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ORIGINAL PAPER

The performance of rooks in a cooperative task depends on their temperament

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Abstract In recent years, an increasing number of studies demonstrated the existence of consistent individual differences in behaviour, often referred to as differences in temperament or personality, in a wide range of animal species. There notably is a growing body of evidence showing that individuals differ in their propensity for risk taking or reacting to stressful situations. This variation has been related to differences in learning abilities or performance in cognitive tasks. In the present study, we examined the consequences of inter-individual variation in boldness on performance in a cooperative task in rooks (*Corvus frugilegus*). Birds were tested individually to measure a number of behavioural parameters related to boldness. The level of a stress-related hormone, corticosterone, in the faeces of each bird was measured under control conditions and after a stress-provoking event. In parallel, we conducted a cooperative string pulling task in which birds were tested in dyads. Successful cooperation depended to a large extent on the temperament of the two partners involved. Temperament, in turn, correlated well with corticosterone levels under stress. Bolder individuals appeared to be more willing to participate in the task, whereas shyer individuals were more influenced by the behaviour of their partner. These findings suggest that a rook's temperament can limit its options of forming successfully cooperating partnerships under stressful conditions.

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Introduction

Cooperation between members of the same species has been the subject of a large number of observational (e.g. Boesch 1994; Noë and Sluijter 1995; Parsons et al. 2003; Scheel and Packer 1991; Silk et al. 2004), experimental (e.g. Chalmeau et al. 1997; Cronin et al. 2005; Hauser et al. 2003; Mendres and de Waal 2000) and theoretical studies (e.g. Nowak et al. 2004; Riolo et al. 2001; Sherratt and Roberts 1998) (see Dugatkin 1997; Noë 2006; Nowak 2006; Sachs et al. 2004 and West et al. 2007 for reviews). Cooperation can be defined as an interaction between individuals that results in net benefits for all of the individuals involved (Bergmüller et al. 2007). Hypotheses tested in experimental studies of cooperation are often derived from theoretical models based on two-player games. The individuals are usually selected by the experimenter, isolated from their social group and confronted with a cooperative task that they have to perform in order to get a reward (for example see: Hauser et al. 2003; Melis et al. 2006; Mendres and de Waal 2000; Stephens et al. 2002). However, two-player models do not take several factors into account that potentially have a strong influence on the occurrence and the patterns of cooperative acts in a group (Heinsohn and Packer 1995; Legge 1996; Noë 2006). For example, tolerance may have considerable influence on cooperation acts in animals (Melis et al. 2006; Petit et al. 1992). Studies on chimpanzees and bonobos (Hare et al. 2007; Melis et al. 2006) showed that individuals that tolerated each other around food were more successful in performing a cooperative task, suggesting that lack of tolerance can act as a constraint that may hamper cooperation. The same authors (Hare et al. 2007; Melis et al. 2006) also suggested that species-specific differences in temperament may partly explain the variance in cooperative ability across species. Moreover, they proposed assessing and controlling social constraints in future cooperation experiments because failure can be due to variables other than cognition.

Recently, the importance of inter-individual variability in animal behaviour has been emphasized in a growing number of publications (Carere and Eens 2005; Groothuis and Carere 2005). Members of the same species were found to differ in their propensity to take risks, to explore new environments, to react to stressful situations (Groothuis and Carere 2005) and can often be classified along a bold–shy continuum (Wilson et al. 1993, 1994). These inter-individual differences in behaviour, which are consistent over time and under different circumstances, are often described as differences in personality or temperament. They have been related to differences in titres of stress hormones, shyer individuals showing a higher plasma corticosterone level than bolder ones (Cockrem 2007; Koolhaas et al. 1999). Inter-individual variations in learning abilities were also found to correlate with temperament, bold individuals performing generally better than shyer ones (Range et al. 2006; Svartberg 2002; Toxopeus et al. 2005).

These findings suggest that temperament may influence many aspects of behaviour, including behaviour shown in cooperation. For example, individual lions and lemurs were found to contribute differently to the cooperative defence of territories. (Heinsohn and Packer 1995) attributed four discrete strategies to lionesses belonging to the same pride namely unconditional cooperator, unconditional laggard, conditional cooperator and conditional laggard. Nunn and Deaner (2004) found that dominance rank, kinship and patterns of parental care only partially explained the variation of behaviours observed in participation of territorial defence in lemurs. Variations in risk taking have also been reported in fish during predator inspection (Brick and Jakobsson 2002; Godin and Davis 1995), which is also often a cooperative behaviour (Dugatkin 1988; Milinski 1987).

The question is: do the differences in temperament between individuals affect the occurrence and the patterns of cooperative actions? Do these differences between individuals play a role in the evolution of cooperation? Till date no empirical study focused on the influence of temperament on cooperation in nature or in the laboratory, but there have been a number of theoretical considerations of the effect of behavioural variation on the evolution and stability of cooperation (Fishman et al. 2001; Fishman 2003; Lotem et al. 1999; McNamara et al. 2004). McNamara et al. (2004) proposed that individual variation in behaviour, due to errors in decision-making or differences in the ability to contribute, can favour cooperation in an Iterated Prisoner's Dilemma game with a fixed maximum amount of possible rounds known to both players.

In the current study, we attempted to identify some consequences of individual temperament on performance in a cooperative task in rooks. Rooks (*Corvus frugilegus*) are Eurasian corvids that nest in large colonies and often forage in large flocks (Madge and Burn 1994). Rooks and other corvids are known for their impressive cognitive abilities in the social (Emery and Clayton 2004; Emery et al. 2007) and physical domain (Helme et al. 2006). Several naturally occurring cooperative behaviours have been described, notably coalitionary support (Emery et al. 2007) and food sharing (Scheid et al. 2008). A recent study on cooperative problem solving in rooks (Seed et al. 2008) showed that these birds quickly solved a cooperative string pulling task without training, and that performance was better in more tolerant dyads. We also used the 'loose string' paradigm (Hirata 2003) in the present study, i.e. two birds had to pull a string simultaneously to obtain a reward. Pulling by a single bird resulted in the string coming loose without moving the reward. We assessed the percentage of success in a cooperative task for each dyad, as well as the individual efforts and amounts of reward taken within dyads. The birds were also tested individually in order to evaluate their temperament and their behaviour without the presence of a partner. We expected bolder birds to be better able to cope with stressful or frightening situations. We predicted that the performance in the cooperative string pulling task would be affected by the respective temperaments of the two partners involved. Following the results obtained in studies on learning abilities, which suggested that bold individuals tend to be more successful than shyer ones (Range et al. 2006; Svartberg 2002; Toxopeus et al. 2005), we predicted that dyads composed of bold individuals would perform better than shyer pairs. Moreover, we expected dyads composed of one bold and one shy individual to perform better than those composed of two shy individuals.

Methods

Subjects and housing

We worked with a captive group of rooks (*Corvus frugilegus*) housed at the Département d'Ecologie, Physiologie et Ethologie in Strasbourg, France. Fourteen birds, ten males and four females, were collected from nests in May 2006, when they were between 2- and 4-weeks old. We took one, two or three birds from the nests depending on the number of chicks present in each nest. We hand reared them in an indoor room until nutritional independency. During handrearing, nestmates were put together in a nest box. Three of the five singletons were put together in a nest box, and the two others were placed in a box with a pair of nestmates. Chicks were fed every 2 h with Nutribird Insect Patee. Birds were marked with coloured leg rings for individual identification. They were housed together in an external aviary, consisting of two parts (16 and 8 m^2; 2 m high) and had access to an indoor experimental room (8 m^2; 2.8 m high) that was divided into three parts by wire mesh panels. The aviary and indoor room were equipped with perches, nest boxes, stones, pine cortex and small plastic toys. Birds were fed three times daily with Nutribird beo and Insect Patee and had ad libitum access to water. All individuals were well habituated to the presence of the experimenters in the aviary and in the adjacent experimental compartment. We sexed the birds when they were 1-year old by using a DNA analysis of blood samples (Fridolfsson and Ellegren 1999). Social behaviour was recorded during focal observations (total of 250 h), ad libitum sampling and scan sampling.

Hormone analysis

Sample collection and preparation

The experimenter (CS) collected for each bird, five samples on days during which no particular stressing event occurred, and five other samples that were collected 1.5 h after an experimentally induced stressful event. Days with and without stressing event were alternated, and each bird was sampled no more than once per day. All samples were collected in November 2007 between 10 and 12 am. To facilitate the collection of the samples, transparent plastic sheets were placed under the perches. The stressing event consisted of the exchange of the dirty plastic sheets with clean ones, which lasted about 5 min. The animals were used to the presence of the experimenter in their aviary, but corvids are generally very frightened during unusual events or procedures. This made the introduction of an additional stressful stimulus superfluous. The droppings were put in small (5 × 8 cm) plastic zipper bags and kept at −20°C. The extraction and analysis of the samples were done at the Department of Natural Sciences of the University of Veterinary Medicine in Vienna. Faecal samples were extracted in ethanol 60%, hydrolysed as described in Kotrschal et al. (1998) and then separated using a high performance liquid chromatography (HPLC) as described by Nakagawa et al. (2003). The amounts of excreted immunoreactive corticosterone metabolites were determined with enzyme immunoassays.

Choice of assay

A subset of four faecal samples was tested with four different enzyme immunoassays. The first used antibodies against corticosterone-3-carboxymethyloxim (Frigerio et al. 2004), the second against 5β-androstane-3α-ol, 11, 17-dione-17-CMO: bovine serum albumin (Möstl et al. 2002), which was also used for ravens (Stöwe et al. 2008). The third was a tetrahydrocorticosterone assay (Nakagawa et al. 2003) and the fourth a cortisone assay (Rettenbacher et al. 2004). The third assay (tetrahydrocorticosterone) gave the best fit with our behavioural observations during sample collection (biological validation method following Touma and Palme (2004) and was therefore chosen for all further samples. For each bird, a mean hormone level was calculated for the five samples after the stressing event and for the five samples collected under control conditions.

String pulling apparatus

The apparatus, which was bolted on the experimental cage at 1.2 m height, consisted of a gliding platform (8 cm × 30 cm) fixed to a metal bar to which a string was attached (Fig. 1). The string allowed the birds to bring the platform in their reach. During individual testing, the string was attached directly on the metal bar, which allowed a single bird to pull in platform. However, during cooperation tests, the 1-m long string went through a pulley, so that the platform moved only when two birds placed in adjacent compartments pulled the string simultaneously. During this cooperation test, the two birds had to be in close proximity (<30 cm), but were separated by a wire mesh panel. We used dog pellets (Mini frolic) that were highly appreciated by all subjects as a reward. Four pellets were placed in line on the platform.

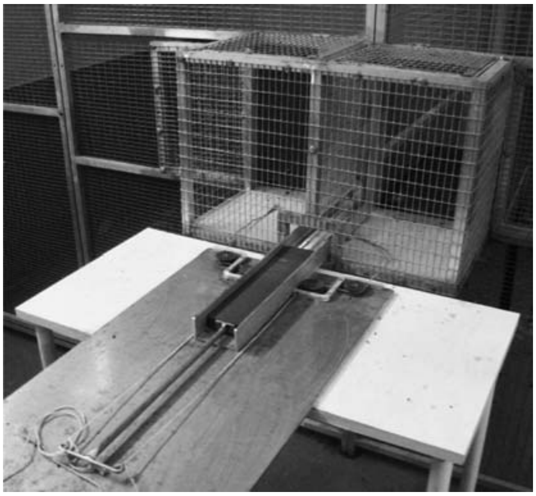

Fig. 1 Apparatus used for the individual ‘fixed string’ and the dyadic ‘cooperative loose string’ tests

Procedure

Training

We habituated the birds to being isolated in the experimental compartment from July to September 2006, when they were between 3- and 6-months old, and trained them daily to pull the string using preferred food items as rewards. If a bird seemed stressed, which was notably due to the separation from the rest of the group, we released it after 1 min. String pulling was trained using standard shaping procedures. One bird never got habituated to being separated. Of the 13 remaining birds, 9 learned to pull the string and 4 birds did not, even after extensive training. This left us with 9 subjects that could be used in the experiment.

Individual testing (August–September 2007)

In the individual "fixed string" test, one bird was isolated in the experimental compartment. For each trial, the experimenter placed four small food items (Frolic pellets) on the platform and waited for the bird to approach and pull the string. After the bird pulled the string and ate the food, the experimenter waited 30 s before pushing the platform back into its initial position and renewing the reward. Each bird ($N = 9$) received 5 test sessions, and 5 trials per session. A session was aborted by releasing the subject if the bird did not come to the platform within 5 min or was obviously too stressed, i.e. continued to fly from perch to perch or against the wire mesh and defecated frequently. For the birds that did not come on the table or came very rarely in the previous tests ($N = 3$ birds), an additional test was performed to elucidate what caused the birds' fearful reaction. In this additional test, the experimenter placed the food directly on the table, ensuring that the access to the food was as easy as possible, and then left the room. A video camera was placed in the room and recorded the behaviour of the bird during 2 min. All individual tests were performed during August and September 2007.

Cooperation test (March–September 2007)

In the "loose string" cooperation test, two birds were isolated in adjacent compartments. The experimenter placed four pieces of food on the platform and waited till the birds came to the apparatus and pulled the string. As the string ran freely over a pulley in this test, the birds had to pull the string simultaneously to move the platform. Each bird had a piece of string of about 15 cm within its reach; thus, if one bird pulled slightly, there was still a chance for the other bird to take the string too. The experimenter waited 30 s after a successful trial before placing the platform at its initial position and putting out four new pieces of food. If one bird pulled the string out of reach for the other bird, the experimenter removed the food from the platform, waited 30 s and replaced the platform and the string at their initial position. After that, four new food items were placed on the platform and the birds could again perform the task. With our nine birds we formed ten dyads in such a way that each bird had at least one 'shy' and one 'bold 'partner; seven birds had two partners and two birds (M and I) had three partners. These two birds were tested with a third partner, because their two initial partners had very similar scores on the bold–shy gradient. The third partner had a very different temperament. We controlled for order effects by starting 5 birds with a bolder and 4 birds with a shyer partner and then alternated partners in each series of trials. Each dyad had 5 test sessions and 5 trials per session, including both successful and unsuccessful trials. The total duration of a test session never exceeded 10 min.

Data collection and analysis

We used all agonistic interactions that occurred between March and September 2007 during focal observations to establish the dominance hierarchy, which was based on displays of submissive behaviour only (avoid, leave, submissive posture). The rank order showed significant linearity (Improved Linearity Test with 10,000 randomizations, $h = 0.84$, $P < 0.001$, Matman–Noldus, Wageningen, the Netherlands). We also assessed the degree of affiliation between birds by analysing their spatial proximity using scan sampling: for each bird, we calculated the nearest neighbour frequencies for all group members. This permitted us to attribute an index of proximity to each dyad, which was the absolute number of times that two birds were nearest neighbours during 112 scans.

In order to quantify the temperament of the birds, we measured the time it took a bird to land near the apparatus after the food was placed on the platform during the individual-fixed string tests (=latency down). We considered the latency to be zero if the bird was waiting at the apparatus before the reward was put in place. We subsequently recorded whether the bird pulled the string and calculated the proportion of trials during which it did (=% pull). If the bird did pull the string, we noted whether the bird stayed at the apparatus and waited for the next trial (=% stay) or flew up on a perch. Finally, after the last trial we measured how long the bird stayed at the apparatus before flying up (=latency up). If a bird did not come at the apparatus during the test, we attributed the value 120 s to the "latency down", because this was the maximum latency observed for a bird before coming down. The four parameters "latency down", "pull", "stay" and "latency up" were strongly correlated (Kendall's coefficient of concordance, $W = 0.95$, $df = 8$, $P < 0.001$). These parameters notably the "latency down" and the "latency up" can be considered as an indicator of the boldness of the birds, because the physical isolation from the group is possibly to induce a moderate stress in social animals and also because birds usually feel more secure at a higher spots. Thus, the shorter the "latency down" and the longer the "latency up", the bolder the bird was considered to be. We used the two latency parameters to rank the birds from 1 (boldest) to 9 (shyest). The other parameters were highly correlated with the resulting rank, but showed several ties.

During the cooperation test, we recorded the latency before each bird landed near the apparatus. We noted the pulling activity of each bird, the degree of synchronization and movements of the platform. When the two birds pulled simultaneously, we noted whether there was a clear asymmetry in their pulling behaviour. We declared pulling to be asymmetrical when one bird just held the string in its bill while the other bird pulled the string and moved back over a distance of at least 20 cm. In order to move the platform fully in reach, the birds had to pull over a combined distance of 40 cm, i.e. 20 cm each when fully symmetrical and 40 cm for a bird pulling alone, given that the other at least prevented the string from running out. Finally, we noted how many pieces of food each bird consumed.

We used a matched pair design in which we coupled each bird with one more and one less bold partner and tested whether there was a significant difference in having a bold or a shy partner for factors that contributed to more or less successful cooperation, using our nine subjects as data points in a sign test. For the birds that were tested with three partners, we used only the boldest partner and the next boldest one in the sign test. Spearman's rank order correlations and Kendall's coefficient of concordance were used to test the association between parameters, using the 10 tested dyads as data points, although these were partially dependent. All statistical tests are two-tailed, and α was set at 0.05. In order to keep the experiment-wise error rate at that level for the cooperation experiments, the rates for the four individual statistical tests were adjusted using the Benjamini and Yekutieli (2001) method following Narum (2006), i.e. for these tests we used an α' of 0.024). Statistical tests were performed with SPSS 13.0; for non-parametric tests we followed Siegel and Castellan (1988).

Ethical note

We had permits from the Direction Départementale de l'Agriculture et de la Forêt to take birds from the wild and from the Direction Départementale des Services Vétérinaires (permit n. 67288) to do experimental work with them. Unfortunately, as there were few birds available, we could not leave chicks in all nests. For the DNA sexing, 0.2 mL of blood was taken by puncturing the brachial vein. Birds were immediately released after this procedure which lasted no more than 5 min. The birds remained in captivity after this study to be used in similar research.

Results

Individual behaviour

Table 1 summarizes the main results obtained for each bird during individual testing. Some birds (K and M) always came to the apparatus before the food was placed on the platform (i.e. a mean latency of 0 s) and one bird (P) never came down (a mean latency of 120 s). There also was considerable variation between birds for % pull and % stay, with extreme values of 0 and 100% for both parameters. Finally, a similar variation was found for the latency before flying up with mean durations ranging between 1 and 65.2 s. The three females (I, V and P) were all found at the shy end of the bold–shy gradient. The tests done without the presence of the experimenter with the three birds that rarely came to the apparatus (the three females I, V and P) gave similar results: the animals did not come more often at the apparatus or more rapidly to take the food if the experimenter was out of the room. There was no significant correlation between the dominance ranks of the birds, and the ranks of temperament assessed during individual testing ($r_S = 0.58$, $N = 9$, $P > 0.1$).

Stress reactions

Faecal corticosterone levels of all birds were clearly higher after stressful events than during control periods (Fig. 2). The hormone levels were not significantly correlated with the bold–shy ranking during control periods ($r_s = 0.317$, $N = 9$, $P > 0.4$), but hormone levels after experiencing stressful events were clearly correlated with the bold–shy gradient, with shyer birds showing higher levels ($r_s = 0.883$, $N = 9$, $P = 0.002$; Fig. 2).

Cooperation test

Percentage of successful cooperation

The percentage of successful cooperation was very variable across dyads and ranged between 0 and 100% (Table 2). Interestingly, some birds were very successful with one partner but not with another. This result could not be explained by the ability to pull the string as both partners of dyads that were unsuccessful (e.g. P and V) were each successful with another partner (e.g. P and B or V and M, see Table 2). In 26 trials, only one of the birds came to the

Table 1 Mean durations (s) and standard deviations of time before coming to the apparatus and before flying up when finished, and percentages of pulling the string and of staying at the apparatus between two trials for each bird during individual testing

Individual (sex)	Bold–shy rank	Dominance rank	Latency down (s)	Latency up (s)	Pull (%)	Stay (%)
M (m)	1	3	0.0 ± 0.0	65.2 ± 32.1	100	100
K (m)	2	5	0.0 ± 0.0	62.7 ± 17.4	100	100
H (m)	3	2	1.8 ± 2.3	47.6 ± 18.9	100	95
B (m)	4	6	2.5 ± 3.0	19.6 ± 13.4	100	80
T (m)	5	4	9.5 ± 13.6	3.0 ± 1.7	100	65
O (m)	6	1	12.4 ± 33.9	2.2 ± 1.3	68	50
I (f)	7	9	87.6 ± 55.4	1.3 ± 0.6	8	0
V (f)	8	7	101.3 ± 45.7	1.0 ± 0.0	4	0
P (f)	9	8	120.0 ± 0.0	1.0 ± 0.0	0	0

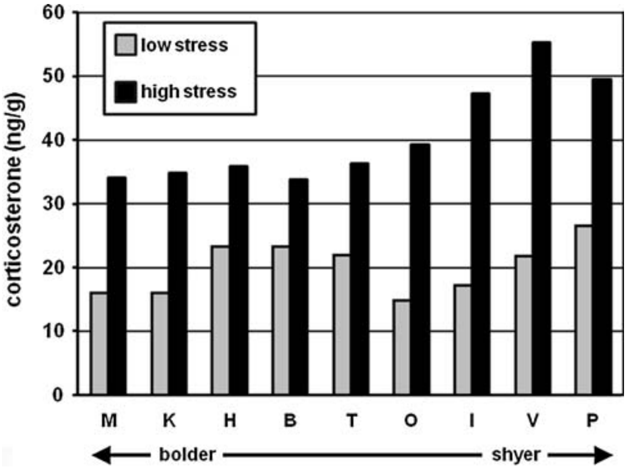

Fig. 2 Average levels of corticosterone in five faecal samples after a stressful event (*black columns*) and during control conditions (*grey columns*). Birds are ranked according to their temperament, the *boldest* being on the left. Individuals I, V and P are females

apparatus and in 21 cases (81%) this bird pulled the string in spite of the absence of a partner. This did not occur more often in the first sessions than in the last sessions and all nine of our subjects did it at least once. However, in the 179 trials in which two birds came to the apparatus, a vast majority (174; 97.8%) pulled simultaneously. In nine cases, one bird had to wait for its partner, but did so in only four cases (involving 2 different birds). In all other cases, both birds were waiting near the platform or arrived as soon as the reward was placed on it and pulled immediately, i.e. their synchronization was the result of external cues rather than active coordination.

Participation with bold or shy partner

Fig. 3 shows the number of times that a bird participated in the task by coming at the apparatus, with the “boldest” and with the “shyest” of the partners with which it was paired. Some individuals (M, K, H or B) did not change their behaviour and always participated well with both types of partners, while others showed a clear difference in their willingness to participate, depending on who their partner was. If birds participated differently depending on their partner, then they participated more often with the bolder of the two. The direct consequence was that all subjects performed better in the cooperative task when they were paired with a bolder partner (sign test: $N = 9$, $P = 0.004$, $\alpha' = 0.024$). The shyer members of dyads were significantly more often the last individual to come to the apparatus (sign

Table 2 Cooperation success with bolder and shyer partners

Subject	Bolder partner			Shyer partner		
	ID	Bold–shy rank	% Cooperation	ID	Bold–shy rank	% Cooperation
M (m)	H	3	100	V	8	84
K (m)	B	4	100	T	5	88
H (m)	M	1	100	I	7	72
B (m)	K	2	100	P	9	84
T (m)	K	2	88	I	7	32
O (m)	M	1	100	I	7	36
I (f)	H	3	72	O	6	36
V (f)	M	1	84	P	9	0
P (f)	B	4	84	V	8	0

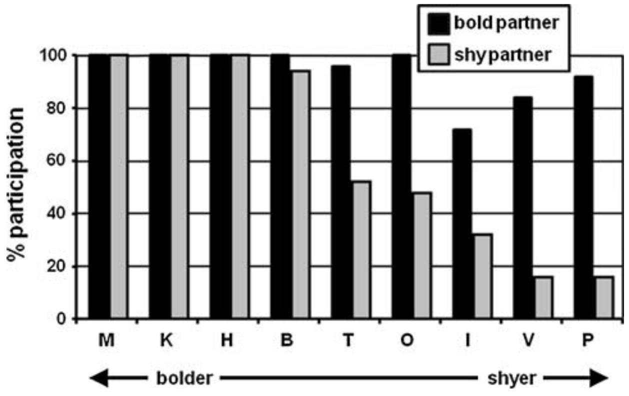

Fig. 3 Percentage of participation of each bird, paired with a "bolder" (*black columns*) or a "shyer" (*grey columns*) partner. Birds are ranked according to their temperament, the boldest being on the left. Individuals I, V and P are females

test: $N = 10$, $P = 0.004$, $\alpha' = 0.024$). Finally, the mean latency before coming down was significantly shorter during the cooperative task than during individual testing (sign test: $N = 7$, $P = 0.016$, $\alpha' = 0.024$).

Asymmetry in pulling

Six dyads showed a strong asymmetry in pulling in spite of holding the string in their beaks simultaneously. This asymmetry increased significantly across sessions (Kendall's coefficient of concordance, $W = 0.68$, $df = 4$, $P < 0.01$), but no significant variation was observed within sessions ($W = 0.37$, $df = 4$, $P > 0.05$), which means that asymmetry in pulling did not vary significantly and systematically within sessions.

Proportion eaten by dominant and subordinate

The average percentage of food items eaten by the dominant of the dyad was 59.9 ± 4.5%. For all dyads, the number of food items eaten by dominant birds was higher than the number eaten by their subordinate partners. The three individuals that were dominant in one dyad and subordinate in the other consumed more than half when dominant and less than half when subordinate.

Proximity during focal observations and success rate in experiment

We ranked the dyads on the basis of the proportion of time they were in proximity during our focal observations. There was no significant correlation between proximity of dyads and their percentage of successful cooperation ($r_S = 0.4$, $N = 10$, $P > 0.05$, $\alpha' = 0.024$).

Discussion

We could classify our nine rooks on a bold–shy continuum on the basis of four highly correlated parameters: the latencies of approaching the apparatus and leaving after the trial, the tendency to stay near the apparatus between trials and the proportion of trials during which the string was pulled. An analysis of faecal hormones showed that the shyer rooks showed stronger increases in corticosterone levels after stressful events than the bolder birds, a general pattern in birds (Carere et al. 2003; Koolhaas et al. 1999). No significant correlation between boldness and dominance rank was found, but gender had a clear effect with the three females being the shyest animals.

The 'temperament' of the birds had a strong influence on their performance in the cooperation task, because combinations of two shy birds (three out of 10 dyads) performed poorly. When at least one partner was bold, however, the couple performed well. The bolder individuals are thus comparable to what Gilby et al. (2008) labelled "impact males" in cooperatively hunting chimpanzees. In dyads with two shy birds, the low percentage of successful cooperation could be explained by the fact that each individual was waiting for its partner to go to the apparatus first. In the present study, the shyest birds were the three females of the group and consequently the patterns observed might be due to differences between sexes. However, the two shyest males behaved in the same way as the females did, that is they participated more often with a bold partner than with a shy partner.

We failed to show a tolerance effect, since more closely affiliated birds did not perform significantly better than birds that were less often found in each others' proximity. This result might be due by the fact that birds were separated by a wire mesh. The variation in performance among dyads was not due to the ability to pull the string either, because all birds performed quite successfully with at least one partner. The high success rates of the seven successful dyads could also not be explained by better coordination, since there were no indications that the animals delayed pulling till the partner was ready to pull too. In 81% of the cases, in which only one bird came to the apparatus, the string was pulled nevertheless and led to a failure, compared to only 2.8% of trials in which the two partners came to the apparatus immediately. Thus, synchrony seems to be explained by a common external cue rather by behavioural coordination (Boesch and Boesch 1989).

A cooperative string pulling experiment conducted with rooks that were not previously trained to perform the task demonstrated that the birds did not understand that simultaneous pulling by both birds was required (Seed et al. 2008). Our results cannot be interpreted as conclusive evidence for or against the notion that rooks 'understand' this type of cooperation task, notably because in our case their coordination can be more parsimoniously interpreted as the result of a reaction to a common cue, as noted earlier. The fact that both obtained access to the reward simultaneously when successful could also partly explain the high performance of the birds (Cronin et al. 2005). In the case in which one shy bird was tested with a bolder partner, the coordination may be explained by the behaviour of the "shy" which waited for its bolder partner to go first to the apparatus before joining it. While performing the cooperative task, birds showed an increasing asymmetry in the pulling behaviour over the sessions. This might suggest that they learned that providing less effort not necessarily resulted in obtaining less. On the contrary, by just holding the string without walking backwards, they ended up closer to the platform with the reward than their diligently pulling partner.

The present experiment provides evidence for an effect of individual temperament on the success of cooperative actions. As already suggested, bold individuals differ from shy ones by their inclination to take risks (Groothuis and Carere 2005), which translates into a different likelihood of participation in cooperation under risky circumstances. In the current experiment, the task proposed was not very risky or costly as all birds were habituated to the apparatus and procedure. However, we nevertheless found an inter-individual difference of boldness during individual testing and our hormone study also showed clear differences in the reaction to mildly stressing events. Thus, it is possible that inter-individual differences in participation appear in naturally occurring cooperation when costs or risks are higher, as in a group-territorial conflict (Heinsohn and Packer 1995; Nunn and Deaner 2004).

We are aware of the limited statistical power of our experiment, which is due to the small number of birds we could use. The consistency of our results makes us confident that the following conclusions are allowed. Differences in temperament, and notably variation along the bold–shy axis, had implications for the performance of individuals in cooperation tasks. The more risk-prone 'bold' individuals appeared to function as catalysers and made it possible for shyer individuals to cooperate under circumstances that they experienced as risky (Groothuis and Carere 2005; Wilson et al. 1994). The shyer animals thus profited from a dilution of perceived risk thanks to the presence of the bolder animal. This compares to a similar effect in predator inspection in which individuals that approach a predator dilute the risk by coordinating their approach. Variation in boldness in interaction with predators has been noticed in several fish species (Brick and Jakobsson 2002; Godin and Davis 1995), among which species for which predator inspection in pairs or groups has been described too (Dugatkin 1988). Combining these two observations, it therefore seems plausible to assume that bolder inspectors will take shyer ones along, which is also evident from our finding that the shyer members of a dyad were usually the last to come to the apparatus. Such mechanism might represent the first step towards a more coordinated cooperation, where individuals actively synchronize their action.

Thus, in species varying from small fish to chimpanzees and lions, cooperation may succeed, because bolder individuals can encourage more fearful conspecifics to engage in cooperative acts under circumstances in which the latter would otherwise not have participated. While none of these studies tested the effect of temperament in an experimental cooperation task, we showed experimentally that shy rooks only take part in a cooperation task when their partner is bold enough to approach the apparatus first.

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