Social manipulation causes cooperation in keas

SABINE TEBBICH, MICHAEL TABORSKY & HANS WINKLER

Konrad Lorenz-Institut für Vergleichende Verhaltensforschung (KLIVV)

Abstract. This study assessed whether keas, *Nestor notabilis*, are able to cooperate in an instrumental task. Seven birds of a captive group were tested in group situations and in dyads. At least two individuals had to manipulate an apparatus to obtain food but only one participant was rewarded. One bird had to push down a lever to enable another one to collect food from a box. The distribution of the two different roles was clearly dependent on hierarchy. The higher ranking individual always obtained the reward and each bird changed its role according to dominance status. Owing to the non-linear hierarchy in the group, each bird participating in cooperative interactions had at least one submissive partner. Therefore, in group situations the reward was distributed symmetrically and cooperation was persistent. In dyadic test situations, three individual keas aggressively manipulated their respective subordinate partners to open the apparatus. Their dominance status enabled them to force cooperation.

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The concept of cooperation can be addressed at two different explanatory levels: the ultimate level of function and the proximate level of mechanism (Petit et al. 1992). At the functional level, the main focus is on the outcome of a cooperative inter-action: the involved costs and benefits. The basic assumption is that in order for cooperative schemes to be adaptive, each individual should perform the required behaviour only if it benefits from the performance at least over a series of interactions. The pay-off does not need to be symmetrical for both or several involved parties (Noë 1990). Different resource-holding powers (Parker 1974) such as size, strength, territory ownership, dominance status within a group, and/or special skills may cause power asymmetries enabling an animal to claim the 'lion's share' (Noë 1990). In principle, there are three possible co-operative solutions to an iterated problem in-volving a reward: (1) sharing of the reward, (2) reciprocity in subsequent encounters, or (3) asymmetric distribution of the reward due to asymmetric relationships.

At the mechanistic level, a critical question is whether participants act in a coordinated manner or whether they achieve the goal independently

and without reacting to each other. Reboreda & Kacelnik (1993) showed that pairs of starlings, *Sturnus vulgaris*, behaved cooperatively in a two-player game. However, this result was reached through the subject's responses to reinforcement of their own behaviour, without the influence of visual perception of the partner. In a similar experimental situation, pigs, *Sus scrofa*, were trained to press a panel to obtain food from a feeding bowl that was separated from the panel. The presence of a submissive partner did not change a dominant pig's solution for acquiring a reward as it could easily displace the submissive partner (Baldwin & Meese 1979). To avoid these possibilities in a test of cooperative abilities, an instrumental task should be selected that forces participants to react to each other's behaviour. The question about the degree of coordination is closely linked to the problem of intentionality and cognitive skills. Povinelli et al. (1992a), for example, suggested from their experiments with chimpanzees, *Pan troglodytes*, that animals may comprehend their partners' role when instrumental tasks necessitate cooperation.

In our study on cooperation in keas, *Nestor notabilis*, we were interested in both the outcome of cooperative interactions and the underlying mechanisms. In contrast to the frequent use of the term 'cooperation' in a functional sense, we use

Correspondence: S. Tebbich, KLIVV, Savoyenstrasse 1a, A-1160 Wien, Austria.

this term in a purely descriptive manner in the sense of 'acting together'. We stress that this does not make any suppositions about the function of the interactions or the involved mechanisms.

Instrumental task-solving that involves co-operation by two or more animals has been studied mainly in mammals (rats, *Rattus norvegicus*: Littmann et al. 1954; pigs: Baldwin & Meese 1979; chimpanzees: Crawford 1937; Boysen et al. 1978; Povinelli et al. 1992a; baboons, *Papio hamadryas*: Beck 1973; macaques, *Macaca mulatta*, *M. tonkeana*: Mason & Hollis 1962; Fushimi 1990; Petit et al. 1992; Povinelli et al. 1992b).

Among birds, keas are an obvious choice to test the ability to solve a cooperative task. They live in mountainous regions of New Zealand between 700 and 2000 m altitude (Campbell 1976; Breejart 1988) and are highly social, remaining in family groups and flocks until they are sexually mature (Jackson 1960; Clarke 1970; Campbell 1976; Breejart 1988). Keas are well known to show a great variety of social behaviour including elaborate play (Keller 1974), which suggests a comparison with mammals. It has been hypothesized that the harsh alpine environment of keas has led to their extremely explorative behaviour and curiosity (Diamond & Bond 1991). Keas persistently investigate and manipulate objects (Keller 1974), which relates to their endurance in instrumental tasks (Kubat 1992).

In this study we examined the development of cooperative behaviour in an experimental set-up. We tested in particular whether these birds are capable of coordinating their behaviour to obtain a food reward and, if so, whether this coordinated behaviour results in food sharing, reciprocity or in the asymmetric distribution of rewards among birds. We used an apparatus that had to be manipulated by at least two birds performing different roles simultaneously. One bird had to push down a lever while the other one could acquire food from a box. Therefore, in a single interaction only one bird initially received a reward. This asymmetry in a single interaction with regard to the distribution of rewards may result in one of several different schemes to solve a cooperative problem. Participants may behave in a coordinated manner and distribute the food rewards symmetrically, either by immediate sharing or by reciprocity resulting from role reversals in subsequent food acquisitions. In dyads in which

the individuals differ in size, dominance status or ability, one partner may acquire a greater proportion of the reward. Under such circumstances the less rewarded participant might stop cooperative behaviour or be forced by its dominant partner to maintain the cooperative role.

GENERAL METHODS

Study Animals and Holding Conditions

We used seven captive keas: two adult males, both 4 years of age at the start of the experiment, three subadult males, 2, 2 and 3 years of age, and two adult females, both 4 years of age. They were all bred at the institute and had been kept with each other since fledging. They were descended from the same breeding pair, and were therefore full siblings. The birds were fed a mixture of vegetables, fruits, seeds, margarine and ox heart. They were housed under outdoor conditions year round in an aviary measuring $15 \times 10 \times 4$ m, which could be divided into three compartments of equal size, each measuring $5 \times 10 \times 4$ m. Thereby, the birds could be easily separated for test periods. The experiments were always done in the same compartment which was equipped with branches at different heights and with tree trunks and rocks on the ground. All keas were colour banded and they are individually referred to by their ring colours (i.e. blue, green, yellow, black, red, white and silver).

Determination of Dominance Ranks

The individual keas were ranked using the directionality of agonistic interactions at the food tray, measured 10 days before and 5 days after the experimental phase each morning once a day. We used the behavioural categories described by Keller (1974), Potts (1977), Diamond & Bond (1991) and Kubat (1992). These included displacements, attacks (referring to all aggressive contact behaviour) and threats (referring to any non-contact aggressive displays, e.g. raising of head feathers, bill gaping and staring; Diamond & Bond 1991). Each 15-min observation session started when the food tray was placed in the cage. The frequency and direction of aggressive behaviour between all pairs of individuals were
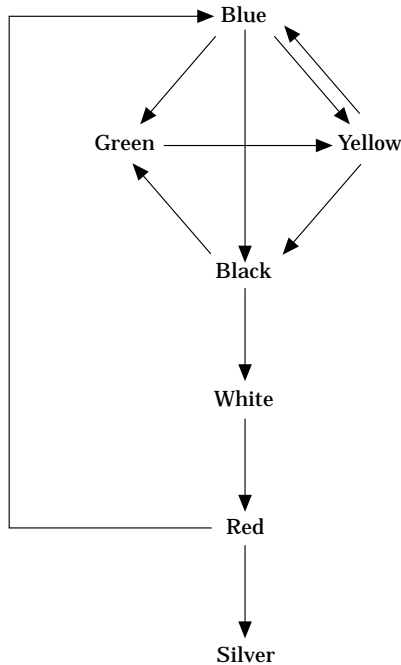
Figure 1. Dominance hierarchy of all keas included in this study. Arrows indicate the directions of the dominance relationship.

recorded and arranged in a matrix. This revealed a non-linear dominance hierarchy (Fig. 1). The number of circular reversals, $d=2.75$, and the linearity coefficient, $k=0.8$, both indicate the degree of linearity (Appleby 1983). Owing to these circular reversals, no bird claimed dominance over all others. Of the 21 dyads between all group members 19 were clearly asymmetric with none or only a few reversed interactions. The latter occurred to a considerable extent between Blue and Yellow, with six being directed from Blue towards Yellow and 13 from Yellow towards Blue. Blue and White were ranked equally (three aggressive interactions in each direction). The directionality of the aggressive interaction at the food tray was consistent with interactions at the test apparatus in all dyads with the exception of the combination Blue/Yellow. At the food tray, Yellow was dominant over Blue, while at the test apparatus Blue was more often aggressive towards Yellow.

Test Apparatus

The test apparatus was a brass seesaw placed on a wooden base (Fig. 2). One end of the 40-cm-long lever had a wooden handle adjusted at 90 degrees and fixed in a horizontal position; a transparent Plexiglas lid was attached to its other end. The lid closed a wooden box measuring $10 \times 10 \times 12$ cm which contained the food reward. A brass weight unbalanced the bar in the direction of the food box. The lid opened when one kea operated the lever either by pushing it down with its leg or by sitting on the handle. This enabled the other bird to acquire the food items from the box. The lid fell back onto the food container once the lever was released, so the bird that pushed down the lever could not obtain the food reward itself. A mechanical resistance limited the speed of the shutting lid which could have otherwise hurt the bird that took out the food. A log 40 cm long and
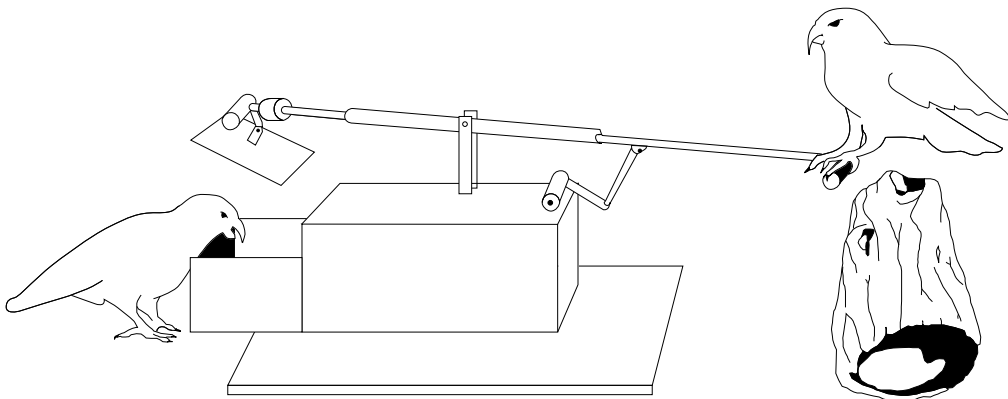
Figure 2. The test apparatus being successfully manipulated by two keas. See text for details of the mechanical function of the seesaw.

20 cm in diameter was placed beneath the handle to improve access. The food reward was a mixture of margarine and cooked yolk, formed into ball-shaped pellets of approximately 8 mm. This had proven to be very attractive to keas in preliminary experiments. We baited the apparatus immediately before the test. This action could be directly observed by the keas.

Data Recording

Each session was recorded on videotape and subsequently transferred to computer files with the help of a data recorder with simultaneous and continuous recording possibilities. We used a computer program specifically written for this type of recording.

GROUP TESTS

In this experiment we assessed whether keas are able to solve a problem that necessitates cooperative behaviour when tested in a group.

Methods

The experimental apparatus was accessible to the whole group and the keas could learn the cooperative task by trial and error without previous individual training. One test session lasted 15 min. The group was tested 20 times within a period of 2 months. We monitored the frequency of pushing down the lever, manipulation of the lid, manipulation of other parts of the apparatus, taking out the food, peering through the lid and the direction and intensity of aggressive interactions. All birds were observed simultaneously and the information was recorded on an individual basis with continuous behavioural observation.

Results

Four out of five males, Blue, Green, Yellow and Black, learned by trial and error within 7 days to push down the lever as well as to take the pellets out of the box while the lid was open. In successful interactions, defined as interactions in which at least one bird was able to obtain a reward, usually two or three birds were engaged: one at the lever and one or two at the food box. In dyadic

interactions (16 out of 76 successful interactions), it was always the subordinate partner who pushed down the lever whereas the dominant bird always took the food reward out of the box.

The five dyads Blue/Green, Blue/Black, Green/Yellow, Black/Yellow and Black/Green were repeatedly successful in getting the food reward. Green, Yellow and Black performed both roles, pushing the lever and taking out the food reward, in accordance with their hierarchical position within the respective dyad. Blue always acquired the food, in all interactions and with all partners. He was about equal in rank with Yellow, and only subordinate to Red who was not involved in cooperative interactions.

Triadic interactions were more frequent than dyadic interactions. In 60 successful interactions one bird pushed down the lever (i.e. the 'donor') and two birds took out food from the box (i.e. the 'recipients'). The distribution of roles in these triadic interactions was rather complex and subject to the combination of participating individuals. It depended clearly on their relative hierarchical positions. The donor was always subordinate to at least one of the two recipients.

The dominant birds at the food box maintained their position through aggressive behaviour in dyadic as well as in triadic combinations. In 55 out of the 76 successful interactions, the donor subsequently tried to approach the food box immediately after leaving the lever. The dominant recipient reacted 38 times by expelling and in 17 cases by tolerating the donor at the food box.

Each bird involved in cooperative interactions in these group tests had at least one submissive partner in dyadic as well as in triadic combinations, owing to the non-linear hierarchy of the group. Therefore, each of the participants was rewarded and the distribution of the rewards was symmetrical (number of rewards: Blue 26, Yellow 17, Green 15, Black 18; pooled data of 15 runs). Cooperative interactions were shown frequently throughout the group tests.

DYADIC TESTS WITH CHANGING PARTNERS

This experiment was designed to determine whether role assumption was the same in dyadic as in group situations and whether cooperation

would persist in successive series of experiments with asymmetrical relationships.

Methods

Two individuals were separated from the other birds for the experimental periods. Each of the 21 possible dyads was tested at least once. Birds that successfully obtained a food reward with at least one partner were tested six times in varying combinations with other birds. The dyad Green/Yellow was tested nine times. One test consisted of two test sessions and two control sessions, each session lasting 5 min and performed in random succession. In control sessions the apparatus was unbaited to determine whether apparatus manipulation was directed towards food acquisition or just motivated by the act of manipulation itself (i.e. play; see Keller 1974). Differences in manipulation frequencies between tests and controls were tested for each pair with a Wilcoxon matched-pairs signed-ranks test.

Results

The frequency of lid manipulation by the dominant participant was significantly higher in test ($\bar{X}=17.9$ times per experiment) than in control ($\bar{X}=7.7$ times per experiment) situations ($N=12$, $P=0.043$), which supports the assumption that this behaviour was directed towards the acquisition of the food reward. The frequency of bar manipulation was higher for all birds in tests ($\bar{X}=1.3$) than in controls ($\bar{X}=0.7$, $N=12$; $\bar{X}$ is the weighted mean of all test pairs) which was a significant difference in three birds in the dominant position ($N=12$, $P=0.01$; $N=12$, $P=0.043$; $N=18$, $P=0.043$) and in two birds in the submissive position ($N=12$, $P=0.05$; $N=12$, $P=0.05$).

As in the group test, four keas (Blue, Green, Yellow and Black) were able to obtain the food reward repeatedly in five different dyadic combinations. The distribution of the two different roles varied consistently with the dominance status of the participants, similar to the group tests. The subordinate bird operated the lever and its dominant partner collected the reward. However, two subordinate individuals ceased to push the lever. After five tests in which no reward had been obtained, one of these birds (Yellow) was repeatedly approached by its dominant partner (Green) when the former was off the apparatus. These
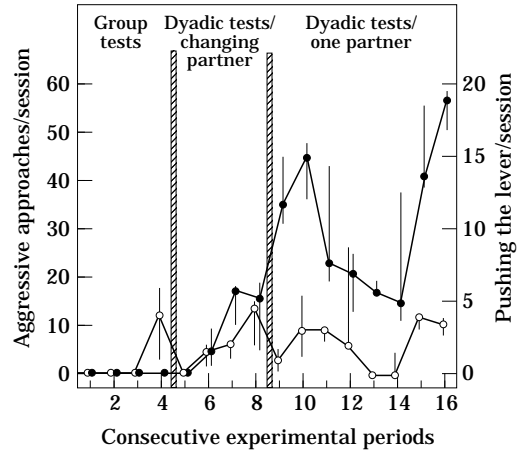

Figure 3. The time course of behaviour shown in dyads of the birds Green (aggressive approach; ●) and Yellow (pushing the lever; ○) during the three experimental phases. Each point represents the median of five test sessions. Vertical lines are inter-quartile ranges.

approaches involved aggressive behaviour of varying intensity. Yellow reacted by moving away from Green, whereupon Green frequently followed it. This led to series of up to 40 approach and retreat sequences in direct succession. This 'chasing' often ended when Yellow reached the apparatus and operated the lever. In the remaining eight tests of this dyad, Yellow pushed down the lever for a total of 25 times, 19 of which occurred after a repeated succession of approaches and retreats. The frequency of approach/retreat sequences increased in the course of the experiments (Fig. 3).

DYADIC TESTS WITH ONE SPECIFIC PARTNER

In this experiment we investigated whether 'aggressive approaching' was a means of forcing the submissive partner into operating the lever and providing access to food for the dominant bird. If this were the case, we should predict the following: (1) aggressive approaching should occur more often in tests with food than in controls without; (2) it should raise the probability that the partner would push down the lever to facilitate food access; and (3) it should occur less frequently when the submissive participant was already performing the desired task or at least
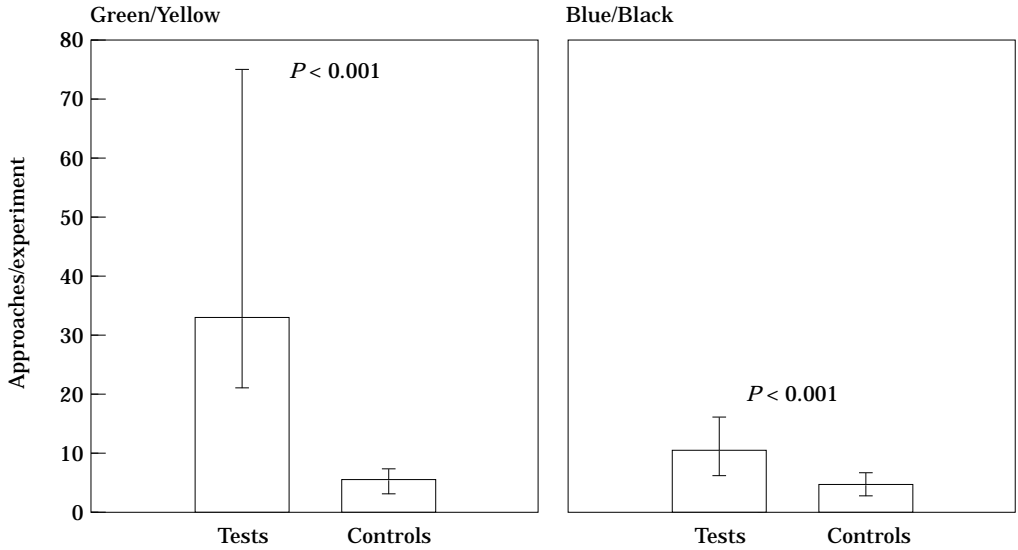
Figure 4. Medians and quartiles of aggressive approaches by the dominant kea per experiment in tests with food and controls without food for two series of 43 test pairs each, with two pairs of individuals. Comparison between tests and controls were made with the Wilcoxon matched-pairs signed-ranks test.

was in a position that would most likely lead to subsequent opening of the lid. Such positions were the lever itself and places from which the submissive participant moved to the lever with an increased likelihood.

Alternatively, if aggressive approaching served to drive the subordinate partner away from the food reward, the probability of approaching should be higher near the apparatus than further away. To test this we compared the probability of aggressive approaching at positions near the apparatus with the probability of this behaviour further away from it.

Methods

The birds of two selected dyads, Blue/Black and Green/Yellow, were tested repeatedly to create iterated situations with the same partner. In control sessions, the seesaw was replaced by a wooden box which resembled the base of the test apparatus in size and form but did not provide a food container and a seesaw. The total experimental period was 21 days for each of two dyads. Two tests and one control session of a dyad were performed on 1 day separated by intervals of 5–10 min. Each session lasted 5 min, and the

succession of tests and controls was randomized. For statistical tests that compared tests and controls one of the two tests was randomly selected and the other discarded to provide equal random likelihoods for rare events in tests and controls.

Two transition probabilities were calculated and compared: (1) the probability of moving from any position on to the lever after being approached and (2) the probability of moving from any position on to the lever without being approached previously. This probability was calculated using the transition frequency to the lever divided by all transitions. Transitions from any position on to the handle were included only when they were direct, that is without any sojourn at other positions except for short stops at the log for less than 4 s. This exception was made because the log was the usual access route to the lever. The limit of 4 s was based on a discontinuity in the data distribution. Transition on to the lever always caused the lid to open.

To assess whether aggressive approaching is dependent on the submissive's spatial position, four space categories were distinguished: lever, log, apparatus (i.e. positions where the bird had physical contact with the apparatus) and
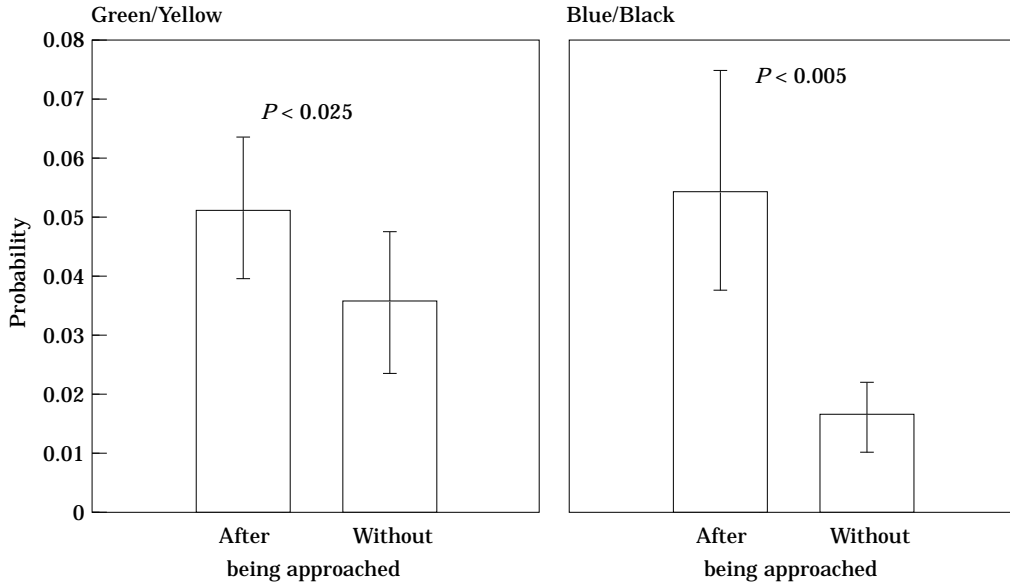
Figure 5. Transition probability of the submissive bird moving to the lever after and without being previously approached. Bars represent the pooled data of 42 tests for two pairs of individuals, error bars represent 95% confidence limits. For the test used see Methods.

the category 'else' which comprised all other positions within the aviary. We measured the probability that the submissive bird moved on to the lever from these spatial categories and the probability of its being approached by the dominant.

For each of the 21 tests the probability of moving on to the lever with and without being approached, the probability of moving on to the lever from different positions, and the probability of approaching a subordinate bird at different positions was tested with the conditional binomial exact test of Rice (1988). The overall probability was obtained by Fisher's procedure of combining tests (Sokal & Rohlf 1981, pp. 779–782).

Results

The two dominant participants Green and Blue both approached their partners significantly more often in tests than in controls (Wilcoxon matched-pairs signed-ranks test: $N=21$, $P=0.0002$, $P=0.0269$; Fig. 4). Both subordinate participants of the two pairs, Yellow and Black, moved significantly more often on to the lever after they had been aggressively approached than when there had been no approach by the dominant (Fig. 5) (Yellow: $\chi^2=53.028$, $df=34$, $N=17$, $P<0.0005$; Black: $\chi^2=42.323$, $df=18$, $N=9$, $P<0.0005$; test see Methods). In both dyads, the transition probability from log on to the lever was significantly higher than that from apparatus and 'else' to the lever (Yellow: $\chi^2=268.526$, $df=34$, $N=17$, $P<0.0005$; Black: $\chi^2=47.498$, $df=20$, $N=10$, $P<0.0005$; test see Methods). In accordance with the third prediction, the probability of approach was significantly lower at the lever and the log than at other positions in both dyads (Yellow: $\chi^2=332.749$, $df=38$, $N=19$, $P<0.0005$; Black: $\chi^2=117.055$, $df=34$, $N=17$, $P<0.0005$; test see Methods). In both dyads, the probability of aggressive approaching was significantly higher at positions of the category 'else' than near the apparatus (Yellow: $\chi^2=378.183$, $df=38$, $N=19$, $P<0.0005$; 'else': $\bar{X} \pm \mathrm{SD}=0.751 \pm 0.256$; 'near': 0.241 ± 0.559; Black: $\chi^2=132.631$, $df=38$, $N=19$, $P<0.005$; 'else': 0.427 ± 0.338; 'near': 0.209 ± 0.308). We therefore rejected the alternative explanation of aggressive approaching serving to keep the submissive bird away from the apparatus.

DYADIC TESTS WITH REVERSED RANKS

In this experiment we asked whether a switch in the dominance rank of a bird would result in the respective change in its behavioural role with regard to the occurrence of aggressive approaching.

Methods

Black/Green as well as Yellow/Black were tested in a dyadic combination. In this combination all birds had the opposite dominance status to that in the previous experiment. All other methods were similar to those of the previous experiment.

Results

In the first of these two dyads, Black immediately approached Green and the latter assumed the submissive role in the first and in all subsequent test sessions. Like Blue and Green in the previous experiment, Black approached Green significantly less frequently when the latter sat on the log or the lever than at other positions ($\chi^2 = 51.4$, $df = 18$, $N = 9$, $P < 0.002$; test see Methods). Aggressive approaching increased the probability that Green sat on the lever ($\chi^2 = 20.704$, $df = 12$, $N = 6$, $P < 0.05$, test see Methods) and it occurred significantly more often in tests than in controls without the seesaw (Wilcoxon matched-pairs signed-ranks test: $N = 9$, $P = 0.028$).

Yellow in combination with Black did not show aggressive approaching. In this combination both birds showed hardly any interest in the apparatus but remained relatively passive. Black was never approached by Yellow and never pushed down the handle.

DISCUSSION

In our experiments the food reward was distributed asymmetrically between the two keas participating in a cooperative task. The dominance hierarchy enabled the higher ranking bird to maintain the preferred position at the experimental food box and to monopolize the food reward. Subordinate birds were allowed only to manipulate the handle of the apparatus.

In group tests, however, all birds involved in manipulations of the seesaw gained access to food rewards with at least one partner because of the non-linear hierarchy. This resulted in a symmetric distribution of the reward which may explain why participants continued to operate the lever throughout the experiments, even without being forced to do so by others. Within the framework of game theory, this situation resembles a Prisoner's Dilemma with N players. Boyd & Richerson (1988) showed that in small groups 'Tit for tat' can be a stable strategy. We do not know, however, whether this situation with symmetrical pay-offs to all participants would have been stable over a long period.

Green, Yellow and Black performed both the food providing and retrieving roles according to their respective dominance status in a dyad or triad. This suggests the importance of rank in role assumption, as proposed by Bertram (1982). Dominant individuals may enforce cooperation on weaker individuals by means of aggressive behaviour such as coercion to deliver food. To an extent, this is also shown in 'producer–scrounger' interactions in which some individuals benefit from the acquisitions of others (e.g. Czikeli 1983). Juvenile keas, for example, will approach adults to obtain access to food (Diamond & Bond 1991). In our experiments, we found a more complex form of compulsion which involved manipulation of one animal to perform a certain type of behaviour that benefits only the other. Another example of manipulative behaviour of this kind is the activation of lazy workers in colonies of the eusocial naked mole-rat, *Heterocephalus glaber*, by their queen. Her shoves activate inherently 'lazy' workers which tend to be larger than and/or less related than infrequently shoved, industrious workers (Reeve 1992).

There was a gradual development in dyadic interactions towards manipulative behaviour of the dominant kea. At first the unrewarded subordinate participants (Yellow and Black) became reluctant to operate the lever of the apparatus voluntarily. Then the dominant participants started to approach their experimental partner aggressively which apparently manipulated the subordinate birds to perform a task that was beneficial to their dominant partners. The submissive birds performed this task significantly more often after being approached than without being approached. It appears as if the dominant birds

had to raise the frequency of aggressive approaches steadily in the course of the experiments because their partners were increasingly reluctant to push down the lever.

In contrast to the group tests, the dominant birds did not try to keep their partners away from the desired resource but approached them significantly more often at a distance from the food box than in its vicinity. They clearly distinguished between different types of behaviour and locations of the subordinate and did not approach when the latter was already in a beneficial position (i.e. lever or log). A somewhat similar manipulation is described as herding, in chimpanzees (Goodall 1968), hamadryas baboons (Kummer 1968), red deer, *Cervus elaphus* (Clutton-Brock et al. 1982) and dolphins, *Tursiops truncatus* (Conners et al. 1992).

In our experiments, sitting on the handle reduced the subordinate's risk of being approached and chased by its dominant partner. Thus the benefit to the subordinate of moving to the handle was the 'withholding to take some action' by the dominant (Taylor & McGuire 1988). The costs of sitting on the handle are more difficult to interpret. The quantification and interpretation of costs is a problem common to many empirical studies on cooperation (Seyfarth & Cheney 1988). In our study, sitting on the handle prevented a participant from performing other activities, such as staying in the preferred position at the food box ('opportunity costs'). The fact that Green and Yellow refused to push down the handle after several dyadic tests in which they were not forced to do so suggests that this behaviour did involve costs. In the fourth experiment, Black was submissive but was not approached by Yellow, and did not operate the lever even though he had frequently done so in the previous experiment when aggressively approached by Blue.

In the last experiment, in which both participants had reversed dominance positions, the dominant participant Black immediately adopted the new role of manipulating the submissive bird Green by means of aggressive approaching. He did not develop this behaviour gradually, but showed aggression towards his partner repeatedly right from the first session of the experiments. Although anecdotal, this may indicate that Black learned this role from prior experience when he had assumed the submissive role. This possibility should be tested experimentally.

Manipulation as a mechanism for cooperation has been suggested by Alexander (1974). Our experiments suggest that dominant keas use a mechanism to force cooperation on subordinates by means of social manipulation.

ACKNOWLEDGMENTS

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