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ORIGINAL PAPER

# Experimental evidence of reciprocal altruism in the pied flycatcher

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**Abstract** Although human behaviour abounds with reciprocal altruism, few examples exist documenting reciprocal altruism in animals. Recent non-experimental evidence suggests that reciprocal altruism may be more common in nature than previously documented. Here we present experimental evidence of mobbing behaviour, the joint assault on a predator in an attempt to drive it away, as reciprocal altruism in the breeding pied flycatcher (*Ficedula hypoleuca*). Given a choice, pied flycatchers assisted in mobbing initiated by co-operating neighbours and did not join in mobbing when initiated by conspecific neighbours which had defected from necessary assistance 1 h before. The results suggest the birds followed a 'tit-for-tat'-like strategy and that mobbing behaviour of breeding birds may be explained in terms of reciprocal altruism.

**Keywords** Reciprocal altruism · Co-operation · Anti-predator behaviour · Mobbing · Pied flycatcher

## Introduction

Reciprocal altruism is a form of mutual co-operation, in which one individual helps a non-relative and receives assistance itself in return some time later (Trivers 1971). While reciprocity is common in human society, the existing literature reveals relatively few cases in nature with experimental documentation and proof (e.g. Clements and Stephens 1995; Dugatkin 1988; Dugatkin et al. 1992; Fischer 1988; Godard 1993; Hauser et al. 2003; Krams et al. 2006a, b; Mendres and de Waal 2000; Milinski 1987; Olendorf et al. 2004; Packer 1977; Packer and Ruttan 1988; Stephens et al. 2002; Taborsky 1987; de Waal 2000; Wilkinson 1984). Recent non-experimental evidence (Krams and Krama 2002) indicates that the mobbing behaviour in birds may be explained in terms of reciprocity, raising the possibility that reciprocal altruism as a part of nest defence may be widespread among animals. However, general experimental evidence is still insufficient.

Several studies have shown that there are two successful survival strategies when a predator is discovered: quietly watching the predator from seclusion and thus escaping its attention or mobbing of the predator to provoke its retreat (Flasskamp 1994; Krams and Krama 2002). Mobbing is the joint assault on a predator performed by prey individuals in an attempt to disable or drive it from the vicinity (Arnold 2000; Curio 1978; Desrochers et al. 2002; Dominey 1983; Shedd 1983). This behavioural pattern occurs in a wide diversity of vertebrate groups, especially in birds and mammals (Altmann 1956; Curio 1978; Pitcher et al. 1986). Prey animals mob predators by emitting repeated, loud and easily localisable calls and by performing stereotyped movements that quickly recruit more prey individuals around a predator (Curio 1978; Dominey 1983). There is a group-size effect (Becker 1984; Robinson 1985) and, therefore, reciprocity among neighbouring individuals may be important for mobbing to be successful (Kruuk 1964; Slagsvold 1980). However, experimental evidence on mobbing as a reciprocity-based behaviour is so far lacking.

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The basic paradigm for most evolutionary models of co-operation has been the ‘prisoner’s dilemma’, where individuals have only two alternatives: to co-operate or to defect (Axelrod and Hamilton 1981). By definition, mutual co-operation gives a higher payoff than mutual defection. However, a defector gains an even higher payoff when paired with a co-operator.

If two territorial neighbours co-operate during mobbing, they have an increased opportunity to drive the predator from their breeding area (Flasskamp 1994; Pettifor 1990). If no neighbour co-operates with the first individual to mob, the lone harasser may be under an increased risk of predation by attracting the predator’s attention (Curio and Regelmann 1985, 1986; Denson 1979; Hoogland and Sherman 1976) while the defector does not increase its own risk of predation. Assuming that certain birds are caught in the ‘prisoner’s dilemma’ and that they are playing some form of reciprocity, they should copy each other’s behaviour according to certain rules (Axelrod 1980; Axelrod and Hamilton 1981; Trivers 1971). The original analysis of the conditions where reciprocity can evolve suggests that animals might follow a simple strategy called ‘tit-for-tat’, which shows an initial bias towards co-operation, followed by each individual copying each of its opponent’s moves. Thus, abandoned by a defector, the mobbing initiator suffers in the initial encounter and then may punish the defector by not assisting in subsequent mobbing initiated by the defector. When joined by a co-operator, the mobbing initiator benefits from increased group size and then later assists in mobbing initiated by the co-operator.

We conducted field experiments to test whether breeding pied flycatchers play tit-for-tat when mobbing in response to a predator. We expected that pied flycatchers would join in mobbing initiated by their co-operating neighbours who assisted them in the test an hour before and we expected them not to assist their non-co-operating neighbours at a simultaneous mobbing nearby. For reciprocal altruism to work, there must be some kind of social control against cheaters who might receive benefits without reciprocating. In communities where the individuals are familiar, a cheater will be recognised and quickly punished when others do not assist in mobbing initiated by the non-reciprocating cheater (Axelrod and Hamilton 1981; Clutton-Brock and Parker 1995).

## Methods

### Study site and general details

Our field setting was a natural population of the pied flycatcher living in dry young pine forests with sparse undergrowth near Kraslava in southeastern Latvia. The fieldwork was performed in May and June 2003 and 2004 while pied flycatchers were feeding nestlings, which were at least 6 days old. Five days was the maximum difference in age of nestlings in two neighbouring nestboxes. The fieldwork was performed between 0700 and 1600 hours under calm, warm and dry weather. All of the males and most of the females observed in this study were yearling individuals (Karlsson et al. 1986; Ojanen 1987; Alatalo et al. 1984). We made observations regarding other bird species living in the study locations.

Concerning specific methods, we colour-marked each adult bird. We placed foam rubber saturated with washable ink by the nestbox entry holes 1–2 days before field observations. The adult birds marked themselves by touching this while entering/leaving their nestboxes. We used a different colour for each nestbox in a triplet. Adult male and female plumages are different, so each adult bird was individually identifiable.

To obtain sufficiently large sample sizes, we constructed 300 identical wooden nestboxes. From these we set up 100 triplets of nestboxes. We arranged each triplet in a triangular pattern. The distance between neighbouring triplets was at least 470 m. We excluded from field study those nestbox triplets where a different species occupied one of the nestboxes, where there appeared to be a nesting failure, or where the nestling age appeared to differ by more than 5 days between the nestboxes. Out of the original 100 nestbox triplets during two seasons, we obtained 44 triplets, which met our experimental criteria. The distance between nestboxes in these triplets was 48–54 m (mean=50.72, SE=3.29). Of these 44 nestbox triplets, we used 35 for the primary experimental situation and a separate 9 for the supplemental experimental situation. We developed our experimental design to evaluate responses in two different situations: primary experimental situation and supplemental experimental situation, which were divided into phase one and phase two.

### Primary experimental situation

Three neighbouring pairs of pied flycatchers lived in nestboxes in a triangular configuration approximately 50 m apart. We randomly identified the nestboxes as A, B and C. To select which nestboxes in each triplet would be designated A and which B, we used a series of coin flips. This provided for random designation of A, B and C positions within each triplet. In *phase one*, we exhibited a predator to nestbox A shortly after the adult bird pair in nestbox B has been secretly captured to prevent them from being able assist in mobbing initiated at nestbox A. To initiate mobbing behaviour, we placed an apparent predator on top of a pre-positioned pole close to a nestbox. In all cases we used life-like stuffed tawny owls (*Strix aluco*) as the predator stimulus. The tawny owl is a common predator of birds in Northern Europe whose presence strongly affects the behaviour of passerine birds (Bautista and Lane 2000). When pied flycatchers find such a predator near their nests, they mob it while uttering characteristic calls that attract other hetero- and conspecific potential prey species to the vicinity (Shalter 1978). We observed the mobbing behaviour for nestbox A birds and any assisting nestbox C birds. As soon as the observations were finished, we removed the predator. We released the nestbox B birds, and normal conditions resumed. For *phase two*, 1 h after the first event, while all three pairs are free, we simultaneously presented predators to both nestboxes B and C. We have created from phase one our experimental setting where nestbox A birds can subsequently choose to assist either the non-co-operating 'defector' neighbour B or the 'co-operating' neighbour C which had not defected. Our question was: how will nestbox A birds respond? We observed the behaviour of the three adult pairs. We hypothesised that the birds in nestbox A would reciprocate in a tit-for-tat fashion by assisting at co-operating nestbox C while ignoring (punishing) the needs of the prior defectors at nestbox B. We noted that this primary experimental situation left open the possibility that if the nestbox B birds had been traumatised or in some way been affected by their prior capture, or if human presence was a factor, then perhaps their mobbing behaviour would be influenced so as to be ineffectual for attracting assistance from the birds in nestbox A. To monitor for this potential interference, we incorporated a supplemental experimental situation as a limited control.

### Supplemental experimental situation

This additional situation was created to evaluate the possibility that capture affected the subsequent alarm calling of the captured birds. Phase one was identical to the primary experimental situation, but phase two was different. As in the primary experimental situation, phase one created a setting where the birds in nestbox A could consider nestbox B to be 'defectors' and nestbox C to be 'co-operators.' For phase two, 1 h after the first event, while all three pairs are free, we presented a single predator to only the defectors in nestbox B. This time our question was the following: will any birds respond and assist at nestbox B? We observed the behaviour of the three adult pairs. We hypothesised that birds from nestbox C might respond if the calling was not impaired, and that perhaps neither nestbox A nor C birds would respond if the previously captured pair B had been affected to a degree to impair their behaviour when B initiated mobbing. Besides evaluating calling efficiency, this experimental situation gave us an opportunity for an additional test of reciprocal altruism. Because the birds in nestbox B are constrained during phase one, according to the idea of reciprocal altruism, the birds of nestbox A should not assist them during phase two.

### Detailed description of experiment

The field design required that we be able to capture and release birds, exhibit a predator, and observe individual behaviour without being overly obvious to birds. To accomplish this we set up small tents as 'blinds' about 10 m away from nestboxes A and B. Concurrent with installing the coloured ink markers, we set up the blinds 1–2 days in advance. Later, during the experiments, we remained inside the blinds except for brief excursions for capture/release and for putting out/retrieving the stuffed predators.

To quickly capture both adult birds at nestbox B, we used mist nets and a remotely closable door on the nestbox. Our objective was to make the captures without being obvious to the birds in nestbox A and C. We always installed the nets and trap door at least 2 h before the trapping procedure. The nets were kept lowered and the trap door open until it was time to trap the two birds. Then, when the two adults were away from nestbox B and not visible, a person stepped out of the blind to raise the nets and returned to the blind. Except for three cases in the primary experimental situation, we were able to capture both nestbox B adults within 2–16 min (mean=8.03, SE=0.59, $n$=32). We abandoned three triplets of the original 35 in the primary experimental situation due to a bird escaping ($n$=1) or inability to quickly capture both birds ($n$=2). All captures for the secondary experimental situation were successful.

The owl position was 1.0–1.5 m away from the nestbox with a base height of 1.2 m above ground level. At the proper time, and while the adults birds were away from the nestbox and out of sight, we momentarily stepped out of the blind and placed the owl on top of the pole. The owl faced the nestbox. After the short observation period ended, we discretely retrieved the owl into the blind.

We objectively scored the mobbing behaviour of each individual bird during phases one and two at each nestbox triplet location. Our scale of pied flycatcher mobbing response used four categories of displays and vocalisations. The final score was the highest valued behaviour observed to last for at least 5 min. Because the perches suitable for mobbing birds varied in distance from the predator at each location, we only scored behaviour and not the specific distance of a mobbing bird's approach to the predator. Although we do not know whether our ranking system is linear in terms of risk and energy expenditure, it is corresponding to species-specific, step-by-step, increasing intensity of mobbing behaviour observed under field conditions (Curio 1959, 1961a,b, 1975; Creutz 1955; Shalter 1978). With no response (0 points), the pied flycatcher investigates the predator from a distance usually without any alarm calls while continuing activities such as foraging or singing. Weak response (1 point) involved frequent approaching and retreating to/from a predator. With average response (2 points), the birds tend to be close to the predator; they restlessly move around the object of alarm by bowing, pivoting, tail-flicking and hovering in the air in front of the predator. Strong response (3 points) involved intense movements and display including dive-attacks on the predator; while mobbing predators, pied flycatchers use 'pik' calls (Bergmann and Helb 1982).

During phase one, the nestbox B birds could not respond to the calls for assistance at nestbox A, and thus were forced into the role of being defectors. The nestbox C birds were free to join and assist in mobbing initiated by nestbox A birds. We defined *assisting* neighbours as leaving the bird's own territory and mobbing the predator in the neighbouring territory, often as close to the predator as the nestbox owners. While the nestbox C birds had the option of remaining in the vicinity of their own nest and from there giving mobbing calls or remaining silent, the nestbox C adults always actively assisted at nestbox A and thus they were co-operators in the eyes of the nestbox A birds.

The field work for both the primary and secondary experimental situations were conducted by teams of three persons. Thus, at least one person was stationed in each blind and humans were not walking from station to station during the experiments.

Phase one of both experimental situations was conducted in the same manner. At least 2 days in advance, selections were made for determining A, B and C; the blinds were set up; and the birds were marked. At least 2 h in advance, the mist nets, remotely activated trap door and predator poles were put in position. After 2 h of waiting, while the nestbox B birds were away from their nest and out of sight, the mist nets were raised. During the next 2–16 min, the nestbox B adults were either trapped inside their nestbox or caught and collected from a mist net. Mist-netted birds were kept quietly inside the blind until release. Once the nestbox B birds were both captured and the nestbox A birds were away from their nest and out of sight, the person at nestbox A discretely placed the stuffed owl on the stand and returned to the blind. The owl was left visible on the stand for about 15 min. During this time, the nestbox A birds always returned to the vicinity of their nestbox and, upon seeing the predator, initiated mobbing behaviour. During this period, we observed and recorded the behaviour of both the nestbox A and C birds. As soon as the 15 min of predator presence ended, and the adult birds had already finished their mobbing behaviour, we quickly and discretely returned the owl to the blind. We then released the captured nestbox B birds. The nestbox B birds returned to their nestbox and resumed feeding nestlings within 8–19 min (mean=12, SE=0.54).

Phase two of the *primary* experimental condition was initiated 1 h after ending phase one (i.e. release of nestbox B birds). During this interval, we remained inside the blinds and monitored to know if the birds became involved in other anti-predator activities. While nestbox B and C birds were simultaneously away from their nests and out of sight, we discretely placed a stuffed owl on the stand at each of these two nestboxes and returned to the blind. The owls were left visible on the stands at nestboxes B and C for about 15 min. During this time, the nestbox B and C birds always returned to the vicinity of their nestboxes and, upon seeing the predator near their nestbox entrance, initiated mobbing behaviour. No birds were caught or trapped. All three pairs were free. During this period, we observed and recorded the behaviour of all three pairs.

Phase two of the *secondary* experimental condition was also initiated 1 h after ending the corresponding phase one (i.e. release of nestbox B birds). This situation involved a single predator appearing only at nestbox B. During the 1-h interval, we remained inside the blinds and monitored to know if the birds became involved in other anti-predator activities. While nestbox B birds were away from their nest and out of sight, we discretely placed a stuffed owl on the stand beside nestbox B and returned to the blind. The owl was left visible on the stand for about 15 min. During this time, the nestbox B birds always returned to the vicinity of their nestbox and, upon seeing the predator near their nestbox entrance, initiated mobbing behaviour. No birds were caught or trapped. All three pairs were free. During this period, we observed and recorded the behaviour of all three pairs.

We found a low density of other non-hole nesting passerines in our study area. The number of passerine birds was similar for each of the 32 primary situation sites. There were between 8 and 10 individuals, including the three pairs of pied flycatchers involved in the experiments (one-way ANOVA, $F_{31}$=0.15, $P$=0.71). Thus, the possible dilution effect during the harassment of predators can be treated as similar over all of the sites. We found the following heterospecific bird species breeding at one or more sites: tree pipit (*Anthus trivialis*), robin (*Erithacus rubecula*), song thrush (*Turdus philomelos*), mistle thrush (*Turdus viscivorus*), willow warbler (*Phylloscopus trochilus*), chiffchaff (*Phylloscopus collybita*), crested tit (*Parus cristatus*), willow tit (*Parus montanus*) and chaffinch (*Fringilla coelebs*). These species are known to mob predators (Snow and Perrins 1997). They were active mobbers during our experiment.

## Results

During phase one of both the primary experimental situation and the secondary experimental situation, where an owl appeared before the nestbox A birds, the adult pair in nestbox C always assisted in mobbing at nestbox A. This happened in all 41 cases.

During phase two, nestbox A birds had a choice to assist nestbox C co-operators, to assist nestbox B defectors or to remain in the vicinity of their own nest and assist neither. In the primary experimental situation, where the owls simultaneously appeared at the nestboxes of nestbox C co-operators and nestbox B defectors, the nestbox A pairs assisted in mobbing initiated by the nestbox C co-operators in 30 out of 32 cases ($\chi^2$=24.5, df=1, $P$<0.0001, Fig. 1). The nestbox A birds never responded to the nestbox B defectors and they remained in the vicinity of their own nestbox in two cases. During phase two of the secondary experimental situation run as a limited control, where an owl appeared only at the nestbox of nestbox B defectors, the nestbox A birds also never responded to the nestbox B defectors and remained in the vicinity of their own nestbox in all nine cases.

During phase two of the primary experimental situation, nestbox C birds were busy defending their own nestbox. During phase two of the secondary experimental situation, the nestbox C birds had a choice to assist nestbox B birds or to remain in the vicinity of their own nest. The result was eight out of nine nestbox C pairs assisting in mobbing at nestbox B ($\chi^2$=5.44, df=1, $P$=0.02). One pair of nestbox C co-operators remained in the vicinity of their own nestbox. These results indicate that mobbing by the previously trapped defectors was as attractive or natural as that exhibited by the other pairs.

We had additional results pertinent to the special concern regarding whether the nestbox B trapped birds subsequently behaved differently from the other birds. The scores for nestbox A bird behaviour during phase one of the primary experimental situation showed mean intensity levels between *average response* and *strong response* in all cases (score range=1–3, mean=2.34, SE=0.11, $n$=32). The nestbox B defectors were observed in phase two to behave at a similar mean intensity of average to strong response (score range=1–3, mean=2.16, SE=0.12, $n$=32). The behaviour of the birds of nestbox A in phase one was similar to that of nestbox B birds during mobbing after release from capture (two-tailed Mann–Whitney $U$ test: $U$=10.0, $P$=0.14). The mobbing intensity also did not differ between the birds of nestbox B during phase two of the primary experimental situation and the birds of nestbox C (score range=1–3, mean=2.28, SE=0.10, $n$=32) during phase two of the primary experimental situation (two-tailed Mann–Whitney $U$ test: $U$=30.0, $P$=0.65).

## Discussion

The comparison of mobbing intensity of the nestbox A birds during phase one of the primary experimental situation with mobbing intensity of the nestbox B birds during phase two of the primary experimental situation and that of the nestbox C birds during phase two of the primary experimental situation showed that mobbing initiators mobbed the predators similarly in all three groups. This provided additional support for the evidence that the refusal of the nestbox A birds to assist the nestbox B defectors should not be attributed to impaired mobbing behaviour from the previously trapped birds. The nestbox A birds did not assist the nestbox B birds despite the fact that the loud mobbing calls usually recruit most individuals from the neighbourhood.

The results of the primary experimental situation and the supplemental experiment are clearly consistent with the idea of reciprocity (Roberts 1998). Mobbing by pied flycatchers has some essential features of a prisoner's dilemma problem with a scale of pay-offs: temptation to defect (T), reward for mutual co-operation (R), punishment for mutual defection (P) and sucker's payoff (S). T is the

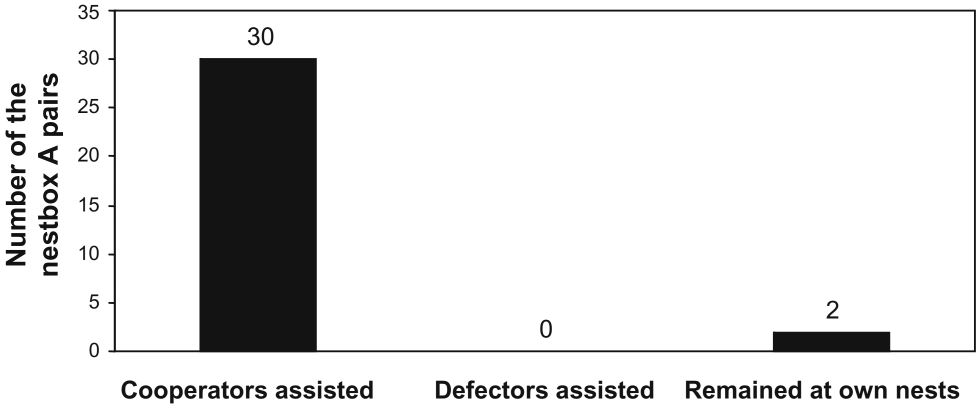

**Fig. 1** Number of the nestbox A pairs of pied flycatchers that assisted co-operators, assisted defectors and remained at their own nest during phase two of the primary experimental situation ($n$=32)

best and S is the worst outcome. Mobbing harassment has been shown to entail a risk of injury or even death to the prey individual engaged in mobbing owing to their proximity to the predator (Curio and Regelmann 1985, 1986; Denson 1979; Hoogland and Sherman 1976; Sordahl 1990). Therefore the *temptation to defect* may pay better than co-operation. Although it is risky to harass a predator, the prey animals may profit from a joint defence against predators because mobbing decreases the risk of being attacked (Pavey and Smyth 1998). Also, the strength of a mobbing response increases with group size and more mobbers increase the chances of successfully driving away a predator (Becker 1984; Robinson 1985; Verbeek 1985). As a predator vacates its immediate foraging area, it gives an opportunity for prey individuals to continue their interrupted daily activities (Pettifor 1990), and this benefit can be shared by individuals within a given area. Hence, the increased inclusive fitness of breeding neighbours is the *reward for mutual co-operation*. If no neighbours squeal and mobbing is not initiated, then the predator may remain in the vicinity for longer times. In this case, no individual increases its risk of predation. However, feeding of offspring is usually not possible while a predator is present, and this is costly. This is the *punishment for mutual defection*. Finally, the initiator of mobbing and its offspring may be under increased risk of predation by attracting the predator's attention, especially if not joined by other neighbouring prey individuals (Krama and Krams 2005). This case could be treated as the *sucker's payoff*. It may seem that this is a three-person game which, in nature, appears to be an *n*-person game. Luce and Raiffa (1957) suggest that multi-player games are much more unstable. However, under our study design, the birds were not able to make coalitions and it indicates that the birds were involved in a stable two-person-like game, which is assumed by the prisoner's dilemma.

A very important condition for reciprocity to evolve is that there must be repeated interactions between the participants, so failing to co-operate on one occasion has a penalty in the future through not having the co-operative act reciprocated next time. For this reason, such behaviours as mobbing are expected to be characteristic of animals that stay together over long periods of time, enough for the roles of donor and recipient to be exchanged many times. A second condition is that cheats can be recognised and penalised. The birds living in breeding communities are not anonymous and their social behaviour such as collective mobbing is evidently based on temporal stability of the breeding communities (Naguib et al. 1999; Krams and Krama 2002) and the positive relationships with conspecific and heterospecific neighbours (Mönkkönen et al. 1997; Forsman et al. 1998). In this field experiment, it appeared that the pied flycatchers could individually identify their neighbours. Our nestbox A pied flycatchers assisted in mobbing initiated by their previously co-operating neighbours and did not assist non-co-operators who had defected in tests 1 h previously. This resembles the first move in the tit-for-tat strategy where only co-operating individuals are supposed to be supported accordingly by their partners on the next move. In this experimental study, co-operating flycatcher families won the reward for mutual co-operation on every encounter. Non-co-operators were immediately punished. The results show that the origin and evolution of mobbing behaviour of breeding pied flycatchers can be explained in terms of reciprocal altruism.

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