You mob my owl, I’ll mob yours: birds play tit-for-tat game

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Reciprocity is fundamental to cooperative behaviour and has been verified in theoretical models. However, there is still limited experimental evidence for reciprocity in non-primate species. Our results more decisively clarify that reciprocity with a tit-for-tat enforcement strategy can occur among breeding pied flycatchers Ficedula hypoleuca separate from considerations of byproduct mutualism. Breeding pairs living in close proximity (20–24 m) did exhibit byproduct mutualism and always assisted in mobbing regardless of their neighbours’ prior actions. However, breeding pairs with distant neighbours (69–84 m) either assisted or refused to assist in mobbing a predatory owl based on whether or not the distant pair had previously helped them in their own nest defense against the predator. Clearly, these birds are aware of their specific spatial security context, remember their neighbours’ prior behaviour, and choose a situation-specific strategic course of action, which could promote their longer-term security, a capacity previously thought unique to primates.

Reciprocal altruism is a form of mutual co-operation, in which one individual helps another and receives assistance in return some time later. Various studies have evaluated the actions of multiple individuals simultaneously cooperating in behaviours known as mobbing or predator inspection, revealing the ability of animals to follow tit-for-tat strategy. However, the mechanisms motivating individuals to cooperate, for example to repulse a predator, are still far from being well understood. Doubts persist whether non-primate species possess the cognitive abilities to remember the outcome of previous interactions and accordingly to select future cooperators. Thus, a number of studies have suggested that animals’ cooperative interactions are motivated only by short-term rewards based on byproduct mutualism or by the need to retain a valuable potential partner. Cognitive skills may also constrain the ability of animals to establish and maintain reciprocity, which could explain why finding evidence for contingent reciprocity in nonhuman animals has been difficult. However, some recent evidence suggests that animals are indeed capable of acting according to their future, rather than current, needs.

Reciprocity denotes a behaviour whereby an organism acts in a manner such that it risks reducing or even losing its fitness while increasing the fitness of another organism, because this other organism is likely to act similarly at a later time. The original analysis of the conditions where reciprocity could evolve suggested that organisms should follow simple strategies such as ‘tit-for-tat’, i.e. an initial bias towards cooperation, followed by each individual copying its counterpart’s moves. Previous experiments with pied flycatchers showed clear response patterns to assist ‘co-operating’ in preference over ‘defecting’ conspecific neighbours based on a prior event, but there arose questions about byproduct mutualism and dominance effects because of the moderately close proximity of the nestboxes (48–54 m apart).

We carried out a field experiment to test whether breeding pied flycatchers can act purely reciprocally when mobbing in response to a predator. We tested this possibility against the hypothesis that the behaviour might be explicable in terms of byproduct mutualism, whereby the activities of an organism provide benefits predominantly for itself and only incidentally to others. We compared the mobbing responses of pied flycatchers for two proximity groups: those breeding either closely or distantly from one another.

Results
In the control subgroups, when an owl was presented at nestboxes #1 of the ‘close’ pairs and the ‘distant’ pairs, adult flycatchers of both subgroups mobbed the predator (Fig. 1). This happened in all 12 cases in ‘close’ pairs control birds and in all 12 cases in ‘distant’ pairs control birds (Fisher’s exact test, P = 1.00). When the owl was...
presented 1 hr later at nestbox #2, all of the previously assisted pairs of flycatchers from nestboxes #1 for both ‘close’ and ‘distant’ groups reciprocated the assistance and arrived to mob the predator at the boxes of their cooperating neighbours (Fisher’s exact test, P = 1.00).

In the experimental subgroups, nestbox #1 birds in phase one had to mob the owl on their own, and were made aware of the “decision” of nestbox #2 birds to defect. When the owl was presented 1 hr later at nestbox #2, all 12 defectors from nestbox #2 were assisted by their ‘close’ neighbours, while only 2 out of 14 defectors were assisted by their ‘distant’ neighbours (Fig. 1). The other 12 birds from the ‘distant’ experimental subgroup pairs were seen to interrupt their feeding and were heard giving alarm calls. These behavioural responses suggest that the uncooperative neighbours of the defectors were indeed aware of the situation at their ‘distant’ neighbour’s nestbox. The incidence of reciprocity in the experimental subgroup of ‘close’ neighbours differed significantly from that of the ‘distant’ group (Fisher’s exact test, P = 0.0001).

Discussion
These results suggest that joining in the mobbing of predators at the nests of near-neighbours might contribute to the protection of one’s own nest, and thus be explicable in terms of byproduct mutualism. It has been shown that a predator tends to leave an area sooner, the more intensely it is harassed29–32. It has also been shown that predators avoid visiting areas where they have been previously harassed29. Thus, prey individuals may profit from a joint defence against predators because their own fitness may be enhanced as a result of the generally reduced probability of predation.

Our results demonstrate that breeding pied flycatchers transition to cooperation behaviours which resemble reciprocity as the distance to a neighbour increases. For distant neighbours, they significantly punished defectors and reliably assisted cooperators. This finding suggests that they are aware of their spatial context, are aware of current and fully capable of remembering previous social interactions with neighbours, change their responses as a result of previous experiences, and choose a situation-specific strategic course of action which might promote their own (self-centered) longer-term security (fitness). This is a demonstration of tit-for-tat strategy, where only co-operating individuals will be supported by their neighbours in the next move. The choice of mobbing or defecting in the distant-neighbour group appears to be an instance of a prisoner’s dilemma. Since harassment of a predator may entail a risk of injury or even death33–35 defection against a non-cooperating individual, rather than cooperation, may be the best option. To mob or not to mob – that is the question, and the answer for a pied flycatcher appears to be a reasonable pattern of responses which incorporates spatial, behavioural, historical, real-time, and future factors.

Methods
Study site and birds. The study was conducted in May and June 2010 and 2011 near Kraslava, southeastern Latvia (55°90’N, 27°19’E). We placed nestboxes in pairs in pine forests with sparse understory, with pairs separated by at least 650 m. ‘Close’ nestboxes were located 20–24 m from one another (mean ± SD = 22 ± 0.96 m; 24 pairs of nestboxes) and ‘distant’ nestboxes 69–84 m from one another (mean ± SD =
80.02 3 3.50 m: 26 pairs of nestboxes). ‘Close’ and ‘distant’ nestbox pairs were further assigned to either an experimental or a control subgroup. In the ‘close’ group, 12 pairs of nestboxes were assigned to the experimental and 12 to the control subgroup. In the ‘distant’ group the corresponding assignment was 14 pairs to the experimental and 12 pairs to the control subgroup.

Since parents should take higher risks while defending larger and older broods, we included in this study only nests with 

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