

Testing mutualism: a commentary on Clements & Stephens

GILBERT ROBERTS

Department of Psychology, University of Newcastle

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Clements & Stephens (1995) reported experiments on non-kin cooperation within pairs of captive blue jays, *Cyanocitta cristata*, pecking for food. In their experiments, the reward regimes were determined by the two-by-two combinations of 'cooperate' and 'defect' keys pressed by the two birds. This experimental determination of payoffs represents an important advance, given the continuing controversy (e.g. Connor 1996) over whether the payoffs involved in cooperation actually fit those of the Prisoner's Dilemma model (Axelrod & Hamilton 1981). In addition to testing birds under a Prisoner's Dilemma regime, Clements & Stephens considered a 'mutualistic' reward regime (where pressing cooperate always gave a higher payoff than pressing defect, and where the highest payoff was obtained when both pressed cooperate). Trials stabilized with both pressing the cooperate key. Clements & Stephens interpreted this result as showing that the birds readily developed mutualism. I argue, however, that the most parsimonious explanation of their results does not involve cooperation, and therefore that their experiment does not provide a test of the establishment of mutualism.

The observation that the jays stabilized on pressing the cooperate key can be explained by arguing that the jays preferred to press the key that always gave the higher reward. Thus, the experiment demonstrates nothing more than choice for a higher reward. The most parsimonious explanation of each jay's behaviour involves no consideration of the behaviour of the other individual, so they cannot be considered to have been cooperating. For behaviour to be classed as mutualistic, there must be some evidence of adaptation specifically for obtaining benefits (e.g. Connor 1995). Thus two birds that have indepen-

dently chosen to feed on a school of fish may happen to benefit from the flushing effect of each other's activities, but they are not mutualists. Two birds that have modified their behaviour to take advantage of the flushing effect of the other are mutualists. In both cases, the birds are acting out of self interest. In both cases, the payoffs fit the mutualism matrix. In the former case, however, choice of school can more parsimoniously be explained without cooperation (the birds would have chosen to feed there anyway, and the presence of the other bird explains only the higher reward not their feeding strategy); in the latter case cooperation is a meaningful concept in explaining their coordinated behaviour. If one considers, as Clements & Stephens do, only the payoff matrix and explicitly defines cooperation in terms of the rewards rather than the behaviour, then one can explain only the rewards and not the behaviour leading to those rewards.

In Clements & Stephens' experiment, there is no evidence that the behaviour of one jay is modified by the presence and behaviour of another, so there is no sense in which they may be said to have been cooperating. Mutualism could be tested by considering strategies that are explicitly defined with reference to the behaviour of another individual. Thus, Clements & Stephens' experiment could be modified by adding a temporal dimension to the task, such that the strategy 'press the cooperate key (at any time, regardless of the other individual's behaviour)' becomes 'press the key at the same time as another individual'. If cooperation developed, such that the birds acted together for mutual benefit, then, as in Clements & Stephens (1995), the birds could be said to be acting out of self interest. In contrast to their experiment, however, in which individuals chose to 'cooperate' regardless of the behaviour of the other (something of a contradiction), this time cooperation is explicitly defined with reference to the behaviour of the other. So, although in the former situation

Correspondence: G. Roberts, Department of Psychology, University of Newcastle, Newcastle upon Tyne NE1 7RU, U.K. (email: gilbert.roberts@ncl.ac.uk).

the most parsimonious explanation of the key-pressing behaviour does not involve the other bird, in the latter situation it must, so mutual cooperation would be a useful concept.

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