

and much less work on understanding the properties or performance of the methods [3]. There is a place for different approaches to reflect the diversity of data and hypotheses being addressed, but it is important that supertree workers justify their choice of method. MRP remains popular largely because of its convenience (as standard phylogenetic software is used to analyse the transformed data), but relying exclusively upon MRP is increasingly difficult to defend.

By proposing a statistical model for the supertree problem, the maximum-likelihood approach is a step in the right direction. Bringing phylogenetic supertrees into the same framework as phylogenetic inference from sequence data should help users focus on the importance of methodological issues, as statistical model selection is now routine when building phylogenies from sequences. In combination with increasingly realistic models of sequence evolution, maximum-likelihood approaches to supertree construction look set to play an important role in the growing field of phylogenomics. Much work remains to be done: it is unclear how well the mathematically convenient exponential distribution models incongruence in real data, and work has only just begun on efficiently estimating optimal trees under this model. Whether or not this particular approach is successful, supertree methods might need to become part of the mainstream toolkit of molecular phylogenetics if systematists are to make proper use of the deluge of genomic sequence data.

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References

- 1 Page, R.D.M. and Holmes, E.C. (1998) *Molecular Evolution: A Phylogenetic Approach*, Wiley-Blackwell
- 2 Bryant, D. (2003) A classification of consensus methods for phylogenies. In *Bioconsensus* (Janowitz, M. *et al.*, eds), pp. 163–184, DIMACS AMS
- 3 Bininda-Emonds, O.R.P. (2004) *Phylogenetic Supertrees: Combining Information to Reveal the Tree of Life*, Kluwer Academic
- 4 Steel, M. *et al.* (2000) Simple but fundamental limits for supertrees and consensus methods. *Syst. Biol.* 49, 363–368
- 5 Wilkinson, M. *et al.* (2007) Properties of supertree methods in the consensus setting. *Syst. Biol.* 56, 330–337
- 6 Wilkinson, M. *et al.* (2005) The shape of supertrees to come: tree shape related properties of fourteen supertree methods. *Syst. Biol.* 54, 419–431
- 7 Steel, M. and Rodrigo, A. (2008) Maximum-likelihood supertrees. *Syst. Biol.* 57, 243–250
- 8 Cotton, J.A. and Wilkinson, M. (2007) Majority-rule supertrees. *Syst. Biol.* 56, 445–452
- 9 Delsuc, F. *et al.* (2005) Phylogenomics and the reconstruction of the tree of life. *Nat. Rev. Genet.* 6, 361–375
- 10 Rokas, A. *et al.* (2003) Genome-scale approaches to resolving incongruence in molecular phylogenies. *Nature* 425, 798–804
- 11 Slowinski, J.B. and Page, R.D.M. (1999) How should phylogenies be inferred from sequence data? *Syst. Biol.* 48, 814–825
- 12 Kubatko, L.S. and Degnan, J.H. (2007) Inconsistency of phylogenetic estimates from concatenated data under coalescence. *Syst. Biol.* 56, 17–24
- 13 Matsen, F.A. and Steel, M.A. (2007) Phylogenetic mixtures on a single tree can mimic a tree of another topology. *Syst. Biol.* 56, 767–775
- 14 Yang, Z. and Nielsen, R. (2008) Mutation-selection models of codon substitution and their use to estimate selective strengths on codon usage. *Mol. Biol. Evol.* 25, 568–579
- 15 Ané, C. *et al.* (2007) Bayesian estimation of concordance among gene trees. *Mol. Biol. Evol.* 24, 412–426

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Letters

Avian mobbing: byproduct mutualism not reciprocal altruism

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Reciprocal altruism [1] is the pinnacle of cooperation and a hallmark of human societies, but has been notoriously difficult to demonstrate in animals. Recently, Krams and colleagues [2] claim to have provided evidence of reciprocal altruism in avian mobbing interactions; this paper was highlighted in a recent Research Focus in *Trends in Ecology and Evolution* [3]. Here we illustrate why the evidence for reciprocal altruism remains equivocal in this context.

To test for reciprocal altruism, Krams and colleagues [2] conducted three sequential experiments using stuffed owls to induce mobbing behaviour in 44 trios (A–C) of pairs of pied flycatchers (*Ficedula hypoleuca*): (i) pair A had an owl placed

at its nest, pair B was caged and pair C was untreated. Pair C mobbed the owl with pair A, while pair B could not (Figure 1a). (ii) An owl was presented at the nests of B and C, while A was left untreated. Pair A mobbed the owl at C more often than at B (Figure 1b). (iii) An owl was placed at pair B while pairs A and C were left untreated. Pair C mobbed at B, but A did not (Figure 1c). Overall, this is suggestive of reciprocal altruism: C helped A, and in return A was willing to help cooperator C, but not defector B. However, reciprocal altruism requires four criteria to be met [1,4]. First, an individual A must invest in an individual B at a cost to itself. Second, individual B must repay the cost to A in the future. Third, the behaviour needs to be contingent: A helps B *because* of a future expectation of reciprocation, and B repays A *because* of the initial act.

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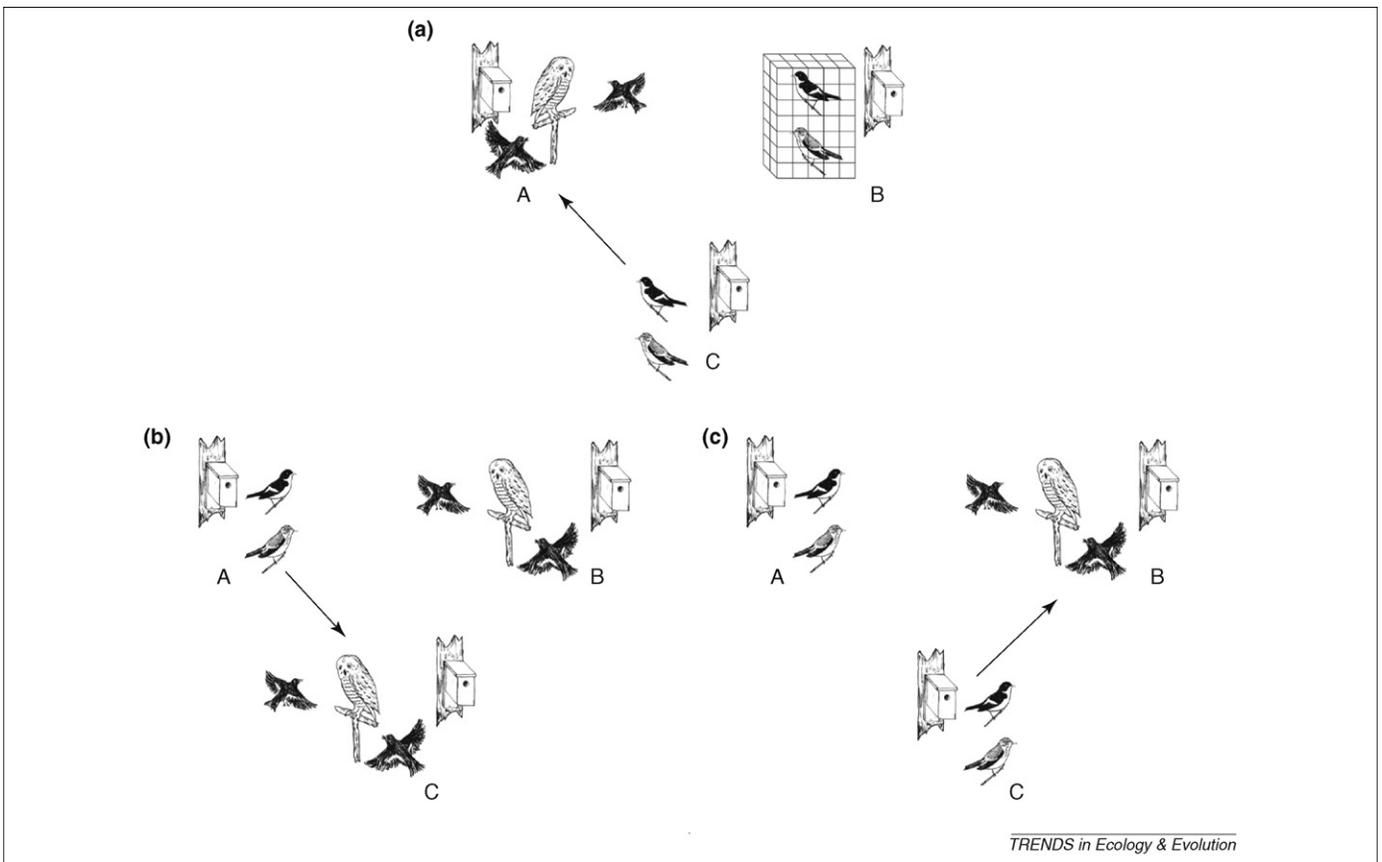


Figure 1. Experimental setup [2]: trios of pairs arranged as shown with 50 m between each. Trials were conducted in order with 1 h in between trials. Stuffed owls were placed 1 m from nests. Reprinted with permission from Ref. [3].

Fourth, the interaction needs to be repeated in order for stability to ensue.

It is possible that pied flycatchers cooperate through reciprocal altruism [2] and birds might have greater cognitive powers than have hitherto been attributed [3]. However, we have three issues with these conclusions. First, why did C mob the owl at A in the first place (Figure 1a)? For reciprocal altruism to be acting, C must have done so because (although the owl posed no immediate threat to C) in the future C might have its own owl to deal with and so would then benefit from A's help. Thus, if C helps A now, then maybe A will help C in the future. This is clearly complicated and potentially unstable (e.g. A might benefit by defecting and fail to return the favour to C). A more parsimonious explanation is that an owl on the territory of A is also of significant threat to pair C, because the territory of an owl is considerably larger than that of a flycatcher. Under this situation, C's initial investment is selfish, not altruistic as required by reciprocal altruism, and if A benefits, it does so through a byproduct mutualism [5]. In a byproduct mutualism, a selfish behaviour by one individual has an incidental but beneficial spin-off for another individual performing the same act. In the case of flycatchers, C benefits by mobbing at the nest of A because it represents an effective way of keeping the owl from its own nest, and through the selfish act of C, A benefits. Because it is based on selfish, not altruistic, interactions, byproduct mutualism carries no incentive for defection, and is hence both simpler and more stable than reciprocal altruism.

Second, why does A mob at C and not B (Figure 1b)? Under reciprocal altruism, this is because A, although perceiving no current threat to itself, chooses to repay the favour dealt by C, because if A requires further help of C in the future, then C might again repay the favour. However, like C's initial act (see above), such apparent reciprocation by A can be explained more parsimoniously through byproduct mutualism. The only difference here is that A has information that C is likely to join in with any mobbing, because A has experienced that C, unlike B, is willing to mob in association with A. Therefore, the reason that A mobbed at C rather than B could simply be due to the fact that C represented a less costly and more effective option than B, because mobbing with others carries lower risks of individual injury and greater likelihood of success than mobbing alone. This alternative explanation does not necessarily involve the complex processes of individual recognition or scorekeeping of previous events that are crucial for reciprocal altruism [1]. It merely requires that A perceives C as a better choice, because of previous evidence that the two pairs are spatially or socially associated in the context of nest defence.

Third, why should A refuse to mob at B (knowing that B did not mob at A) and yet C (knowing little about B) should decide to do so (Figure 1c)? This result is the most interesting because, under reciprocal altruism, A does not mob at B *because* B did not help A previously and hence A is retaliating for B's earlier defection. However, an alternative explanation is that A is simply doing what is best for A and using prior experience to balance costs and benefits of

self-interested mobbing, which A might expect to do so alone if it is at the nest of previously nonassociated B. By contrast, without any such prior experience, C might assume some baseline likelihood that B would choose to mob, as they did initially with A. Thus, A's decision not to mob at B can be explained by sensible investment rather than punishment by defection. As argued above, the mechanisms involved here are potentially much less complex and cognitively demanding than those required for reciprocal altruism. This alternative route to 'cooperative' mobbing based upon the expected benefits from byproduct mutualism would appear more parsimonious and more likely to have evolved in this context.

In conclusion, interactions that might appear reciprocal do not necessarily provide evidence for reciprocal altruism. Unless the first move can be shown to be altruistic (at least in the short term) and that any subsequent return is strictly contingent upon such altruism, then we are most likely observing some form of byproduct mutualism. Showing both that initial and reciprocal acts are costly and that

each are performed multiply by pairs of individuals over time would go a long way to providing the evidence necessary for reciprocal altruism. Thus, although the results of the Krams *et al.* [2] are clearly thought provoking and consistent with reciprocal altruism, parsimony would suggest that they are more likely to be explained by more simple and more common forms of cooperation.

References

- 1 Trivers, R.L. (1971) The evolution of reciprocal altruism. *Q. Rev. Biol.* 46, 35–57
- 2 Krams, I. *et al.* (2008) Experimental evidence of reciprocal altruism in the pied flycatcher. *Behav. Ecol. Sociobiol.* 62, 599–605
- 3 Wheatcroft, D.J. and Price, T.D. (2008) Reciprocal cooperation in avian mobbing: playing nice pays. *Trends Ecol. Evol.* 23, 416–419
- 4 Axelrod, R. and Hamilton, W.D. (1981) The evolution of cooperation. *Science* 211, 1390–1396
- 5 Brown, J.L. (1983) Cooperation—a biologist's dilemma. *Adv. Stud. Behav.* 13, 1–37

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Letters Response

Response to Russell and Wright: avian mobbing

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As noted in Russell and Wright's letter [1], Krams and colleagues [2] conducted three experiments examining cooperative mobbing of predators by pairs of pied flycatchers (*Ficedula hypoleuca*). Russell and Wright [1] argue that these experiments can be parsimoniously explained as byproduct mutualism, which assumes only that pairs directly benefit whenever they mob a predator either at their own or a neighbor's nest. It can be hard in practice to distinguish between byproduct mutualism and alternatives such as reciprocity, because the assumptions that underlie them—fitness payoffs associated with different behaviors—are notoriously difficult to measure in nature [3].

We agree that the results of the first two experiments performed by Krams and colleagues [2] can potentially be explained as either reciprocity or byproduct mutualism. However, the third experiment of Krams and colleagues [2] ('secondary phase two' in their original article) is much more difficult to explain as byproduct mutualism. In this experiment, a predator model was presented at the nests of breeding pairs (A), while a second set of breeding pairs (B) was prevented from joining the subsequent mob. Later, when the predator was placed at the nests of the B pair, the A pair did not join in, while a third, unmanipulated pair almost always joined the mob. To explain why the A pairs

declined to join the mobs at the B pairs' nests, Russell and Wright [1] suggest that, due to the potential costs of mobbing alone at another nest, pairs only mob at a neighbor's nest if they expect these neighbors to mob as well.

There is a significant problem with this interpretation. Given that all birds in the area are equally aware of existing mobs, it is difficult to accept that the decision of a pair whether or not to mob should depend on how they expect their neighbors to behave, when the decision could instead be based on what is actually occurring. During the experiments of Krams *et al.* [2], the B pairs always mobbed predators at their own nests, meaning that the A pairs would be assured that they would not be mobbing alone. Following an explanation with byproduct mutualism, pairs should directly benefit whenever they join mobs at any neighbor's nest. As a result, it is unclear why the A pairs would decline to join existing mobs, unless they were reciprocating against the B pairs for defecting previously.

Whatever the interpretation, the results of Krams *et al.* [2] are noteworthy not only for their demonstration that pairs do not assist previously uncooperative pairs but also that this happens so consistently across experiments. Their findings suggest that extended research into this and other similar avian systems offers us one of the best chances to understand the evolution of cooperation in nature.

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