Cooperation among lions: an overlooked theory

In her recent *TREE* article[1], Sarah Legge concluded that: 'The recent papers on cooperation (and the lack of it) in lions show clearly that the IPD [Iterated Prisoner's Dilemma] and its solutions are not necessarily the appropriate paradigm for cooperation. Perhaps lions are finally escaping the Prisoner's Dilemma?' Discussing alternative theories, she states that 'Aside from kin selection, cooperation has been categorized into three non-exclusive types: group-selected behaviour, reciprocity and mutualism.'

Unfortunately, she missed one additional, alternative, theory that I proposed in 1976 (Ref. 2) and that I later discussed in a series of papers[3,4]. This theory suggests that the investment in the welfare of the group is the cost (handicap) of proving the honesty of the individual's claim for social status. Such investment, which often looks like altruism, is in fact a selfish character that contributes to the direct fitness of the investor.

This alternative theory is based on the Handicap Principle. As long as that principle remained unacceptable, it was understandable why the theory was not considered as a possible explanation for the investment in group life. However, now that the principle has been accepted, there is no reason why the theory should not be considered. This theory is supported by observations on the behaviour of the Arabian babbler, a group territory bird, which my students and I have studied over the past 25 years[5]. Like the lions, individuals in such groups are dependent on one another for survival and breeding. In babbler groups, aggression is replaced by frequent displays of 'apparent altruism'. The reproductive success of different individuals is highly skewed and is correlated to the individual's social status. This theory could also account for the behaviour of the lions, in which the skew in reproductive success among cooperating members[6] is achieved, like the babblers, with comparatively little show of aggression.

Whether the suggested alternative theory is applicable to the case of the lions or not, I would also like to draw the readers' attention to the fact that, unlike my theory, all other theories mentioned by Legge, including that of kin selection, are based on mechanisms of indirect selection and are hence vulnerable to social parasites that may destroy the social systems that are based on these theories[7].

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Reply from S. Legge

The thrust of my article was not an attempt to provide a comprehensive review of all the theories pertaining to cooperation. In the sentence that Zahavi quotes in the first paragraph of his letter, I actually summarize other authors' categorizations of cooperation[1]. My own comment is that the current approach to the problem of cooperation is unnecessarily restrictive, and although alternatives have been suggested, researchers, on the whole, continue to focus disproportionate attention on reciprocity and the Iterated Prisoner's Dilemma in particular. I agree that social status (as an extension of the Handicap Theory) is relevant to the theory of cooperation, however, my article was not the place to critique its merits.

Although social status may be an attractive way to deal with cooperation in some species, the idea is not readily applicable to lions. Zahavi cited Packer and Pusey[2] as evidence for reproductive skew without aggression. However, this paper deals with male lions, not females. The recent *Science* paper by Heinsohn and Packer[3] explicitly looks at the mechanisms for cooperation between females. Female groups are stable over time, reproductive success is equitable, and there is no discernible dominance hierarchy[4]. The point of this recent work is that lionesses recognize 'cheaters' but do not punish them, in contradiction to reciprocity theory. Heinsohn and Packer[3] found that one third of the lionesses consistently lagged behind, yet if lionesses were competing for status during the territorial encounter, one might expect a more enthusiastic response from each individual.

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Arthropod evolution: on informative data and sound methodology

In their recent *TREE* article, Osorio *et al.*[1] argue that new data support monophyly of arthropods. However, the article presents characters that are not compatible with Manton's Uniramia concept. The authors support the Mandibulata concept, which is widely accepted[2–5]. However, within the Mandibulata, close relationship between myriapods and insects is rejected. There are two major faults in their argumentation: (1) many well-known characters are not mentioned, and (2) the characters they describe are not evaluated. For instance, they do not discuss whether *engrailed* expression, *Eve* expression in the nervous system, *Hox* genes, and the 'similarities' of the nervous system, show synapomorphies of crustaceans and insects, and outgroup comparisons are missing. An important argument is the similarity of the optic lobes in higher malacostracans and insects, but the authors do not state precisely what they conclude from this observation. Should the complex optic lobes be considered a synapomorphy, then insects must have evolved within the malacostracan clade! Since the inner chiasm is absent in lower Malacostraca (Leptostraca)[6] and in outgroup crustaceans, this feature must have evolved within the Malacostraca. A further argument of Osorio *et al.* is that molecular data support their conclusion. Unfortunately, published molecular studies support nearly any combination of higher arthropod taxa[2,4,7,8]. Information content of conserved DNA sequences often is very low and has not been estimated a priori in nearly all published molecular studies[9].

Only few of the putative apomorphies supporting the Tracheata are discussed by Osorio *et al.* Here is a more complete list[10]: postantennal sense organ (pseudoculus, Tîmîsvary organ) present; second antenna absent in adult, though present in early embryos, simultaneously areas of tritocerebrum reduced; mandibular palp absent; maxillae uniramous, with (originally) two endites; second maxilla fused basally, not masticatory; first movable article of legs ('coxa') with movable stylus and coxal vesicle; exopods absent; primary (i.e. limbless) abdomen of the mandibulate groundplan absent (see, for example, stem-line mandibulates[11]); antennal nephridia absent; digestive glands absent; tracheal system with segmental pair of pleural openings (a unique pattern absent in other arthropods); malpighian tubules.

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