

strongly support the notion⁶ that benzo-diazepine, GABA and perhaps glycine receptors interact with the same chloride ion channels.

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Another interpretation of communal breeding in green woodhoopoes

LIGON AND LIGON¹ presented information which they stated "suggests helping is a strategy for personal gain", and concluded that their observations "do not support an interpretation of helping behaviour relying on kin-selected altruism." Obtaining critical evidence on these two points is difficult, perhaps justifying presentation of preliminary data. Nevertheless, it should be pointed out that their results are open to other interpretations and, in my view, they are entirely consistent with my proposed theory² incorporating kin selection and individual selection, which they rejected.

Ligon and Ligon apparently invoked the personal-gain theory because the helpers showed no evidence of discrimination in their feeding of nestlings according to genetic relatedness. They did not actually demonstrate any personal gain; they merely inferred that it must exist because they saw that some helpers were not related to the young they fed. I consider this to be insufficient evidence on which to base the interpretation of personal gain. The few data presented are equally compatible with a zero-gain or even a loss (that is, altruism) hypothesis, as long as, on average, helping causes a gain in inclusive fitness to the helper. The apparent eagerness of helpers to feed young could be similarly explained.

Although personal gain to helpers by helping has been invoked by many authors and seems highly likely (for review see ref. 3), I know of no case in which a personal gain in terms of direct (individual) fitness

has been convincingly demonstrated. Although there is some evidence for this⁴, firm empirical data based on a strong-inference hypothesis are lacking. Apparently, Ligon and Ligon considered that their observations of a few helpers feeding unrelated young was inconsistent with kin-selection theory. They did not give their reasoning, but it seems to be based on two points: lack of discrimination of genetic relatedness in feeding efforts, and presence of presumed personal gain.

Discrimination was not evident in the few cases described, but the sample is unfortunately quite small (three cases). It may be of interest that a similar, though insignificant, lack of discrimination has been shown in jays (Fig. 1 of ref. 5). Even some parents in communal birds sometimes fail to discriminate between their own young and that of others (p. 375 of ref. 6), but one would not interpret this as evidence that parents in general have no genetic interest in their young. In any case, discrimination is not a necessary feature of kin selection⁷⁻¹², even though some authors have written as if it were¹³.

Personal gain, although inconsistent with altruism, is entirely consistent with kin selection. This is not always evident in writings on kin selection^{13,14}, but, as clearly shown by Hamilton¹¹, the concept of inclusive fitness specifies that genetic costs and benefits be accounted across all relatives (not just offspring), regardless of the sign of the effect. My theory² for the evolution of helping was based on a combination of kin selection and individual selection. Although I called helpers 'altruists', altruism or sacrifice by the helper was not a necessary or even desirable part of the theory, which is equally applicable when personal gain to the helper is involved.

As kin selection requires neither discrimination by relatedness nor individual sacrifice, it is difficult to see how the data of Ligon and Ligon are inconsistent with kin selection. The important condition is that the indirect fitness (inclusive fitness minus direct or individual fitness¹²) be raised by helping, and the Ligon did not consider this point.

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LIGON AND LIGON REPLY—Brown's major criticism of our report¹ is that we rejected his theory² incorporating both individual and kin selection in the evolution of avian helper systems. Actually, we questioned only kin-selected or phenotypic altruism^{3,4} in one kind of bird. Because green woodhoopoes can gain breeding status and helpers by first being helpers, whether or not they are related to the nestlings aided, we suggested that helping is a strategy for personal gain. For example, older birds gain and hold new breeding positions as a result of the support provided by younger individuals⁵. The system we describe corresponds to Hamilton's⁴ selected category and can also be referred to as cooperation⁶, reciprocal altruism⁷, reciprocity³ or mutualism⁸. Kinship ties may or may not be present but are not required for this kind of behavioural interaction.

Brown proposes alternative explanations for our observations. We feel that because of the many unknown factors related to kin-selection theory⁹ the most parsimonious explanation for avian helping behaviour is personal or direct gain¹⁰, when this can be ascertained. Very recently, Brown¹¹ has acknowledged that kin selection may not always be involved in communal helper systems, and Brown and Brown¹² have urged abandonment of the term 'altruism' to refer to avian helping behaviour. Both points are addressed in our report and we support both suggestions.

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