
Tree Swallows and TIT FOR TAT

Response to Koenig

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Koenig's (*Ethol. and Sociobiol.* 9:73-84, 1988) review of Lombardo's (*Science* 227:1363-1365, 1985) experiment testing the TIT FOR TAT model of reciprocity correctly concluded that the experiment did not demonstrate the existence of reciprocal altruism between parent and conspecific nest intruder tree swallows. However, his review contained errors that preclude a fair evaluation of the experiment and interpretation of its results. Here I respond to these criticisms, reexamine tree swallow behavioral ecology, and suggest that the lack of aggression between parents and intruders can best be modeled as by-product mutualism. I reiterate that the balance between parental aggression and nonaggression toward intruders can be maintained by TIT FOR TAT.

KEY WORDS: Prisoner's Dilemma; Reciprocal altruism; Reciprocity; Restraint; TIT FOR TAT; Tree Swallow.

INTRODUCTION

The task of unambiguously demonstrating reciprocal altruism (RA) in nonhuman animals presents a daunting challenge to empirical biologists. Ligon (1989) discussed two reasons for this. First, there is no consensus on how RA should be defined or recognized in nature (e.g., see Koenig 1988; Rothstein and Pierotti 1988; Seyfarth and Cheney 1988; Taylor and McGuire 1988; Ligon 1989). Second, empirical work has been unable to keep pace with theoretical advances. Consequently, nearly all reported cases of RA have been subsequently criticized or reinterpreted (e.g., see Waltz 1981; Connor 1986; Koenig 1988; Rothstein and Pierotti 1988; Wilkinson 1988). For example, in his careful review of studies that claimed to provide evidence of RA in birds, Koenig (1988) critically reexamined my experiment (Lombardo 1985) with tree swallows (*Tachy-*

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cineta bicolor) that tested and supported the TIT FOR TAT (TFT) model of reciprocity (Axelrod and Hamilton 1981). I agree with many of Koenig's criticisms, but his criticism contained errors that preclude a fair interpretation of the experiment and its results.

Here I respond to Koenig by 1) reviewing tree swallow behavioral ecology, 2) discussing the difficulties in using the terms RA, reciprocity, and restraint to describe animal behavior, 3) responding to specific criticisms, and 4) suggesting another explanation for the maintenance of nonaggression in this system.

TREE SWALLOW BEHAVIORAL ECOLOGY

Conspecific intruders (nonbreeders in Lombardo [1985]) are common at Tree Swallow nests throughout the breeding season (e.g., see Kuerzi 1941, Tyler 1942, Sheppard 1977, Stutchbury and Robertson 1985; Lombardo 1986a, 1987a,b). Intruders include sexually mature individuals of both sexes, and late in the breeding season, recently fledged birds (Lombardo 1986a). Leffelaar and Robertson (1985) and Stutchbury and Robertson (1985, 1987a) showed that sexually mature intruders at nests during egg laying, incubation, and the early nestling period are searching for exploitable breeding opportunities (e.g., nest usurpation). I showed that intruders are not helpers at the nest (Lombardo 1986a) and that the hatching year intruders that are common late in the breeding season are searching for potential future nest sites (Lombardo 1987a). Since then, Robertson and Stutchbury (1988) and Lombardo (unpublished data) have observed intruders committing infanticide.

Because intruders do not help breeders, and the evidence suggests that intruders are in search of present or future breeding opportunities, intruders and parents have a conflict of interest. Intruders present several threats to parental reproductive success: 1) intraspecific killing during fights between adults over nest site ownership (Kuerzi 1941; Lombardo 1986b; Robertson et al. 1986), 2) nest usurpation (Stocek 1970; Leffelaar and Robertson 1985), 3) cuckoldry (but see Leffelaar and Robertson 1984), 4) mate loss that results when an intruder drives away a same-sex resident (Kuerzi 1941; Stocek 1970; Leffelaar and Robertson 1985), 5) intraspecific brood parasitism (Lombardo 1988), 6) infanticide (Shelley 1934; Robertson and Stutchbury 1988; Lombardo, unpublished data), 7) the disruption of parental feeding schedules (Lombardo 1986a), 8) the transmission of disease and ectoparasites from intruders to nestlings (cf. Brown and Brown 1986), and 9) the attraction of diurnal avian predators to the nest (Lombardo 1987b).

Despite the conflict of interests between parents and intruders during the nestling period, the interactions between them were generally nonaggressive (Lombardo 1987b), suggesting that restraint (see later) was employed by both sides (Lombardo 1985). I hypothesized that the conflict be-

tween parents and intruders resembled the Prisoner's Dilemma (PD) game (see Lombardo 1985 for details) and that the nonaggression between parents and intruders could be modeled by reciprocity as described by the TFT model. TFT predicts restraint in conflict before a competitor's act of defection, retaliation after defection, and forgiveness if the opponent cooperates (Axelrod and Hamilton 1981). After a simulated act of defection by intruders, parents behaved as predicted by the model.

DIFFICULTIES IN USING RECIPROCAL ALTRUISM, RECIPROCITY, AND RESTRAINT TO DESCRIBE ANIMAL BEHAVIOR

A central issue of Koenig's criticism was that my experiment did not demonstrate RA. This criticism is correct but misleading. I never claimed that my experiment was intended to demonstrate RA. In fact, I stayed away from the concept because it is an onerous one. I attempted to show how restraint in aggression existed in this system and could be maintained by TFT. Restraint in conflict is an important precursor in the evolution of RA and other forms of cooperation because for cooperation to evolve, interactants must not "cheat" or "defect" on the first move (Axelrod and Hamilton 1981).

I believe that the foundation for Koenig's criticism was the mistaken equation of the term "*reciprocity*" with the biological concept of RA (Rothstein and Pierotti 1988). Although Trivers' (1971) original concept of reciprocity involved individuals trading benefits, a reciprocal interaction can also involve a give-and-take of harmful behaviors or attacks. Nevertheless, reciprocity is often used synonymously with RA (e.g., see Axelrod and Hamilton 1981; Brown 1983; Rothstein and Pierotti 1988; Taylor and McGuire 1988; Ligon 1989). Within this historical context, Koenig's criticism is understandable.

I concur with Williams (1966) and Rothstein and Pierotti (1988) that when biologists use nonbiological terms such as "*reciprocity*" to describe biological phenomena the terms should be used in the same ways that they are used in every day speech. Therefore, the term reciprocity includes all behavioral interactions in which actors engage in like-for-like behaviors regardless of their beneficent or harmful effects. Thus, reciprocity need not equal RA, but RA is a type of reciprocity. However, unless it is explicitly demonstrated that individuals have traded fitness increasing benefits while incurring a fitness decreasing cost in doing so, we should not assume or invoke RA (Koenig 1988).

Because TFT is a model of RA (Axelrod and Hamilton 1981), Koenig's criticism that my experiment did not demonstrate the existence of RA or TFT is understandable. However, TFT does not equal RA and individuals that alternately harm or attack one another may employ TFT (Rothstein and Pierotti 1988; Axelrod, personal communication). The point of my paper was

to show that mutual nonaggression could be maintained by TFT, not that the system was based on RA.

The underlying issue is whether we should consider restraint to be altruism and thus whether it can be modeled with RA or TFT. Axelrod (1984, p. 96) considers restraint to be altruism because the restraining actor is “. . . foregoing proceeds that might have been taken.” I agree with Koenig’s (1988) suggestion that we should be cautious before invoking RA in systems where antagonists appear to display restraint because demonstrating true restraint in nonhuman animals is difficult. The problem is separating those cases where an individual does not do something (e.g., attack, steal food, attempt an extra-pair copulation) because the costs of doing so outweigh the benefits from those cases where an individual accepts a fitness cost by not performing a particular behavior. I consider only the second to be an example of true restraint. A familiar example demonstrates this point. Consider a young child in a candy shop. The child would be truly showing restraint by not stealing candy if the shopkeeper was not present and there was no chance of his/her being caught stealing. Here the benefits of stealing outweigh the costs of being detected. However, if the shopkeeper were present, or there was a chance of being caught and punished for stealing, the child that did not steal candy would not be showing restraint. Here the costs of being caught stealing outweigh the benefits of obtaining candy. It is difficult to see how restraint without the promise of subsequent material benefit could evolve in the absence of a moral system (cf. Alexander 1987). For these reasons, I no longer consider the mutual nonaggression between parents and intruders to be an example of restraint (see later).

RESPONSE TO KOENIG

Throughout his criticism, Koenig referred to tree swallow nest intruders as helpers. He was incorrect. Lombardo (1985, p. 1364) stated that “. . . non-breeders were not cooperating with parents in the rearing of young.” The discussion of intruder behavior above provides further evidence that these birds are not helpers at the nest as commonly defined in the avian literature (cf. Brown 1987). Therefore, Koenig’s challenge (1988, p. 78) that one must demonstrate that parents gain by having the “helpers” feed young as one requirement for the interaction to involve RA was inappropriate within the true context of parent-intruder interactions in this species. More importantly, calling these intruders helpers when they do not help confuses the evaluation of the phenomenon because it affects the construction of the payoff matrix describing the interaction between intruders and parents.

Koenig claimed that the references that I used to support the critical assumption that intruders can lower parental reproductive success and possibly usurp nests were irrelevant. My experiment mimicked an effect (infanticide) that was known (e.g., see Shelley 1934). Kuerzi (1941) documented

harassment of breeders by intruders and intraspecific killing of adults during fights between breeders and nest intruders early in the breeding season. These references provided support for the assumption that an intruder defection coupled with parental nonaggression would result in “. . . the lowering of parental reproductive success. . .” (Lombardo 1985, p. 1364). Thus, there is ample documentation that intruders can lower parental reproductive success. However, Koenig was correct in that these references provided only weak support for the idea that intruders may usurp nests. Subsequent verification that intruders pose a threat to parental reproductive success and that they sometimes usurp nests can be found in Stoczek (1970), Leffelaar and Robertson (1985), Lombardo (1986, 1988b), Stutchbury and Robertson (1987a), and Robertson and Stutchbury (1988).

Koenig (1988) should be credited for constructing a set of possible payoff matrices to describe the parent-intruder interactions based on the information in Lombardo (1985). However, his belief that the asymmetrical payoffs to parents and intruders are a “. . . possibly fatal complication for applying this paradigm to the interaction” (Koenig 1988, p. 78) does not reflect current understanding as payoffs need only be measured in terms relative to one another (Axelrod 1984, p. 17; Seyfarth and Cheney 1988). Therefore, the payoff earned by a parent from an unopposed defection (T) need not equal a payoff of T earned by an intruder so long as the inequalities that define PD ($T > R > P > S$ and $R > (T + S)/2$) are met separately for each interactant. R is the payoff for mutual cooperation, P is the payoff for mutual defection, and S is the payoff for cooperating when a competitor defects.

Payoffs need not be in the same currency either (Axelrod 1984; Seyfarth and Cheney 1988). Therefore, PD can be used to model circumstances where parents gain from nonaggression by having their reproductive effort proceed unhindered and intruders gain from nonaggression by learning the locations and characteristics of potential future nest sites (e.g., Lombardo 1985). Seyfarth and Cheney (1988) discuss how asymmetries in the costs and benefits of behaviors being exchanged between interactants makes the empirical demonstration of RA and reciprocity difficult.

Nonaggression Between Parent and Intruder Tree Swallows Reexamined

The lack of aggression between parents and intruders during the nestling period may be more accurately modeled as by-product mutualism (Brown 1983) by both participants rather than by TFT in which individuals trade benefits. Individuals often perform egoistic acts that only incidentally benefit others as a by-product. If nonaggression is the result of by-product mutualism, then the inequalities that define PD (i.e., $T > R > P > S$ and $R > (T + S)/2$) are not met because $R > T$, precluding the evolution of TFT (Axelrod and Hamilton 1981).

In the context of parent-intruder interactions late in the breeding season,

parents that are nonaggressive toward intruders in order to avoid the costs of aggression, aid intruders by allowing them to learn the location and characteristics of potential future nest sites. This lowers costs of migration for intruders, making them effective competitors for those sites in the future. They know exactly where to go the next spring and what to defend when they get there (Baker 1978). Koenig (1988) correctly noted that intruders may gain knowledge that could be useful in future breeding attempts even if they do not interfere with parental efforts, suggesting that $R > T$. Thus, for intruders, I now hypothesize that $R \geq T$ late in the season (*contra* Lombardo 1985).

Late in the season when successful breeding is impossible, intruders have nothing substantial to gain by harming parental reproductive success. Koenig (1988) correctly identified this point as a flaw in my original argument. Because adult return rates are only 40–50% (Kuerzi 1941; DeSteven 1978; Lombardo 1986a; Robertson and Stutchbury 1988), intruders that evict the same-sex parent have little to gain because the probability of mating with the remaining parent is small (Robertson and Stutchbury 1988). Recently fledged intruders also have little to gain because they are sexually immature and cannot breed.

Intruders that visit nests and avoid behaving in ways that could lower parental reproductive success in order to avoid parental retaliation, benefit parents by not interfering with parental reproductive effort. By passively mobbing predators, intruders only secondarily aid parents while they learn the location, identity, and probable behavior of the potential predator (Shields 1984).

When parents attack a nonaggressive intruder they may receive a score of T but pay the energetic costs of aggression and risk accidental injury (e.g., see Arcese 1987). These costs devalue T relative to R , and may drive it below R .

However, there is an unavoidable cost to parents of mutual nonaggression that may cause $T > R$. By allowing intruders to visit their nests, parents may expose their offspring to ectoparasite infection (e.g., mites). Although mite infestations are common and can have a significant negative effect on parental reproductive success in swallows (Moss and Camin 1970; Brown and Brown 1986), observations from 1980–1983 suggested that the phoretic spread of mites from nest to nest by intruders was not an important threat to parental reproductive success in tree swallows (Lombardo 1987a). Thus, the cost of the phoretic spread of mites is insufficient to favor parental aggression toward intruders late in the season and R probably remains above T .

My experiment demonstrated that the behavior of parent tree swallows toward intruders late in the nestling period was based on a conditional strategy (cf. Dugatkin 1988). Parents ignored intruders unless attacked by them. If attacked, they reciprocated and attacked in return. Thus, the balance between nonaggression and aggression between parents and intruders may be maintained by a TFT-like conditional strategy as suggested by Lombardo

(1985). TFT, except for the first move, is a conditional strategy in which individuals do whatever their competitor did on the previous move regardless of whether the move was cooperate or defect (Axelrod and Hamilton 1981). The first move in TFT is unconditional cooperation. In the tree swallow context, the first parental move (nonaggression) is best modeled as by-product mutualism (Brown 1983). Subsequent parental moves are modeled by TFT. It is not necessary for an interaction to include the trading of benefits for it to be maintained by TFT (Rothstein and Pierotti 1988; R. Axelrod, personal communication). The value of viewing parental aggression toward intruders this way is that it makes no assumptions about the payoffs to the interactants and thus is a preferred explanation for this phenomenon.

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