

Forum

Acceptance by the splendid fairy-wren of parasitism by Horsfield's bronze-cuckoo: reexamination of Brooker and Brooker's equilibrium model

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Acceptance of cuckoo parasitism by hosts appears maladaptive and poses a challenge for behavioral ecologists (Dawkins and Krebs, 1979; Rothstein, 1982). Two main hypotheses have been proposed to account for this phenomena: evolutionary lag and evolutionary equilibrium. According to the evolutionary lag hypothesis, rejection would lead to higher fitness than acceptance, but the genetic variant capable of rejection has not appeared in the host population (Rothstein, 1975) or has not yet reached fixation (Davies and Brooke, 1989; Dawkins and Krebs, 1979; Kelly, 1987). According to the evolutionary equilibrium hypothesis, rejection may not spread because it incurs some costs which make it even less adaptive than acceptance (Brooker and Brooker, 1990; Davies and Brooke, 1989; Lotem et al., 1992; Rowher and Spaw, 1988; Zahavi, 1979). The extent to which the evolutionary lag and the evolutionary equilibrium hypotheses account for acceptance of brood parasites is still a matter of debate (Davies et al., 1996; Lotem et al., 1995; Rothstein, 1990).

Brooker and Brooker (1996) have recently published data from a 17-year study of a splendid fairy-wren (*Mahurus splendens*) population parasitized by Horsfield's bronze-cuckoo (*Chrysococcyx basalis*) in Western Australia. They argue that "of the two explanations for the lack of rejection, neither really stands up to scrutiny with respect to the splendid fairy-wren" (p. 396). Instead, they propose a new model for evolutionary equilibrium based on the life history and population structure of the host species. According to their model, pure acceptance of parasitic eggs and chicks is an evolutionarily stable strategy (ESS; Maynard Smith and Price, 1973), regardless of how costly rejection of parasitic eggs might be.

Although we endorse the use of equilibrium models in the study of avian brood parasitism, we find some problems in the specific model proposed by Brooker and Brooker. Namely, we suspect that their model cannot be stable. Brooker and Brooker's (1996) model is built on two stages. First, they suggested that: "a strategy of total acceptance in response to parasitism could be just as profitable as rejection if the accepters are more likely than rejecters to renege after they have been parasitized" (Brooker and Brooker, 1996: 402). Rejecters cannot outrun accepters by renegeing as often as they do because the "likelihood of renegeing is constrained by the number of offspring already produced" (Brooker and Brooker, 1996: 402).

There are, however, individual differences. Fairy wrens can be divided in "successful" and "less successful" (Brooker and Brooker, 1996). The "less successful" individuals would benefit from rejecting cuckoo eggs because "the accepters would have insufficient time to lay the extra clutches they require" (p. 402). Why does not rejection spread if it is beneficial for the "less successful" individuals? Here is where the second step of the model comes in:

among the [successful] birds, accepters will be able to produce *just as many* offspring as rejecters. Ultimately, accepters will prevail in the population, not because they are accepters per se, but primarily because they are multibrooded, sedentary, territorial birds whose success lies in their acquisition and retention of the quality habitat that ensures their renegeability (Brooker and Brooker, 1996: 402–403, italics added).

Does this model provide a framework where acceptance of parasitic eggs is an ESS, regardless of how small the costs associated with rejection are? We argue below that it does not.

As stated in Brooker and Brooker's paper, acceptance would be, at best, as good as rejection. As a consequence, it would not be stable because it could be invaded by genetic drift. But the argument is actually more subtle (Brooker LC, personal communication). Horsfield's bronze cuckoo females remove one fairy-wren egg at laying. A fairy-wren that accepts the cuckoo egg can expect to raise, from its first unparasitized clutch, n offspring (normally three), while an individual that ejects or buries the cuckoo egg will raise $n - 1$ (two) offspring from the parasitized clutch (because the loss of one egg that has been removed by the cuckoo cannot be recovered by ejection or by cuckoo egg burial). Considering that the probability of renegeing is constrained by the number of offspring already produced, the removal of one egg by the cuckoo can lead to acceptance being more profitable (as opposed to "just as profitable") than ejection of cuckoo eggs. For instance, if renegeing is maladaptive when there are more than three fledglings in the territory, a ("successful") accepter will eventually raise two full broods, making up six fledglings, while a ("successful") ejecter will produce six fledglings only if it is not parasitized, five fledglings if it is parasitized in one of the broods, and four fledglings if it is parasitized twice. But, as is easily seen, this argument can be made to work in the opposite direction just as easily: if renegeing is maladaptive when there are more than two fledglings in the territory, an accepter will only manage to raise three chicks, while a parasitized ejecter will raise five offspring if its first brood is parasitized or four if parasitized twice. Hence, when the probability of renegeing is constrained by the number of offspring already produced and the cuckoo removes one egg from parasitized nests, only under very restricted and artificial conditions will acceptance be more profitable than rejection if there are no rejection costs. Thus, a *fixed* renegeing threshold of *exactly* three or six fledglings will favor acceptance, but a threshold of two, four, five, or seven will not. And even in this restricted situation, to guarantee that acceptance is more profitable than rejection we must further assume that chick mortality only occurs through whole-clutch predation (broods either fail completely or succeed completely).

Another flaw in Brooker and Brooker's argument is that it ignores rejection by desertion: a female that deserts a parasitized brood and renegees loses nothing in terms of chick production (as compared with an accepter) and gains time and reduces the foraging effort involved in raising a cuckoo chick. In other words, in the absence of rejection costs, the proposed model is unstable against a host mutant that rejects parasitism by nest desertion, which is quite a common rejection method among cuckoo hosts (Davies and Brooke, 1988; Moksnes et al., 1993; Rothstein, 1990).

We move now to the second stage of the model. If acceptance is *as profitable as* rejection for "successful" individuals,

and less profitable for "less successful" individuals, accepters will not prevail, they will be selected against. If the division of the population in "successful" and "less successful" breeders depended on the quality of their territories, as suggested by Brooker and Brooker (1996), or on some phenotypic difference, some offspring of successful breeders would end up in low-quality habitat and would belong to the "less successful" breeding class. Hence, to maximize their fitness, successful breeders must ensure that their less successful offspring have the highest possible reproductive success (so far as this does not jeopardize the reproductive success of their more successful offspring). As a result, if rejection led to higher reproductive success in low-quality territories, and if it was selectively neutral in high-quality territories, successful breeders would maximize their fitness by having rejecter offspring, and acceptance will not be favored. The fact that most fairy wrens breed in their natal territory or an adjacent one (Russell and Rowley, 1993) does not change this conclusion, because the difference between the "successful" and "less successful" individuals is precisely that the "less successful" individuals do not reproduce fast enough to replace themselves and the vacancies have to be filled with offspring from "successful" individuals.

It seems clear, then, that for acceptance to be an ESS it would have to be *more profitable* than ejection. However, as we have argued above, under the circumstances described by Brooker and Brooker acceptance will not be more profitable than rejection, unless there are some costs associated with rejection. In other words, pure acceptance cannot be an ESS for splendid fairy-wrens regardless of the magnitude of rejection costs; it can only be an ESS if there are recognition errors or other rejection costs (Davies and Brooke, 1989; Rothstein, 1990; Zahavi, 1979) or an advantage of being parasitized (Smith, 1968).

Although we find Brooker and Brooker's (1996) equilibrium model unconvincing, they have made an important contribution showing that the life-history characteristics of the splendid fairy-wren and other Australian passerines (e.g., multibrooded, sedentary, high reneatability) may reduce the impact of cuckoo parasitism and probably make acceptance less costly than in some Northern Hemisphere cuckoo hosts. This makes the equilibrium hypothesis quite realistic because even a small rejection cost will be sufficient to make acceptance better than rejection. Yet, it should also be noted that if the impact of parasitism is as small as Brooker and Brooker suggest, the selective advantage of rejection can be very small and the host may still be in evolutionary lag despite a long history of interaction with the cuckoo (see Davies and Brooke, 1989; Kelly, 1987). In summary, we believe that the available data on this cuckoo-host system do not allow discrimination between the evolutionary lag or the evolutionary equilibrium hypotheses.

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Why do splendid fairy-wrens always accept cuckoo eggs?

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Rodríguez-Gironés and Lotem (this issue) are correct in claiming that acceptance cannot be more profitable than rejection unless there are some costs pertaining to rejection. In a detailed optimality model for reed warblers *Acrocephalus scirpaceus*, Davies et al. (1996) clearly show this to be true. Yet, even when rejection costs are relatively large, hosts will do better to reject when the risk from parasitism is high. Davies et al. (1996) estimate that it will pay reed warblers to reject whenever the parasitism rate is greater than 19-41%, despite ejection/recognition costs of between 0.5 and 1.25 eggs in parasitized clutches and recognition costs of 0.4-1.2 eggs in unparasitized clutches.

Optimality model A

The relative payoffs from the various strategies of acceptance, desertion and ejection are as follows (see also Brooker and Brooker, 1996; Davies and Brooke, 1989; Davies et al., 1996):