

COMMENTARY

ON TESTING THE HAMILTON-ORIANS HYPOTHESIS FOR THE ORIGIN OF BROOD PARASITISM¹

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Brood parasitism has long been of interest to ornithologists, but little is known about its evolutionary origin. Hamilton and Orians (1965) proposed that one factor favoring the evolution of brood parasitism might be nest destruction during egg laying. Because most birds lay a clutch of eggs over a series of days, and because successive eggs are ovulated soon after the previous egg is laid, females become physiologically committed to laying their next egg within hours of laying the previous egg of the clutch. Thus, if the nest is destroyed during the laying period, the female is faced with the problem of where to lay the physiologically committed egg and might benefit by laying it in another bird's nest.

Recently, Rothstein (1993) reported an attempt to test the Hamilton-Orians Hypothesis experimentally. He removed nine Red-winged Blackbird (*Agelaius phoeniceus*) nests after females had laid their first egg and monitored surrounding conspecific nests, as well as the old nest site, for the appearance of eggs on subsequent days. He found no evidence of parasitism, but did find single eggs deposited near three of the old nest sites. Rothstein (1993) concluded that while the experiment had the potential to provide support for the Hamilton-Orians Hypothesis, the results instead argue against it. Here we argue that Rothstein's experiment provided only limited additional evidence of a pattern already evident from previously published results; i.e., that Red-winged Blackbirds do not lay parasitically in response to nest loss. We further suggest that evidence from Red-winged Blackbirds alone is inconsequential to the validity of the Hamilton-Orians Hypothesis, and we discuss problems with intraspecific testing of the hypothesis in general. Finally, we outline why a comparative approach is more appropriate and how it could be applied.

Rothstein (1993) acknowledged that published studies (e.g., Gibbs et al. 1990; Harms et al. 1991) indicate there is virtually no brood parasitism in Red-winged

Blackbirds, but argued that because of this, a link between experimental nest destruction and brood parasitism in this species would indicate the potential generality of this selection pressure for "all or most bird species" (Rothstein 1993, p. 1001). This argument relies on the premise that nest destruction is not a regular feature of Red-winged Blackbird nesting ecology. Although Rothstein (1993) suggested that most nest failure in Red-winged Blackbirds involves predation that leaves nests intact, he also indicated that nests are sometimes destroyed. Data from a variety of locations confirm that nest failure is frequent among Red-winged Blackbirds, due to harsh weather or flooding (e.g., Goddard and Board 1967; Picman et al. 1988) and especially predation (e.g., Robertson 1972; Caccamisse 1976). A number of studies also indicate that these events often result in partial or complete nest destruction (e.g., Case and Hewitt 1963; Goddard and Board 1967; Robertson 1972; Lenington 1980; Picman et al. 1988; Harms et al. 1991). While it is clear that nest destruction occurs regularly, and at all stages of the nesting cycle, it is also evident from previously published studies (collectively involving hundreds of nests) that brood parasitism in this species is virtually absent. Gibbs et al. (1990) demonstrated its absence using DNA profiling of parents and offspring (see also Westneat 1993). Harms et al. (1991) found it to be *extremely* rare (0.5%), even when they included potentially false positives. Most studies on Red-winged Blackbirds do not mention it. Although many of these studies were not explicitly designed to identify parasitic eggs, most included regular nest searches and egg checks, and in some cases, molecular techniques that are powerful for detecting parasitism. Thus, parasitism should have been previously identified if it were a regular response to nest loss during laying. Hence, it is clear from a much larger number of nests, which included repeated natural experiments, that Rothstein's (1993) experiment could not provide evidence of a general link between nest destruction and parasitism.

While Rothstein's (1993) study provides additional evidence of the absence of conspecific brood parasitism in Red-winged Blackbirds, because brood parasitism does not occur with any regularity, intraspecific studies of this species seem unlikely to provide insight into the evolution of brood parasitism. However, we suggest that no single species (including one in which brood parasitism is known to occur) can provide a strong test of the Hamilton-Orians Hypothesis. This is because the hypothesis explicitly refers to nest destruction as a factor favoring the *initial* evolutionary development of parasitism, while experiments on a single species can only provide information about the selection pressures *currently* maintaining parasitism. The latter may or may not be those that originally selected for parasitism. Studies indicate conspecific brood parasitism can be a finely tuned reproductive strategy (e.g., Jackson 1993; Lyon 1993). In such cases, it is likely to have

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been substantially modified from its original condition as a result of selection for increased efficiency. Thus, while some species do lay parasitically in response to nest destruction (e.g., Feare 1991), inferences from these patterns about the initial evolution of brood parasitism are tenuous. Conversely, the absence of parasitism following nest destruction in any one species does not argue against the Hamilton-Orians Hypothesis unless one applies evolutionary hypotheses deterministically. Frequent nest loss during laying might be necessary for the evolution of brood parasitism, but it may not be sufficient. Preadaptations to brood parasitism, such as the ability to locate other birds' nests or remember their locations (also see Hamilton and Orians 1965), may also be necessary. Because preadaptations may be taxonomically restricted, the evolution of brood parasitism might be constrained in particular taxa despite frequent nest losses during laying. Thus, the egg laying response of a particular taxon to nest loss does not constitute a test of the Hamilton-Orians Hypothesis.

The comparative method (see Harvey and Pagel 1991) provides one possible means for testing the generality of the Hamilton-Orians Hypothesis. Unlike intraspecific studies, the comparative approach can identify evolutionary trends because it assesses variation in one or more traits across a range of taxa. As a result, it uncovers repeated instances of correlated evolution, and therefore greatly reduces the problem of recent adaptation within a particular taxon obscuring the relationship. The Hamilton-Orians Hypothesis makes the comparative prediction that nest predation is more frequent among those taxa currently exhibiting brood parasitism than in their closest sister taxa without brood parasitism. The hypothesis can be supported regardless of whether, within each taxon, parasitism is presently triggered by nest loss. In a comparative analysis, Red-winged Blackbirds would represent one datum with a certain level of nest loss. If the Red-winged Blackbird were the sister taxon of a group exhibiting brood parasitism and suffering higher nest predation, the Hamilton-Orians Hypothesis would be supported. However, only repeated instances of this situation would constitute evidence for the evolutionary generality of the Hamilton-Orians Hypothesis. While this analysis could only include taxa that are not obligate parasites, and therefore build nests, it would only be confounded with respect to the Hamilton-Orians Hypothesis if the evolution of brood parasitism systematically influenced rates of nest predation. An additional advantage of the comparative approach is that by applying analytical techniques that control for phylogenetic effects (Pagel and Harvey 1991), the potentially confounding effects of preadaptations are either eliminated (because they are likely correlated with phylogenetic relationship) or more easily controlled statistically.

In sum, we do not dispute Rothstein's (1993) finding that female Red-winged Blackbirds do not lay eggs parasitically in response to nest destruction (though we believe this was evident from previously published results). However, we suggest that this observation does not constitute evidence either for or against the Hamilton-Orians Hypothesis for the evolution of brood parasitism, because the hypothesis refers explicitly to the evolutionary origin of the behavior and it cannot be

evaluated by the absence of parasitism in a particular species. We believe that the hypothesis is testable using a comparative analysis that considers frequency of nest loss and the presence of brood parasitism across taxa.

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