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BROOD PARASITISM AND THE HAMILTON-ORIANS HYPOTHESIS REVISITED[1]

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To account for the evolutionary origin of avian brood parasitism, Hamilton and Orians (1965) suggested that parasitism might begin if nests are destroyed during laying leaving birds with the dilemma of having to lay subsequent, physiologically committed eggs in a clutch but no nest of their own in which to lay them. Laying parasitically in conspecific nests would then be the most adaptive option for such birds and this behavior might lead to obligate interspecific parasitism. My paper (Rothstein 1993) presented a straightforward experimental test of the first step in the Hamilton-Orians Hypothesis (HOH). I removed the nests of laying Red-winged Blackbirds (*Agelaius phoeniceus*) and concluded (p. 1003) that my results "... argue against it [the HOH], at least for the Red-winged Blackbird ..." because none of the affected females laid parasitically. Yezerinac and Dufour (1994) present two criticisms of my paper. These are as follows. (1) I should have known that I would elicit no parasitism because other studies found little or no intraspecific parasitism (IP) and no link between nest loss and such parasitism in Red-winged Blackbirds, i.e., my study had little potential to bear on the Hamilton-Orians Hypothesis. (2) To really test the HOH, one should do a comparative study on many species.

For criticism 1 to be valid, one has to be convinced of the following two points. (1) Data published prior to my paper were sufficient to show that IP is always virtually absent in Red-winged Blackbirds and that there is no link between nest destruction and the rare cases of IP that do occur. (2) The HOH can only be tested in species with known IP and a link between parasitism and nest loss. Addressing this first point, Yezerinac and Dufour cite a number of studies to show that nest loss is common in Red-winged Blackbirds and stress that reports of IP are virtually nil. However, none of these studies was an experimental (i.e., manipulative) one and most predate the time (early 1980s) when researchers realized that IP is a common, adaptive behavior in many seemingly nonparasitic species (rather than a rare aberrant behavior of no significance). So most of these studies were done when people were simply not looking for IP, which is difficult to detect (Yom-Tov 1980, MacWhirter 1989), and the number of species with frequent IP is now known to be much higher than was assumed 10–15 years ago (compare reviews by Payne 1977, Yom-Tov 1980, MacWhirter 1989). My paper cited only those two studies in which researchers were intent on detecting IP in Red-winged Blackbirds (Westneat [1993] was published after my paper went to press). As regards these two studies, Gibbs et al. (1990) dealt with only 36 nests in Ontario and sampled DNA markers in nestlings not eggs. Conspecific parasitic eggs often have low hatching success (Petrie and Møller 1991) so evidence of parasitism will be underrepresented among nestlings. In the second paper, Harms et al. (1991) documented a low (0.4%) incidence of IP in 7,805 nests from one area in eastern Washington. While cases of apparent IP may have included some false positives as Yezerinac and Dufour argue, some cases of IP were probably missed when parasitic eggs were laid 1–3 days after a host finished laying (nests were checked every three days). One simply cannot conclude from these two studies that IP is virtually absent throughout the species' range. I worked over 1,200 km from where these studies were performed on a subspecies (*A. p. neutralis*) with plumage and presumably genetic differences from the subspecies (*A. p. nevadensis* and *A. p. phoeniceus*) studied by the other authors.

Among studies cited by Yezerinac and Dufour, only Harms et al. (1991) tested for a link between IP and nest destruction. However, their sample of parasitized nests was small, their means of analysis very indirect and their relevant data were not tested statistically. Although Harms et al. found no definite evidence of such a link, their data do not negate this possibility as nest destruction preceded 44% of their cases of IP. Harms et al.'s analysis was worth reporting as it had the potential to show a link, but it is far from the last word on the question. Furthermore, the HOH would be supported if IP is not a usual response to nest loss but tends to be linked to nest loss when it (IP) occurs.

Yezerinac and Dufour's assertion that my manipulation is of little or no value misses an essential point about science: no matter how numerous our observations and how clear trends seem to be, we usually cannot be certain that we understand a system until we manipulate it and determine that it changes in the expected direction. So no matter how convincing the pre-existing nonmanipulative data were (and they were not at all convincing in this case) for a lack of a relationship between nest loss and IP, my experiment would still be worthwhile doing and reporting. Yezerinac and Dufour stated that my "... experiment provided only limited additional evidence of a pattern already evident from previously published results. ..." Logically then they would have made the same criticism had I done my experiment on a species for which nonmanipulative studies suggested a link between IP and nest loss (which they argue would have been an appropriate species) and had I induced parasitism, as in previous studies (Emlen and Wrege 1986, Feare 1991, Stouffer and Power 1991) they fail to criticize.

Next I address Yezerinac and Dufour's belief that the HOH can only be tested in a species with IP. Even if I could have been certain that Red-winged Blackbirds

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everywhere have virtually no IP, my experiment would still have been of value because the HOH deals with the transition from no parasitism to parasitism. My paper emphasized that previous studies indicate that Red-winged Blackbirds appear to have very low rates of IP and that experimentally induced parasitism in such a species would provide especially strong support for the HOH.

I agree somewhat with the authors' second major argument, namely that a comparative approach would be valuable and in fact I emphasized (p. 1004) that data on other species are needed. I also stressed (p. 1003) that my results apply only to the Red-winged Blackbird and not to the general validity of the HOH. Furthermore, it is not a foregone conclusion that a comparative approach is superior in this case as Yezerinac and Dufour argue by simplifying the contrast between my study and their proposed one as a single species versus a comparative study. While my study was on a single species, it employed experimental methods and therefore has certain advantages that are absent from comparative studies (Harvey and Pagel 1991).

Even if an appropriate comparative study were to show a link between IP and high levels of nest predation, correlation in such studies does not prove causation (Harvey and Pagel 1991). Species with high levels of IP could have high levels of nest predation because something about IP leads to more nest predation. Yezerinac and Dufour acknowledge this problem, so it is unclear why they are so intent on arguing for the superiority of the comparative approach. This is basically the same criticism these authors leveled against my paper; i.e., studies done at the current time do not necessarily tell us about initial conditions. Furthermore, even if the IP-predation link is found, what does that tell us about the evolutionary increase of parasitism in species in which IP is rare or absent? My experiment speaks to that issue, unlike the proposed comparative approach, because it could have shown that the behavior necessary for the HOH is present (regardless of the level of IP known to occur). Although it is worth doing, a great deal of caution is needed in using the incidence of nest predation in a comparative study. Unlike many features considered in comparative studies (such as body size, secondary sexual characteristics, etc.), predation is not strictly an intrinsic aspect of a species' biology but is instead largely imposed in a proximate sense by the environment. As such, its incidence often varies greatly within a species according to season, year, habitat, geography, etc.

The authors miss two other values of my paper. First, I presented what may be the first proof of "physiologically committed eggs" in free-ranging birds, because I found eggs laid on the substrate at three of nine nest sites. Secondly, that eggs were wasted by being laid on the substrate indicates that the birds I tested have no tendency whatsoever towards IP and that such parasitism is rare at best in yet another part of the Red-winged Blackbird's range.

Nothing Yezerinac and Dufour say changes the message of my study. The only seemingly substantive difference here is that the authors say my study is "inconsequential" to the HOH and I say it is relevant because I failed to induce IP. But even this is not a substantive difference because I stressed that an experimental study on a single species is limited in value in that it cannot lead to an overall rejection of the HOH. But we have to start with one species and my paper may stimulate experiments on additional species with varying levels of IP and this may allow us to assess the overall importance of the HOH.

If there is a substantive difference here, it is in our approaches to science, or at least to this issue. Yezerinac and Dufour are basically saying that I should have made the same conclusion from the literature that they made. They are willing to accept Harms et al.'s analysis and other indirect data as proof that there is no relation between nest loss and the rare cases of IP that occur and I am not. Although I am more critical as regards to what one can conclude from data in the literature, I am also more open to the kinds of data I think are worth considering as I see considerable value in both experimental and comparative approaches, as do the authors (Harvey and Pagel 1991) of the general treatise Yezerinac and Dufour (1994) cited in arguing for the putative superiority of the comparative approach.

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