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## Seasonal sex allocation by Common Grackles? Reply

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We thank Howe (2010) for his comments on our recent paper (Maddox and Weatherhead 2009) in which we replicated his 1977 study of Common Grackles (*Quiscalus quiscula*). In our study, we did not challenge sex-ratio theory or that there are well-documented cases of adaptive sex allocation by birds, nor did we question

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that contingent behavior is both a common and important ecological phenomenon. Thus, we have little argument with much of Howe's (2010) essay. At issue is simply how to interpret Howe's (1977) results in light of ours (Maddox and Weatherhead 2009).

Howe's (1977) methods did not allow him to determine hatching sex ratios and fledging sex ratios for the same nests, nor could he determine the sex of most nestlings that starved. Thus, his conclusion that female grackles adaptively adjusted the sex ratio of their offspring to match seasonal changes in food rested on the assumption that primary sex ratios did not differ between his study populations or within the same population between years, and that nestling starvation was male biased. Our methods allowed us to determine hatching and fledging sex ratios in the same nests and to determine the sex of nestlings that starved. We found no evidence that females adjusted sex ratios seasonally and no evidence that male nestlings were more likely to starve.

We offered two possible explanations to interpret the difference between our results and Howe's (1977): (1) Howe's populations exhibited both adaptive sex allocation and male-biased nestling mortality whereas ours did neither or (2) the interpretation that Howe's populations exhibited adaptive sex allocation and male-biased nestling mortality resulted from failed assumptions. We acknowledged that neither explanation could be dismissed, but argued that the latter explanation seemed more plausible. In contrast, Howe (2010) argues that the former explanation (i.e., the Illinois and Michigan populations are different due to contingent behavior) is more compelling, and thus that his original interpretation of the Michigan data was correct.

Whether or not nestlings of one sex starve more could be a function of either sex-specific costs and competitive ability and food availability, or result from contingent parental behavior whereby one sex is favored. Differences in these factors presumably explain why sexual size dimorphism does not consistently result in male-biased mortality among different species of blackbirds. Howe uses this interspecific variation to argue that sex-biased mortality could also differ among populations of Common Grackles, thereby explaining the disparity between his results and ours. Given the central importance of data versus assumptions to the issue at hand, it is critical that the distinction be kept clear: Howe did not present evidence of differential mortality by sex; he assumed that it occurred (anecdotal evidence of a male bias from an unspecified number of dead nestlings notwithstanding). We found no evidence of sex-biased mortality and think that ecological similarities between study populations (e.g., high nestling starvation, both populations are migratory, similar nesting habitat and nesting phenology) make it unlikely that nestling starvation was male biased in Howe's study

when it was not in ours. If so, we are left with the similarly implausible requirement that grackles preferentially fed daughters in Michigan but not in Illinois, and that this difference in behavior did not result in substantially different starvation rates in the two populations.

Howe argues that offspring sex ratio is a contingent trait and that contingency in allocating offspring sex should occur as commonly as contingency occurs in other aspects of ecology. Therefore, we should reasonably expect that nearby populations of the same species might often behave differently (e.g., Howe's research on voles to which he refers), as might the same population in different years. Because of the methods available at the time of his study, however, Howe had to combine data collected in different years or places. For example, only once during his study did he collect both hatching and fledging sex ratio data during the same year, and those data were obtained from two sites approximately 20 km apart. Were these two Michigan populations "doing something different?" Even were they not, chance alone could produce differences in hatching and fledging sex ratios between populations when sample sizes are small. The potential for both contingent behavior and sampling error add to the importance of collecting all the pertinent data (hatching sex ratio, fledging sex ratio, sex-specific mortality) from the same population at the same time, as we did in Illinois. Therefore, Howe's (2010) "contingency" argument actually weakens his interpretation of his data while strengthening the view we favored originally (Maddox and Weatherhead 2009), that it is more parsimonious to interpret the apparent difference between his study and ours as resulting from the failure of one or more of Howe's (1977) assumptions.

More broadly, our effort to repeat Howe's (1977) study illustrates the generally acknowledged difficulty in replicating ecological research, despite the importance of doing so (Palmer 2000, Kelly 2006). Even had we conducted our study on Howe's Michigan study sites and obtained the same results we got in Illinois, the difference between Howe's results and ours could have been a consequence of ecological changes that might have occurred in the time between the two studies. If future research consistently fails to replicate important ecological results, then it may indeed be true that most of those results were contingent on conditions unique to the time and place of each study. Such an outcome would greatly increase the challenge of trying to identify general ecological principles. Hopefully the importance of this issue will encourage others to repeat important studies, and editors to publish the results.

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