

William T. Wcislo

Commentary: Solitary behavior in social bees

Professor George Eickwort was killed in an automobile accident on 11 July 1994 (see Wcislo et al. 1994). The preceding manuscript (Eickwort et al. 1996) was essentially complete, except for revisions, up-dating references, and related editorial matters. I attended to these matters at the request of the second and fourth authors, both of whom participated in the field work and were listed as authors on the original manuscript. I have the notes, data, and original manuscript pertaining to this study. Revisions to a posthumous manuscript pose a problem, because the senior author might not have agreed to proposed changes. The aim of this commentary is to clarify what substantive revisions I made to the original manuscript, so readers can distinguish my additions from George Eickwort's original thinking. Revisions were made using three formal reviews from the journal, comments from an associate editor, two informal reviews previously solicited by Eickwort (see Acknowledgements, Eickwort et al. 1996), and three reviews that I solicited.

The original manuscript exclusively focused on the hypothesis that the Gothic population of *Halictus rubicundus* represented an evolutionary reversion to solitary behavior from an eusocial population. The authors equated loss of sociality with "brood loss", and asked whether solitary behavior is based on an evolutionary deletion of the first brood of their social ancestors (i.e., foundresses immediately produce a brood of reproductives), or on deletion of the second brood. In an extensive discussion of offspring sex ratio, they rea-

soned that these two evolutionary pathways to solitary behavior generate different predictions about the observed sex ratio. Since sex ratio differs between broods of eusocial populations, an evolutionary retention of the first brood (deleting the second) predicts a female-biased sex ratio, while retention of the second brood predicts an equal or male-biased sex ratio. The observed sex ratio in solitary *H. rubicundus* is more similar to the second brood of social populations, so they concluded that the solitary population deleted the first brood. Their argument assumed, however, that sex ratio evolution was slow relative to the rate at which social behavior was lost, and therefore observed patterns of sex ratio investment are not obscured by the length of time a population is solitary. This may be unlikely (e.g. Fisher 1958). Secondly, they did not consider the hypothesis that observed differences in sex ratio might be due to a facultative mechanism which alters the sex ratio in response to environmental conditions (e.g. Mueller 1991), and differences do not necessarily imply there has been an evolutionary reversion. I revised the manuscript to address these alternative interpretations.

A different, and more conventional, way to view loss of sociality is as the loss or suppression of worker behavior. The original manuscript contained no mention of this possibility, nor did it discuss mechanisms which might be involved in the loss or suppression of worker behavior. This is a particular problem because the original focus on brood deletion implicitly assumed that all (or most) females of the first brood become workers (i.e., one way to lose worker behavior is to delete the first brood). In fact, however, first-brood halictine females can become reproductives or workers, depending on environmental and social conditions (e.g. Michener 1990). These considerations were incorporated into the revisions.

The occurrence of solitary behavior (or modified brood structure) in a high-altitude population is consistent with a second hypothesis that was not mentioned in the original manuscript, but is discussed

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in the revised version: there has been no evolutionary change, and the observed behavior results from a developmental system which permits facultative expression of different phenotypes under different environmental conditions. During my discussions with G.C. Eickwort, he agreed that this alternative hypothesis could not be rejected and needed to be discussed in the paper, but he did not agree that it was more likely, nor more parsimonious.

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