NOTE

A COMMENT ON BOBISUD’S PAPER ON
EVOLUTION OF CANNIBALISM

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One of Bobisud’s (1976) models for the evolution of cannibalism is discussed. His analysis is criticised for not being based on the principle of individual selection. Assuming the operation of that principle, we show by simulating his model that cannibals may establish themselves in a non-cannibal population. This will happen both in cases where Bobisud concluded cannibalism to be optimal and in cases where he concluded cannibalism not to be optimal.

Recently, Bobisud (1976) analysed the evolution of cannibalism in a predator–prey system. The prey was assumed to have a three-stage history; eggs (E), larvae (L), and adults (A) laying eggs. An evolutionary variable, c (being a parameter in the ecological model), was defined as the coefficient of cannibalism. For a given c, the system has the following equilibria: \( \hat{E}(c) \), \( \hat{L}(c) \), and \( \hat{A}(c) \).

Bobisud’s criterion for positive selective value is that the derivative of the equilibria of the prey with respect to the evolutionary variable, c, are all positive, when evaluated at \( c = 0 \), i.e.

\[
\left. \frac{d\hat{E}(c)}{dc} \right|_{c=0} > 0, \quad \left. \frac{d\hat{L}(c)}{dc} \right|_{c=0} > 0, \quad \text{and} \quad \left. \frac{d\hat{A}(c)}{dc} \right|_{c=0} > 0
\]
However, this is not an appropriate criterion for evaluating whether or not a cannibalistic trait will be established in a population. Rather, Bobisud's criterion answers the problem of whether the equilibrium densities will increase or not, should cannibalism prove to be favoured by natural selection [as defined for instance by Fisher (1930); see also Pianka (1974, pp. 9-12)] and therefore be established in the population. **Thus, Bobisud's analysis is insufficient for answering under what conditions cannibalism represents an evolutionary optimal strategy.** Primarily, this is the point we want to make by this note! However, by simulating one of Bobisud’s models we show below that cannibalism will actually be selected, even under much wider conditions than originally proposed. That is, Bobisud seems to have indicated the right answer, but for wrong reasons. Elsewhere we present a more complete re-analysis of Bobisud’s models (Reed and Stenseth, 1978).

In addition to the criterion applied by Bobisud, he mentions five other criteria: (i) Expected time to extinction, (ii) predator-to-prey ratio, (iii) increased stability of equilibrium (i.e. decreased or more negative real parts of the eigenvalues), (iv) increased region of attraction of the equilibrium (which in the limiting case is what Holling (1973) coined “resilience”), and (v) increased “robustness” (i.e. insensitivity to inclusion of terms other than those already included in the model). As is the case for Bobisud’s criterion, these latter criteria all presume the operation of group selection.

In general, the operation of group selection cannot be ruled out as a mechanism producing adaptations. Many authors (e.g. Maynard Smith, 1976) have presented convincing arguments showing that group selection may be assumed unimportant and that only individual selection (or the special form called kin selection, cf. Maynard Smith (1964)) seems necessary to explain most phenomena earlier attributed to group selection. Thus, any theoretical investigation should first verify whether or not individual selection can be shown to favour the trait under study. That is, “the principle of adaptation must be recognized at no higher a level of organization than is absolutely necessary” (Williams, 1966, p. 130). In our simulations we presume the operation of individual selection only: Individual selection operates by maximizing individual fitness defined as “the per capita rate of increase of the sub-population of phenotypes endowed with that life history” (León, 1976, p. 304), i.e. \( \frac{dN_i}{dt} N_i \).

Bobisud’s model for cannibalistic larvae [i.e. his Eqs. (1)-(4)] will, as an example, be analysed. For discussion of the model structure and definition of parameters, see Bobisud’s original paper. It is sufficient for our purpose here, to define the predator density as \( P \), the egg density as \( E \), the larval density as \( L \), and the adult density as \( A \). Eggs laid by adults develop into larvae which again develop into adults. The larval stage may supplement their diet by eating eggs produced by relatives. The effect of cannibalism is assumed to be an increased