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SYMPOSIUM

Sociogenetics in Insects

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Genetics of Social Behaviour in Honey Bees
(Apis mellifera L.)

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Cooperative behavior and intense regulative interactions between members of a social group are basic characteristics of highly eusocial insects. Often colonies of social insects are addressed as superorganisms, since polyethism and the caste system result in many operational similarities to true biological organisms. The fundamental genetical difference to the individual organism is its "intra-individual" genotypic variation. Consequently this results in within-colony selection among individuals. Thus, for understanding selective processes in populations of social insects we will have to consider both individual and group or colony level selection.

Classical quantitative genetic analysis refers to genetic variation among characters of individual organisms only. In social groups, however, we often find behavior which is expressed in groups but not in isolated group members. Individuals may behave differently when removed from their social context. For example colonies of honey bees (Apis mellifera L.) operate like homothermic organisms, whereas each individual worker has to be considered as poikilothermic organism. In this study the alarm reaction is used to quantify effects of worker interactions on the group phenotype in honey bees.

MATERIALS AND METHODS

Honey bees with highly variable alarm behavior had been available from a diallel breeding project for the analysis of defensive behavior (for details see Moritz et al. 1986). Capped worker brood of a low line (L), a high line (H) and two hybrid colonies (LxH and HxL) was allowed to emerge in an incubator (35°C, 60% RH). Freshly emerged workers were placed in groups of 40 into screened containers and fed with pollen and honey ad libitum. Various compositions of these groups were tested. Pure L, H, LxH and HxL groups, and mixed groups of L and H bees (L+H) were established. Also, freshly emerged worker bees from two unrelated colonies with similar reactivity to IPA, were combined at different ratios. After 4 days the groups were tested in a metabolic bioassay described previously (Moritz et al. 1985). The test groups were exposed to a 5 second flush of isopentyl acetate, a major compound of the alarm pheromone, and the reaction of the test bees was quantified by measuring the short term increase of O2-consumption or CO2 production.

RESULTS

Fig.1a shows the results of the first set of experiments in which workers with highly different phenotypes were combined (L+H). There is no significant deviation from linearity in this data set, implying that mainly additive interactions between the group members affect the group phenotype. The average reaction of genetic hybrid groups (HxL or LxH) did not significantly differ from the in vitro mixed groups of 20 L

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workers with 20 H workers. Fig. 1b shows the reactions of the combined
groups of workers from colonies which have a similar low reactivity in
the present bioassay. There is a significant deviation from linearity
and mixed groups apparently reacted stronger than pure groups.

![Graph](image)

Fig. 1. Reaction of mixed test groups to a 5 second exposure of IPA.
X-axis: Frequency of highly reactive workers in the group; Y-axis:
O₂-consumption (a) or CO₂-production (b) in µl/bee/min. a) Test
groups are combinations of 40 workers from preselected H and L colo-
nies. ± = mean ± SE of 5 test groups; * = mean of 40 test groups from
genetical hybrid colonies (H x L and L x H respectively). b) Workers from
colonies with similar reactivity were combined in various ratios.

DISCUSSION

Group behavior is determined by both additive and non-additive
interactions of the group members. In the case of strong phenotypic
differences, the additive variance overrode the nonlinear interactions.
The non-additive component only appeared when workers with similar
phenotypes were combined. The non-linear interactions found in this
study are similar to overdominance phenomena found for individuals.
Reactions of the mixed genotype groups were stronger than those of the
strongest reacting pure group. Since overdominance is thought to be
one of the key factors for heterosis and hybrid vigor, genotypic with-
in-group variability might similarly affect group vigor. In this light
the multiple mating of honeybee queens also may be a result of selec-
tion for genetic heterogeneity within the colony.

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