## "Division of labor in heterogeneous ant colonies"

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Abstract: The composition of social groups has profound effects on their function, from collective decision-making to foraging efficiency. But few social systems afford sufficient control over group composition to precisely quantify its effects on individual and collective behavior. Here we combine experimental and theoretical approaches to study the effect of group composition on individual behavior and division of labor (DOL) in a social insect. Experimentally, we use automated behavioral tracking to monitor 120 colonies of clonal raider ants, with controlled variation in three key correlates of social insect behavior: genotype, age, and morphology. We find that each of these sources of heterogeneity generates a distinct pattern of behavioral organization, including the amplification or dampening of inherent behavioral differences in mixed colonies. Theoretically, we use a well-studied model of DOL to explore potential mechanisms underlying the experimental findings. We find that the simplest implementation of this model, which assumes that heterogeneous individuals differ only in response thresholds, could only partially recapitulate the empirically observed patterns of behavior. However, the full spectrum of observed phenomena was recapitulated by extending the model to incorporate two factors that are biologically meaningful but theoretically rarely considered: variation among workers in task performance efficiency and among larvae in task demand. Our results thus show that different sources of heterogeneity within social groups can generate different, sometimes non-intuitive, behavioral effects, but that relatively simple models can capture these dynamics and thereby begin to elucidate the basic organizational principles of DOL in social insects.