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Emergent division of labor among clonal ants

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ABSTRACT

Division of labor is thought to be central to the success of social species like ants and humans, but how does it arise? We used automated behavioral tracking in an unusual, clonal ant to show that division of labor can emerge in response to increasing group size. These behavioral changes were accompanied by rapid increases in colony performance.

A group of clonal raider ants, hand-painted so as to be individually recognized by our tracking software. Image credits: Daniel Kronauer ©

What are the benefits of living in society? Sociality has long been proposed to be beneficial because groups can divide labor among individuals to increase their efficiency. Some of the most sophisticated forms of division of labor are found in social insects, such as honeybees, termites and ants, which live in colonies that can count millions of individuals but are integrated to such a degree that they often seem to function as a single organism. In social insect colonies, work is often divided between highly specialized, morphologically differentiated castes (e.g. large, fertile queens and one or more castes of smaller, sterile workers). These extreme forms of division of labor are thought to be highly beneficial, but they only appeared after sociality was established. To evolve from solitary ancestors, sociality must have initially generated benefits in small, simple groups consisting of similar, undifferentiated individuals. How the division of labor and its hypothesized benefits could have arisen under such conditions remains unclear.

To investigate this question, we used an unusual ant species, the clonal raider ant (Photo 1), whose social organization naturally resembles these conditions. This species has no queens; instead, colonies are made up of morphologically and genetically identical workers that can perform all the tasks necessary for the colony, like nursing, foraging and laying eggs.

This implies that—at least in principle—they could live on their own, without the need of a social group.

With this convenient study system, we set out to measure division of labor and fitness (that is, colony performance) in experimental colonies over a size range corresponding to the onset of group-living (1 to 16 ants). Measuring fitness (survival, reproduction) was straightforward, but the tools needed to measure behavior and division of labor were not available, so we had to develop them from scratch. We built a setup to record images from many colonies in parallel, and wrote custom software to automatically detect and identify each ant in those images, based on individual color-marks painted on the ant's thorax and abdomen.

Using these methods, we found that division of labor self-organizes surprisingly early, in colonies of as few as six workers. As group size increased, individual workers became more specialized and colonies became behaviorally more diverse, even though all ants had the exact same genotype and age. In parallel with those effects on behavior, fitness also rapidly increased with group size: ants in larger colonies lived longer and had more offspring than ants in smaller colonies, and their offspring also grew faster.

We wondered whether our observations were compatible with the best-known mathematical model for self-organized division of labor, in which small intrinsic differences between individuals drive them to specialize in different tasks. For this, Chris Tokita and Corina Tarnita from Princeton University joined the project.

Initially, our and their instincts were that social interactions were necessary to explain our observations. Thus, they set out to construct a model incorporating social interactions among individuals that they hoped would better match the data, while using the established model as a baseline to compare against. Their theoretical analysis, however, revealed that the well-known model could easily reproduce our empirical results.

Moreover, an exploration of the model also bore predictions we had not yet explored. Theoretical analyses suggested that larger groups were more homeostatic, or in other words that they were better able to maintain stable conditions inside the colony. Homeostasis is an essential property of life, and as such is inherently linked to fitness. Going back to our empirical data, we found that larger colonies were indeed more homeostatic, which is a likely explanation for why they also did better in our experiments. For example, larger colonies almost never left the young unattended (that is, there was generally at least one ant at the nest to take care of the larvae), while small colonies often did.

As a whole, our results show that several important colony properties (division of labor, homeostasis and increased fitness) can naturally emerge in very small social groups composed of very similar individuals. These benefits, arising from small increases in group size alone, could promote social cohesion at early stages of group-living and might provide an evolutionary "stepping-stone" towards more complex forms of social organization. Beyond the evolution of sociality, these results might also have implications for the study of other "major transitions in evolution" (steps in the evolution of life where smaller entities formed larger entities, then differentiated and became inter-dependent), such as the evolution of multicellularity and the associated emergence of cell differentiation.