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How army ants' iconic mass raids evolved

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Image #1 Army Ants reproduced with permission from "Army Ants: Nature's Ultimate Social Hunters" by Daniel J.C. Kronauer; Image #5 painted clonal raider ants photograph by Daniel Kronauer. Credit: #1: Daniel J.C. Kronauer, #5: Daniel Kronauer

Army ants form some of the largest insect societies on the planet. They are quite famous in popular culture, most notably from a terrifying scene in Indiana Jones. But they are also ecologically important. They live in very large colonies and consume large amounts of arthropods. And because they eat so much of the other animals around them, they are nomadic and must keep moving in order to not run out of food. Due to their nomadic nature and mass consumption of food, they have a huge impact on arthropod populations throughout tropical rainforests floors.

Their mass raids are considered the pinnacle of collective foraging behavior in the animal kingdom. The raids are a coordinated hunting swarm of thousands and, in some species, millions of ants. The ants spontaneously stream out of their nest, moving across the forest floor in columns to hunt for food. The raids are one of the most iconic collective behaviors in the animal kingdom. Scientists have studied their ecology and observed their complex behavior extensively. And while we know how these raids happen, we know nothing of how they evolved.

A new study in *Proceedings of the National Academy of Sciences* led by Vikram Chandra, postdoctoral researcher, Harvard University, Asaf Gal, postdoctoral fellow, The Rockefeller University, and Daniel J.C. Kronauer, Stanley S. and Sydney R. Shuman Associate Professor, The Rockefeller University, combines phylogenetic reconstructions and computational behavioral analysis to show that army ant mass raiding evolved from a different form of coordinated hunting called group raiding through the scaling effects of increasing colony size.

The researchers discovered that the ancestral state to army ants' mass raids is the rather different-looking group raids that their non-army ant relatives perform. The evolution of mass raids from group raids happened tens of millions of years ago and the transition from group raids to mass raids is perfectly correlated with a massive increase in colony size.

"All of these ants are within the subfamily Dorylinae," said Chandra. "The first doryline ants, which were not army ants, lived in small colonies of a few hundred workers. When army ants evolved their foraging behavior from group to mass raiding, they also massively expanded their colony sizes. Army ant colonies now have tens of thousands—and often millions—of ants."

Kronauer's Laboratory of Social Evolution and Behavior at The Rockefeller University studies the clonal raider ant *Ooceraea biroi*, a relative of army ants. Clonal raider ants are almost the only ant species that can be kept in a lab and experimented on indefinitely. They are also genetically tractable in that researchers can make mutants or transgenic lines to compare. But they are also poorly understood, understudied, and hard to find in the field. The mass raiding of army ants is well studied and described; however group raiding is not. And understanding group raiding is key to understanding the evolutionary trajectory to mass raiding.

"My goal has always been to study how social behavior evolves and is controlled, and how army ants have evolved," said Kronauer. "A few years ago we discovered that the way clonal raider ants forage is through raids that are similar to army ant raids."

To understand how the raids are structured and organized, the team collected a large number of video recordings of many colonies raiding under controlled conditions.

"Our goal was to understand what are the underlying behavioral rules the ants follow and how a raid emerges out of the behavior of individual ants," said Gal. "Tracking individuals in a dense colony is a challenge and does not have a generally applicable solution. This is especially true for small ants that like to form dense clusters such as raider ants."

The researchers overcame this challenge by using a custom computer vision software developed in the lab named anTraX that tracked and identified the ants based on small color marks painted on their abdomen and thorax. The method allowed them to collect accurate trajectories for all the ants for several weeks with minimal human effort, and without requiring expensive high-resolution cameras.

In a small nest of 25 ants they used 5 sets of colors and painted each ant with a unique set of colors. The researchers placed a single fire ant pupa (the prey) in the foraging arena outside of the nest. The nest sends out a scout to look for food. Once the scout finds the food, she lays a pheromone trail back to home. Inside the nest she releases, what researchers believe to be, a recruitment pheromone that attracts the ants to her. They spill out of the nest and follow her trail to the food in a group raid.

As the researchers increased the colony size, the number of scouts sent to forage also increased and they began to see more coordinated search activities. This same behavior is seen in army ants, but at a scale of tens of thousands or often millions of ants, with a very large increase in the number of scouts.

"Our behavioral analysis shows that group raids have stereotyped structure, and that they are conserved across the Dorylinae. Because the transition from group to mass raids over evolutionary time is perfectly associated with massive increases in colony size, we wondered whether this had something to do with the transition in raiding behavior," said Chandra. "We gradually scaled our colonies up from 10 through to 100 ants and we saw this very nice increase in coordinated search behavior as you increase colony size."

"Our experiments show that in larger colonies, the ants become more synchronized in their leaving of the nest to scout. In other words, when an ant leaves, the chances that more ants will follow her are higher in large colonies. While we cannot directly say much about the actual mechanism underlying this observation, we know from other complex systems that an increase in synchronicity is a result of stronger positive feedbacks between individuals," said Gal. "In the army ant size limit, this will result in what we know as a mass raid."

But the resemblance to army ant behavior seen as colony size increased was not limited to temporal synchronization. The experiments also showed that army ants and their relatives follow the same set of behavioral rules when searching for food. A few army ants leave the nest at first with no pheromone trail outside. They hesitantly step out and then appear to waver, turn around, and run back in. But there are ants inside the nest that want to leave, so they push them back out, or they take their place. Because each ant that leaves and returns is laying a pheromone trail the group is slowly extending the trail from the nest in bursts. This 'pushing party' is how army ants create a column of ants leaving the nest and traveling quite far away. As the researchers expanded the clonal raider ants' colony size, they observed the same behavior.

"It's hard to see in the small colonies because there are so few ants," said Chandra. "But we show statistically that this really is happening and we have instances where it's quite dramatic. So, even in small colonies of clonal raider ants, each ant seems to be following very similar rules for search behavior compared to an army ant, although it might not look like it at first glance. And as you increase colony size, the interactions between these ants lead to greater coordination, you start to see more obvious 'pushing parties' and you start to actually see spontaneous columns of ants leaving the nest."

To doubly test this, the team experimented with two colonies of 5,000 workers each, which is an order of magnitude larger than seen in natural colonies for this species. In these studies the raids displayed all four of the characteristic features of army ants' mass raids: a large number of ants that participate in the raid, a bifurcating trail that enables army ants to raid multiple prey sources, a recruitment that happens outside the nest at the raid front, and a spontaneously initiated raid.

At small colony sizes, these rules manifest as group raids, and as colony size increases—either experimentally or over evolutionary time—these rules give rise to mass raids. The team concluded that expansions in colony size in the ancestors of army ants are sufficient to have caused the transition from group raiding to mass raiding behavior.

"Probably the most common pattern is that collective behavior evolves via natural selection acting on and tweaking the interaction rules that the individual animals follow," said Kronauer. "But our study is a nice example of a different mechanism: scaling effects associated with group size can give you dramatically different outcomes in terms of collective behavior, even though the individual rules don't change much."

Gal agreed, "Of course, it has been long known that changing group size can have a dramatic effect on emergent collective behavior. This has been shown both theoretically and experimentally. We have now shown that this effect can also be harnessed by evolution, and that collective behavior can be adapted over evolutionary timescales without actually modifying the behavior of individuals."

As far as is known, the coordinated behavior of clonal raider ants is one of the most complex social behaviors that can be induced or studied in the lab. The authors are currently working on a detailed study of how individual ants behave during the course of the raid, and how the structure of the raid responds to variation in environment and colony composition.

"We suspect that the ants specialize to some extent on specific tasks," said Chandra. "There's probably some very interesting division of labor going on, and there's also clearly complex communication—the ants use several different pheromones to talk to each other and to organize the raid. And there are several decisions the colony must make in the course of the raid. It's an incredibly rich behavior and there are many questions we could ask in the future and we're laying the groundwork for that."

More information: Vikram Chandra et al, Colony expansions underlie the evolution of army ant mass raiding, *Proceedings of the National Academy of Sciences* (2021). DOI: 10.1073/pnas.2026534118

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