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The conundrum of spontaneous (un)cooperation in pine sawflies

by Antti Miettinen[1] | Master student; Carita Lindstedt[1] | Postdoctoral Research Fellow

[1]: Centre of Excellence in Biological Interactions, Department of Biological and Environmental Sciences, University of Jyväskylä, Finland

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ABSTRACT

Would you puke to save your group? The dramatic group defence of the common pine sawfly (Diprion pini) larvae can help us understand why individuals do not always use their full potential to cooperate with others. Our study suggests that interactions between species determine how costly it is to cooperate. This in turn affects the frequency of cooperating and cheating individuals in groups of pine sawflies.

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It might seem that there is always someone who works a little less than others in a group. Especially if the participation in a collective effort comes with the price. This may be the case with groups of people aiming at a common goal and is widely detected with other organisms in nature as well. Perhaps surprisingly, the behaviour of the common pine sawfly (Diprion pini) can help us understand why individuals do not always use their full potential to cooperate with others in a group and what is the price of cooperation.

One of the key puzzles that evolutionary biologists aim to solve is when and why organisms should cooperate with other members of their species, and when and why they choose not to.

Fortunately, the group-dwelling lifestyle of the common pine sawfly (D. pini) offers a good opportunity to study what affects cooperative behaviour in nature. Larvae of this species live in large groups on pine trees, and collectively defend themselves against predators and parasites. The higher the proportion of defending individuals is, the more protected all group members should be from attacks by their enemies, such as birds and parasitoids.

When threatened, the common pine sawfly larvae exhibit a striking defence display by arching their back and regurgitating (i.e. throwing up) a resinous bubble of sticky defence fluid that they have stored in their defensive glands. All of this happens in concert with other members of the larval group. Or as is the case sometimes, with the exception of some individuals not participating in this cooperative effort.

In our study, we found that participation in this common defence is costly for the larvae. We studied this by simulating repetitive predator attacks on selected individuals and monitoring their performance and immune responses. Consequently, we found that the larvae pay a significant price for defending. Larvae that were forced to defend on a daily basis were more likely to die before they reach the pupal stage, and also had a weaker ability to defend themselves in future encounters with predators and parasites, compared to the control group. For example, the regularly defending larvae produced less and weaker defence fluid than their controls.

We also found that the 'willingness' to participate in the common defence, and how costly it was for the larvae, depended on the chemical content of the larvae's diet. We found that for example, having to defend regularly reduced the immune responses of larvae only when the larvae fed on pine needles with a high resin content. Host plant quality of pine sawflies also varies widely in nature. Thus, these manipulated conditions simulated natural ecological interactions faced by pine sawflies. Therefore, our study shows that these different interactions jointly determine how many cooperators and free-riders there are in pine sawfly groups.

Finally, we found that irrespective of the manipulated conditions, male larvae were always more likely to be freeloaders in group defence than their sisters. Males also clearly benefited from their 'cheating' as non-defending male larvae grew faster than males participating in the defence more often.

These results shed light on why it can be beneficial to cheat in a group effort. Non-defending, or 'cheating', larvae in our study may have done so to save energy. These cheats directly benefited from it by growing faster. In addition, larvae that were forced to defend less often than their peers had a better capacity to defend themselves in future encounters against predators and parasites. Host plant quality combined with attack rate, i.e. interactions between different species, had a large impact on these costs.