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<RH>*Commentary*/The cultural evolution of emergent group-level traits

<CT>**Explaining group-level traits requires distinguishing process from product**

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<C-AB>**Abstract:** Smaldino is right to argue that we need a richer theory of group-level traits. He is wrong, however, in limiting group-level traits to units of cultural selection, which require explanations based on group selection. Traits are best understood when explanations focus on both process (i.e., selection) and product (i.e., adaptation). This approach can distinguish group-level traits that arise through within-group processes from those that arise through between-group processes.

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We agree with Smaldino's thesis: many important aspects of human behavior are best described as group-level traits, emergent properties of social groups characterized by differentiation and organization. Crowdsourcing provides a vivid and contemporary illustration. Wikipedia is the product of an immense collaboration of specialists organized into different roles like author and editor. Such a work cannot be expressed by or reduced to any one of its millions of contributors. How should we make sense of group-level properties like this? According to Smaldino, theory

leans too heavily on the N -person prisoner's dilemma model in which groups do best when everyone contributes but individuals do best by withholding contributions. This model forces us to think about social groups and behavior in terms like "cooperation," "freeriding," and "altruism." Many group-level properties, especially those with emergent, rather than additive properties, do not fit into this framework.

Although sympathetic to Smaldino's call for a richer theory of group-level traits, we disagree that group-level traits necessarily constitute "a unit of cultural selection that is not encompassed by selection on individuals" (sect. 1, para. 2). This assertion seems to yoke together group-level traits and group-level selection. As we will argue, this need not be the case. The deeper problem is that Smaldino does not clearly distinguish selection from adaptation. Making sense of phenotypic evolution (including group-level traits) is best done by focusing on both process (i.e., building models of selection to determine why one phenotype results rather than another) and product (i.e., studying adaptations to infer the historical selective pressures). Focusing on group-level traits without explicitly modeling selection processes results in a phenomenological approach that obscures and confuses alternative mechanistic explanations. Smaldino gets caught in this trap when discussing caste differentiation in eusocial insects: "the trait [caste differentiation and social organization] does not *emerge* from the collection of individuals possessing those properties, but is merely a statistical description of their organization" (sect. 3, para. 5). It is not obvious why a Roman Legion (discussed in sect. 2) represents a group-level trait, while an insect colony does not. What would help is an understanding of both the consequences of the traits and how they evolve.

To illustrate our point, let us imagine a group of individuals stranded on an island, isolated from the rest of the world. For the sake of argument, we endow these individuals

with the capacity for division of labor and trade (as Smaldino notes, a crucial ingredient in the emergence of group-level traits). Capacities like these emerge over evolutionary timescales. Because we are interested in the emergence of group-level traits over historical timescales, we can take these capacities as given. Though capable of division of labor, our hypothetical islanders do not practice it. Instead, they embody Marx's manifesto: no one is a specialist; everyone is a generalist. During the day, all are fisherman; at night, all philosophers.

Suppose now that some individuals specialize, exclusively fishing or philosophizing. With increasing returns to specialization, these innovators produce more fish or more knowledge than their comrades. If the islanders value leisure – and who does not? – they can have more of it by trading with each other. Fishers trade their surplus catch to philosophers in exchange for knowledge (or whatever it is that philosophers produce). And both parties enjoy more leisure. Specialization-and-trade will quickly spread throughout the community. The benefit of division of labor has transformed our society into one that is differentiated. An outside observer might argue that the economy should be understood as an emergent, group-level trait. But what process caused this trait? Surely not group selection, as there were no competing groups. Instead, the emergent, group-level trait resulted from within-group forces in which individuals made choices to maximize utility.

The observer might then object that this hypothetical fishing-and-philosophizing economy does not, in fact, constitute a group-level trait. After all, the products of labor flow to individuals; they are not properties of groups. Fair enough. Suppose now that fishermen discover that they can catch more fish by working together in collaborative teams, complete with differentiated roles and social organization. (As with division of labor, we are assuming the capacity for collaboration, not explaining it.) These groups fish together for some time, reap

profits that are then split among group members, and then individuals go their separate ways. Smaldino argues that ephemeral co-ops like this constitute trait groups but are not “consistent enough over time to constitute a unit of selection” (sect. 3, para. 5). Maybe so. But in our example, the group-level trait results from individuals maximizing utility, not group selection.

Finally, let us suppose that the island is bridged to other islands. People are free to move to whichever island they so desire. On some islands, philosophizing is an individual affair, and so knowledge systems are limited. On other islands, philosophers long ago founded academies in which knowledge could be shared and therefore grows further and faster. Islands with academies are far more attractive to immigrants than islands without them. When migrants vote with their feet, group-level traits can spread through a group-level process (Boyd & Richerson 2009). In addition, philosophically starved islanders might emulate their more successful neighbors by founding academies, representing another form of group selection (Boyd & Richerson 2002). In both cases, a group-level trait spreads because of group-level selection.

Although we agree with Smaldino that more attention must be paid to group-level traits, we want to stress that this focus on adaptation must be combined with a focus on selection. Group-level traits, as defined by Smaldino, may arise through group selection, but they may also arise through within-group processes. When multiple processes operate simultaneously, it is all the more crucial to understand how they interact in generating adaptation.

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<RFT>**References** [Karthik Panchanathan, Sarah Mathew, and Charles Perreault] [KP]

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