Behavioral Ecology

The official journal of the
ISBE
International Society for Behavioral Ecology

Behavioral Ecology (2021), XX(XX), 1–2.

Invited Commentary

Proximate and ultimate processes may explain "task syndromes": a comment on Loftus et al.

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Groups are comprised of individuals that differ from one another in their behavior and in their task performance, thus affecting group-level outcomes. In their review, Loftus et al. (2020) propose a comprehensive set of hypotheses for how task performance may be linked with other behavioral tendencies of individuals, which they refer to as "task-independent behavioral variation" or "personality." As they review, individuals in a social insect colony perform different tasks, such as foraging, brood care, and nest maintenance. and consistent differences among individuals in task-independent behaviors occur at both the worker and colony levels (Jandt et al. 2014). Hypotheses for how task-independent behavioral diversity may affect the collective behavior of colonies have been proposed (Pinter-Wollman 2012) and tested empirically (e.g., Neumann and Pinter-Wollman 2019). However, evidence that task performance is linked with task-independent behavioral diversity is scant. Some studies that have examined this link did not find evidence for a connection between task performance and task-independent behavioral tendencies. For example, in *temnothorax* ants, there is task-independent behavioral diversity in worker activity. However, individuals that are highly active, or "diligent," do not all specialize in the same task, and some very active individuals perform a large array of tasks without specializing in any task (Pinter-Wollman et al. 2012). Furthermore, in honey bees, task-independent fast cognitive phenotypes relate to both high performance in nursing tasks and early onset of foraging activity (Tait and Naug 2020). Thus, individuals classified as fast cognitive types are diligent in both tasks and do not specialize in one particular task.

Our ability to link task-independent behavioral variation with task specialization might depend strongly on differences in the physiological mechanisms that underlie these behaviors, their ultimate function, and environmental conditions. Task performance and task-independent behaviors may emerge from different genetic, neurobiological, or other physiological mechanisms. For example, individuals that perform different tasks express different genes (e.g., scouting in honey bees [Liang et al. 2012] and brood care in ants [Walsh et al. 2018]). Furthermore, there are genetically heritable task-independent learning behaviors (Cook et al. 2020). Examining the overlap between genes that are expressed when performing certain tasks and genes that underlie task-independent behaviors may help determine the level to which the different types of behaviors are linked. For example, in the Argentine ant, *Linepithema humile*, the *Lhfor* gene is downregulated in foragers (Ingram et al. 2005) and has low levels of expression in exploratory individuals (Page et al. 2018). Thus, rather than "switching the focus from genetic diversity to behavioral variation itself" (Loftus et al. 2020), studying the synergies between genetic and behavioral diversity may reveal links between task-independent behaviors and task performance.

Task performance and task-independent behaviors might differ substantially in their ultimate function. Loftus et al. (2020) define "task" as "any behavior that positively affects the fitness of conspecifics within a social group by providing a good or service to those conspecifics." According to this definition, the predominant selective pressure on task performance occurs at the level of the group. However, task-independent behaviors are not defined in the context of the group and, therefore, can be subject to other selective pressures, for example, at the level of the individual. While, in social insects, the fitness of the individual can be tightly linked with the success of the group because, in many social insects, workers are sterile, this is not the case in all social insects or in other social animals. One of the goals of Loftus et al. (2020) is to extend the concept of tasks beyond social insects. However, the ultimate function of performing a task (to help others in the group) and task-independent behaviors (to benefit oneself) can be very different—weakening the potential links between the two types of behavior. As Loftus et al. (2020) propose, feedback between individual behavior and colony function may align conflicting selective pressures and lead to links between task-independent behaviors and task performance.

Finally, the physical environment might have an important role in facilitating the links between task-independent behaviors and task performance. For example, individuals that are highly exploratory might become "scouts" that recruit individuals to new foods in environments where food is scarce and scattered across large distances. However, in environments in which food is abundant and uniformly distributed, exploratory individuals might not become specialized. In social insects and other social animals, the actions of individuals might influence the physical environment (e.g., through nest construction and food storage). Thus, the feedback between the behavior of individuals and the environment in which they live might facilitate links between individual behavior and collective outcomes and, therefore, between task-independent behaviors and task performance.

To summarize, when investigating the links between task-independent behavioral variation and task specialization, it is important to consider the physiological mechanisms that underlie these behaviors, their ultimate function, and the environmental conditions in which the behaviors are performed.

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Received 31 October 2020; editorial decision 2 November 2020; accepted 2 November 2020.

doi: 10.1093/beheco/araa126

Handling editor: Leigh Simmons

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