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groups, within-individual behavioral variation may vary among in-
Westneat et al. 2009). This approach partitions variance; in social
cialization and its functional consequences. They incorporate sev-
eral important ideas, and they confront, with mixed success, two
fundamental issues in behavioral ecology.

Loftus et al. adopt the statistical definition of personality that is
embedded in the behavioral reaction norm approach (Dingemanse
et al. 2010), applicable to any repeatedly expressed trait (e.g.,
Westneat et al. 2009). This approach partitions variance; in social
groups, within-individual behavioral variation may vary among in-
dividuals, and variation in both may vary among groups. Moreover,
different behaviors may be associated into syndromes. This multi-
level multivariate vision of behavior is a powerful tool for statistical
natural history, yet to be widely employed.

Loftus et al. also distinguish between the behaviors that define a
task (e.g., behaviors specifically associated with obtaining a group
benefit) and task-independent behaviors. They propose two poten-
tional controversy ideas about this distinction. First, they suggest
that individuality in task-independent behavior may, through vari-
ous feedbacks, lead to task specialization. Many, especially stu-
dents of the social insects, may dismiss this idea because castes are
often determined very early or via predictable life-history shifts.
I bet applying the multilevel, multivariate framework will reveal
more variation than usually assumed, but note that Loftus et al.
do not explain the relative influence of early-life individuality and
feedback affecting task specialization as opposed to other develop-
mental pathways.

Loftus et al. also broaden the idea of tasks to include role taking
in other social groups, also a potentially controversial stance.
However, I contend this broad view of tasks generates more widely
applicable ideas about sociality. Two examples occurred to my
ornithological mind: 1) male–female pairs raising offspring and
2) ephemeral groups (flocks) that forage together. Many biparental
birds exhibit parental care roles. Often these are sex specific (Ryser
et al. 2016), but no one has asked if prereproductive behavioral
differences contribute to role taking. Few have assessed vari-
ation in role taking or how it may affect reproductive performance
(but see Both et al. 2005). Because sociality probably arose from
small family units with parental care, extending the idea of tasks
produces more fine-grained assessment of the evolutionary ante-
cedents of complex sociality.

Foraging flocks provide an uneasy fit to the Loftus et al. frame-
work. Social foragers often exhibit producer–scrounger dynamics
(Barnard and Sibly 1981). Producers search for new food sources,
and once found, public information leads to scroungers exploiting
the newly found food. Although flexible role taking occurs, individ-
uals tend to specialize (Morand-Ferron et al. 2011). Earlier workers
had proposed that role taking might emerge from role-independent
individuality (Ensminger 2011; Katsnelson et al. 2008). That devel-
opmental sequencing and positive feedbacks might contribute to so-
cial structure in social foragers is still poorly investigated. However,
scroungers are social parasites and reduce group level fitness,
making flocking birds an awkward fit to the framework. Loftus et al.
acknowledge social parasitism, but do not confront the challenge of
defining either the causes or consequences this wrench-in-the-works
would have on their vision of social development and evolution.

Loftus et al. also tackle two big issues with mixed success. First,
they explicitly incorporate the tension between personality and
plasticity. This is simultaneously nuanced and muddled, thereby in-
dadvertingly highlighting the challenge. Personality is by definition
a constraint on some forms of plasticity, but the framework posits that
it can be created by other forms of plasticity. That is, differences in
task-independent behavior can produce differences in propensity
for certain tasks (a form of sequential multidimensional plasticity,
Westneat et al. 2019). Missing from the framework are clear criteria
for distinguishing differences in underlying biology from pseudo-
personality. The former would be evident if individuals exposed to
the same environment behave differently, but the latter arises from
individuals with the same behavioral tendencies being exposed to
different environments, creating differences. The distinction is rele-
rent; brood care takers are exposed to dramatically different envir-
onsments than are foragers. A similar lack of clear criteria concerns
developmental and activational plasticity. These differ in the time
course of effects, which unfortunately are likely continuous, causing
blurring of the distinction. Short-term feedbacks generate subtle ties
in links between plasticity and personality and will be challenging
to disentangle empirically.

The second idea is that social feedbacks affect social struc-
ture within groups. Feedbacks may influence the developmental
process, in which case they add even more complexity to the
interplay between developmental and activational plasticity.
Feedbacks also may occur over evolutionary time. Loftus et al.
briefly describe an exciting but relatively vague vision of group
level and individual fitness consequences of task syndromes
within social groups. Evolutionary feedbacks can occur through
many routes, with the interactive effects on fitness of the pheno-
types of social partners a key element (Araya-Ajoy et al. 2020).
Teasing apart pathways to social evolution will be an immense
challenge. The Loftus et al. framework provides some new ideas but
much work remains.

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Variation and change in behavior: a comment on Loftus et al.

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Variation and change are different but easily confused (Gordon 1991). Variation is due to differences among individuals at a point in time. A reaction norm, due to differences among genotypes in their response to a particular environmental condition, leads to variation among genotypes at a point in time (Gupta and Lewontin 1982). By contrast, change happens over time. Developmental plasticity is a trajectory over time, from changes in how individuals respond to conditions (Sultan 2015).

This article puts together the idea of variation among individuals in behavior, how individuals differ at a particular point in time, and behavioral change over time in response to changing conditions. Differences among individuals in how they change over time are called a reaction norm or “behavioral type.” This represents change over time in behavior as a consequence of something else that is static and inherent, or “pre-existing,” as the authors put it.

The authors suggest that in any group of animals, there is a fixed set of the optimal mixture of behavioral types. They argue that the “probability of suboptimal mixtures decreases” when individuals vary less over time and thus stick to particular specialized types. This is not consistent with other arguments they present for why it is adaptive for individuals to change over time in response to changing conditions. If the optimal response for each individual shifts in response to changing conditions, then isn’t it likely that whatever is optimal for the group shifts as well?

The authors argue, as many have, that in a social insect colony, individuals differ in task because they differ in pre-existing behavioral types (reviewed in Gordon 2016). This is similar to threshold models of task allocation (Beshers and Fewell 2001), but the proposal here is to break down the threshold into two parts. First, there are differences among individuals in pre-existing behavioral type; second, these differences in behavioral type affect the threshold or probability of performing a certain task. That some kinds of behavior are associated with others seems uncontroversial, and many kinds of individual variation could lead to variation in task performance. For example, one ant might be more likely than others to encounter more things, perhaps because it moves around a little faster than others, and this ant might then be more likely to respond to those things by picking them up and moving them. The suggestion here would be to call the speed at which an ant moves around and bumps into things its behavioral type, and its tendency to pick those things up its task performance.

However, in social insects, colonies are the reproductive individuals: colonies send out reproductives that mate and then form new colonies. Thus, selection acts on variation among colonies, and not on variation among individuals within colonies (Jandt and Gordon 2016).

It is an open question how much of the variation among colonies that is ecologically important, and shaped by natural selection, is the result of variation in the distribution of individuals of different types within colonies. It could also be that all the individuals in one colony are different from all the individuals in another colony, in ways that are ecologically relevant and thus open to natural selection. For example, harvester ant colonies in the desert vary in how they collectively manage water loss using olfactory interactions of outgoing and returning foragers, and natural selection is shaping this variation among colonies (Gordon 2013). Recent work suggests that colonies differ in worker expression of genes associated with biogenic amines that influence the workers’ response to current humidity and to olfactory interactions (Friedman et al. 2020). If all the workers in one colony differ from all of the workers in another, differences among colonies in behavior do not arise from differences in the distribution of particular types within colonies.

In general, there is much to learn, for all animal groups, about how individuals vary in response and how this variation plays out over time. A further question is how much the ecologically important differences among groups arise from differences in the groups in the distribution of particular types, and how much they arise from differences between one group and another that all group members share.

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