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Understanding foraging patterns that achieve colony-level macronutrient regulation

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Several studies of ants and honeybees have shown that colonies forage so as to regulate macronutrient intake to specific targets. Moreover, when a regulating mixture of diet choices is not available (e.g., if one macronutrient is over-represented in all choices), colony survival declines -- ostensibly because of the accumulation of unavoidable surpluses of macronutrients. These observations are consistent with predictions of the geometric framework (GF) of Simpson and Raubenheimer, but little is known about the behavioral mechanisms that eusocial insects use to achieve macronutrient regulation. To this end, we have developed a novel economic framework (EF) of nutrition that encapsulates the GF while also modeling the effect of ecologically rational behaviors that achieve regulation under typical dietary conditions and lead to deleterious allocations otherwise. The EF suggests designs for new experiments that use two mutually deficient diets to probe foraging behavior further than is currently possible with the GF. Additionally, it provides testable predictions for how foragers will allocate to three or more food sources that vary in only two macronutrients. In this latter case, a continuum of foraging allocations is available that satisfies the regulating condition of the GF. However, the EF is able to predict allocations that will be preferred within that continuum. Moreover, the EF predicts how macronutrient supplements commonly given to agricultural honeybee colonies can destabilize an existing healthy foraging allocation. So the EF provides new insights into apiculture and the nutritional components that have been implicated in colony collapse disorder. More generally, this foraging framework also encapsulates two classical results from solitary and social foraging theory, the ideal free distribution (IFD) and the marginal value theorem (MVT), and explains why these results may not apply when there is macronutrient co-limitation. Thus, the EF potentially is a unifying framework for solitary, social, and eusocial foraging theory.