Research Statement Rebecca Clark

Nutritional physiology and life-history evolution in insects

The acquisition and allocation of nutrients influences evolution and ecology across levels of complexity, from the growth and development of individual organisms to driving the dynamics of ecosystem function. My goal is to identify how behavior and nutrition interact to shape growth and fitness across an array of organisms, from solitary animals to complex adaptive systems. Out of myriad requirements, three bulk nutrients that drive animal survival, growth, and reproduction are the macronutrients protein and carbohydrate; and the element Phosphorus. Parallel approaches developed in animal nutrition and freshwater ecology indicate that organisms are sensitive to both the absolute and relative amounts of these nutrients. My central aims are to determine how these nutrient constraints translate into fitness consequences across different system types (solitary to eusocial), and to determine how constraints are counterbalanced by the behavioral and physiological mechanisms that organisms have evolved to cope with nutrient heterogeneity.

Nutrition and behavior shape colony growth in leaf-cutter ants

Eusocial groups solve the same organizational and developmental challenges as individual organisms: they must sustain predictable growth trajectories, while coping with variation in food amounts and quality. Further, they do this in a social context. My research employs whole-colony manipulations of diet quality and quantity, to determine how nutrient inputs shape survival, behavioral interactions, and colony growth / composition in ants.

Characterizing the growth of a complex tri-trophic system. Leafcutter ants have evolved an obligate, symbiotic, nutritional relationship with a fungus - their sole food source. Workers collectively balance effort between supplying the fungus with leaves, and feeding fungus to developing brood, under growth conditions that shift with age and season. In newly-formed colonies of the desert leafcutter ant *Acromyrmex versicolor*, the ratio and growth of ants to fungus changes depending on colony size, even under abundant leaf availability, causing a previously undiscovered selective bottleneck during early colony development (C.V. Refs 5, 9). New colonies experience high queen mortality prior to first worker emergence. In addition, I found that leafcutter colony growth does not actually stabilize until months later, when colonies reach a threshold worker number that enables a robust division of labor between foraging and brood provisioning.

How nutrient limitation shapes a terrestrial trophic system. Leading hypotheses suggest leafcutter foraging decisions and colony growth result from combined, interacting factors, including leaf quality and the fungus garden's physiological state; factors that are impossible to disentangle in the field. I developed a new artificial diet and lab measurement methods to demonstrate, via p, c and Phosphorus supplementation, that nutrient quality influences foraging rates, fungus performance (growth), and ant population growth and structure (in prep). However, the nature of the diet effect depended on the specific identity of the added nutrient, manifesting as parallel growth increases or decreases in the fungus garden and the ant population, or changes in the ant population alone. This suggests that physiological allocation of different nutrients by the fungus affects how nutrient additions are passed along to the ants. Nutrient addition experiments in other terrestrial trophic systems, predominantly in grasslands, also frequently show shifts between trophic compartments that do not match predictions based on studies of nutrient limitation at the individual level. This highlights a need for continued experiments to determine why nutrient limitation effects do not always translate as expected. Within the leafcutter system, I plan to apply techniques developed to characterize nutrient flux in solitary insects to determine why colony-level responses differed for p, c, and Phosphorus (see below). I hypothesize that the response is a product of three interrelated elements: flexible nutrient allocation by the fungus garden under varying nutritional conditions, selective feeding and management by the ants based on fungus quality, and foraging decisions driven by a combination of ant-detected leaf characteristics and feedback from the fungus garden (Fig. 1).

Foraging behavior can be modified in multiple ways to buffer nutrient limitation. In leafcutter colonies, I found that colonies respond to changes in the size of the fungus garden by both shifts in total worker activity and worker switching between tasks. The boost in total activity suggests that inactivity serves an important function in colonies: maintaining a reserve workforce to counteract environmental perturbations. At present, it is unknown to what degree such shifts in activity and task allocation reflect generalized responses to nutrient limitation in social systems. For example, honey bees respond to changes in stored pollen levels by recruiting new foragers, not via changes in individual foraging effort (Fewell and Bertram 1999). Colonies are also likely to respond to resource limitation by shifting which resources they collect. Expansion across a spectrum of solitary to social systems will help test the generality of the growth constraints identified so far and provide a picture of how nutrition and behavioral responses have evolved to regulate social insect colony growth.

Nutrient inputs underlie a life-history trade-off in crickets

For my postdoctoral work, I switched from social to solitary insects to strengthen my foundation in techniques to characterize nutrient regulation and flux through major metabolic pathways. Many insect species are genetically polymorphic for dispersal capability, with flight-capable and flightless morphs co-occurring within the same population. In the wing-dimorphic cricket *Gryllus firmus*, during early adulthood, flight-capable females have metabolically active flight muscle, but postpone egg production, while flightless females have non-functional flight muscles but 200-400% larger ovaries. Thus, there is a life-history trade-off between allocation to flight versus reproduction in early adulthood. Flight muscle maintenance is accompanied by increased triglyceride production and reduced allocation of biosynthesized lipids to the ovaries. Historically, studies of the physiological mechanisms that generate this and other life-history trade-offs considered the role of food largely as a simple energetic input. Using ideas developed in the context of the Geometric Framework of nutrition, we hypothesized that intake of specific macronutrients - protein and carbohydrate – would directly affect nutrient utilization and allocation, and thus the generation and maintenance of alternate life-history strategies. Indeed, alternate morphs have distinct nutrient regulation strategies: flight-capable crickets are sensitive to nutrient balance, whereas flightless crickets only respond to food total caloric content. Food nutrient content also has direct consequences for body composition and mass gain for both morphs (C.V. Refs 6, 10), and modulates nutrient allocation, respiratory metabolism, activity patterns, lifespan, and lifetime reproductive output (Refs 10, 11, and in prep). Efforts are ongoing to link nutrient regulation strategies to specific effects on intermediary metabolism and organismal energetics, via studies employing respirometry, radio- and stable- isotope tracers, enzyme kinetics, and analytical chemistry.

Nutrient heterogeneity and life-history evolution in the field. An outstanding question remains from lab experiments: given the clear effects of diet on feeding and nutrient allocation in the lab, how does nutrient heterogeneity in the field affect cricket population structure and dispersal? Wing-dimorphism is a widespread trait in insects, but the degree to which different environmental factors contribute to its generation and maintenance is known only from a limited number of specialized cases. Given that crickets occur across a wide range of habitat types, that dispersal characteristics vary within and between species, and that crickets occupy an important trophic position in many terrestrial systems, they will be an informative group for testing ideas about the evolution of dispersal. For example, dispersal can arise either as a strategy to escape from suboptimal environments, or as a method to opportunistically move into new habitats when local environmental conditions are highly favorable. Currently, little is known about what crickets actually eat in the wild or how this affects morph determination and dispersal.

Organisms manage to thrive in environments of overabundance and scarcity, thanks to sophisticated behavioral and physiological control mechanisms. The two insect systems I study, and approaches I use, show promise for determining how multiple, interacting nutrients affect the evolved metabolic control systems used by solitary insects, and how these effects scale up to complex social systems.

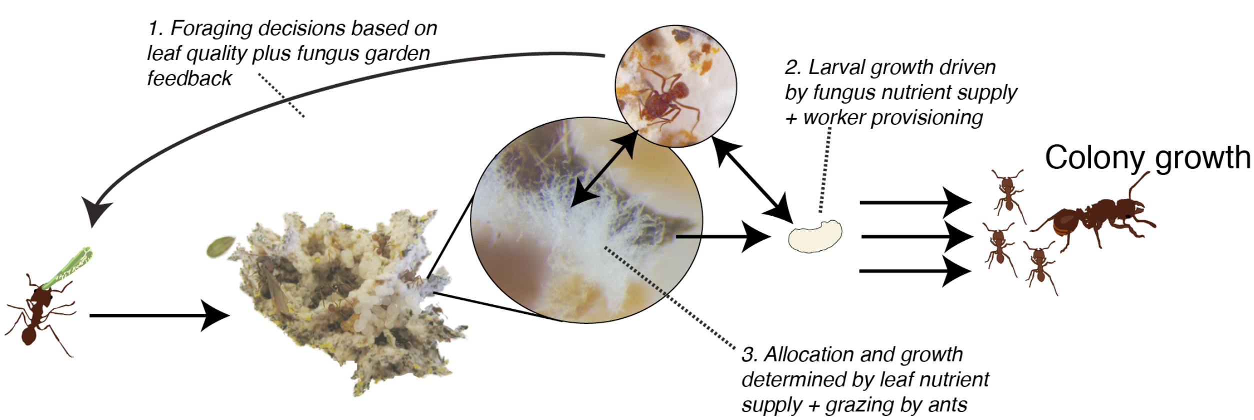

Fig. 1. Conceptual diagram outlining factors shaping colony responses to nutrient limitation in leafcutter ant colonies. In social insects, information and regulation at the individual level lead to shifts in behavior to promote survival and reproduction at the colony level.