

Metabolic 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 with metabolic control systems to shape growth and fitness across organisms, from solitary animals to complex adaptive systems. Out of myriad requirements, four nutrients that drive animal survival, growth, and reproduction are the macronutrients protein, carbohydrate, and lipid; and the element Phosphorus. Parallel approaches developed in animal nutrition and freshwater ecology indicate that organisms are sensitive to both absolute and relative amounts of these nutrients. My central aims are to determine how nutrient constraints translate into fitness consequences across different system types (solitary to eusocial insects), and to determine how constraints are counterbalanced by the behavioral and physiological control mechanisms that organisms have evolved to cope with nutrient heterogeneity. I use insects as focal organisms because they are ubiquitous, diverse, and have short generation times.

I. 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.

Establishment and 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 (Kang et al. 2011, Clark and Fewell 2014). New colonies experience high queen mortality prior to first worker emergence. However, 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 an artificial diet and lab measurement methods to demonstrate, via p, c and Phosphorus supplementation, how nutrient quality influences foraging rates, fungus performance (growth), and ant population growth and structure (Clark and Fewell, submitted). The influence of diet depends heavily on the specific type of added nutrient. It manifests either as parallel growth increases or decreases in the fungus garden and the ant population, or as changes in the ant population alone. Therefore, physiological allocation of different nutrients by the fungus affects whether or how nutrients are passed on to the ants. Nutrient addition experiments in other terrestrial trophic systems, predominantly in grasslands, also often show shifts between trophic compartments that do not match predictions from studies of nutrient limitation at the individual level. This highlights a need for functional experiments to

determine why nutrient limitation effects do not translate as expected. Within the leafcutter system, I plan to apply techniques for measuring 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 condition, and foraging decisions driven by a combination of ant-sensed leaf characteristics and feedback from the fungus garden (Fig. 1). Outcomes from this work will provide a framework for thinking about how nutrient regulation strategies have evolved across complex social systems.

Foraging behavior can be modified in multiple ways to buffer nutrient limitation. I found that leafcutter colonies respond to changes in the size of the fungus garden by both shifts in total worker activity and worker switching between tasks (in prep). The boost in total activity suggests that inactivity has 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 may also respond to resource limitation by shifting which resources they collect. Expansion across a spectrum of solitary to social systems will test the generality of the growth constraints identified so far and provide a picture of how nutrition and behavioral responses have evolved to shape social insect colony growth.

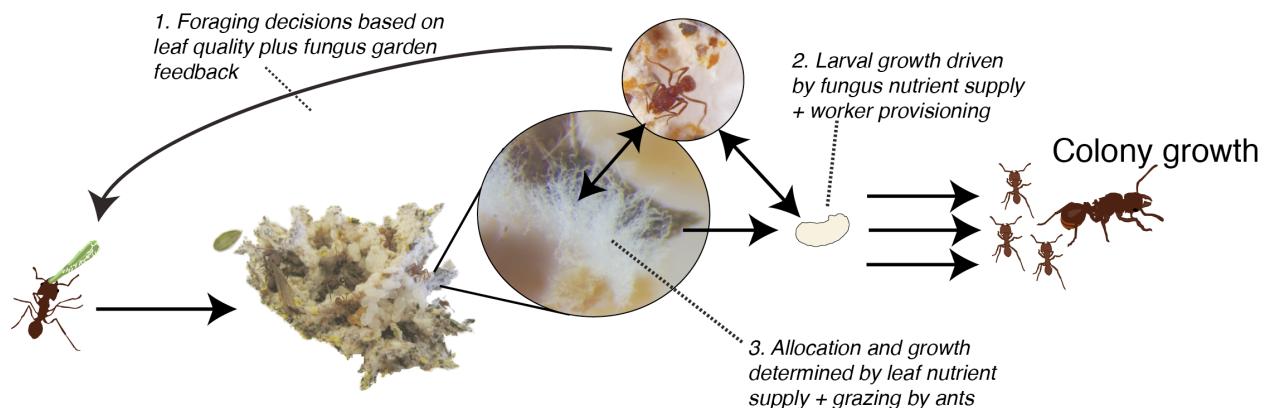


Figure 1. Conceptual diagram outlining hypothesized ways in which leafcutter ant colonies respond to nutrient limitation. In social insects, information and regulation at the individual level lead to shifts in behavior to promote survival and reproduction at the colony level.

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

For my postdoctoral work, I switched to wing-polymorphic insects to strengthen my foundation in biochemical techniques for studying the evolution of nutrient regulation and flux through metabolic pathways. Many insect species are genetically polymorphic for dispersal capability: flight-capable and flightless morphs co-occur within the same population. In wing-dimorphic crickets, 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 (Fig. 2). Thus, there is a life-history trade-off between allocation to flight versus reproduction in early adulthood. Flight muscle maintenance is accompanied by

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increased triglyceride production and limited 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 specific intake of protein and carbohydrate directly affects nutrient utilization and allocation, and thus influences the generation and maintenance of alternate life-history strategies. Indeed, the morphs have distinct nutrient regulation strategies: flight-capable crickets are very sensitive to nutrient balance, whereas flightless crickets simply eat in response to total food caloric content. Food nutrient content has direct consequences for body composition and mass gain for both morphs (Clark et al 2013; 2015), and modulates nutrient allocation, respiratory metabolism, activity patterns, lifespan, and lifetime reproductive output (Clark et al 2016; Zera et al 2016; in prep). Our subsequent efforts to link nutrient regulation strategies to effects on intermediary metabolism and organismal energetics suggest there are separate metabolic control mechanisms involved in generating the morph differences, versus generating physiological responses to food nutrient content. Improved understanding of how those control mechanisms work will have a broad impact on how we think about interactions between organisms and their nutritional environment – an important emerging topic.

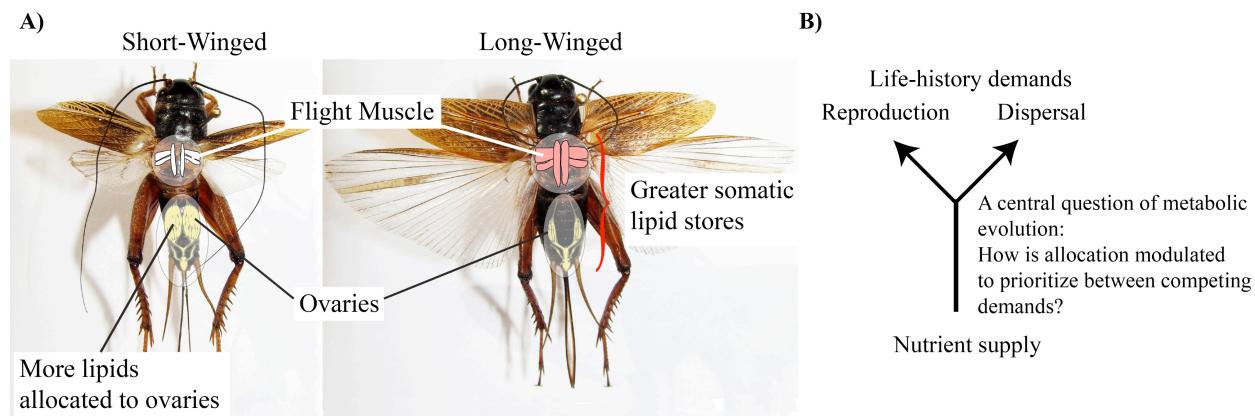


Figure 2. A) Overview of the life-history trade-off between dispersal and reproduction in wing-dimorphic crickets. B) Classical model of how life-history trade-offs result from differential allocation of limited resources to competing functions.

Nutrient heterogeneity and life-history evolution in the field. An outstanding question remains from lab findings: given the clear effects of diet composition on feeding and allocation in the lab, how does nutrient heterogeneity in the field affect animal performance, population structure, and dispersal? Wing-dimorphism is a widespread trait across insects, but the degree to which different environmental factors contribute to its generation and maintenance is known only from a few specialized cases. Given that crickets occur across a wide range of habitat types, that dispersal characteristics vary within and between species and over time, and that crickets occupy an important trophic position in many terrestrial systems, they are an informative group for testing ideas about the evolution of dispersal under changing environmental conditions. 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 environmental conditions are favorable.