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Stoichiometry Driven Patch Foraging: A Nutrient Explicit Dynamic State-Variable Model

Theoretical biologists studying foraging behavior have long ignored nutrient specific models; instead most have utilized the energetics paradigm, black-boxing the specifics of the organism's resources. The integration of nutritional ecology, ecological stoichiometry, and optimal foraging theory is an emerging area of study that may lead to significant insights in all of these areas. In this model we explore the connection between predation risk, nutrient acquisition and allocation using a dynamic state-variable model. Organisms show temporal variation in their elemental construct throughout their life times, this is because they perform different biological functions at different stages in their life history. It follows that in order to achieve these different constructs, organisms will need to alter the nutrients that they intake. How organisms obtain and allocate resources may also depend on their state, such as the individual's fat reserves, body size, or shell size.

In order to understand how a nutrient explicit approach may alter our understanding of state-dependent behavior we have constructed a model based on the life history of physid freshwater snails (*Physidae* sp.). This system allows us to separate nutrients that are used for body growth and shell growth. Snails that forage in phosphorus-rich patches achieve faster body-growth, where a snail's clutch size is dependent on their body mass. Individuals foraging in calcium-rich patches may accomplish faster shell-growth, which decreases an individual's predation risk. We use a dynamic state-variable model to see how this would affect foraging on patches with differing phosphorus to calcium ratios, and how initial body sizes, shell sizes and predation risk influence their foraging behavior and morphology over their lifetime.

Previous work in this area has shown that initial state variables can influence behavior and future state variables in two different ways. The "asset protection principle" predicts a negative feedback loop between initial states through time, where individuals with a higher reproductive value (based upon some of the state variables), would be more risk averse because they have more fitness assets built up that they could lose. Individuals with lower reproductive value are predicted to use more risky behavior because they have less to lose. The outcome over time is that individuals all converge on the similar state values. However, a second phenomenon of state-dependent predation risk can work as a positive feedback loop, where small differences in initial state result in diverging state values. The model that we put forth investigates whether integrating nutrients that affect different state-variables that perform different biological functions can produce both phenomena.