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## ON THE BROADENING OF INSECT-PLANT RESEARCH

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"When a herbivore moves onto a host plant, it gets the outside of the plant as well as what is inside." ". . . in attempting to understand the ecological and evolutionary distribution of herbivores among their host plants, it is easy to forget that what might be termed the carnivory regime [and climate regime] of a host plant individual or population are as much traits of a plant as is its chemical profile." "When we ask why a caterpillar feeds on only one particular host species, it may be as much that it is highly adapted to the predator risks and desiccation regimes of that plant as that it is adapted to the plant's internal chemistry," (Janzen 1985: 141). Such statements and sentiments are commonplace in the recent literature (e.g., ". . . how and where a herbivore feeds is undoubtedly influenced by its natural enemies," (Hawkins and Lawton 1987:790). Almost any field study of the biology of a herbivore in relatively wild circumstances quickly reveals the veracity of this view.

It is easy to forget Hairston, Smith, and Slobodkin's (1960) seminal paper on this subject because it did not separate the two core questions. (1) Why don't all the herbivores eat up all the green world? Because most of the green world is inedible to any given species of herbivore. (2) Why don't the herbivores that can readily consume a species of plant eat their host into oblivion? Because the carnivory and climate regimes stop them. They focused on the second question, leaving the first question unturned, and it has been this first question that has been the fashion of the day for the past two decades.

Bernays and Graham (1988) are quite correct to stress that the research balance needs a shift back to exploring both of the above questions. A major profitable direction will be exploring the balance between the two across a multiplicity of species and life forms. What proportion of herbivorous insect migration is driven by carnivore accumulation, seasonal climate change, and seasonal change in food availability? How much of herbivore host specificity is driven by the value of matching the colors and textures of specific backgrounds? How much of the pattern of herbivore distribution is simply ecological fitting by immigrants to

the multiple challenges of carnivores, weather, and host chemistry? The questions are almost infinite in number and characteristically involve second- and third-order interactions.

A broadening of herbivore ecology and evolutionary biology into this area will be much slower and less neat than were the two decades of chemical ecology. There is no analogue to the phytochemists that were waiting in the wings, looking for broader meaning to their research. Likewise, there is no huge body of literature, analogous to the phytochemical literature, to be mined for ideas and trends. Carnivores are much less discrete; you cannot put a carnivore regime in a bottle and send it to a co-worker for clean data. Arthropod carnivores are intrinsically of less interest to society than are plant secondary compounds, and also less familiar to the lay public. The intrapopulation and intraindividual variation in the carnivory regime of a plant species is enormous, and can never be documented with the finality of a secondary compound profile. The carnivory regime cannot be measured in vacuo, nor derived from the Latin name of the plant; that is to say, two species of *Passiflora* can easily have grossly different carnivory regimes, yet nearly identical secondary compound profiles. The carnivore regime can even less easily be brought into the laboratory and tested on a herbivore in a way that reflects usefully on the plant-herbivore interaction. Finally, as humanity degrades her few remaining natural habitats even further, the carnivore regime is far more easily degraded and altered than is the secondary compound profile of a plant species.

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