Model Systems in Behavioral Ecology

Integrating Conceptual, Theoretical, and Empirical Approaches

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3 Peeling the Onion: Symbioses between Ants and Blue Butterflies

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My first encounter with entomology was not a success. As a sophomore in college, I was attracted by a listing in the course catalog for "Terrestrial Arthropods," taught by Charles L. Remington. I knew little about insects, but I could spend hours watching a line of ants running along a sidewalk. The introductory lecture had me hooked, but then came the laboratory practical: cockroach vivisection. The cockroaches in question were not the familiar denizen of kitchen cabinets, but rather *Gromphadorhina portentosa*, the Madagascar hissing roach. True to their name, these blackish-brown insects, the size of a baby's fist, can hiss by driving air out of their spiracles when disturbed. The sound of that hissing made my hair stand on end. They had the tangy odor of warm armpits, and I found them hideous.

At that first lab, we were each expected to pick up our roach at the front of the room, take it back to our lab bench, and dissect it. I loitered at the end of the line, and when the time came, stood for a long time looking into the bin of cockroaches. The teaching assistant wasn't impressed: "Well, go ahead—just pick it up!" I made a quick lunge, but my target scuttled deftly out of my grasp, its tibial spurs rasping against my palm. That was that. The teaching assistant was by now completely exasperated. "Come on, everyone is waiting!"

I burst into tears, seized my books, and ran the entire six blocks down "Science Hill" to my dormitory. There, I discovered a note on my door telling me that I'd been accepted into a special seminar on "Personal Journalism" taught by Loudon Wainwright, a writer I greatly admired, who for many years ran a thoughtful column in the back pages of *Life* magazine. I felt I could never show my face in Terrestrial Arthropods again.

Years later, I remember proudly presenting Mr. Wainwright with my first published paper over lunch in New York: "Parasitoids as selective agents in the symbiosis between lycaenid butterfly caterpillars and ants." He was about sixty then, a big man with a bushy white beard, a little like a Santa Claus. He glanced down at the paper and gave me a wry smile: "Catchy title." I realized at that moment how far I had come from my escape into personal journalism. While cramming the title with every term I could imagine that might be useful to a computer abstracting service, I hadn't given style a moment's thought.

So I'm definitely not someone who was committed to studying insects

since childhood. I still feel slightly unsettled when confronted with large insects with hairy legs, and I am interested to observe that my three-year-old daughters switch from delight to horror if I place a live swallowtail butterfly on my hand and show them its black legs.

However, I developed a passion for butterflies when I returned to Terrestrial Arthropods a year after my disgrace, and it's a passion that has held me ever since. I can no longer step outdoors without finding myself straining to catch a glimpse of that elusive flutter of wings. Part of their appeal is aesthetic, but butterflies offer more than that. As another of my undergraduate professors, G. Evelyn Hutchinson, once explained to me in an offhand remark, "The wings of a butterfly are the only place where the laws of evolution are printed in color on a single page." I have never overcome my dislike of killing them, but there are few activities I prefer to chasing and observing butterflies. I have surprisingly frequent dreams of discovering new species with intricate and impossible wing patterns, or migrating with flocks of metallic blue *Morphos*.

I have reviewed more technical aspects of my research elsewhere (Pierce 1987, 1989; Pierce et al. 1991; Pierce & Nash 1999). Here I focus on how I first came to study ants and butterflies in the family Lycaenidae, and on some of my early experiences as an experimental field ecologist. I try to explain how each new finding contributed to or extended our conceptual understanding of ecology and evolution. I describe reasons why lycaenids, their attendant ants, host plants, and natural enemies have proved to be a model for the study of insect/plant interactions, chemical communication, mutualism, biodiversity, conservation, and the evolution of complex life history traits. Where possible, I delineate the features that I continue to find intriguing about the natural history of the system, and how they might be valuable in addressing further questions about adaptation and evolution.

Choosing a System

I wanted to do my Ph.D. on insect/plant interactions. I was impressed by Paul Ehrlich and Peter Raven's proposal that butterflies and their host plants coevolved, and that this process of coevolution had, in fact, shaped most of organic life as we know it (Ehrlich & Raven 1964). However, when I started my degree at Harvard, two of the three entomologists in the department, E. O. Wilson and Bert Holldobler, specialized in ants. At that time, Wilson had just published *Sociobiology*, and the evolution of intraspecific cooperation, particularly the origin of altruistic behavior, was a topic of intense discussion among my fellow students. Bob Trivers was still at Harvard, and W. D. Hamilton was spending the year there as a distinguished visitor. I remember meeting Hamilton at the Estabrook Woods near Concord, Massachusetts, where he had been digging insects out of rotting wood, and with a

glint in his eyes, held out both hands dripping with brown slime toward me. "Forgive me if I do not shake your hand," he said softly.

My choice of a thesis topic was motivated then by a combination of passion and pragmatism. Although everything about ants and the evolution of complex social behavior was fascinating, I couldn't shake my initial inclination toward butterflies. This was only semirational: I can't explain why butterflies seem so much more captivating than anything else, but the fact remains that they do. I recognized early on that it was important to select a topic that would sustain my interest long enough to be able to complete a dissertation.

After graduating from college, I had received a year-long traveling fellowship to Australia to visit Ian Common's laboratory at the Commonwealth Scientific Industrial Research Organization (CSIRO) in Canberra, where Charles Remington was then on sabbatical. A friend that I made at CSIRO, Roger Kitching, had told me about a family of butterflies whose caterpillars associated with ants. This seemed to present a unique opportunity to combine all of my developing interests in a single system. I was fortunate to be supported on both fronts: Robert Silberglied and Bert Holldobler were my thesis advisors at Harvard. Silberglied was immensely knowledgeable about all things involving Lepidoptera, and Holldobler had pioneered the study of "myrmecophilous" interactions, analyzing the relationship between staphylinid beetles and the ants whose nests they inhabit (Holldobler 1971).

As I have at almost every critical juncture in my professional life, I wrote to Charles Remington to seek his advice, this time about the feasibility of studying ant-associated butterflies in the Lycaenidae for my dissertation. He replied straight away to say that there were several suitable species to be found near the Rocky Mountain Biological Laboratory in Colorado, not far from where I grew up. This convinced me, and I wrote a proposal to study the evolution of interspecific cooperation between caterpillars of the family Lycaenidae and ants. My initial approach to this problem was not so much why as how: I was interested in the mechanisms involved in initiating and maintaining interspecific interactions, including the signals involved in interspecies communication. This provided an accessible entry point into a complex system.

I had the problem in mind, but I had yet to see the actual insects involved. I headed out to Colorado. I still didn't have a driver's license, partly because I rarely had access to a car. I had lived away from home since I was thirteen, and the general expense was more than my family or I could afford while I was in college. However, my father, a geologist who enjoys any kind of field expedition, drove me over to Red Rocks Park, where we had had some success collecting butterflies with a graduate student from Yale, Bob Pyle, and a high school student named Mark Epstein on a Fourth of July butterfly count. I found my first lycaenid caterpillar feeding on alfalfa beside the parking lot of Red Rock's gigantic outdoor amphitheater. I knew what it was

the moment I saw it, and I can feel that thrill of recognition even today. It was a late instar of *Plebejus melissa,* the Orange-Margined Blue, feeding on flowers, and it was being assiduously tended by several small black ants.

Shortly afterwards, I moved up to the Rocky Mountain Biological Laboratory (RMBL) just outside Crested Butte to find a system that I could study for my thesis. My inability to drive became a serious liability, but fortunately, the youngest son of family friends, Paul Mead, had just graduated from high school and was willing to join me as a field assistant for the summer, along with his truck.

At RMBL, it was my great fortune to be taken under the wing, figuratively and almost literally, of an expert on lycaenid butterflies, Paul Ehrlich. During my first few days at the Lab, he took Paul Mead and me flying in his small plane over a number of field sites that hosted populations of *Glaucopsyche lygdamus,* the Silvery Blue. The caterpillars of this species were tended by numerous species of ants, and Ehrlich and his students had analyzed the relationship between the butterflies and their host plants, several different species of lupine (Breedlove & Ehrlich 1968; Dolinger et al. 1973). Ehrlich then drove us to some of the best localities, and essentially laid the groundwork for our summer's research. Another ecologist interested in coevolution, John Downey, had made the first intensive study of the ant associates of another lupine-feeding lycaenid several years earlier, and he also provided invaluable information about the behavior of the ants and caterpillars. He put me in touch with R. E. Gregg, who painstakingly helped me identify the attendant ants.

Cost/Benefit Analysis of a Mutualism

From the outset, I had decided to do a cost/benefit analysis of the association between *G. lygdamus* and its attendant ants. However, my initial approach focused entirely on the butterflies. While at first it seemed obvious that the caterpillars were providing food for ants through secretions from specialized glands, it was less clear what the ants were doing for the caterpillars. Earlier work suggested that the caterpillars benefited primarily because ants did not attack them; normally, ants are serious predators for lepidopteran larvae. However, it also seemed possible that attendant ants were more than just appeased, that they actually protected the lycaenids from their enemies.

After several messy attempts, Paul and I settled on using sticky barricades made from a viscous, gooey substance called Tanglefoot © to exclude ants from tending caterpillars in the field. We compared untended caterpillar survivorship with that of tended counterparts. Such "ant exclusion" experiments are standard fare in ecology field courses today, but we were among the first to apply these techniques to a large sample of plants under field conditions. I owe the suggestion of this approach to Bob Robbins, now at the Smith-

sonian, who gave me a number of helpful ideas early in my graduate work. In experiments at three field sites over two years, we found that ant-tended caterpillars of *G. lygdamus* were four to twelve times more likely to survive to pupation than their untended counterparts (Pierce & Mead 1981; Pierce & Easteal 1984). The ants were primarily effective against a suite of parasitoids that attacked the larvae and pupae. Paul and I were thrilled and more than a little bit amazed when our paper describing this result, with its dismally uncatchy title, was accepted for publication in *Science* in 1981. In his book, *Curious Naturalists*, Niko Tinbergen argued that the most important thing a young scientist can do is to gather data, because the data helps establish self-confidence, and this was certainly my experience.

In the meantime, however, I had also learned some of the disadvantages of working with this system. *G. lygdamus* had only one brood a year, and population numbers could vary dramatically from one year to the next. We tried to augment our experimental possibilities by studying two populations that occurred at different altitudes: one near Gunnison, Colorado, became active at least a month earlier than the one near Crested Butte, and this meant that we could conduct two sets of field experiments in one season. However, the fluctuation in numbers, while interesting, presented difficulties for someone working on the time frame of a Ph.D. For example, in the summer of 1982, my collaborator from Australia, Roger Kitching, came out to Crested Butte for the field season, and we recall seeing exactly three individuals the entire summer. This extreme fluctuation was not unusual: Ehrlich and his colleagues had previously documented the extinction of the population near Crested Butte (Ehrlich et al. 1972).

Moreover, we were never able to induce males and females of *G. lygdamus* to mate with each other, and this clearly restricted the kinds of experiments we could do. Larger butterfly species can often be hand-paired, but small and delicate Lycaenidae are usually not so obliging. The host plants, perennial species of lupines, also presented difficulties. We could not easily pot them and move them around the habitat.

A Tractable Experimental System

By working as a teaching assistant in one or two courses every semester, and acting as a tutor in one of the residential houses on campus, I finally saved enough money for a return visit to Australia in December 1979. Roger Kitching had moved from CSIRO to Griffith University in Brisbane, where he had started to study another species of lycaenid whose caterpillars associate with ants (Kitching 1976, 1983). In contrast to the North American lycaenids I had become familiar with, whose caterpillars were tended only intermittently by many species of ants, the caterpillars of *Jalmenus evagoras* are constantly tended, and specifically by only a few species of ants in the

genus *Iridomyrmex*. One of Roger's students, Martin Taylor, had a small culture of these butterflies in a field house on the roof of Griffith's School of Australian Environmental Studies. I could hardly believe my eyes. Instead of the single, slug-like caterpillar gingerly caressed by half a dozen eager ants to which I was accustomed, here were clusters of spiny black caterpillars and pupae, seething with so many ants that it was difficult to distinguish them beneath the moving layer of legs, bodies, and antennae.

Martin and a friend, Mark Elgar, then took me to Mount Nebo, a location just outside Brisbane, to see the butterflies in the field. The road, now so familiar, is nauseatingly winding, and my car-sick stomach spent much of the journey telling me that this was not the place for a long-term study. By the time we reached the field sites, I made a headlong scramble out of the car to keep from throwing up all over my colleagues. Despite this inauspicious introduction, my relationship with *J. evagoras* was love at first sight.

As at RMBL, I was again fortunate to be befriended at Mount Nebo by an invaluable ally. Charmaine Lickliter had built her own house and lived "on the mountain" for many years. She knew everything about self-reliance. She showed me how to design a gravity-feed toilet (useful if the electricity is cut), raised all her own food and flowers, and recounted fascinating outback lore such as the uses of emu oil and how it could slip out of glass containers. Her back yard was a haven for kookaburras, cockatoos, and shy little wallabies called paddymelons. She acted as though it was perfectly normal for a single woman who couldn't even drive (I finally learned the first summer there) to spend the year living in a large, upside-down watering tank while studying the behavior of butterflies and ants. She helped me in countless ways over the years, even providing her own paddock as a breeding ground for the butterflies. She never seemed to tire of daily accounts of insect happenings, and her support and friendship made an intangible but enormous difference to my ability to do fieldwork there every summer for the next ten years.

In contrast to *G. lygdamus*, *J. evagoras* afforded a marvelously tractable system. Host plants and ants are easily cultured in the laboratory, designated butterfly matings are not difficult to achieve, and the species overwinters in the egg stage. This means that eggs can be transported in small vials, stored in a cold room, and brought out of diapause when host plants and ants are readily available. All stages aggregate, which makes them easier to find and introduces some interesting complications to their ecology and evolution. Moreover, rather than crawling off into the leaf litter to pupate in hidden locations, the full-grown caterpillars of *J. evagoras* pupate in the open, like clusters of grapes lined up along the stems of their *Acacia* host plants. Pupae are tended by ants, and this has been a helpful feature in studying the relationship between *J. evagoras* and its associated ants. For example, to learn more about the chemicals involved in attracting ants, we can take surface washings from pupae that cannot regurgitate or defecate in the process.

Moreover, because individuals pupate in locations that are highly visible to us as well as to potential mates, it has been possible to analyze their mating behavior with the kind of detail seldom possible in field studies of an insect.

Lycaenids, Ants, and Their Host Plants

Research on lycaenid/ant associations led me back in a somewhat unexpected way to my original interest in insect/plant interactions, and more specifically to butterfly/plant coevolution. One of the most striking findings from our work on *J. evagoras* and its associated ants started with the observation that caterpillars secret amino acids, the building blocks of proteins, as well as simple sugars as rewards for attendant ants (Pierce et al. 1987; Pierce 1985, 1989). It seemed likely that these amino acids and the nitrogen they contained played a central role in the currency of exchange between these mutualistic partners (Pierce 1989; Baylis & Pierce 1993; Pierce & Nash 1999). The growth rate of colonies allowed to forage on caterpillar secretions far exceeded that of their counterparts raised without access to these secretions (Nash 1989; Pierce & Nash 1999). Moreover, caterpillars raised on plants that had been enriched through the application of fertilizer attracted more ants and survived longer than their counterparts on plants that had not received treatment. Laboratory analysis confirmed that the foliage of these fertilized plants had a higher content of nitrogen, phosphorous, and other minerals, and female butterflies preferred to lay eggs on these high-quality plants (Baylis & Pierce 1991).

In their paper on coevolution, Ehrlich and Raven mentioned more than once that "in the Lycaenidae, ants . . . may further modify patterns of food plant choice" (p. 588), and their prediction proved to be true. Moreover, it helped to account for some of the diversity of host plant use exhibited by the Lycaenidae, much of which appeared to be unexplained by their central paradigm, which rested upon the importance of plant secondary chemistry in governing the relationships between butterflies and their host plants. They emphasized that toxic secondary metabolites could exclude competition from other herbivores and potentially provide both attractants and a means of defense for butterflies that could detoxify and/or sequester them; the butterflies could then radiate in this new adaptive zone.

Our findings suggested that in the Lycaenidae, host plant chemistry could also play a role in mediating the "enemy free space" surrounding a caterpillar (e.g., Atsatt 1981). In this case, however, it is the nutritional quality of the host plant that is critical in determining a caterpillar's ability to maintain its defense force. By feeding on plants that are sufficiently rich in protein, the caterpillar can satisfy not only its own needs, but also those of its attendant ants. If this premise is true, one might expect Lycaenidae that reward ants with amino acid secretions to feed only on plants or plant parts that are

also rich in proteins. Indeed, the Lycaenidae are well-known as a group for their predilection for nitrogen-rich parts of plants, including terminal foliage, flower, and seed pods (Mattson 1980). Furthermore, a survey of a great number of species, each scored for its degree of ant association and its choice of host plant, revealed a striking association between being tended by ants and feeding on legumes (Pierce 1985; Fiedler 1991, 1995). Not only are legumes rich in nitrogen (one reason why beans are considered nutritious), but unlike most other kinds of plants, legumes have symbiotic bacteria in their roots that can fix atmospheric nitrogen. Thus one might expect them to vary less over evolutionary time in their composition of nitrogen compared with other plants.

However, the general significance of the strong correlation between ant association and legume feeding is still unresolved. It is possible that the association of these two traits in the Lycaenidae might simply be the result of historical accident. For example, if a proto-lycaenid fed on legumes and also happened to be ant-associated, the descendants of this lycaenid might be legume-feeding and ant-associated without this correlation having a particular functional significance. However, if one could show that legume feeding and ant association had evolved together in a number of independent instances, it would provide support for the hypothesis that these two characteristics are in fact functionally linked. Our limited knowledge of the evolutionary history of the Lycaenidae has made it hard to assess how many times ant association and legume feeding have evolved together.

Partly as a consequence, members of my laboratory and I have been working toward estimating the phylogeny of the Lycaenidae using molecular characters (e.g., Braverman 1989; Blair 1995; Mignault 1996; Taylor et al. 1993; Campbell 1998; Campbell et al. 2000; Rand et al., in press). The foundation for this task was laid by Colonel John Eliot. In 1973, he published a classification of the family based on morphological characters, delineating the major groups and suggesting their historical relationships. In sampling our taxa, this work has been invaluable, and I have been impressed and humbled by his careful and insightful analysis.

degree of fine-tuning involved in meting out this cost is impressive: caterpillars even modify the amount of secretion they produce per capita depending upon their social context. When they are in groups, they are able to maintain a threshold level of ant guard at a lower cost, and they therefore secrete correspondingly fewer droplets per capita as rewards for ants (Axén & Pierce 1998).

The significant cost to the caterpillars of cooperating with ants is interesting because selection should favor any participant in the interaction that can still reap the benefits at a minimum cost. For example, if the chemicals necessary to fool ants into tending caterpillars are cheaper to produce than nutritious rewards, selection should favor parasitism of ants by lycaenids rather than the mutualism observed in this system.

This switch from mutualism to parasitism has evolved repeatedly in the Lycaenidae (Cottrell 1984; Pierce 1995). For example, species in at least two genera, *Maculinea* and *Lepidochrysops*, are "phytopredaceous." Caterpillars spend their early instars feeding on plants, and then drop to the ground, where they are picked up by workers of their host ant species and carried into the brood chamber of the nest. Here, chemically camouflaged and undetected by the adult ants, they consume the helpless brood. The caterpillars of other Lycaenidae, such as the species of the Australian genus *Acrodipsas*, never go through a plant-eating stage, but spend their entire lives consuming ants. In an even more sophisticated twist on this theme, some lycaenids, such as the Japanese species *Niphanda fusca*, enter the ant nest, but have mastered the signals made by brood to elicit regurgitations from adult ants. These "cuckoo" species are fed entirely on ant regurgitations through a process called trophallaxis.

Convergent origins of parasitism, including both carnivorous and cuckoo-like behaviors, are exhibited by individual species in a number of genera whose other members are all plant-eating and apparently mutualistic. These include representatives from *Spindasis, Ogyris, Arhopala,* and *Chrysoritis* (Pierce 1995). The reverse relationship, that of mutualism arising from parasitism in these myrmecophilous relationships, has yet to be documented.

Life History Evolution: Parasitism Arising from Mutualism

Another key finding from research on *J. evagoras* and its ant associates was the demonstration that the caterpillars pay a dramatic metabolic cost for maintaining an ant guard (Pierce et al. 1987; Baylis & Pierce 1992). Larvae raised in the greenhouse without attendant ants pupate at a much larger size than their tended counterparts, and these pupae become larger adults. Since size is correlated with fecundity in females (Hill & Pierce 1989), and lifetime mating success in males (Elgar & Pierce 1988; Hughes et al. 2000), ant association therefore represents a significant cost for these butterflies. The

Species-Specificity and Chemical Communication

The species-specific relationship between certain species of Lycaenidae and ants parallels the host plant specialization exhibited by many species of phytophagous insects. Research to date has only scratched the surface of possible mechanisms involved. How do ants recognize the lycaenids with which they associate, and vice versa? And just as the evolution of host plant specialization in phytophagous insects remains a conundrum, a satisfying evolutionary explanation for why some lycaenids are allied with only a single species of ant whereas others are generalists is likewise unknown.

Given the importance of ants for their survival, it seemed reasonable that females of *J. evagoras* might use ants as cues in finding suitable host plants upon which to lay eggs. Nevertheless, I was surprised when our experiments showed that females not only use attendant ants as cues in laying eggs, but can tell the difference between different species (Pierce & Elgar 1995; Pierce & Nash 1999). I was even more astonished when my student, Ann Fraser, and a postdoctoral associate, Tom Tregenza, recently showed that females can tell the difference between various populations of attendant ants, and are more likely to lay eggs on plants containing workers from their natal populations (Fraser 1997 and unpublished results). How females distinguish between different populations, and the possible selective advantages of such fine-tuned behavior, remain to be determined.

Another open area for research on species-specificity is the biochemistry of the signals involved in ant/caterpillar recognition. The lycaenids that are tended by ants secrete substances that appease ants and gain favorable recognition. In the case of species-specific interactions, these signals would appear to be highly specialized. A pairwise analysis of the surface secretions of a suite of lycaenid caterpillars and their respective ant associates could provide considerable insight into the signals used by ants in species-specific recognition, and possibly in brood recognition (Pierce 1989). Many lycaenids, including *J. evagoras*, also stridulate to attract attendant ants, and these interspecific acoustical signals may contribute significantly to the fine-tuning of their interactions (Travassos & Pierce, in press).

Since all known attendant ants species have alternative food sources, it seems unlikely that there has been any kind of "coevolution" between ants and lycaenids in the Ehrlich/Raven sense of the term. However, some of our work on the phylogeny of different genera with species-specific ant associations has indicated strong conservatism on the part of the lycaenids for ants within a particular subfamily (Pierce & Nash 1999 and unpublished results). It would appear that once a relationship has been established, speciation is more likely to occur within the association than outside. In other words, ant-associated taxa tend to have ant-associated sister groups, and sister groups tend to be associated with related ant species. Perhaps this is because the numerous complex behaviors and biochemical mechanisms necessary to achieve specificity in the first place influence the evolutionary trajectory of a particular lineage. In this respect, the ant fauna might be considered a template against which the lycaenids have diversified.

Biogeography

I was struck by the qualitative difference between the *Jalmenus*/ant relationship and the *Glaucopsyche*/ant relationship. These species may reasonably be regarded as representative of their respective continents, although they are

both on the high end of their respective ant-associated spectra. Lycaenids such as *J. evagoras*, have been described as "obligately" ant-associated, in the sense that caterpillars and pupae are never found without ants, and their survivorship is negligible if attendant ants are experimentally excluded. Their relationship also involves a high degree of specificity: while juveniles of *J. evagoras* are known to associate with several species of ants, all are in the genus *Iridomyrmex*. Other species of Lycaenidae in Australia exhibit even greater specificity. For example, *Hypochrysops ignita* has been observed feeding on seventeen different host plant families, yet the larvae are tended by only one species of ant, *Papyrius* sp. (*nitidus* group). At one of our field sites in Australia, *J. evagoras* and two of its close relatives, *J. ictinus* and *J. daemeli*, all co-occur on the same host plant species, brigalow (*A. harpophylla*). However, each associates exclusively with its own species of attendant ants.

This kind of obligate ant association, frequently combined with species-specificity and ant-dependent oviposition, is essentially unknown among North American taxa, and uncommon in the Palearctic. However, more than a third of the myrmecophilous Lycaenidae in Australia have obligate associations with ants, and such associations are likewise well-developed in South Africa. The records available from India, while sketchy, hint at a number of strongly ant-associated taxa. This distribution of ant-associated Lycaenidae led me to speculate about whether it might have been generated by a Gondwanaland-Laurasia split in ant-associated and non-ant-associated lineages (Pierce 1987). For this pattern to be explained by such a faunal split, the evolutionary history of the Lycaenidae would also have to reflect this division, and the pattern of ant association should track it.

Ideally, to investigate this pattern further, we would want to conduct a detailed analysis of phylogeny, ant association, and biogeographic distribution for each clade within the Lycaenidae. Our understanding of the phylogeny of the Lycaenidae is still too limited to permit such a detailed analysis. However, only one of the thirty-three tribes of Lycaenidae recognized by Eliot (1973) is unique to the Holarctic, and all others have representatives in biogeographic regions derived from both Gondwanaland and Laurasia. Thus a simple phylogenetic explanation—in this case, two main lineages, one obligately ant-associated and the other not, one Gondwanan and the other Laurasian—is not tenable. In addition, current ideas about the origin of butterflies suggest that the Gondwanan/Laurasian split occurred before the diversification of the lycaenids. Nevertheless, the pattern may well reflect biogeographic history if the lycaenids have responded to an ancient dichotomy in critical aspects of their biology such as the distribution of host plants (*Acacia*, for example) or attendant ants.

The biogeographic distribution of highly ant-associated Lycaenidae remains a truly fascinating pattern that begs explanation. After all, the preponderance of obligately ant-associated lycaenids in Australia and South Africa

is not the result of a distinctive biogeographic distribution of a single taxon. It reflects the distribution of a suite of species interactions, including obligate ant associations (both parasitic and mutualistic ones), host plant affiliations, and selection pressures exerted by parasitoids and predators.

Ant Association and Its Evolutionary Consequences: Speciation and Extinction

Ant association has an important impact on the demography of lycaenids such as *J. evagoras*. Both larvae and pupae require appropriate species of attendant ants as well as suitable host plants in order to survive. Their populations are often small, localized, and patchily distributed (Smiley et al. 1988; Taylor et al. 1993; Costa et al. 1996). As a result, lycaenids are likely candidates for a peripheral isolate model of speciation, whereby evolutionary change is concentrated in small, marginal, isolated, or semi-isolated populations.

Such a propensity for speciation may in turn lead to amplified rates of diversification. However, small population sizes may also contribute to the negative component of the evolutionary demographic, extinction. Many species of Lycaenidae are recognized as endangered, and these taxa have frequently featured as emblems for conservation biology. Examples include the Large Blue in the United Kingdom, the Arionides Blue in Japan, the Karner Blue and Xerces Blue in the United States, the Brenton Blue in South Africa, and Illidge's Blue in Australia. As our research has indicated, highly specialized lycaenids such as these are likely to be more sensitive to environmental perturbations because their life histories are so complex. Moreover, both theory and observation have shown that small, inbred populations are prone to extinction (Saccheri et al. 1998). Lycaenid butterflies and ants may therefore provide a model not only for understanding mechanisms generating diversity, but processes leading to the loss of diversity.

Final Thoughts on Finding a System and an Approach

I doubt I would have continued to study lycaenids if their interactions hadn't proved to be so multidimensional. I never set out to study or establish a model system; the work just progressed. My interests were simple to start with—an assessment of the costs and benefits of the interaction for each partner of a putative mutualism. Exploration itself was part of the goal, and each new peel of the onion revealed a fresh and equally fascinating layer. In particular, I gained an appreciation for the different levels at which this and all other natural systems can be analyzed. And to a greater extent than I

would have ever anticipated, I learned that a detailed understanding of natural history and behavior is essential in considering broader issues. One of my postdoctoral advisors, Dick Southwood, exhorted students to "Know thy barnacles!" with reference to Darwin's classic study. By this he meant that a deep knowledge of a particular group of organisms assists enormously in providing a general understanding of the principles of ecology and evolution.

Model systems usually have a suite of desirable traits, depending on the questions they are used to explore. A geneticist might favor organisms that have a small genome size and fast generation time, and afford the possibility of manipulating the genetic background. A behavioral ecologist might favor organisms with complex interactions and close relatives exhibiting diverse life histories. In both cases, experimental tractability can be critical. For a behavioral ecologist, it usually helps to study organisms where individuals and/or units of selection can easily be identified, especially when trying to measure something as elusive as lifetime reproductive success.

My students and I have discussed whether it might be better to start with a systematic and phylogenetic framework for a particular group before working on specific aspects of behavioral ecology. My own development took the reverse approach: I was drawn to studying life history evolution through my interest in lycaenid behavioral ecology. But because history counts so much in understanding biological systems, I have wondered at times whether it wouldn't have been better to have started by building the structure upon which to hang the questions. This would argue for systematics first.

However, such logic ignores one thing: the importance of a passionate interest. For myself, I would always advocate setting sails with the subject closest to the heart before spending time collecting navigational charts. It was my field experience with living animals that informed the kinds of questions I wanted to ask about their evolutionary history. Without that initial inspiration, I might not have persisted, especially in difficult times. And it was the many forms of support from friends, family, and colleagues that helped me develop ideas, deepen my interest, and in many cases, simply do the work. I still rely on good friends, and reveries of caterpillars seething with ants and butterflies winking on and off in the Australian bush to get me through another faculty meeting and another Massachusetts winter.

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