13. BUTTERFLY–ANT MUTUALISMS

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INTRODUCTION

At some stage in every elementary biology course the idea of interaction between species is introduced. This is sometimes accompanied by a chart consisting of a 3×3 matrix labelled with two mythical entities, 'species A' and 'species B'. The matrix is composed of pluses, minuses and zeros: 00 is the trivial case in which there is no interaction; $+-$ (or $-+$) denotes parasitism or predation; $--$ signifies competition, and -0 (or $0-$), interference; $+0$ (or $0+$) indicates commensalism; and $++$ is mutualism. The category 00 is invoked rather more often than is probably justified. If one is not interested in interaction *per se*, the temptation is strong to treat one's organism in isolation. This, almost without exception, is misleading. A hypothetical 100-year-old ecologist, who joined this Society in the year of its founding and who would be duly honoured at an anniversary meeting such as this one, would immediately understand why. He would have witnessed the development of ecology from glorified natural history to a major scientific discipline and would be fully aware that a feature of the evolution of ecology has been an increasing recognition that the natural world is complex, and that food webs are intricate networks. Research into $+-$ interactions has been a popular study area ever since the fundamentals of ecological theory were formulated in the early days of the discipline. Competition $(--)$ and interference (-0) have not been lagging far behind: again, many of the most far-reaching results in early ecology, both theoretical and empirical, directly addressed these issues, especially competition.

So what of $++$ and $+0$? Our old man (his sex is assumed on the basis of the make-up of the founding membership of this Society) will remember little emphasis on these topics throughout his career as an ecologist. Mutualism $(++)$ is here taken simply to denote an interaction in which the fitness of each party is increased by the action of its partner. There has, however, been a flurry of theoretical interest in mutualism over the past decade or so (see Boucher 1985), and this stimulated development of models of the population dynamics of mutualists (May 1981; Addicott 1984; Wolin 1985; Pierce & Young 1986; reviewed in

Boucher, James & Keeler 1982) and of their evolution (e.g. Trivers 1971; Roughgarden 1975; Wilson 1980; Axelrod & Hamilton 1981; Keeler 1981, 1985; Maynard Smith 1982; Axelrod 1984; Vandermeer 1984; Law 1985; Templeton & Gilbert 1985). Commensalism (+0) has yet to generate an extensive literature of its own, perhaps because it is rather uninteresting: after all, effectively only one party is doing the interacting.

The reasons why mutualism has attracted so much theoretical interest lie, I believe, primarily with the emergence of social biology. Altruistic social interactions that appear to contradict the central survival-of-the-fittest dogma of a Darwinian theory of evolution with its emphasis on the fitness of the *individual* have always been an enigma to evolutionary biologists. It was only with the work set in motion by Hamilton (1964) that we have been able to feel comfortable in an established evolutionary framework with such social 'anomalies'. However, kin selection arguments necessarily only apply within species; alternative models to explain the evolution of co-operation between species have been necessary (Trivers 1971; Axelrod & Hamilton 1981). In fact, interspecific mutualism provides us with the ideal opportunity to explore such proposed mechanisms of social evolution as reciprocal altruism, in the absence of the complicating factor of kin selection. Only recently (May 1981) have refinements to standard Lotka–Volterra models made possible the mathematical description of mutualistic systems (see Addicott 1984 for a discussion).

From an empirical point of view, mutualism is amenable to study for a number of reasons. First, it is common. With the exception of pollination syndromes, the phenomenon may not be as obvious as predation, but mutualism, it is becoming apparent, is a major evolutionary theme: from mycorrhizal fungi associated with plant roots to microorganisms in the guts of termites. The extent of mutualism in nature will not, I think, be fully realized until we have a more complete understanding of microbial ecology. Second, the strength of these associations is highly variable: many occasionally ant-tended aphid species survive well in the absence of ants, while neither the termite nor its gut microorganisms can survive independently when forcibly parted. This range of relationship, from loosely facultative to strictly obligate, gives us a corresponding range of systems suitable for different kinds of experimental approach. If a given group displays a trend in the strength of its mutualism, then it may be possible through the use of comparative studies to identify those ecological correlates that have been critical in driving its evolution. Third, because mutualists are often highly depen-

dent upon each other, it is likely that the selective forces shaping the association are strong and therefore *identifiable*. It is possible to recognize key components of an organism's biology simply by elucidating what costs and benefits it experiences from associating with its partner. Thus, in the case of the aphid–ant relationship, we can surmise that defence from predators and parasites is a significant evolutionary 'problem' for the aphid. Fourth, although a mutualism is, by definition, two-sided, there exist, in many cases, asymmetries between the two parties involved. For instance, for some lycaenid butterfly species the presence of tending ants is imperative if the larvae are to survive while the ants, although they benefit nutritionally from the lycaenid larvae, can survive in their absence. This facilitates experimental manipulations because ant exclusion results only in the extinction of the butterflies, permitting quantification of ant performance in the absence of the mutualist. Assuming a hypothetical situation in which the asymmetry was reversed so that the ants could not survive without the butterflies, it would be possible to reconstruct the 'other side of the story', thereby completing an overall picture. Finally, it is worth adding that the output of evolutionary and ecological theoreticians in the form of testable predictions and models is in itself major incentive for empiricists to study mutualism.

A conceptual framework for studies of mutualism has only recently been available. Such a framework is necessary because mutualisms are necessarily complex: co-operation invariably entails exchange and communication, both of which are likely to confound simple analysis. This complexity does not stop at the straightforward level of the relationship between the two parties involved, but other, extrinsic, factors also intrude. A study of the termite–micro-organism mutualism should go beyond a mere analysis of the actual relationship and include, for example, the impact of the termite's diet on the 'ecology' of the protozoa. Thus a study of mutualism must usually entail the kind of multi-dimensional exercise envisioned by Price *et al.* (1980) in their model of interaction among three trophic levels, or Janzen (1985) in his discussion of diffuse effects of mutualism. It is important to recognize that trade between the two participants generally does *not* involve the transfer of a common currency. Thus, while ants derive nutrition from their aphid mutualists, the reward to the aphids is protection from natural enemies — the life/dinner principle for mutualists. It is extremely difficult to compare, on a simple cost–benefit basis, the relative contribution of each species to the other's fitness. Although a number of studies of mutualism have discussed this problem (for example Schemske

1983; Addicott 1986), I know of none that has satisfactorily quantified the costs and benefits to each party in terms of each one's reproductive success.

Lycaenid butterflies and their attendant ants exemplify all these advantages and disadvantages, as will become clear in what follows. They have, however, some special features which, to my mind, make them especially suitable for studies of mutualism. Even within a single butterfly genus, the types of association can be quite varied. Species may be completely untended; they may have the ability to deter ants from attacking them without actually being tended; they may be loosely facultative in being tended only occasionally by a number of different ant species; or they may be obligately tended by members of a single species of ant. Various permutations of these categories also exist. Lycaenids are particularly amendable to large-scale comparative analysis because, as butterflies, they have traditionally attracted the attention of naturalists, which means that extensive records of their natural histories exist. For the same reasons, they have, unlike many groups of insects (including, unfortunately, the ants), been reasonably well classified, although debate still exists concerning the placement of the riodinids, which I here include in my discussion with the cautionary note that they might yet prove to be a separate family (Eliot 1973). It is also possible to culture many of the relevant species of both ants and butterflies in the laboratory, permitting the kind of carefully controlled experimental manipulation that I consider to be an essential complement to field studies.

What follows is an account of my work on such a lycaenid–ant mutualism, that of *Jalmenus evagoras*, a lycaenid ranging from the temperate south of Australia to subtropical regions just north of Brisbane, and its main attendant ant species, *Iridomyrmex anceps*. Although I am not entirely sure that the methods that I will describe together constitute the correct prescription for 'an exact ecology', my collaborators and I have, by means of a combination of experimental, comparative and biochemical techniques, been able to build up a reasonable picture of the dynamics of this mutualism. We have attempted to import the essential elements of the field into the laboratory, and we have employed a number of laboratory-style manipulations of the system in the field. My intention was first to identify costs and benefits of the association, and second to provide a qualitative sense of the direction and magnitude of those costs and benefits through the use of quantitative techniques.

NATURAL HISTORY

The Australian genus *Jalmenus* contains at least nine species whose larvae associate with dolechoderine ants (Common & Waterhouse 1981). One of the these species, *Jalmenus evagoras*, has been the focus of investigation for the past 5 years (Kitching 1983; Pierce 1983, 1984, 1985; Pierce & Elgar 1985; Pierce & Young 1986; Pierce *et al.* 1987; Elgar & Pierce 1988; Smiley, Atsatt & Pierce 1988). Species in the genus *Jalmenus* have interesting and variable life-histories. For example, at least five of the species appear to have obligate, species-specific associations with ants, in the sense that larvae are never found without ants in the field and are only ever found with one species of ant, whereas others, including *J. evagoras*, are known to associate with several species of congeneric ants. Two 'species groups' of ants in the genus *Iridomyrmex*, *I. anceps* and *I. rufoniger* are particularly important associates of *J. evagoras* in our study sites. The taxonomy of these groups has yet to be resolved. For convenience, I will refer to them here as *I. anceps* and *I. rufoniger* (although this nomenclature is misleading in that we know that the *I. rufoniger* tending *J. evagoras* is distinct morphologically from the *I. rufoniger* tending *J. daemeli*. In all cases, we have deposited reference specimens with the Australian National Insect Collection). Like their lycaenid partners, attendant ant species also vary in many aspects of their biology, such as body size, tending behaviours and nest construction. Larvae and pupae often aggregate on host plants, which include approximately twenty species in the genus *Acacia*, and are also extremely localized where they occur, most likely as a result of their dependence upon ants. Thus individuals in natural populations are easily marked and observed in the field for their entire lifetimes. We have had no difficulty in rearing species of *Jalmenus* with their attendant ants on potted food plants in the laboratory.

COSTS AND BENEFITS FOR LYCAENIDS

The general approach that we have used in assessing the costs and benefits of the association for each party involved has been through the use of exclusion experiments, conducted both in the field and the laboratory. These have used sticky barricades to confine the distributions of ants, potted host plants to culture lycaenid larvae and manipulate their distributions in the field, and artificial nest boxes to house queenright (i.e. containing a queen) attendant ant colonies and control their distributions in the field.

Our first ant exclusion experiments were designed to assess the benefit that lycaenid butterflies receive from associating with ants, and in particular we wanted to see whether attendant ants protected larvae from parasites and predators. Ant defence of larvae has been demonstrated for a number of other species (Ross 1966; Pierce & Mead 1981; Pierce & Easteal 1986; DeVries 1987). To do this, we excluded ants from tending larvae in the field by applying a sticky barricade of Tanglefoot (The Tanglefoot Company, Grand Rapids, Michigan) around the bases of the larval host plants. Controls were treated in the same manner, except that Tanglefoot was smeared around only half the stem, allowing ants continued access to the larvae. In addition, we secured clear, plastic drop cloths coated with Tanglefoot beneath each tree to catch any larvae or pupae that might drop off. In this way, we could be sure that disappearances from the trees were due to differential predation by aerial predators and not simply due to larvae dropping off plants without ants (Pierce & Easteal 1986).

We have now repeated the ant exclusion experiments five times over three seasons at three different sites at Mount Nebo, Queensland (152° 47'E/ 27° 23'S), in order to assess how patchiness in space and time of predators and parasitoids might influence the outcome of the experiment. What we have discovered so far is that although the natural enemies of *J. evagoras* do indeed vary from site to site and year to year, the net effect of ant removal is always the same (Fig. 13.1): larvae and pupae deprived of attendant ants cannot survive (Pierce *et al.* 1987, and unpublished).

The benefit that juveniles of *J. evagoras* receive from associating with ants is survival, and we reasoned that, unless the lycaenids were actually fooling their attendant ants and parasitizing them in some way, the cost that the lycaenids would be able to pay for their association might be considerable. In particular, since larvae and pupae produce food secretions for attendant ants, we suspected that maintaining attendant ants might affect larval development. To look at this question, we compared the development of larvae raised with and without attendant ants in the laboratory.

Our experiment revealed both a benefit and a cost of ant attendance for lycaenid larvae. The benefit is that, in addition to guarding juveniles, the presence of attendant ants shortens larval duration, thereby reducing the time that larvae are exposed to the threat of predators and parasitoids (but see Henning 1984). Thus larvae with ants took approximately 23 days to pupate, whereas those without ants took about 29 days. The cost, however, is expressed as a reduction in adult size. For example, females
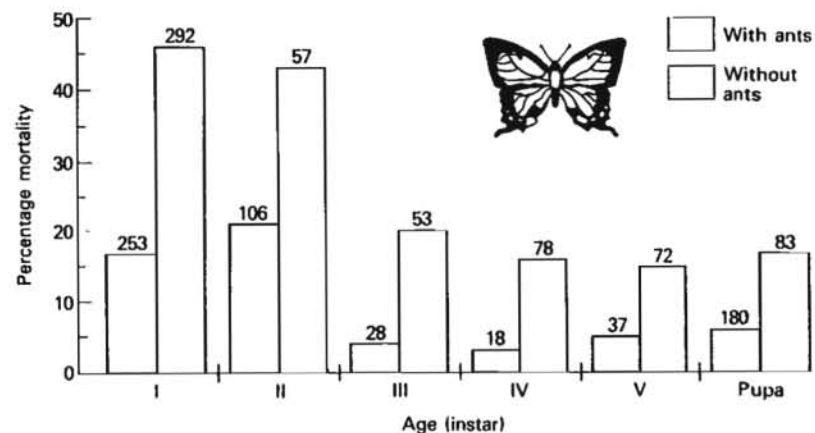

FIG 13.1   Benefit to butterflies. Diagram depicts the age-specific mortality due to predation of juveniles of *Jalmenus evagoras* in an ant-exclusion experiment at Mount Nebo, Queensland; sample sizes are given above each bar (redrawn from Pierce *et al.* 1987).

that are tended by ants pupate at a weight that is approximately 20% lighter than their untended counterparts. Since ant attendance also shortens development time, we found no significant difference in growth rates between larvae raised with and without ants. In the presence of ants, larvae simply pupate earlier at a much smaller size (Pierce *et al.* 1987).

It remained to determine whether smaller size indeed represented a cost to the butterflies. We examined females and males separately in this analysis. First, we raised freshly mated females in the laboratory, collected all of the eggs laid by each individual, and found a highly significant correlation between size and fecundity in this species. Second, we measured the mating success of individual males in the field, and compared this with their forewing length relative to all other males involved in competition for female mates at the same time. When a pupa is about to eclose, as many as twenty males may gather around it, forming a 'mating ball'. The males engage in a frenzied scramble as the pupa ecloses and copulation takes place before a teneral female has even had time to expand her wings. Pairs remain mating on a tree for several hours. Dissections of field-caught females indicate that females mate only once, although in the laboratory we have been able to induce them to mate more than once on rare occasions. Mating in *J. evagoras* does not always involve the formation of a visually dramatic mating ball, and eclosing females are frequently found by single males. However, virtually every

mating is readily observable because of the highly localized distribution of the butterflies and the long copulation time. We were able to mark individual males as they eclosed in the field, and then follow them for their entire lifetimes (or until they emigrated) to see how many matings they achieved. Again, we found that relatively bigger individuals tended to do better: there was a significant relationship between lifetime mating success and relative forewing length in males (Elgar & Pierce 1988). Thus we can conclude that size can influence both fecundity in females and lifetime mating success in males, and that a reduction in size represents a considerable cost from the point of view of the butterflies.

We also discovered that whereas tended larvae pupate sooner than their untended counterparts, tended pupae develop significantly more slowly. This slightly lengthened exposure to predators and parasitoids may represent an additional cost of ant attendance (Pierce *et al.* 1987).

COSTS AND BENEFITS FOR ATTENDANT ANTS

By comparison with the lycaenids, which are readily identifiable and easy to work with, we know very little about the costs and benefits of associating with *J. evagoras* for its attendant ants. Few quantitative data exist describing the benefits that ants receive in any of their apparently mutualistic interactions with other insects (but see Degen *et al.* 1986; Fiedler & Maschwitz 1988; and Buckley 1987 for review). It is easy to see why this is the case: ants that nest underground are difficult to work with, and, perhaps more importantly, they present a serious difficulty in deciding what unit to measure. Should we be assessing benefits to individual foraging ants, or to individual colonies? And, when we are working with a large, amoeboid polygynous and polydomous 'colony' that can extend as a single, self-compatible unit for distances of more than a kilometre, then what is the right unit to measure? Ecologists have approached this difficulty in different ways. Some have settled on individual foraging ants as the units of measurement (e.g. Lanza & Krauss 1984), whereas others have concentrated on colony and group level dynamics (e.g. Brian 1983; Sudd & Sudd 1985; Gordon 1986). We have attempted to study benefits at the levels of both the individual forager and the colony.

Several lines of evidence suggest that colonies of *I. anceps* receive substantial rewards for their efforts. First, simple inspection of the association indicates that this is the case: numerous attendant ants continuously groom and lick the larvae, and solicit secretions from a specialized organ on the seventh abdominal segment. Ants invariably establish nest extensions or 'bivouacs' containing brood at the base of trees containing larvae of *J. evagoras*, and it seems highly unlikely that they would move their 'central place' in this way unless the foraging rewards are high.

Second, we reasoned from our earlier work that tended pupae might develop slightly more slowly than their untended counterparts because of their need to feed attendant ants. Unlike larvae that alter their feeding behaviour in response to ants, pupae are essentially restricted in their expendable resources. To examine this possibility, we compared the weight loss of tended and untended pupae during a 5-day period. Pupae matched for age and size were divided into two groups, and half were placed on poles from which they could be tended by workers from a queenright laboratory colony of *I. anceps*. The remaining half were placed on adjacent poles where ants had been excluded. Pupae that were tended by ants for only 5 days lost 25% more wet weight than their untended counterparts. Thus pupae may supply rewards for ants by diverting metabolic resources from metamorphosis (Pierce *et al.* 1987).

Third, we attempted to measure the weight of the food harvested by attendant ants. A representative tree infested with sixty-two juveniles of *J. evagoras* was selected for observation, and the rate of ants travelling up and down the tree was measured at 2-hour intervals over a 24-hour period. We then took the wet and dry weights of each individual ant (Fig. 13.2). By comparing the dry weights of individual ants travelling to and from larvae of *J. evagoras*, we estimated that the daily biomass removal from a tree containing sixty-two juveniles of *J. evagoras* was about 400 mg. The mean dry weight of a worker of *I. anceps* is about 0.4 mg, so, if we use 10% as an estimate of biomass conversion from one trophic level to the next, then the net food removed from larvae on this single, representative tree was equivalent to the production of about 100 new workers of *I. anceps* in one day (Pierce *et al.* 1987).

Finally, we have measured how the secretions of lycaenid larvae contribute to colony growth and investment into reproductives. My student, David Nash, and I have collected nests of an attendant ant species, *I. rufoniger*, and are rearing them in the laboratory on water and an artificial diet (Bhatkar & Whitcomb 1970) supplemented by the secretions of differing numbers of larvae of *J. evagoras* feeding on potted host plants. The starting nests for this experiment are comprised of sister queens taken from polygynous colonies in the field, each provisioned by an equal number of workers and a similar weight of brood. The nests are housed in glass test tubes to allow observation of both growth rates and the investment into different castes. Each colony is fed equal and small
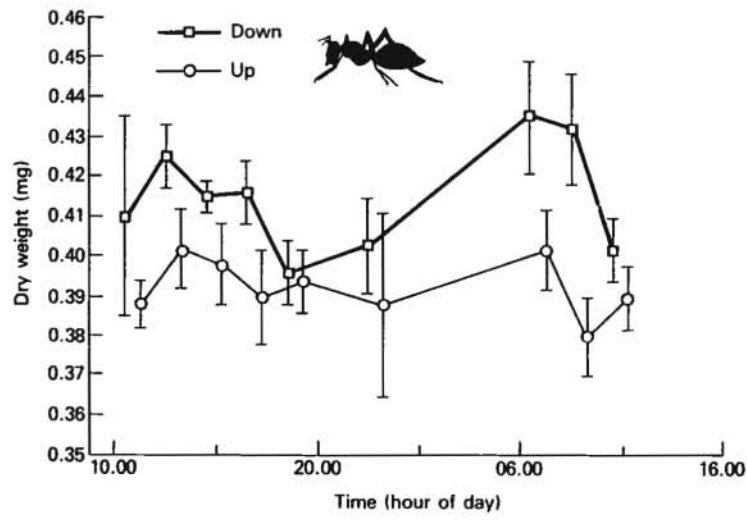
FIG 13.2 Benefit to ants. Graph illustrates differences in dry weights of ants foraging on a tree containing sixty-two juveniles of *Jalmenus evagoras* over a 24 h period. 'Up' weights are means for ants travelling up the tree and 'down' weights are means for ants travelling back down again. Bars represent standard errors; sample sizes are over twenty in all time zones, except 22:30, when they are both 7 (redrawn from Pierce *et al.* 1987).

amounts of ant diet to supplement the larval secretions. Although the nests are still growing, our preliminary results (after 40 days) indicate that those nests whose workers have been allowed access to host plants containing lycaenid larvae have significantly higher growth rates (as reflected by numbers of eggs laid) than nests whose workers are foraging on host plants with no larvae.

Although this experiment supports the idea that the interaction between *Jalmenus evagoras* and its attendant ants is indeed mutualistic, it raises many new questions. How would factors such as colony size, age and diet influence the results of the study? These characteristics are doubtless crucial in determining the effect that lycaenids have on the population dynamics of the ants, and they are characteristics which naturally vary in the field. However, they continue to present a challenge to our understanding of the interaction because they are difficult to study even in the laboratory, let alone under field conditions.

Finally, we are still in the process of measuring the costs of the association for the attendant ants. One of the methods that we are using is

simply to measure the metabolic cost to the ants of foraging on larvae and pupae (Nielsen, Torben & Holm-Jensen 1982; Peters 1983; Dreisig 1988; Fiedler & Maschwitz 1988). We also hope to gain information about the nature of both the costs and the benefits involved through a consideration of the foraging decisions made by ants when presented with larvae placed at different distances from the nest.

THE BIOCHEMISTRY OF LARVAL SECRETIONS OF SPECIES OF *JALMENUS* AND THEIR ATTRACTIVENESS TO ANTS

Unlike the 'honeydew' of aphids, the secretions of the Lycaenidae come from specialized exocrine glands. In addition to having an unusually thick cuticle (Malicky 1970), as well as larval and pupal stridulatory organs (Kitching 1983; Pierce & Elgar 1985), the larvae of species of *Jalmenus* possess at least three sets of glands that appear to be adaptations for associating with ants, two of which are probably important in ant appeasement and reward (Kitching 1983): epidermal glands called 'pore cupolas' scattered all over the surface of the larva (Malicky 1969, 1970), and, in the middle of the seventh abdominal tergite, the 'dorsal organ' (Newcomer 1912; Maschwitz, Wust & Schurian 1975). In general, this secretion is produced only when the ants have signalled the caterpillar in the right way, although a few species are known to produce secretions in the absence of ants (Hinton 1951).

We sampled these secretions to determine whether they constituted a genuinely nutritional reward for the attendant ants or whether they were merely a form of chemical trickery whereby the lycaenids are able to fool the ants into tending them. The latter is clearly the case in parasitic lycaenids such as the Large Blue, *Maculinea arion*. We found that both the pore cupolas and the dorsal organ of *J. evagoras* produce free amino acids, especially serine (at a concentration of about 30 mM from the dorsal organ). By conducting choice experiments in the field, we were also able to show that serine was one of the preferred amino acids of *I. anceps*: workers could definitely distinguish between different amino acids, and alanine, histidine, leucine and serine were highly significantly preferred over water alone. Different colonies varied in the total amount that they drank and in their preferences, although the rankings of preference between colonies were similar.

As serine is the main amino acid secreted by *J. evagoras* and is also one of the preferred amino acids of *I. anceps*, it seemed possible that serine was an important currency in the interaction. By scoring the rate of

ant attendance on pupae which differed in their attractiveness to ants, and by assaying the total amount of serine secreted by the pupae, we established that there was a strong correlation between the amount of serine secreted by a pupa and its attractiveness to ants. While this correlation does not establish cause and effect, it clearly suggests that serine has a critical role to play in this association (Pierce 1983; N. E. Pierce, unpublished).

Given the apparently stringent requirements of tended *J. evagoras* larvae in terms of amino acid output, it seemed likely that nitrogen limitation could influence lycaenid host plant choices. By releasing free-flying females of *J. evagoras* in a bush house, and providing them with a choice between fertilized (i.e. nitrogen-rich) and unfertilized potted host plants, my student Matthew Baylis and I found that females preferred to lay eggs on fertilized trees rather than on the unfertilized controls. Moreover, larvae that were raised on fertilized trees attracted more attendant ants and survived better than their counterparts on unfertilized controls. These results provided strong evidence that ovipositing females can respond to different levels of nitrogren in their host plants, though it is not clear what proximate cues they use in recognizing these plants, or whether other compounds that may covary with nitrogen are involved in the interaction (see Mattson 1980; Scriber & Slansky 1981; Myers 1985).

Further, if nitrogen is of particular importance to lycaenids that associate with ants, I reasoned that these lycaenids might have a predilection for feeding on protein-rich plants. Fortunately, excellent records of host plant use and ant association are available for Australia, South Africa and North America, and, for the species of these regions, there is indeed a strong correlation across all the lycaenids between ant association and feeding on relatively nitrogen-rich food plants, such as legumes (Pierce 1987).

SPECIES SPECIFICITY IN LYCAENID–ANT INTERACTIONS

Species specificity is of particular interest in the study of lycaenid–ant associations because in many ways it lies at the heart of the problem: an understanding of how and why interactions are species-specific will help resolve questions about the ecological mechanisms promoting both facultative and obligate mutualism, as well as the chemical communication between the lycaenids and their ant partners. We have approached this problem from two perspectives: the point of view of the ovipositing

butterflies, and the point of view of their attendant ants. Although much of this work is still in preparation for publication, I present it here both as a direction for future research, and as an indication of some of the methodological problems inherent in studying a complex system.

Because attendant ants are essential for the survival of *J. evagoras*, we suspected that ants might play an important role in the host-finding behaviour of the female butterflies. The oviposition behaviour of females of *J. evagoras* has proved to be exceptionally tractable for field studies, in part because of the dense and localized occurrence of populations of *J. evagoras*, and in part because the larvae and pupae aggregate, and females are attracted to conspecific juveniles during oviposition (Pierce & Elgar 1985). In order to test whether females respond to ants during oviposition, we arranged potted host plants in a circular arena in the field. These were provisioned with equal numbers of late instar larvae, and ants were allowed to tend larvae on half of the plants for several days, whereupon treatments were switched to control for possible host plant or position effects. This experiment demonstrated that females did indeed use ants as cues during oviposition, and that they were far more likely to lay egg masses on plants with larvae and ants than on plants with larvae but without ants. We then repeated the same experiment, but used juveniles of the homopteran, *Sextius virescens*, to attract ants (rather than conspecific juveniles). Again, females preferred plants with homopterans and ants (Pierce & Elgar 1985).

This satisfied our curiosity about whether females responded to workers of *I. anceps* during oviposition, but it did not tell us whether females could distinguish between different ant species. In an 'ant smorgasbord' experiment, we offered females of *J. evagoras* a choice between host plants inhabited by different species of ants. The ants were introduced into the field in artificial nest boxes, and allowed to forage on honeydew produced by juveniles of *S. virescens*, which were placed on potted host plants adjacent to the ant nests and attached to them by stick bridges. Two potted plants were positioned beside each treatment as controls: one contained equal numbers of homopteran juveniles that were not tended by ants, and the other contained homopteran juveniles that were tended by workers of *I. anceps*, the species that commonly attends larvae of *J. evagoras* in the field. Twelve different ant species were simultaneously presented to ovipositing females of *J. evagoras* in this manner. Females actively avoided several of the ant species, treated a number as if there were no ants present (laying as many egg masses on plants with ants as on plants without ants), and preferred to oviposit only on those trees where the homopterans were tended by *I. anceps*, the

common ant associate. However, females were indifferent to another attendant ant, *I. rufoniger*, that we have observed occasionally associating with larvae of *J. evagoras* in the field.

In a sequel to the ant smorgasbord experiment, we ran an experiment to determine whether workers of *I. anceps* were better tenders than workers of *I. rufoniger*. Three colonies of each species were arranged in the field in an area not inhabited by either ant species. Each colony was allowed to tend larvae of *J. evagoras* feeding on potted host plants. Twenty-five first instars were placed on each tree, and their survival was monitored daily for two weeks. At the end of two weeks, only about 15% of larvae tended by *I. rufoniger* remained on each plant, whereas about 60% of those tended by *I. anceps* were still surviving. Thus, under these experimental conditions, *I. anceps* was clearly a better tender than *I. rufoniger*. We concluded that selection has favoured species-specific identification of ants by ovipositing butterflies only for those species that provide adequate protection to insure high survival of their lycaenid associates (but see Law & Koptur 1985). The actual mechanism by which females discriminate different ant species in the field is still not known.

Our second approach to the question of species specificity took the perspective of the ants. Can ants distinguish between different species of Lycaenidae, and do they prefer larvae of the species they normally associate with? This work was done with four lycaenid/ant pairs: *J. evagoras / I. anceps*, *J. daemeli / I. rufoniger*, *J. pseudictinus / Froggatella kirbyi*, and *J. ictinus / I. purpureus*. In each case, ants were housed in artificial nest boxes in the laboratory, and allowed access to larvae feeding on potted plants of a single species, *Acacia irrorata*. In a mix-and-match experiment, five first instars of each lycaenid were offered to each ant species, and the survival of these larvae was monitored every day for 2 weeks. This demonstrates that, in addition to their normal lycaenid associate, there was little latitude in acceptance between ants and lycaenids. Workers of *I. rufoniger* accepted *J. daemeli* (their normal associate) and *J. evagoras*, and workers of *F. kirbyi* accepted *J. pseudictinus* (their normal associate) and *J. daemeli*. In all other cases, larvae of 'foreign' lycaenid species were attacked and consumed.

However, we also found that in another laboratory situation, a separate colony of *F. kirbyi* actively tended larvae of both *J. evagoras* and *J. daemeli*. The host plant in this instance was *A. decurrens* rather than *A. irrorata*, and the colony in the first experiment was reared on dilute honey and chopped cockroaches, whereas the colony in the second was reared on an artificial diet (Bhatkar & Whitcomb 1970). In other respects, our experimental protocol was very similar. These apparent experimental inconsistencies point toward an important consideration: variation in colony responses to larval secretions. Thus our future experiments in this area will include not only replicates of larvae, but also replicates of attendant ant colonies, and consideration of possible host plant effects. Such preference tests should also probably be run under field conditions, since colony diet may well influence ant behaviour. Likewise, the ant smorgasbord experiment should probably be run again using multiple ant colonies, rather than simply one colony per species.

Once we had managed to culture the four different species of *Jalmenus* in the laboratory, we were interested in comparing the secretions produced by each species for its attendant ants. We were able to raise all four species successfully on potted plants of *A. irrorata*, hoping to control for possible differences in the secretions caused by host plant species effects. The amino acid profile secreted by each species was unique. The secretions of *J. evagoras* were the simplest, containing primarily serine and small amounts of leucine, whereas those of *J. pseudictinus* contained a complex blend of histidine, arginine, serine, leucine, alanine and others. The secretions of *J. daemeli* did not contain amino acids, but showed a consistent, broad peak in the profile that probably corresponds to a small peptide.

If different species of *Jalmenus* secrete unique amino acid profiles, do the respective ant associates of these species prefer different combinations of amino acids? We had to return to the field to answer this question, and we set up 'drinking-straw' experiments in the field for each of these species. The different ant associates clearly varied in their amino acid preferences, both quantitatively and qualitatively. One species, *I. rufoniger*, was less attracted to amino acids and much preferred to forage on sucrose solutions instead. Not too surprisingly, this was the species whose usual lycaenid partner, *J. daemeli*, did not secrete amino acids. However the remaining two species, *I. purpureus* and *F. kirbyi*, both foraged actively on amino acids, and on different ones from those preferred by *I. anceps*. Moreover, although each species differed significantly in its amino acid preferences, the colonies within each species also varied significantly in the total amount consumed, as well as in preferences for certain amino acids. This was strong evidence again that colony level variation *must* be taken into account in studies of lycaenid–ant interactions. How did the preferences of the ants match up with the secretions of their lycaenid associates? For the remaining two species pairs, *J. ictinus / I. purpureus* and *J. pseudictinus / F. kirbyi*, the Spearman rank correlation between the relative concentrations of amino acids produced by larvae and the amino acids preferred by their attendant ants

was significant, indicating that the lycaenids may indeed secrete those amino acids that their ant associates prefer. Now the compelling question remains: why do the different ant species differ in their preferences for different amino acids? Doubtless their preferences are related in some way to their metabolic needs, and, since ants rely so heavily on chemical communication, my guess is that the preferred amino acids may be important building blocks for commonly used pheromones. For example, serine is a direct precursor for formic acid, and thus might be of particular importance for formicine ants that secret formic acid in relatively large quantities.

A POSSIBLE PRE-ADAPTATION ON THE PART OF ANTS FOR TENDING LYCAENID LARVAE

In addition to being a highly desirable food source, the amino acids secreted by different species of lycaenids might also be involved in recognition: that is, the food itself might act as a communication signal for the ants. It is clear from the results of the bioassays described above that ants can distinguish between different amino acids, and hence it seems possible that amino acids could also act as discriminating substances in chemical communication. The unique amino acid profiles secreted by each species of *Jalmenus* could therefore be not only the product of the food preferences of their associated ants, but also the cue that the ants use in favourably recognizing the larvae so that they choose to tend them rather than attack them.

As a signal, epidermal secretions of lycaenid butterflies operate on several levels of recognition (Hölldobler & Michener 1980). Larvae of all parasitic and many mutualistic species are somehow able to ensure species-specific recognition by their ant associates, and larvae of parasitic species that are carried into the nest by ants are clearly capable of mimicking ant brood signals. There is no evidence, however, that the initial appeasement and adoption of lycaenid larvae by host ants is ever colony-specific, although it is conceivable that, once a colony has adopted a larva, it can somehow impart to it a colony-specific odour (Vander Meer & Wojcik 1982).

As mentioned before, larvae of many species of lycaenids are tended by only one species of ant or several closely related species of ants. This is particularly true of parasitic larvae that are carried into the ant nest (Cottrell 1984). In these unusual species, such as the Large Blue, *Maculinea arion*, the larvae become carnivorous on the ant brood, completing their development and pupating in the ant nest. Larvae of these species are invariably carried into the brood chambers of their host's nest where they are treated as if they were brood; clearly they are able to mimic not only species-specific signals, but also brood-specific signals of their host ants. We shall discuss these two types of signals as distinct from one another, although it is possible that any discriminating substances that ensure brood recognition are the same as those responsible for species recognition, but vary, for example, in their relative concentrations. In this context, we use the term 'discriminating substances' suggested by Hölldobler & Michener (1980) to describe exocrine secretions that identify individuals between species, or brood within species. It is still unknown whether identification is based on odours that are genetically controlled, environmentally conditioned, or a combination of both.

As yet we have little evidence that amino acids in the epidermal secretions of lycaenids could act as communication signals for attendant ants (beyond their nutritive function), but two observations indicate that this is possible. First, when we examined the combined amino acid profiles of approximately fifty pupae from each of five colonies of *I. anceps*, we found that their profiles matched those obtained from larvae and pupae of *J. evagoras* in the sense that they all contained significant amounts of serine (as well as a variety of unidentified peptides.) Second, we noticed that workers of *Pheidole megacephala*, a species of ant whose workers are hostile to larvae of *J. evagoras* and attack them upon encounter, were completely indifferent to a solution of the amino acid serine, whereas workers of *I. anceps* literally stood on top of each other to drink this solution. Other studies (Inouye & Waller 1984; Lanza & Krauss 1984) have also shown that honey-bees and ants (species of *Leptothorax* and *Monomorium*) can distinguish between different amino acids. These behaviours demonstrate two things: (1) there are differences in the dietary preferences of particular ant species, and (2) the striking contrast in response suggests that amino acids at least have the potential to function as discriminating substances.

It is possible that the recognition and nutritive functions of amino acid secretions are interrelated, the former being a ritualized adaptation of the latter. Regurgitation of amino acids by larvae has been considered important for dietary reasons in the evolution of the Hymenoptera (Maschwitz 1966; Wust 1973; Hunt 1982), and perhaps epidermal secretions of amino acids by the larvae and pupae of ants have also become important in species or brood recognition. Interestingly, Walsh & Tschinkel (1974) found that the absence of protein in the diet of *Solenopsis invicta* resulted in an inconsistent response by workers to their own brood.

Several researchers (Fielde 1903; Jaisson 1975; Le Moli 1978; see

Carlin 1988 for review) have shown that, in certain situations, brood of one species of ant will be tolerated by workers of a wide variety of alien ants, and Hölldobler (1973) has postulated that brood-tending pheromones may occupy a high position in a hierarchical order of recognition pheromones. This may also be true of the 'brood' substances produced by lycaenids. *Maculinea teleius*, a lycaenid that in Japan is always associated with ants in the genus *Myrmica*, has also been discovered in the brood chambers of a nest of *Lasius niger* (Fukuda *et al.* 1978). In this instance brood-recognition signals must have overridden any other signals produced by the larvae and induced workers of *L. niger* not only to carry larvae of *M. teleius* into the brood chamber of their nest, but also to treat them there as brood, even though *Lasius* and *Myrmica* are members of different ant subfamilies.

For parasitic species of Lycaenidae that are actually carried into the ant nest, it is not difficult to imagine that the larvae are mimicking an ant brood signal. My suggestion here, however, is that even those species that are not carried into the nest may be mimicking some critical *portion* of the brood stimulus that causes ants to care for, groom and protect them exterior to the nest.

This analogy between the behaviour shown by ants towards lycaenid larvae and their brood relies in part on the idea that there exists a generalized component of the brood signal that is identifiable to many species of ants. If lycaenid larvae do in fact mimic such a generalized signal, this could also account for why many lycaenids are accepted by a wide variety of tending ants. For example, as many as eleven different species of ants have been recorded as tending the larvae of *Plebejus icarioides* (Downey 1962). These putative gustatory and/or olfactory signals may act in conjunction with tactile stimuli in insuring brood recognition. For example, Brian (1975) has shown that features such as size, shape, turgidity and hairiness of brood are important variables in brood recognition by various species of *Myrmica*.

A number of similarities exist between ant–brood and ant–lycaenid associations even among those lycaenids whose larvae are not carried into the ant nest. The chemical attractants in both cases appear to be non-volatile 'surface' attractants (Wilson 1971; Walsh & Tschinkel 1974; Brian 1975); adult ants must make contact with or come very close to making contact with larvae or pupae before recognizing them. In addition, these attractants are stable in nature. Walsh & Tschinkel (1974) observed that workers of *S. invicta* would respond normally to dead brood for at least 21 hours, and Robinson & Cherrett (1974) also found that workers of *Atta cephalotes* responded to brood killed by freezing.

Similarly, I have observed that attendant ants persist in tending carcasses of the larvae of *Glaucopsyche lygdamus* and *J. evagoras* for up to a week following death.

Moreover, the behaviour shown by tending ants toward lycaenid larvae is also remarkably similar to the behaviour shown toward brood. In particular, ants spend considerable amounts of time licking and grooming larvae, just as they do their brood. They sometimes appear to show great fidelity to larvae; in one case I observed several marked individual workers continue to tend the same larva of *Glaucopsyche lygdamus* for 10 days. This kind of fidelity has also been documented for ants tending homopterans (Ebbers & Barrows 1980). Finally, ants tending lycaenid larvae also spend considerable time grooming themselves, as do ants in nest brood chambers, perhaps thereby spreading substances gleaned from the larvae over their own bodies.

As more is learned about the nature of ant pheromones, the mechanism by which lycaenid larvae have broken the communication codes of their host ants will surely be elucidated. One of the greatest difficulties in determining the nature of ant brood pheromones has been distinguishing whether workers are responding to a food stimulus or to an actual communication signal. Bioassays that can discriminate between these responses may be extremely difficult to design. It is possible, for example, that substances such as amino acids that originally acted as phagostimulants for ants have evolved to function as communication signals. Glancey *et al.* (1970) observed that workers of *Solenopsis invicta* placed corn grits treated with homogenized extracts of their own juveniles with the brood in their nests. Henning (1983) also used the technique of Glancey *et al.* to examine the response of attendant ants to the tissue of lycaenid larvae (*Aloeides dentatus* and *Lepidochrysops ignota*) extracted with dichloromethane, with similar results. However Walsh & Tschinkel (1974) were unable to repeat the assay of Glancey *et al.* when they had modified the nest design to create a separate, discrete brood chamber, and suggested that the brood response may have been confounded with a food response.

There are many gaps in our understanding of the proximate mechanisms that maintain the association between lycaenids and ants, particularly in our understanding of the biochemical nature of the secretions of lycaenid larvae. The notion that free amino acids can be secreted in particular combinations and concentrations to create unique, recognizable profiles provides an attractively parsimonious mechanism for a chemical communication code in an animal that can distinguish the difference between different amino acids. Nevertheless, it is hard to

imagine that this information alone could signal ants to tend larvae rather than attack them, and it seems likely that larvae produce compounds other than amino acids that are also involved in the recognition process. Recent work has focused on the possible significance of cuticular hydrocarbons produced by social insect hosts and their guests. The termitophilous beetle *Trichopsenius frosti* synthesizes a hydrocarbon pattern identical to that of its host, *Reticulitermes flavipes* (Howard, McDaniel & Blomquist 1980), and the myrmecophilous beetle *Myrmecaphodius excavaticollis* appears to acquire species-specific hydrocarbons from each of at least four different species of *Solenopsis* hosts (Vander Meer & Wojcik 1982).

TOWARD A MORE EXACT ECOLOGY

What can an analysis of lycaenid butterflies and ants tell us about mutualism in general? In essence, this study has at least three long-term goals: (1) to measure the costs and benefits for both partners in a mutualism; (2) to consider some of the pre-adaptations of both parties that may have promoted the evolution of the mutualism; and (3) to assess possible evolutionary consequences of the interaction. Clearly, the association that lycaenid butterflies have with ants has profoundly shaped their evolution and subsequent diversification, and I have discussed these evolutionary considerations elsewhere (Pierce 1987). However, more empirical studies are needed before ecologists will be able to reach any general appreciation for the importance of mutualism in generating or maintaining diversity, or otherwise structuring natural communities.

What we require is a comparative framework: we need to have more studies of particular mutualistic systems from which to generalize. Such a framework will be necessary in order to assess whether there are particular features of organisms that predispose them to associate symbiotically, and whether such associations are then likely to have characteristic evolutionary outcomes (c.f. Law 1985). Consider two possible examples. First, mutualisms often appear to give rise to parasitism, especially in situations where the pay-offs are highly asymmetrical, as exhibited by a number of lycaenid–ant interactions. To predict why and when this might occur, we need to know more about selective forces that determine the *degree* of association found between different mutualists: under what circumstances and how commonly can we expect obligate interactions to arise? How can an obligate dependence on the

part of one or both partners affect population structure and subsequent evolution of both? Second, the results shown here suggest that ant mutualists are 'keystone' participants in the interaction between lycaenids, their host plants, parasites and predators. If we were to remove ant mutualists from our Australian *Acacia* communities, diversity would decrease significantly. While the ecological literature abounds with discussions of whether competition and/or predation are important in structuring communities, relatively few attempts have been made to assess the relative importance of mutualism as a mechanism in either generating or maintaining community diversity. In part this is because the necessary data do not yet exist.

We could speculate about the importance of learning more about the role of mutualism in natural communities by taking a hypothetical example. Consider an effort aimed at reforestation following the destruction of tropical rain forests. Even if we were able successfully to replant the appropriate species in their native habitats, such an effort at regeneration might nevertheless completely fail if the appropriate, mutualistic pollinators and seed dispersers for these plants had gone extinct in their absence. For specialized, obligate mutualists, this is clearly a possibility.

The results of this research show that working toward a more exact ecology can yield benefits in terms of a better understanding of complex species interactions. By 'exactness', I refer to several main approaches, one being the implementation of technological innovations such as HPLC in analysing and quantifying (in this case) lycaenid secretions, the second being a quantitative and experimental approach in weighing out costs and benefits for each partner and determining the mechanisms underlying species interactions, and the third being the use of comparative studies in looking for ecological correlates of particular life-history traits. For example, had we not discovered that lycaenids secrete amino acids as rewards for attendant ants, we might never have scrutinized the role of nitrogen in lycaenid–host plant interactions. And, had we not found that different amino acids were being secreted by different lycaenid species, we would never have enquired further into how the biochemistry of ant nutrition might be related to chemical communication. However, I thank Evelyn Hutchinson for providing what is certainly the most fitting summary to the work discussed here: when I told him about the theme of this symposium, he remarked, 'Well, it's all very well to aim toward a more *exact* ecology, as long as no one makes the mistake of thinking that, by doing so, they will discover a more *simple* ecology.'

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