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Ant Plant Interactions

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Cover illustration: The neotropical ant *Azteca ovaticeps* takes a Müllerian body, rich in glycoegen, from the trichilium at the base of a petiole on the myrmecophytic tree *Cecropia* sp. Drawn by Rosemary Wise.

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Extrafloral nectarines of herbs and trees: modelling the interaction with ants and parasitoids

Suzanne Koptur

Plant tissue lost to consumers is a physiological cost to a plant. Over evolutionary time, a variety of plant defences have evolved which enable plants to avoid or better survive herbivory. Plants are rooted, and cannot flee, so their defences operate at the site of attack. Much research has been done on the mechanical and chemical defences of plants, but biotic defences have received less attention, perhaps because they require greater field study. Biotic defences of plants are dynamic, and there are compelling reasons to study them. Most plant species have multiple defences, since no single line of defence works against all herbivores. By gaining a better understanding of how plants benefit from mutualisms with biotic protective agents we gain insight into complex interactions that shape community structure.

Extrafloral nectarines and plant defence

Evidence for ants visiting extrafloral nectarines and providing protection against herbivores is abundant (Bentley 1977*a*; Buckley 1982; Beattie 1985; Jolivet 1986). Ants visiting nectarines on vegetative parts of the plant body may protect foliage (Janzen 1966, 1967; Bentley 1976; Tilman 1978; Koptur 1979, 1984; Kelly 1986) which can translate into greater seed set and increased fitness for the plant (Koptur 1979; Stephenson 1982; Barton 1986). Nectarines on or near reproductive structures can provide ant protection of ovules and seeds (Elias and Gelband 1975; Bentley 1977*b*; Deuth 1977; Inouye and Taylor 1979; Schemske 1980, 1982; Keeler 1981*b*; Horvitz and Schemske 1984). However, ant protection is by no means universal (e.g. O'Dowd and Catchpole 1983; Tempel 1983; Boecklen 1984; Heads and Lawton 1984; Lawton and Heads 1984; Whalen and Mackay 1988; Rashbrook *et al.* Chapter 16, this volume; Mackay and Whalen Chapter 17, this volume), and the benefits to plants from ants vary both geographically (Koptur 1985; Barton 1986; Kelly 1986; Koptur and Lawton 1988) and temporally (Tilman 1978; Schemske and Horvitz 1988; Cushman and Addicott Chapter 8, this volume).

Extrifloral nectaries also attract predators and parasitoids of the plant's herbivores (Leius 1967, Price *et al.* 1980, Washburn 1984;

1985). Parasitoids

systems (de Bach 1964; Crepps 1975; Altieri *et al.* 1977; Hassell 1982) and in natural situations (Washburn and Cornell 1981; Hassell Waage 1984; Hassell 1985; Weis and Abrahamson

1986), especially in areas where ants are not abundant (Keeler 1985; Koptur and Lawton 1988).

The nature of the mutualism

A mutualism is 'any interaction in which two (or more) species benefit from the presence of the other species' (Addicott

cases it is probable that the indirect benefits of a mutualistic extend beyond the individual mutualist paying for the interaction Mutualistic interactions in which a number

sides of the interaction are called diffuse (Addicott (Law 1985), and are usually facultative (Koptur 1979).

have noted that interactions between mutualistic species tend to specificity (Schemske 1983; Harley and Smith 1983; Howe 1984; 1985). The tendency for non-specificity or

the interplay between antagonistic and mutualistic interactions differentiation the equilibrium to be unstable (Law and Koptur 1986).

Mutualisms mediated by extrifloral nectaries are non-specific nectar can be taken by a variety of animals, whose behaviour

Baker 1989; DeVries Chapter 12, this volume). These actions will be distinguished here from the often obligate, mutualisms of myrmecophytes, in which there are a greater mediating factors (domatia, food bodies, and sometimes also nectaries).

sitoids, and predatory insects. The consequences of these actions on plant fitness are measurable, and are important order to understand the dynamics of mutualisms in (Thompson 1988).

Extrifloral nectaries: a quantitative defence

Chemical defences of plants have been categorized as either qualitative (toxins, effective against specialist herbivores) or quantitative (e.g. digestibility reducers, effective against generalists) (Rhoades and Cates 1976); plants that are apparent (long-lived and/or abundant) tend to have quantitative defences, while non-apparent plants may utilize qualitative defences more effectively (Feeny 1976). Typically, there are specialist herbivores that can circumvent qualitative chemical defences, even utilizing protective chemicals for their own nutrition or defence (Bernays and Woodhead 1982).

McKey (1988) compares and contrasts chemical and biotic plant defences and notes that, in situations where extrifloral nectaries function on young leaves, biotic protection replaces phenological defence. In many plant species, however, extrifloral nectaries function on mature leaves and/or other parts of the plant body. In general, biotic protection supported by extrifloral nectaries can be considered quantitative for three reasons:

1. More nectar supports greater visitor activity and increases protection.
2. Ants can control a wide variety of phytophagous insects.
3. Parasitoids attracted to nectaries are often taxonomic generalists.

Many plants with extrifloral nectaries are abundant, widespread, and/or long-lived, and could certainly qualify as 'apparent'. The generalized defence supported by extrifloral nectaries may facilitate colonization of new areas, where the plant can strike up a facultative mutualism with non-co-evolved ants, e.g. Old World vetches that grow in north America and are protected by an introduced ant (Koptur 1979).

In habitats where ants are scarce, plants with extrifloral nectaries are less abundant (Keeler 1979*a*, 1980*b*, 1981*a*). Certain plants lose their ant-related traits when ants are absent (Rickson 1977). Removing nectaries from plants substantially reduces the number of ants on a plant (Koptur 1979) unless there are few ants to begin with, or ant-tended homopterans are involved (see below). The more nectar that is offered, the more carbohydrate is available, and many ant species recruit to good resources (Carroll and Janzen 1973; Bentley 1976; Taylor 1977).

As the exception that proves the rule, plants with extrifloral nectary-mediated defence have a small number of specialist herbivore species (in their native habitats) that circumvent the biotic protection. The presence of ants on a plant may create 'enemy-free space' (Lawton 1978; Aisatt 1981; Jeffries and Lawton 1984) for herbivores specialized for survival among ants (Janzen 1966, 1967; Koptur 1984; Heads and Lawton 1985; Joliver Chapter 26, this volume). Certain insect herbivores secrete honeydew and are tended by ants (Way 1963; Hill and Blackmore 1980; Messina 1981; Briese 1982; Fritz 1982; Sudd 1983; Takeda *et al.* 1983; Whalen and Mackay 1988;

Chapters 8–10, this volume) and may thus be protected from their parasitoids (Pierce and Mead 1981; Horvitz and Schemske 1984; Maschwitz *et al.* 1984; Smiley *et al.* 1988; Pierce *et al.* Chapter 11, this volume). Other herbivores may obtain protection by feeding inside structures which are tended outside by nectar-drinking ants (Washburn 1984; Compton and Robertson 1988, Chapter 10, this volume; Koptur and Lawton 1988).

Specialized herbivores that are immune to ant defence may be especially devastating to plant fitness in situations where ant protection is so complete that the natural enemies of these herbivores are virtually excluded (Compton and Robertson 1988; Koptur and Lawton 1988). The effects of the different guilds (herbivores, ants, and parasitoids) on plants depends on their interactions with each other, which can vary spatially (Gilbert 1975; Gilbert and Smiley 1978; Koptur 1985; Smiley 1985, 1986; Barton 1986; Kelly 1986; Koptur and Lawton 1988) and temporally (Clancy and Price 1986; Schemske and Horvitz 1988; DeVries Chapter 12, this volume).

Habitat considerations

The diversity and abundance of herbivores on a plant are related to many factors, including habitat heterogeneity and structural diversity; host plant abundance, distribution, density, and architecture or structure; and seasonal phenology (Strong *et al.* 1984). In addition, biotic interactions between plants and non-phytophagous insects can influence the herbivores utilizing a given host plant (Price *et al.* 1980, 1986; Hassell and Waage 1984). The complex interactions between herbivores and host plants vary in different situations (Deno and McClure 1983; Thompson 1988). The relative benefit from different guilds of protective agents may therefore vary, resulting in different patterns of protection, herbivore damage, and diversity in different situations.

The structural diversity of plants influences herbivore diversity in plants of different lifeforms (Lawton 1983) and successional stages (Southwood *et al.* 1983). Pioneer plant species experience greater herbivore pressure, especially on mature foliage (Coley 1983*b*; Newbury and Foresta 1985). Bentley (1976) found ant abundance and plants with nectaries to be more common in clearings and forest edges than in closed forest; Schupp and Feener (Chapter 13) find nectar-mediated ant defence to be more common in light-dependent, tropical woody plant species than climax species. Balsas (*Ochroma pyramidalis* Bombacaceae) (O'Dowd 1979) and certain *Inga* (Mimosaceae) are examples of such successional plants.

Life history considerations

Annual plants have herbaceous tissues, most of which actively photosynthesize and are therefore appealing to herbivores. Herbs that utilize biotic

protection usually have the extrafloral nectaries in positions that enhance protection of flowers and fruits, to maximize seed protection during the sole reproductive opportunity. Temperate annuals with extrafloral nectaries near the inflorescences include the common vetch, *Vicia sativa*, which has axillary flowers on short pedicels and stipular nectaries in very close proximity (Koptur 1979), and the partridge pea, *Cassia fasciculata*, which has inflorescences in the axil of each leaf that bears a petiolar nectary (Barton 1986; Kelly 1986).

Tropical herbs are usually perennials, but many of these also have inflorescence-associated extrafloral nectaries: the neotropical ginger *Costus pulverulentus* (Zingiberaceae) has nectaries on the inflorescence bracts, which are visited by ants which repel dipteran ovule predators (Schemske 1980). Other tropical herbs with similar strategies include *Aphelandra deppeana* (Acanthaceae) (Deuth 1977) and *Calathea ovandensis* (Marantaceae) (Horvitz and Schemske 1984). There are also examples of temperate perennial herbs which use this strategy: *Helianthella quinquevenis* (Asteraceae) has nectaries on the phyllary bracts of the composite inflorescence (Inouye and Taylor 1979) and *Vicia sepium* has stipular nectaries quite similar to those of the annual *V. sativa* (Koptur, personal observation).

It is in perennials, especially woody ones, that extrafloral nectaries are more commonly associated with vegetative parts of the plant body, presumably because, even when ovules and seeds are not directly protected, a reduction in the amount of damage to leaf tissue can have a significant impact on eventual seed reproduction in either the same year or a following year. *Catalpa speciosa* (Bignoniaceae) has foliar nectaries, and Stephenson (1982) found that ants visiting these nectaries decreased loss of leaf tissue and increased seed setting on protected branches. In some species of *Inga*, nectaries function at a time other than flowering (Koptur 1984), yet the resulting damage reduction may increase fruit production.

Biotic defences are 'mobile' defences (Coley *et al.* 1985), for although secretory structures involve a non-returnable investment, their secretory activity is regulated by the plant and is often temporary (e.g. on young leaves only while they are expanding). The same long-lived leaves may economize by investing in generalized defences that involve one-time investments (e.g. lignins and tannins) rather than prolonging the biotic protection (nectaries) that involves high maintenance costs (McKey 1988). Examples of this strategy include rainforest legume trees *Leonadoda africana* in the Old World (McKey 1984) and *Inga* spp. in the New World (Koptur 1984). It is more common for herbaceous plants to have extrafloral nectaries which function for the major part of their lives (e.g. *Vicia sativa* (Koptur and Lawton 1988) than for woody plants.

Extrafloral nectaries, establishment, and survival

Extrafloral nectaries are probably more important in the successful survival of perennials to reproductive age than that of annuals. Some annuals do not have functional nectaries until the time of flower formation (e.g. *Vicia sativa*). Nectaries can play a significant role in the survival of juvenile *Inga* trees to reproductive maturity: if an unlucky sapling is totally defoliated (entirely reproductive if one or two pierid caterpillars spend their fifth instar feeding on the leaves) there is a high probability of death (Table 15.1). Ants visiting nectaries on seedlings and saplings can repel ovipositing Lepidoptera, remove eggs, harass caterpillars, and thereby minimize damage; parasitoids fed by nectaries may also shorten the feeding life of certain herbivores. Certain herbaceous species, however, have extrafloral nectaries functioning on the cotyledons (e.g. the castor bean *Ricinus communis*, Euphorbiaceae), suggesting an adaptive advantage of nectar production in seedling establishment.

Costs and inducibility of extrafloral nectar production

Herbs have a larger relative proportion of their biomass actively photosynthesizing than do woody plants. Therefore, they have greater vulnerability to herbivores. Herbs have lower maintenance costs than woody plants, and there is generally greater net productivity in herbaceous vegetation. An acceptable short-term approach to measuring fitness in plants is to calculate cost as the amount of carbon required to produce and maintain a structure (Mooney 1972; Chapin 1989); benefit is the carbon gain resulting from the structure, and can be estimated experimentally or by simulation (Mooney and Gulmon 1982). Using biomass as a rough indication of carbon investment, woody plants invest more in their structures than do perennial herbs, which in turn invest more than do annuals. A given volume of nectar (of a certain sugar concentration or amount of carbon) will therefore be less expensive for a herb than a woody plant, and for an annual than a perennial.

Perhaps this is why inducible extrafloral nectar production has been found (so far) to be more common in herbs than in trees (see below). Many plants increase levels of chemical defence in response to herbivore attack (Fowler and Lawton 1985). There is preliminary evidence that some plants may respond to damage from herbivores by secreting more extrafloral nectar (Koptur 1989) and nectar of different constitution (Smith *et al.* 1990), which are potentially adaptive responses if more biotic protection results. Smith *et al.* (1990) have found that herbaceous *Impatiens* secrete nectar higher in amino acid concentration subsequent to artificial herbivory. My own experiments with herbaceous *Vicia* have shown increases in nectar volumes and sugar concentrations with moderate levels of damage; but experiments with woody *Pithecellobium* and two *Inga* species have had negative results for induction

Table 15.1. Effects of artificial and natural defoliation on survival of *Inga* saplings.

% Leaf area destroyed	Number of individuals	No.	% Survival 1 year later
(a) Artificial defoliation of <i>I. densiflora</i> in Monteverde, Costa Rica			
25	8	8	100
50	10	9	90
75	9	6	67
100	10	2	20
(b) Natural defoliation of <i>Inga</i> by caterpillars of <i>Dismorphia</i> spp. (Pieridae)			
<50	15	14	93
80-95	15	3	20

(Koptur 1989). However, Stephenson (1982) observed that nectar production increased in woody *Catalpa* with greater natural defoliation.

Ants versus parasitoids: trees versus herbs

Ants remove or deter herbivores on the surface of plants; protection takes place before the herbivores cause much damage, and the benefit from producing the nectar accrues largely to the nectar-producing individual. Parasitoids visiting nectaries are more likely to encounter and parasitize herbivores on plants secreting nectar. The parasitoid larvae eventually emerge, killing the herbivore egg, larva, or pupa. If herbivore lifespan is shortened and plant consumption is reduced, there will be direct benefit to the individual nectar-producing plant. However, an indirect benefit of parasitized herbivores not becoming reproductive adults is experienced by all plants of that species in the vicinity, and indeed by other plants susceptible to that herbivore.

My work has led me to wonder how these traits are selected for by the various guilds of biotic protective agents, especially in the situations where parasitoids are more important than ants as nectary visitors. Two examples contrast the life history and ecological situations.

1. *Inga* are legume trees, with foliar nectaries that support fairly effective ant-guards in neotropical, lowland wet forests. The same species of *Inga* occur in upland wet forests where ants are rare, and do not regularly visit nectaries: here there can be no ant protection, but most trees of the species secrete extrafloral nectar. Caterpillars on upland trees are parasitized frequently than their lowland counterparts, suggesting that parasitoids

lowland tree does.

2. *Vicia sativa* (vetch) is a temperate annual legume herb, with nectaries in close proximity to the flowers. Ants visit these nectaries, effective in reducing the numbers of surface-feeding Lepidoptera, but ineffectual against the many phytophagous adult beetles. Some of lepidopteran and beetle herbivores oviposit in the flowers and be controlled by
posit in/on the larvae or in flowers and developing fruit. The support the two guilds of protective agents simultaneously.

Modelling extrafloral nectary mutualisms

It is easy to see how ants that deter herbivores could promote associations between ants and plants. which a novel type that secretes extrafloral nectar arises: Type-A secrete nectar, of N , in proportions p and q ($p + q = 1$).

Let d = an individual of Type-A's effect on itself

z = its effect on every other member of the group

b = benefit due to nectary visitors

c = cost of nectaries and nectar

So $d = b - c$ (benefit of action minus the cost).

When $b > c$, the effect on self will be positive.
any benefit

the short term, phytophagous insects disturbed on more likely to oviposit and/or feed directly on Type-B plants.

on every other member of the group ($Np - 1$; 1 is that individual itself). Therefore, changes in fitness from the nectar secreted by be calculated as follows (f_x = fitness of Type-X plants):

$$f_A = d + (Np - 1)z \quad (15.)$$

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The effect on Type-B plants from Type-A plants is:

$$f_B = Npz \quad (15.2)$$

The type with the higher fitness increases its proportionality in the next generation. So, for Type-A to be selected,

$$f_A > f_B, \text{ and}$$

$$d + (Np - 1)z > Npz \quad (15.3)$$

$$d > z$$

Namely, net benefit to self must be greater than benefit of action to other members of the group for the trait to be selected. Ants will remove more herbivores from Type-A plants, thereby increasing f_A , and the nectar-producing type will be selected.

If, however, there are no ants present, some parasitoids may select for nectaries (via the same model) if they reduce herbivore pressure on individual plants that secrete nectar (e.g. by shortening the life of parasitized herbivores, especially eliminating the late instars that eat more, or by parasitizing eggs that will then not hatch, or produce short-lived larvae). Not all parasitoids will do this, and if they do not, the cost of nectar production will not be offset by an immediate benefit to the individual nectar producer:

$$c > b, d \text{ will be negative}$$

Therefore, $d < z$.

If the cost of nectar production is non-zero ($c > 0$), d will be less than z , and Type-B plants (non-producers) will be selected. Even if nectar secretion and parasitoids reduce overall herbivore numbers (by preventing some larvae from becoming reproductive adults), this will benefit all members of the population equally (both Types A and B) so that the fitness of Type-B will be greater (as they do not have any cost to bear) and the nectar secreting trait will be selected against. Again, $d < z$, because c will detract from b for Type-A, whereas $c = 0$ for Type-B).

How, then, are nectaries selected and/or maintained in areas where ants are not present in numbers sufficient to afford protection? In a population of upland *Inga*, with no ants present the nectaries are visited by parasitoids and herbivores are parasitized. It may be possible to understand why most plants secrete nectar if we consider the basic selection model with the homogeneity assumption relaxed. Consider that the population may be sub-structured and that selection may operate between groups within the deme (the large breeding population).

The plant that secretes extrafloral nectar will increase the likelihood of its

herbivores being parasitized. The parasitized herbivores may continue feeding on the plants for some time, so the benefit is not necessarily immediate, unless the herbivore eats less than its non-parasitized counterparts. This problem (having to sustain parasitized herbivores) may not be that important as *all* individual plants in the area will have herbivores, i.e. no extra cost is involved from foliage feeding on nectar-secreting individuals over and above that cost to non-secretors. The greatest protective benefit may arise from the parasitized herbivore not living to reproduce, therefore decreasing the numbers of herbivores in the next generation. As many herbivorous insects have adults that move some distance (e.g. Lepidoptera), the eggs that might have been laid by a given parasitized larva would have produced larvae feeding not only on the plant that produced the nectar, but on other individuals of that species in the vicinity. There is, therefore, the potential for all plants susceptible to that herbivore and growing in the vicinity of the nectar-producing individual to benefit from the nectar.

For *Inga*, the deme is determined by strong-flying, far-ranging pollinators (hawkmoth and hummingbird) and seed dispersers (mammal and bird). Trait groups are smaller groups within which ecological interactions take place: for *Inga* we will consider the groups defined by herbivore oviposition range. (This is certainly a continuous function, the oviposition frequency falling off with distance from the original larval food plant; but here we will consider it, for simplicity, as discrete.) These trait groups are small compared to the deme: herbivorous Lepidoptera on these trees are mostly smaller and less vagile than the pollinators and seed dispersers.

Let each trait group be characterized by a certain density of Types A and B. The more Type-A (nectar secretors) there are in a trait group, the greater that trait group's fitness will be, and that trait group will be represented proportionately more in the next generation.

Let f_A and f_B represent fitnesses within a trait group (as in Wilson (1980)). Within a deme, there will be a large number of trait groups (T) each characterized by a single density (of Type-A) and frequency (of Type-A).

Let p_{mn} = the proportion of trait groups containing m Type-A and n Type-B, $m + n = N$.

The fitnesses of the two types over the entire deme (F) consist of the weighted averages of fitness for each type over all trait groups (mixing occurs throughout the whole deme, so this is justified). As defined previously, $d = a$ Type-A individual's effect on itself, and $z =$ its effect on every other member of the group:

$$F_A = \frac{\sum_0^{\infty} p_{mn} [d + (m-1)z]}{\sum_0^{\infty} p_{mn} m} \tag{15.4}$$

$$F_B = \frac{\sum_0^{\infty} p_{mn} nmz}{\sum_0^{\infty} p_{mn} n} \tag{15.5}$$

Even if individual fitnesses indicate otherwise, trait groups with more Type-A individuals in them can have enhanced fitness under certain circumstances, which will increase the fitness of Type-A over the entire deme (Wilson 1980).

Consider a four-species system, with the two types of plant (A and B), one parasitoid, and one herbivore. The interactions between all these entities are shown in Table 15.2. Self effects are negative (intraspecific competition). The direct effect of one entity on another is expressed as positive, negative, or none (+, -, or 0).

Table 15.2. Interactions between nectar-secreting plants, non-secreting plants, parasitoids, and herbivores.

Y	The effect of X on Y			
	X:Type-A plant (with nectar)	Type-B plant (without nectar)	Parasitoids	Herbivores
Type-A plant	-	-	0	-
Type-B plant	-	-	0	-
Parasitoids	+	0	-	+
Herbivores	+	+	-	-

We can specify basic difference equations for each species, using

- P = density of parasitoids (1,2—from herbivores on Type-A,B plants)
- H = density of herbivores (1,2—on Type-A,B plants)
- N = density of plants (1,2—Type-A and Type-B plants)
- A = attack rate of parasitoids on herbivores (1,2—for herbivores on Type-A,B plants)
- r = rate of increase (r_1 —for plants; r_2 —for herbivores)
- K = carrying capacity (K_1 —plants; K_2 —herbivores per individual plant)
- L = effect of herbivores on plants

The plant population growth equation has density dependence, so that growth slows as the carrying capacity is approached. The effect of herbivores

on plants (L) also limits population growth, relative to the number of herbivores at time t :

$$N_{t+1} = N_t \exp [r_1 \{1 - (N_t/K_1)\}] - LH_t \quad (15.6)$$

For herbivores, population growth is positively affected by plant density (N) at time t . Herbivore carrying capacity is defined on a per plant basis, and limits the increase of herbivores. Herbivore population growth is negatively affected by parasitoid density and the efficiency of parasitoids in finding the herbivores (A):

$$H_{t+1} = H_t \exp [r_2 \{1 - (H_t/NK_2)\}] - AP_t \quad (15.7)$$

Using the Nicholson-Bailey equation (Nicholson and Bailey 1935), parasitoid population growth is directly related to herbivore density at time t , and is self-limiting by both the attack rate on herbivores (A) and the parasitoid density at time t . As in equation (15.7), these two entities are inversely related: with a low rate of attack, more parasitoids can be accommodated in available herbivore hosts.

$$P_{t+1} = H_t (1 - \exp[-AP_t]) \quad (15.8)$$

The Nicholson-Bailey model assumes that parasitoids encounter prey in direct proportion to prey density, and that these encounters are distributed randomly among the available prey (Hassell 1978). The Nicholson-Bailey model shows increasing oscillations, but the density dependence in the basic herbivore equation renders the parasitoid equation (above) stable.

For the four-species system, with two types of plants, the equations are elaborated as follows. First, the densities at time t are defined (Part I, equations (15.9)–(15.12)). Then, the densities at time $t + 1$ are defined (Parts II–IV, equations (15.13)–(15.16)).

Part I

(a) Parasitoid density on Type-A plants at time t is a function of the proportion of Type-A plants in the population. The more Type-A plants in a group, the greater the attraction to parasitoids. The combined attraction is greater than that expected by a simple linear relationship up to the maximum of a pure population of Type-A. If x = the proportion of Type-A plants, the function is defined as

$$fnQ(x) = 2x - x^2$$

This gives the following equation for parasitoids on Type-A plants:

$$P_{t,A} = P_t fnQ(N_{t,A}/(N_{t,A} + N_{t,B})) \quad (15.9)$$

Parasitoid density on Type-B plants is simply the remainder of the total number of parasitoids at time t less the density on Type-A:

$$P_{t,B} = P_t - P_{t,A} \quad (15.10)$$

(b) Herbivore densities at time t are similarly divided between the two types of plants, with the number of herbivores on Type-A plants directly related to the proportion of Type-A plants in the population. Herbivores on Type-B plants are the remainder of the total less the density on Type-A plants:

$$H_{t,A} = H_t (N_{t,A}/(N_{t,A} + N_{t,B})) \quad (15.11)$$

$$H_{t,B} = H_t - H_{t,A} \quad (15.12)$$

Part II

Plant densities at time $t + 1$ (the next generation) are expressed for Type-A and Type-B plants separately. The plant rate of increase and carrying capacity are, of course, the same for each type of plant, as is the effect of herbivore damage on both types of plants:

$$N_{t,A,t+1} = N_{t,A} \exp [r_1 - ((N_{t,A} + N_{t,B})/K_1)] - LH_{t,A} \quad (15.13)$$

$$N_{t,B,t+1} = N_{t,B} \exp [r_1 - ((N_{t,A} + N_{t,B})/K_1)] - LH_{t,B} \quad (15.14)$$

Part III

Herbivore density at time $t + 1$ is a combination of herbivores supported on Type-A plants and Type-B plants. Both groups of herbivores have the same rate of increase and the same carrying capacity per plant, but the attack rate of parasitoids is greater on Type-A than on Type-B plants:

$$H_{t+1} = H_{t,A} \exp [(r_2(1 - H_{t,A}/(N_{t,A}K_2)) - A_1P_{t,A})] + H_{t,B} \exp [(r_2(1 - H_{t,B}/(N_{t,B}K_2)) - A_2P_{t,B})] \quad (15.15)$$

Part IV

The density of parasitoids at time $t + 1$ is determined by using the Nicholson-Bailey equation on the subdivided population. The first part of the following equation represents parasitoids from herbivores on Type-A plants, the second part represents those from herbivores on Type-B plants:

$$P_{t+1} = H_{t,A} (1 - \exp[-A_1P_{t,A}]) + H_{t,B} (1 - \exp[-A_2P_{t,B}]) \quad (15.16)$$

The equations were used to construct a simple simulation model. The BASIC program (shown in Appendix 15.1) then does the following:

1. Uses the above difference equations, and specifying initial population densities (N) for each type of plant, and the values for the various parameters.
2. Creates a number (T) of trait groups (using a random number generator), with mean density N_i and variance V_i for each species (plant type). The method of setting up the proportion of each plant type used here is not ideal (see Appendix 15.1).
3. For each trait group, the equations are iterated a number (I) of times to obtain densities at $t + I$. $I =$ The amount of time spent in the trait group, and the simplest case is used here, i.e. one generation ($I = 1$).
4. The densities of each trait group are added, and divided by T , to obtain average densities for the global population.
5. Repeating from step 2 above a number of times (generations), the simulation is achieved.

Behaviour of the model

The community undergoes stable oscillations, i.e. all entities persist, within certain limits of the various parameters of the model. Starting with equal numbers of Type-A and Type-B plants at a designated carrying capacity for plants and herbivores, stability is achieved when the magnitude of the effect of herbivores on plants is less than the magnitude of the attack rate of parasitoids on Type-A plants ($L < A_1$). Stability is also achieved when the relative magnitude of parasitoid attack rate on Type-A vs. Type-B plants is more than 10:1 ($A_1 > 10(A_2)$).

Starting with a large number of Type-B plants (no nectaries), the community can be invaded by Type-A. The speed of invasion of Type-A is not affected by the magnitude of A_1 : for both $A_1 = 0.1$ and 0.3 , the numbers of Type-A plants match Type-B numbers after 10 generations. This is probably due to the self-regulating effects of A in the parasitoid population growth equation (15.8).

The reverse situation (many Type-A plants, few Type-B) is less easily invaded by Type-B. This is because the small size of A_2 , the attack rate of parasitoids on herbivores on Type-B plants, does not enhance the representation of trait groups with the same magnitude as Type-A plants can upon invasion (above).

When the effect of herbivores on the plants is too great ($L > 0.05$) relative to the reproductive capacity of plants and the parasitoid attack rates, plants do not persist and the simulation is unstable, with all species going to zero.

If the initial number of Type-A plants is zero, after a number of generations the parasitoids do not persist, with $A_2 = 0.01$, but if A_2 is increased to 0.1, parasitoids do persist.

Other considerations

The cost of producing extrafloreal nectar could also be included in this model, by using two different values for plant reproductive capacity in equations (15.13) and (15.14): r_{11} for Type-A plants, and r_{12} for Type-B plants. The cost of nectar production could be experienced as a direct fitness cost that lowers the reproductive rate very slightly, so that $r_{11} < r_{12}$. Existing estimates of cost of extrafloreal nectar production are 1–2 per cent or less (e.g. O'Dowd 1979); the effect of this cost on the reproductive capacity would presumably be even less than that (though there is no experimental basis for this assumption), suggesting that the appropriate difference in r values might be as little as 0.0001. This elaboration of the model has not yet yielded satisfactory results.

No benefit to parasitoids from nectar is included in the parasitoid growth equation. The beneficial effects on adult parasitoid longevity and reproductive fitness (egg production) could be expressed only if there were a parasitoid r . However, most biologists do not consider this parameter to be of importance in parasitoid population growth.

Differences in generation time are always a consideration in modelling plant-herbivore interactions, and it is interesting here to consider the implications for annuals (where, simplistically, there could be a one-for-one match with the herbivore species) versus perennials. For perennial plants, there is always a component of future herbivory on that individual plant: the cost incurred in secretion of extrafloreal nectar and support of parasitized caterpillars one year may not yield any benefit that same year, but would in the future (a delayed-reward type of individual selection). For annuals, extrafloreal nectar production to support parasitoids may appear to be an altruistic act. Altruistic, that is, unless one considers the potential kin selection for increase in the number of Type-A (nectaried) plants, another dimension to the structured deme.

Discussion

The model presented here is in an early state of development and the results are only preliminary. Moreover, the full biological situation is far more complex than has been shown here. Many kinds of selection operate at once. There is direct selection by some parasitoids (e.g. those that kill eggs). There are different generation times involved with trees and herbivores; would it be more realistic to hold herbivore numbers as a constant? The model points out certain parameters that it is essential to measure accurately:

1. What is the cost to plants of producing nectar? How does this cost affect their rate of increase?
2. What is the effect of herbivores on plant fitness?

3. What are attack rates of parasitoids on herbivores? Do they differ on plants with nectaries and without, and what is the magnitude of that difference?

Modelling is a useful tool for field ecologists for two reasons. Firstly, one can test with a model whether or not a particular scenario (selective process, population change, etc.) can theoretically occur, and within what limits. Secondly, the results one obtains indicate what parameters of natural population predictions. This exercise has indicated the necessity of measuring several parameters, enumerated above, encountered in the study of plant-ant-parasitoid-herbivore interactions. It has compared and contrasted the interactions between plants bearing extrafloral nectaries with their two main guilds of protective agents, ants and parasitoids. And most importantly, this exercise has revealed the different ways in which selection might operate between ants and plants versus parasitoids and plants. The first is direct, straightforward, and easily demonstrated; while the second is indirect, more complex, and needs to be tested.

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Appendix 15.1. BASIC program for simulation described in this chapter

Note: The variable designations here differ in some cases from the equations in the paper.

Designated variables in this model

A1	attack rate of parasitoids for herbivores on Type-A plants
A2	attack rate of parasitoids for herbivores on Type-B plants
D	generation
H	density of herbivores
H1	density of herbivores on Type-A plants
H2	density of herbivores on Type-B plants
K1	plant carrying capacity
K2	herbivore carrying capacity per plant
L	effect of herbivores on plants
M	average density (initial)
N1	density of Type-A plants
N2	density of Type-B plants

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P	density of parasitoids
R1	plant <i>r</i> (reproductive capacity)
R2	herbivore <i>r</i> (reproductive capacity)
T	number of trait groups
T1	total density of plants

```

00010 DIM N1(20), N2(20), P1(20), P2(20), P(20), H1(20), H2(20), H(20), S1(4),
S2(5), M(4)
00020 OPEN "DATA.1" FOR OUTPUT AS #1
00030 INPUT "DO YOU WANT ALL TRAIT GROUPS LISTING (Y/N) "A$
00040 IF NOT(A$="Y" OR A$="y" OR A$="n" OR A$="N") THEN 30
00050 M(1)=60:M(2)=60:M(3)=100:M(4)=160
00055 PRINT#1, "M(1)="M(1); "M(2)="M(2); "M(3)="M(3); "M(4)="M(4)
00060 T = 20
00070 DEF FNB(I)=EXP(R1*(S-I**T))
00080 DEF FNC(I)=EXP((R2*(1-I/K2)-Q1*(Q2)))
00090 DEF FNA(I) = INT(0.5+(X+1)*RND(1))-1
00100 DEF FNC(X)=2**X-X**X
00110 A1 = 2:A2 = 0:A3 = 0:R1 = 1:K1 = 600:I = .05:R2 = 1:K2 = 10
00115 PRINT#1, "A1="A1; "A2="A2; "R1="R1; "K1="K1; "I="I; "R2="R2; "K2="K2
00116 PRINT "A1="A1; "A2="A2; "R1="R1; "K1="K1; "I="I; "R2="R2; "K2="K2
00120 PRINT #1, "PLANT A, PLANT B, POID, HERBV"
00124 PRINT #1, "GEN, POP SIZES, MEANS, VAR."
00125 PRINT "GEN, POP SIZES, MEANS, VAR."
00126 PRINT #1, "1 "
00127 PRINT "1 "
00130 GOSUB 150
00140 GOTO 300
00145 H(T)=P(T)=N1(T)=N2(T)=0: GOTO 150
00150 FOR G = 1 TO 19
00160 N1(G)=FNA(M(1)): IF N1(G) < 0 OR N1(G) > M(1) THEN 160
00170 N2(G)=FNA(M(2)): IF N2(G) < 0 OR N2(G) > M(2) THEN 170
00180 P(G)=FNA(M(3)): IF P(G) < 0 OR P(G) > M(3) THEN 180
00190 H(G)=FNA(M(4)): IF H(G) < 0 OR H(G) > M(4) THEN 190
00210 NEXT G
00220 GOSUB 700
00230 N1(T)=INT(0.5+(T*M(1)/2)-S1(1))
00240 N2(T)=INT(0.5+(T*M(2)/2)-S1(2))
00250 P(T)=INT(0.5+(T*M(3)/2)-S1(3))
00260 H(T)=INT(0.5+(T*M(4)/2)-S1(4))
00280 IF H(T) <= 0 OR P(T) <= 0 OR N2(T) <= 0 OR N1(T) <= 0 GO TO 145 ELSE GOTO
290
00290 RETURN
00300 REM NOW ALL 20 TRAIT GROUPS ARE SET UP
00310 GOSUB 510
00320 D=2
00330 FOR G=1 TO T
00340 IF A$="y" OR A$="Y" THEN PRINT#1, N1(G); N2(G); P(G); H(G)
00345 IF A$="y" OR A$="Y" THEN PRINT N1(G); N2(G); P(G); H(G)
00346 T1=N1(G)+N2(G)
00347 IF T1>0 THEN H1(G)=H(G)*N1(G)/T1: H2(G)=H(G)-H1(G) ELSE
H1(G)=0:H2(G)=0:H2(G)=0:H2(G)=0:H2(G)=0:H2(G)=0:
00350 IF T1>0 THEN P1(G)=P(G)*FNC(N1(G)/T1): P2(G)=P(G)-P1(G) ELSE
P1(G)=0:P2(G)=0:P(G)=0
00355 P(O)=INT(0.5+H1(G)*(1-EXP(-A1*P1(G)))+H2(G)*(1-EXP(-A2*P2(G))))
00360 S=1-(N1(G)+N2(G))/K1
00370 N1(O)=N1(G)*FNB(H1(G))
00380 N2(O)=N2(G)*FNB(H2(G))
00390 IF N1(G)>0 THEN Q1=A1:Q2=P1(G):H(O)=H1(G)*FNC(H1(G)/N1(G)) ELSE
H1(G)=0:H(O)=0
00400 IF N2(G)>0 THEN Q1=A2:Q2=P2(G):H(O)=H2(O)+H2(G)*FNC(H2(G)/N2(G))
ELSE H2(G)=0
00440 NEXT G
00450 PRINT#1, D;
00455 PRINT D;
00460 GOSUB 620
00470 FOR J9=1 TO 4
00472 M(J9)=INT(2*(S1(J9)/T))

```

```

00474 NEXT J9
00480 GOSUB 150
00485 GOSUB 510
00490 D=D+1
00500 IF D=21 THEN GOTO 750 ELSE GOTO 330
00510 GOSUB 620
00512 FOR G=1 TO 4
00513 PRINT #1,S1(G);
00514 PRINT S1(G);
00515 NEXT G
00520 FOR G=1 TO 4
00530 PRINT#1, FNZ(S1(G)/T);
00535 PRINT FNZ(S1(G)/T);
00540 NEXT G
00550 FOR G=1 TO 4
00560 PRINT#1, FNZ(ABS(S2(G)-S1(G)^2)/T)/(T-1);
00565 PRINT FNZ (ABS(S2(G)-S1(G)^2)/T)/(T-1));
00570 NEXT G
00571 PRINT#1," "
00572 PRINT" "
00580 RETURN
00590
00600
00610
00620 GOSUB 700
00623 FOR G=1 TO 4
00624 S2(G)=0
00625 NEXT G
00630 FOR G=1 TO T
00632 S2(1)=S2(1) +N1(G)*N1(G)
00640 S2(2)=S2(2) +N2(G)*N2(G)
00650 S2(3)=S2(3) +P(G)*P(G)
00660 S2(4)=S2(4) +H(G)*H(G)
00665 NEXT G
00670 RETURN
00680
00690
00700 FOR G=1 TO 4:
00702 S1(G)=0
00704 NEXT G
00710 FOR G=1 TO T
00712 S1(1)=S1(1) + N1(G)
00714 S1(2)=S1(2) +N2(G)
00716 S1(3)=S1(3) +P(G)
00718 S1(4)=S1(4) +H(G)
00720 NEXT G
00740 RETURN
00750 END

```

16

Bracken and ants: why is there no mutualism?

V. K. Rashbrook, S. G. Compton, and J. H. Lawton

Introduction

One of the advantages of studying a plant as cosmopolitan and ubiquitous as bracken fern (*Pteridium aquilinum* (L.) Kuhn), is that ecological comparisons can be made between different areas of its world-wide range (Lawton 1982, 1984; Compton *et al.* 1989). Bracken was initially assumed to be relatively immune to herbivory and thought to possess a scant arthropod fauna (Darwin 1877). However, although the plant does contain an array of secondary plant compounds (Lawton 1976; Cooper-Driver *et al.* 1977), it is by no means under-exploited by insect herbivores in comparison with other common plant species, and supports a diverse arthropod fauna in different parts of its range. Areas surveyed so far include continental Europe (Simmonds 1967), the UK (Lawton 1976, 1982), Papua New Guinea (Kirk 1977, 1982), south-west USA (Lawton 1982), Hawaii (Lawton 1984), Australia (E. Shuter and M. Westoby, unpublished work), New Zealand (Winterbourne 1987), and South Africa (Compton *et al.* 1989).

The extrafloral nectaries of bracken were first noted by Darwin (1877) and Lloyd (1901) and a comprehensive account of their variation in structure, distribution, and activity is given by Page (1982). Ants are by far the most frequently observed visitors to bracken nectaries. Although Tempel (1983) and Lawton and Heads (1984) also recorded parasitic hymenoptera at the nectaries in the USA and UK respectively, it was not established whether they utilized bracken herbivores as hosts. No parasitic wasps or predators other than ants have been observed at the nectaries in South Africa (Rashbrook 1989). Therefore, ants are the only group likely to offer the prospect of defending bracken from herbivores and hence to enter into a mutualism with the plant.

As Bentley (1977*a*) pointed out, no defence mutualism can exist between ants and plants unless the plants are actually vulnerable to their herbivores and ants constitute a meaningful defensive force. Testing the importance of herbivory is most readily achieved in plants for which an accurate measurement of sexual reproductive output can be made (Waloff and Richards 1977; Whitham and Mopper 1985). Due to its vegetative mode of reproduction, an

References to Part 3

- Addicott, J. F. (1984). Mutualistic interactions in population and community processes. In *A new ecology* (ed. P. W. Price, C. N. Slobodkinoff, and W. 16, pp. 438-55. John Wiley & Sons, New York.
- tropical understorey community. *Nature*, **336**, 574-5.
- Airy Shaw, H. K. (1980a). A partial synopsis of the Euphorbiaceae-Australia (excluding *Phyllanthus*, *Euphorbia* and *Calyxopappus*). *Kew Bulletin*, **577-700**.
- Airy Shaw, H. K. (1980b). The Euphorbiaceae of New Guinea. *Kew Additional Series*, **8**, 1-243.
- Altieri, M. A., von Schoonhoven, A., and Doll, J. (1977). in insect pest management systems: a review illustrated by *PANS*, **23(2)**, 195-205.
- Alsatt, P. R. (1981). Lycaenid butterflies and ants: selection for enemy-free space. *American Naturalist*, **118**, 638-54.
- Barton, A. M. (1986). Spatial variation in the effect of ants on an extrafloral nectar. *Ecology*, **67(2)**, 495-504.
- Bazzaz, F. A. and Pickett, S. T. A. (1980). The physiological ecology of succession. *Annual Review of Ecology and Systematics*, **11**, 287-310.
- Beattie, A. J. (1985). *The evolutionary ecology of anti-plant mutualisms*, 182 pp. Cambridge University Press, Cambridge.
- Beckmann, R. L.
- Ipomoea pandurata* (L.) G. F. W. Mey (Convolvulaceae). *American Journal Botany*, **68**, 72-9.
- Bentley, B. L. (1976). Plants bearing extrafloral nectaries and the associated community: interhabitat differences in the reduction of herbivore damage. *Ecology*, **57**, 815-20.
- Bentley, B. L. (1977a). Extrafloral nectaries and protection by pugnacious bodyguards. *Annual Review of Ecology and Systematics*, **8**, 407-27.
- Bentley, B. L. (1977b). The protective function of ants visiting the nectaries of *Bixa orellana* (Bixaceae). *Journal of Ecology*, **65**, 27-38.
- Bentley, B. L. (1981). Ants, extrafloral nectaries, and the vine life-form: an interaction. *Tropical Ecology*, **22**, 127-33.
- Bernays, E. A. and Woodhead, S. (1982). Plant phenols utilized as nutrients by phytophagous insect. *Science*, **216**, 201-3.
- Bishop, Y. M. M., Fienberg, S. E., and Holland, P. W. (1975). *Discrete analysis: theory and practice*. MIT Press, Cambridge.
- Blom, P. E. and Clark, W. H. (1980). Observations of ants (Hymenoptera: Formicidae) visiting extrafloral nectaries of the barrel cactus *Ferocactus gracilis* (Cactaceae) in Baja California, Mexico. *Southwestern Naturalist*, **25**, 181-96.
- Boecklen, W. J. (1984). The role of extrafloral nectaries in the herbivore defence of *Cassia fasciculata*. *Ecological Entomology*, **9(3)**, 243-9.
- Bolton, B. (1976). The ant tribe Tetramoriini (Hymenoptera: Formicidae): constituent

References to Part 3

- genera, review of smaller genera and revision of *Triglyphothrix* Forel. *Bulletin of the British Museum (Natural History)*, *Entomology*, **34**, 281-378.
- Briese, D. T. (1982). Damage to saltbush by the coccid *Pulvinaria maskelli* Olliff, and the role played by an attendant ant. *Journal of the Australian Entomological Society*, **21(4)**, 293-4.
- Brokaw, N. V. L. (1985). Treefalls, regrowth, and community structure in tropical forests. In *The ecology of natural disturbance and patch dynamics* (ed. S. T. A. Pickett and P. S. White), pp. 53-69. Academic Press, Orlando.
- Brokaw, N. V. L. (1987). Gap-phase regeneration of three pioneer tree species in a tropical forest. *Journal of Ecology*, **75**, 9-19.
- Brown, W. L., Jr. (1973). A comparison of the Hylean and Congo-West African rain forest ant faunas. In *Tropical forest ecosystems in Africa and South America: a comparative review* (ed. B. J. Meggers, E. Ayensu, and W. D. Duckworth). Smithsonian Institution Press, Washington.
- Buckley, R. C. (1982). Ant-plant interactions: a world review. In *Ant-plant interactions in Australia* (ed. R. C. Buckley), pp. 111-41. W. Junk, The Hague.
- Carroll, C. R. and Janzen, D. H. (1973). Ecology of foraging by ants. *Annual Review of Ecology and Systematics*, **4**, 231-57.
- Caughley, G. and Lawton, J. H. (1981). Plant-herbivore systems. In *Theoretical ecology: Principles and applications* (ed. R. M. May), pp. 132-66. Blackwell, Oxford.
- Chapin, F. S. III. (1989). The cost of tundra plant structures: evaluation of concepts and currencies. *American Naturalist*, **133**, 1-19.
- Clancy, K. M. and Price, P. W. (1986). Temporal variation in three-trophic-level interactions among willows, sawflies, and parasites. *Ecology*, **67(6)**, 1601-7.
- Coley, P. D. (1983a). Herbivory and defensive characteristics of tree species in a lowland tropical forest. *Ecological Monographs*, **53**, 209-33.
- Coley, P. D. (1983b). Intraspecific variation in herbivory on two tropical tree species. *Ecology*, **64(3)**, 426-33.
- Coley, P. D. (1987). Interspecific variation in plant anti-herbivore properties: the role of habitat quality and rate of disturbance. *New Phytologist*, **106** (Suppl.), 251-63.
- Coley, P. D. (1988). Effects of plant growth rate and leaf lifetime on amount and type of anti-herbivore defense. *Oecologia*, **74**, 531-6.
- Coley, P. D. and Aide, T. M. (1990). A comparison of herbivory and plant defenses in temperate and tropical broad-leaved forests. In *Herbivory: tropical and temperate perspectives* (ed. P. W. Price, T. M. Lewinsohn, W. W. Benson, and G. W. Fernandes) pp. 25-49. John Wiley and Sons, New York.
- Coley, P. D., Bryant, J. P., and Chapin, F. S. III. (1985). Resource availability and plant antiherbivore defense. *Science*, **230**, 895-9.
- Compton, S. G. and Robertson, H. G. (1988). Complex interactions between mutualisms: ants tending homopterans protect fig seeds and pollinators. *Ecology*, **69**, 1302-5.
- Compton, S. G., Lawton, J. H., and Rashbrook, V. K. (1989). Regional diversity, local community structure and vacant niches: the herbivorous arthropods of bracken in South Africa. *Ecological Entomology*, **14**, 365-73.
- Cooper-Driver, G., Finch, S., Swain, T., and Bernays, E. (1977). Seasonal variation in secondary plant compounds in relation to the palatability of *Pteridium aquilinum*. *Biochemical Systematics and Ecology*, **5**, 177-83.
- Crepps, W. F. (1975). Influence of specific non-crop vegetation on the insect fauna of small-scale agroecosystems. M.Sc. thesis. University of California, Davis.

- Croat, T. B. (1978). *Flora of Barro Colorado Island*. Stanford University Press, Stanford.
- Cronquist, A. (1981). *An integrated system of classification of flowering plants*. Columbia University Press, New York.
- Darwin, F. (1877). On the glandular bodies of *Acacia sphaerocephala* and *Cecropia peltata* serving as food for ants. With an appendix on the nectar-glands of the common brake fern, *Pteris aquilina*. *Botanical Journal of the Linnean Society*, **15**, 398-409.
- De Bach, P. (1964). *Biological control of insect pests and weeds*, 844 pp. Reinhold, New York.
- Denno, R. F. and McClure, M. S. (1983). *Variable plants and herbivores in natural and managed systems*. Academic Press, New York.
- Death, D. (1977). The function of extrafloral nectaries in *Aphelandra deppeana* Schl. & Cham. (Acanthaceae). *Brenesia*, **10/11**, 135-45.
- DeVries, P. and Baker, I. (1989). Butterfly exploitation of an ant-plant mutualism: adding insult to herbivory. *Journal of the New York Entomological Society* (in press).
- Douglas, M. M. (1983). Defense of bracken fern by arthropods attracted to axillary nectaries. *Psyche*, **90**, 313-20.
- Duffey, S. S. (1986). Plant glandular trichomes: their partial role in defence against insects. In *Insects and the plant surface* (ed. B. E. Juniper and T. R. E. Southwood), pp. 151-72. Edward Arnold, London.
- Elias, T. S. (1983). Extrafloral nectaries: their structure and distribution. In *The biology of nectaries* (ed. B. L. Bentley and T. S. Elias), pp. 174-203. Columbia University Press, New York.
- Elias, T. S. and Gelband, H. (1975). Nectar: its production and functions in the trumpet creeper. *Science*, **189**, 289-91.
- Feeny, P. P. (1976). Plant apparency and chemical defense. *Recent Advances in Phytochemistry*, **10**, 1-40.
- Fiala, B., Maschwitz, U., Tho, T. Y., and Helbig, A. J. (1989). Studies of a South East Asian ant-plant association: protection of *Macaranga* trees by *Crematogaster borneensis*. *Oecologia*, **79**, 463-70.
- Foster, R. B. and Brokaw, N. V. L. (1982). Structure and history of Barro Colorado Island. In *The ecology of a tropical forest. Seasonal rhythms and long term changes* (ed. E. G. Leigh, Jr., A. S. Rand, and D. M. Windsor), pp. 67-81. Smithsonian Institution Press, Washington, DC.
- Fowler, S. V. and Lawton, J. H. (1985). Rapidly induced defences and talking trees: the devil's advocate position. *American Naturalist*, **126**(2), 181-95.
- Fritz, R. S. (1982). An ant-treeshopper mutualism: effects of *Fornica subsericea* on the survival of *Vanduzeeo arguata*. *Ecological Entomology*, **7**, 267-76.
- Gilbert, L. E. (1975). Ecological consequences of a coevolved mutualism between butterflies and plants. In *Coevolution of animals and plants* (ed. L. E. Gilbert and P. H. Raven), pp. 210-40. University of Texas Press, Austin.
- Gilbert, L. E. and Smiley, J. T. (1978). Determinants of local diversity in phytophagous insects: host specialists in tropical environments. *Symposium of the Royal Entomological Society of London*, **9**, 89-104.
- Goodland, R. (1971). A physiognomic analysis of the cerrado vegetation of central Brazil. *Journal of Ecology*, **59**, 411-19.
- Gould, S. J. and Vrba, E. S. (1982). Exaptation—a missing term in the science of form. *Paleobiology*, **8**, 4-15.

- Harley, J. L. and Smith, S. E. (1983). *Mycorrhizal symbiosis*. Academic Press, London.
- Harper, J. H. (1977). *Population biology of plants*. Academic Press, London.
- Hassell, M. P. (1978). *The dynamics of arthropod predator-prey systems*. Princeton University Press, New Jersey.
- Hassell, M. P. (1980). Foraging strategies, population models and biological control: a case study. *Journal of Animal Ecology*, **49**, 603-28.
- Hassell, M. P. (1982). Patterns of parasitism by insect parasitoids in patchy environments. *Ecological Entomology*, **7**, 365-77.
- Hassell, M. P. (1985). Insect natural enemies as regulating factors. *Journal of Animal Ecology*, **54**, 323-34.
- Hassell, M. P. and Waage, J. K. (1984). Host-parasitoid population interactions. *Annual Review of Entomology*, **29**, 89-114.
- Hawkins, C. P. and MacMahon, J. A. (1989). Guilds: the multiple meanings of a concept. *Annual Review of Entomology*, **34**, 423-52.
- Heads, P. A. (1986). Bracken, ants and extrafloral nectaries. IV. Do wood ants (*Fornica lugubris*) protect the plant against insect herbivores? *Journal of Animal Ecology*, **55**, 795-809.
- Heads, P. A. and Lawton, J. H. (1984). Bracken, ants and extrafloral nectaries. II. The effect of ants on the insect herbivores of bracken. *Journal of Animal Ecology*, **53**(3), 1015-31.
- Heads, P. A. and Lawton, J. H. (1985). Bracken, ants and extrafloral nectaries. III. How insect herbivores avoid ant predation. *Ecological Entomology*, **10**, 29-42.
- Hespenheide, H. A. (1985). Insect visitors to extrafloral nectaries of *Byrnia aculeata* (Sterculiaceae): relative importance and roles. *Ecological Entomology*, **10**(2), 191-204.
- Hill, M. G. and Blackmore, P. J. M. (1980). Interactions between ants and the coccid *Icerya seychellanum* on *Aldabra* Atoll. *Oecologia*, **45**, 360-5.
- Horvitz, C. C. and Schemske, D. W. (1984). Effects of nectar-harvesting ants and an ant-tended herbivore on seed production of a neotropical herb. *Ecology*, **65**(5), 1369-78.
- Howe, H. F. (1984). Constraints on the evolution of mutualisms. *American Naturalist*, **123**, 764-77.
- Hubbell, S. P. and Foster, R. B. (1986). Canopy gaps and the dynamics of a neotropical forest. In *Plant ecology* (ed. M. J. Crawley), pp. 77-96. Blackwell Scientific Publications, Oxford.
- Huxley, C. R. (1986). Evolution of benevolent ant-plant relationships. In *Insects and the plant surface* (ed. B. E. Juniper and T. R. E. Southwood), pp. 257-82. Edward Arnold, London.
- Inouye, D. W. and Taylor, O. R. (1979). A temperate region plant-ant-seed predator system: consequences of extrafloral nectar secretion by *Helianthella quinquevervis*. *Ecology*, **60**, 1-7.
- Janzen, D. H. (1966). Coevolution of mutualism between ants and acacias in Central America. *Evolution*, **20**, 249-75.
- Janzen, D. H. (1967). Interaction of the Bull's-Horn acacia (*Acacia corrigera* L.) with one of its ant inhabitants (*Pseudomyrmex ferruginea* F. Smith) in eastern Mexico. *Kansas University Science Bulletin*, **47**, 315-558.
- Janzen, D. H. (1973). Dissolution of mutualism between *Cecropia* and its *Azteca* ants. *Biotropica*, **5**, 15-28.
- Jeffree, C. E. (1986). The cuticle, epicuticular waxes and trichomes of plants, with

- reference to their structure, functions and evolution. In *Insects and the plant surface* (ed. B. E. Juniper and T. R. E. Southwood), pp. 23-64. Edward Arnold, London.
- Jeffries, M. J. and Lawton, J. H. (1984). Enemy free space and the structure of ecological communities. *Biological Journal of the Linnean Society*, **23**, 269-86.
- Jolivet, P. (1986). *Les fourmis et les plantes—un exemple de coevolution*, 245 pp. Société Nouvelle des Editions Boubee, Paris.
- Keeler, K. H. (1979*a*). Distribution of plants with extrafloral nectaries and ants at two elevations in Jamaica. *Biotropica*, **11**, 152-4.
- Keeler, K. H. (1979*b*). Species with extrafloral nectaries in a temperate flora (Nebraska). *Prairie Naturalist*, **11**, 33-7.
- Keeler, K. H. (1980*a*). The extrafloral nectaries of *Ipomoea leptophylla* (Convolvulaceae). *American Journal of Botany*, **67**, 216-22.
- Keeler, K. H. (1980*b*). Distribution of plants with extrafloral nectaries in temperate communities. *American Midland Naturalist*, **104**, 274-80.
- Keeler, K. H. (1981*a*). Cover of plants with extrafloral nectaries in four northern California habitats. *Madrono*, **28**, 26-9.
- Keeler, K. H. (1981*b*). Function of *Mentzelia nuda* (Loasaceae) postfloral nectaries in seed defense. *American Journal of Botany*, **68**(2), 295-9.
- Keeler, K. H. (1981*c*). A model of selection for facultative nonsymbiotic mutualism. *American Naturalist*, **118**, 488-98.
- Keeler, K. H. (1985). Extrafloral nectaries on plants in communities without ants: Hawaii. *Oikos*, **44**, 407-14.
- Keeler, K. H. (1989). Ant-plant interactions. In *Plant-animal interactions* (ed. W. G. Abrahamson), pp. 207-42. McGraw-Hill Book Co., New York.
- Keeler, K. H. and Kaul, R. B. (1979). Morphology and distribution of petalifer nectaries in *Ipomoea* (Convolvulaceae). *American Journal of Botany*, **66**, 946-52.
- Kelly, C. A. (1986). Extrafloral nectaries: ants, herbivores and fecundity in *Cassia fasciculata*. *Oecologia*, **69**, 600-5.
- Kempf, W. W. (1973). A new *Zacryprocerus* from Brazil, with remarks on the generic classification of the tribe Cephalotini (Hymenoptera—Formicidae). *Studia Entomologica*, **16**, 449-62.
- Kirk, A. A. (1977). The insect fauna of the weed *Peridium aquilinum* (L.) Kuhn (Polypodiaceae) in Papua New Guinea: a potential source of biological control agents. *Journal of the Australian Entomological Society*, **16**, 403-9.
- Kirk, A. A. (1982). Insects associated with bracken fern *Peridium aquilinum* (Polypodiaceae) in Papua New Guinea and their possible use in biological control. *Acta Oecologica/Oecologia Applicata*, **3**, 343-59.
- Kopur, S. (1979). Facultative mutualism between weedy vetches bearing extrafloral nectaries and weedy ants in California. *American Journal of Botany*, **66**, 1016-20.
- Kopur, S. (1983). Flowering phenology and floral biology of *Inga* (Fabaceae: Mimosoideae). *Systematic Botany*, **8**, 354-68.
- Kopur, S. (1984). Experimental evidence for defense of *Inga* (Mimosoideae) saplings by ants. *Ecology*, **65**, 1787-93.
- Kopur, S. (1985). Alternative defenses against herbivores in *Inga* (Fabaceae: Mimosoideae) over an elevational gradient. *Ecology*, **66**(5), 1639-50.
- Kopur, S. (1989). Is extrafloral nectar production an inducible defense? In *Evolutionary ecology of plants* (ed. J. Bock and Y. Linhart), pp. 323-39. Westview Press, Boulder.

- Kopur, S. and Lawton, J. H. (1988). Interactions among vetches bearing extrafloral nectaries, their biotic protection agents, and herbivores. *Ecology*, **69**(1), 278-83.
- Kopur, S., Smith, A. R., and Baker, I. (1982). Nectaries in some neotropical species of *Polypodium* (Polypodiaceae): preliminary observations and analyses. *Biotropica*, **14**, 108-13.
- Kusnezov, N. (1957). Numbers of species of ants in faunae of different latitudes. *Evolution*, **11**, 298-9.
- Laine, K. J. and Niemelä, P. (1980). The influence of ants on the survival of mountain birches during an *Oporinia autumnata* (Lep., Geometridae) outbreak. *Oecologia*, **47**, 39-42.
- Law, R. (1985). Evolution in a mutualistic environment. In *The biology of mutualism: ecology and evolution* (ed. D. H. Boucher). Croom Helm, London.
- Law, R. and Kopur, S. (1986). On the evolution of non-specific mutualism. *Biological Journal of the Linnean Society*, **27**, 251-67.
- Lawton, J. H. (1976). The structure of the arthropod community on bracken. *Botanical Journal of the Linnean Society*, **73**, 187-216.
- Lawton, J. H. (1978). Host-plant influences on insect diversity: the effects of space and time. In *Diversity of insect faunas* (ed. L. A. Mound and N. Waloff), pp. 105-25. Blackwell, Oxford.
- Lawton, J. H. (1982). Vacant niches and unsaturated communities: a comparison of bracken herbivores at sites on two continents. *Journal of Animal Ecology*, **51**, 573-95.
- Lawton, J. H. (1983). Plant architecture and the diversity of phytophagous insects. *Annual Review of Entomology*, **28**, 23-9.
- Lawton, J. H. (1984). Non-competitive populations, non-convergent communities, and vacant niches: the herbivores of bracken. In *Ecological communities: conceptual issues and the evidence* (ed. D. R. Strong, D. Simberloff, and L. G. Abele), pp. 67-100. Princeton University Press, Princeton.
- Lawton, J. H. (1986). Biological control of bracken: plans and possibilities. In *Bracken. Ecology, land use and control technology* (ed. R. T. Smith and J. A. Taylor), pp. 445-52. Parthenon Publishing, Carnforth, England.
- Lawton, J. H. (1988). Biological control of bracken in Britain: constraints and opportunities. *Philosophical Transactions of the Royal Society of London B*, **318**, 335-55.
- Lawton, J. H. and Heads, P. A. (1984). Bracken, ants and extrafloral nectaries. I. The components of the system. *Journal of Animal Ecology*, **53**, 995-1014.
- Lawton, J. H. and McNeill, S. (1979). Between the devil and the deep blue sea: on the problem of being a herbivore. In *Population dynamics* (ed. R. M. Anderson, B. D. Turner, and L. R. Taylor), pp. 223-440. Blackwell Scientific, Oxford.
- Lawton, J. H., MacGarvin, M., and Heads, P. A. (1986). The ecology of bracken-feeding insects: background for a biological control programme. In *Bracken. Ecology, land use and control technology* (ed. R. T. Smith and J. A. Taylor), pp. 285-92. Parthenon Press, Carnforth, England.
- Leigh, E. G., Jr., Rand, A. S., and Windsor, D. M. (ed.) (1982). *The ecology of a tropical forest. Seasonal rhythms and long-term changes*.
- Leius, K. (1967). Influence of wild flowers on parasitism of tent caterpillar and codling moth. *Canadian Entomologist*, **99**, 444-6.
- Lenzen, N. R. and Brubaker, C. L. (1987). Extrafloral nectaries in Leguminosae: review and original observations in *Erythrina* and *Munca* (Papilionoideae; Phaseoleae). *Bulletin of the Torrey Botanical Club*, **114**, 437-47.

- Lloyd, F. E. (1901). The extra-nuptial nectaries in the common brake, *Pteridium aquilinum*. *Science*, **13**, 885–90.
- MacGarvin, M., Lawton, J. H., and Heads, P. A. (1986). The herbivorous insect communities of open and woodland bracken: observations, experiments and habitat manipulations. *Oikos*, **47**, 135–48.
- McKey, D. (1979). The distribution of secondary compounds within plants. In *Herbivores: Their interaction with secondary plant metabolites* (ed. G. A. Rosenthal and D. H. Janzen), pp. 55–133. Academic Press, New York.
- McKey, D. (1984). Interaction of the ant-plant *Leonardoxa africana* (Caesalpiniaceae) with its obligate inhabitants in a rainforest in Cameroon. *Biotropica*, **16**, 81–99.
- McKey, D. (1988). Promising new directions in the study of ant-plant mutualisms. In *Proceedings of the XIV International Botanical Congress* (ed. W. Greuter and B. Zimmer), pp. 335–55. Koeltz Königstein/Taunus.
- McKey, D. (1989). Interactions between ants and leguminous plants. In *Legume biology* (ed. J. Zarucchi and C. Shitton). Missouri Botanical Gardens, Louis.
- McLain, D. K. (1983). Ants, extrafloral nectaries and herbivory on the passion *Passiflora incarnata*. *American Midland Naturalist*, **110**, 433–9.
- Maschwitz, U., Schroth, M., Manel, M., and Yow Pong,
- ing symbiotic plant-ant partnerships. *Oecologia*, **64**, 78–80.
- Messina, F. J. (1981). Plant protection as a consequence of an mutualism: interactions on goldenrod (*Solidago* sp.). *Ecology*, **62**, 1433–40.
- Mooney, H. A. (1972). The carbon balance of plants. *Annual Review of Ecology Systematics*, **3**, 315–46.
- Mooney, H. A. and Gulmon, S. L. (1982). Constraints on leaf in reference to herbivory. *BioScience*, **32**, 198–206.
- Morais, H. C. (1980). Estrutura de uma comunidade de formigas arbóricolas vegetação de campo cerrado. M.Sc. thesis, Universidade Estadual de Campinas, SP, Brazil.
- Morais, H. C. and Benson, W. W. (1988). Recolonização de vegetação de após queimada, por formigas arbóricolas. *Revista Brasileira de Biologia*, **48**, 459–66.
- Newbury, D. and Foresta, H. (1985). Herbivory and defense in pioneer, gap, understorey trees of tropical rain forest in French Guiana. *Biotropica*, **17**(3), 238–44.
- Nicholson, A. J. and Bailey, V. A. (1935). The balance of animal populations. *Proceedings of the Zoological Society of London*, **1935**, 551–98.
- O'Dowd, D. J. (1979). Foliar nectar production and ant activity on a neotropical tree, *Ochroma pyramidalis*. *Oecologia*, **43**, 233–48.
- O'Dowd, D. J. (1980). Pearl bodies of a neotropical tree, *Ochroma pyramidalis*: ecological implications. *American Journal of Botany*, **67**, 543–9.
- O'Dowd, D. J. (1982). Pearl bodies as ant food: an ecological role for some leaf emergences of tropical plants. *Biotropica*, **14**, 40–9.
- O'Dowd, D. J. and Catchpole, E. A. (1983). Ants and extrafloral nectaries: no evidence for plant protection in *Heliconium* spp.—ant interactions. *Oecologia*, **59**(2–3), 191–200.
- Oliveira, P. S. (1988). Sobre a interação de formigas com o pequi do cerrado, *Caryocar brasiliense* Camb. (Caryocaraceae): O significado ecológico de nectários extraflorais. Ph.D. thesis, Universidade Estadual de Campinas, São Paulo, Brazil.
- Oliveira, P. S. and Leitão-Filho, H. F. (1987). Extrafloral nectaries: their taxonomic distribution and abundance in the woody flora of cerrado vegetation in southeast Brazil. *Biotropica*, **19**, 140–8.
- Oliveira, P. S. and Oliveira-Filho, A. T. (1990). Distribution of extrafloral nectaries in woody flora of tropical communities in Western Brazil. In *Herbivory: tropical and temperate comparisons* (ed. P. W. Price, W. W. Benson, T. M. Lewinsohn, and G. W. Fernandes). John Wiley and Sons, New York.
- Oliveira, P. S., Silva, A. F. da, and Martins, A. B. (1987). Ant foraging on extrafloral nectaries of *Qualea grandiflora* (Vochysiaceae) in cerrado vegetation: ants as potential anti-herbivore agents. *Oecologia*, **74**, 228–30.
- Page, C. N. (1982). Field observations on the nectaries of bracken, *Pteridium aquilinum*, in Britain. *Fern Gazette*, **12**, 243–5.
- Pagel, M. D. and Harvey, P. H. (1988). Recent developments in the analysis of comparative data. *Quarterly Review of Biology*, **63**, 413–40.
- Pemberton, R. W. (1988). The abundance of plants bearing extrafloral nectaries in Colorado and Mojave desert communities of southern California. *Madrono*, **35**, 238–46.
- Pierce, N. E. and Mead, P. S. (1981). Parasitoids as selective agents in the symbiosis between lycaenid butterfly larvae and ants. *Science*, **211**, 1185–7.
- Price, P. W., Bouton, C. E., Gross, P., McPherson, B. A., Thompson, J. N., and Weis, A. E. (1980). Interactions among three trophic levels: influence of plants on interactions between insect herbivores and natural enemies. *Annual Review of Ecology and Systematics*, **11**, 41–65.
- Price, P. W. and Clancy, K. M. (1986). Interactions among three trophic levels: gall size and parasitoid attack. *Ecology*, **67**(6), 1593–600.
- Price, P. W., Westoby, M., Rice, B., Aitsatt, P. R., Fritz, R. S., Thompson, J. N., and Mobley, K. (1986). Parasite mediation in ecological interactions. *Annual Review of Ecology and Systematics*, **17**, 487–505.
- Putz, F. E. (1984). The natural history of lianas on Barro Colorado Island, Panama. *Ecology*, **65**, 1713–24.
- Putz, F. E. and Windsor, D. M. (1987). Liana phenology on Barro Colorado Island, Panama. *Biotropica*, **19**, 334–41.
- Rand, A. S. and Rand, W. M. (1982). Variation in rainfall on Barro Colorado Island. In *The ecology of a tropical forest. Seasonal rhythms and long-term changes* (ed. E. G. Leigh, Jr., A. S. Rand, and D. M. Windsor), pp. 47–59. Smithsonian Institution Press, Washington, D. C.
- Rashbrook, V. K. (1989). Interactions between ants, herbivorous insects and bracken (*Pteridium aquilinum*), a fern with extrafloral nectaries. M.Sc. thesis. Rhodes University, South Africa.
- Rhodes, D. F. (1979). Evolution of plant chemical defense against herbivores. In *Herbivores: Their interaction with secondary plant metabolites* (ed. G. A. Rosenthal and D. H. Janzen), pp. 3–54. Academic Press, London.
- Rhodes, D. F. and Gates, R. G. (1976). Toward a general theory of plant anti-herbivore chemistry. In *Biochemical interaction between plants and insects* (ed. J. W. Wallace and R. L. Mansell), pp. 168–213. Plenum Publishing Co., New York.
- Rickson, F. R. (1977). Progressive loss of ant-related traits of *Cecropia peltata* on selected Caribbean islands. *American Journal of Botany*, **64**, 585–92.
- Rickson, F. R. (1980). Developmental anatomy and ultrastructure of the ant-food bodies (Beccarian bodies) of *Macaranga triloba* and *M. hypoleuca* (Euphorbiaceae). *American Journal of Botany*, **67**, 285–93.

- Ridley, H. N. (1910). Symbiosis of ants and plants. *Annals of Botany*, **24**, 457-85.
- Ridley, M. (1983). *The explanation of organic diversity*. Oxford University Press, Oxford.
- Ridley, M. (1986). The number of males in a primate troop. *Animal Behaviour*, **66**, 1848-58.
- Rodriguez, E., Healey, P. L., and Mehta, I. (ed.) (1984). *Biology and chemistry of rithomes*. Plenum Press, New York.
- Schemske, D. W. (1980). The evolutionary significance of extra floral nectar production by *Cosmos woodsorum* (Zingiberaceae): an experimental analysis of ant protection. *Journal of Ecology*, **68**, 959-67.
- Schemske, D. W. (1982). Ecological correlates of a neotropical mutualism: ant assemblages at *Cosmos* extrafloral nectaries. *Ecology*, **63**, 932-41.
- Schemske, D. W. (1983). Limits to specialization and coevolution in plant-animal mutualisms. In *Coevolution* (ed. M. H. Nitecki) pp. 67-109. Press, Chicago.
- Schemske, D. W. and Horvitz, C. C. (1988). Plant-animal interactions and production in a neotropical herb: a path analysis. *Ecology*, **69**(4), 1128-37
- Schupp, E. W. (1986). *Azteca* protection of *Cecropia*: ant occupation juvenile trees. *Oecologia*, **70**, 379-85
- Simmonds, F. J. (1967). Possibilities of biological control of bracken *aquilinum* (L.) Kuhn (Polypodiaceae). *Pest Articles and News Summaries* (C), 200-3.
- Smiley, J. T. (1985). *Heliconius* caterpillar mortality during establishment with and without attending ants. *Ecology*, **66**, 845-9.
- Smiley, J. T. (1986). Ant constancy at *Passiflora* extrafloral nectaries: effects caterpillar survival. *Ecology*, **67**(2), 516-21.
- Smiley, J. T., Aitsart, P. R., and Pierce, N. E. (1988) butterfly, *Jahnenus evagoras*, in response to host ants and plants. *Oecologia*, 416-22.
- Smith, L. L., Lanza, J., and Smith, G. C. (1990). floral nectar of *Impatiens sultani* increase after simulated herbivory **71**(1), 107-15.
- Snelling, R. R. (1973). The ant genus *Conomyrma* in the United States. *in Science, Natural History Museum of Los Angeles County*, **238**, 1-6
- Sokal, R. R. and Rohlf, F. J. (1981). *Biometry*, 2nd edn. W. H. Freeman Company, New York.
- Southwood, T. R. E., Brown, V. K., and Reader, P. M. (1983) vegetation in space and time: a comparison of insects' habitat successional stages. *Researches on Population Ecology*, **3** (Suppl.), 61-74.
- Stephenson, A. G. (1982). limiting herbivory and increasing fruit production. *Ecology*, **63**, 663-9.
- Strong, D. R., Lawton, J. H., and Southwood, T. R. E. (1984). *Insects on plants* well Scientific Publications, Oxford
- Sudd, J. H. (1983). Distribution of foraging wood aphids. *Insectes Sociaux*, **30**(3), 293-307
- Sudd, J. H. and Sudd, M. E. (1985). Seasonal changes in the (*Formica lugubris*) to sucrose baits. *Ecological Entomology*, **10**, 89-97.
- Takeda, S., Kinomura, K., and honeydew excretion and
- Taylor, F. (1977). Foraging behavior of ants: experiments with two species of myrmecine ants. *Behavioral Ecology and Sociobiology*, **2**, 147-67.
- Taylor, J. (1986). The bracken problem: a local hazard and global issue. In *Bracken. Ecology, land use and control technology* (ed. R. T. Smith and J. A. Taylor), pp. 21-42. Parthenon Publishing, Carnforth, England.
- Tempel, A. S. (1983). Bracken fern (*Pteridium aquilinum*) and nectar-feeding ants: a nonmutualistic interaction. *Ecology*, **64**, 1411-22.
- Tho, Y. P. (1978). Living in harmony. *Nature Malaysiana*, **3**, 34-9.
- Thompson, J. N. (1988). Variation in interspecific interactions. *Annual Review of Ecology and Systematics*, **19**, 65-87.
- Tilman, D. (1978). Cherries, ants and tent caterpillars: timing of nectar production in relation to susceptibility of caterpillars to ant predation. *Ecology*, **59**, 686-92.
- Waloff, N. and Richards, O. W. (1977). The effect of insect fauna on growth, mortality and natality of broom, *Sarothamnus scoparius*. *Journal of Applied Ecology*, **14**, 787-98.
- Washburn, J. O. (1984). Mutualism between a cynipid gall wasp and ants. *Ecology*, **65**, 654-6.
- Washburn, J. O. and Cornell, H. V. (1981). Parasitoids, patches, and phenology: their possible role in the local extinction of a cynipid gall wasp population. *Ecology*, **62**(6), 1597-607.
- Way, M. J. (1963). Mutualism between ants and honeydew producing Homoptera. *Annual Review of Entomology*, **8**, 307-44.
- Webster, G. L. (1967). The genera of Euphorbiaceae in the southeastern United States. *Journal of the Arnold Arboretum*, **48**, 303-430.
- Weis, A. G. and Abrahamson, W. G. (1985). Potential selective pressures by parasitoids on a plant-herbivore interaction. *Ecology*, **66**(4), 1261-9.
- Wells, H. and King, J. L. (1980). A general 'exact' test for N x M contingency tables. *Bulletin of the Southern California Academy of Sciences*, **79**, 65-77.
- Whalen, M. A. and Mackay, D. A. (1988). Patterns of ant and herbivore activity on five understory Euphorbiaceous saplings in submontane Papua New Guinea. *Biotropica*, **20**(4), 294-300.
- Whitham, T. G. and Mopper, S. (1985). Chronic herbivory: impacts on architecture and sex expression of piñon pine. *Science*, **228**, 1089-91.
- Wilson, D. S. (1980). *The natural selection of populations and communities*. Benjamin Cummings, Menlo Park.
- Wilson, E. O. (1976). Which are the most prevalent ant genera? *Studia Entomologica*, **19**, 187-200.
- Winterbourne, M. J. (1987). The arthropod fauna of bracken (*Pteridium aquilinum*) on the Port Hills, South Island, New Zealand. *New Zealand Entomologist*, **10**, 99-104.
- Wolf, P. G., Hauffer, C. H., and Sheffield, E. (1988). Electrophoretic variation and mating system of the clonal weed *Pteridium aquilinum* (L. Kuhn) (bracken). *Evolution*, **42**, 1350-55.
- Zar, J. H. (1984). *Biostatistical analysis*. 2nd edn, p. 201. Prentice-Hall, Englewood Cliffs, New York.