

# Induced indirect defence in a lycaenid–ant association: the regulation of a resource in a mutualism

Anurag A. Agrawal<sup>1\*</sup> and James A. Fordyce

<sup>1</sup>*Department of Botany, University of Toronto, 25 Willcocks Street, Toronto, ON, Canada M5S 3B2*

<sup>2</sup>*Section of Evolution and Ecology, and Center for Population Biology, University of California, 1 Shields Avenue, Davis, CA 95616, USA*

Indirect defences involve the protection of a host organism by a mutualistic partner. Threat of predation to the host organism may induce the production of rewards and/or signals that attract the mutualistic partner. In laboratory and field experiments we show that threatened lycaenid butterfly larvae (*Plebejus acmon*) produce more nectar rewards from their gland and were tended by protective ants twice as much as controls. Ant attendance did not affect the leaf consumption or feeding behaviour of larvae in the absence of predators. Inducible nectar production and indirect defence in this system may be a mechanism by which larvae provide rewards for services when they are needed the most. Such a system may stabilize the mutualistic association between lycaenid larvae and ants by preventing exploitation by either partner.

**Keywords:** mutualism; ant–caterpillar association; *Plebejus acmon*; symbiosis; tending; tritrophic interactions

## 1. INTRODUCTION

Defence against predators and parasites has been usefully divided into direct and indirect mechanisms (Takabayashi & Dicke 1996). Direct defences are those that act directly on the enemy via deterrent chemicals or toxicity and may result in risk avoidance (i.e. fleeing the area). Indirect defences act through a third party. For example, ants often tend homopterans and protect them against predators and parasitoids (Buckley 1987) (this has also been called biotic defence) (Agrawal 1998*b*). Direct and indirect mechanisms of defence are common in nature and can be expressed constitutively or they can be induced following a threat of predation or initial attack (Karban & Baldwin 1997; Agrawal *et al.* 1999*a*; Tollrian & Harvell 1999).

When defence is indirect, there is strong potential for mutualism between top predators and host organisms; top predators benefit by being provided shelter and/or food and host organisms benefit by having predators or parasites removed. Such mutualisms, which are mediated by defence against threatening predators and parasites, have been well described for many associations, including those between ants and plants (Davidson & McKey 1993), ants and caterpillars (Pierce *et al.* 1987; Cushman *et al.* 1994), predators or parasitoids and plants (Takabayashi & Dicke 1996), endophytic fungi and plants (Clay *et al.* 1993) and crabs and coral (Stachowicz & Hay 1996).

In any mutualism, be it obligate or facultative, there should be a tendency to cheat, that is to take resources or services from the partner without reciprocating (e.g. Addicott & Bao 1999). The problem of not reciprocating because of selfish interest has been conceptualized as the prisoner's dilemma (Axelrod & Hamilton 1981); partners should not invest in mutualism if they cannot assess whether their partner will invest. This issue has

stimulated a great deal of theoretical investigation attempting to reconcile the predominance of mutualism in nature with the theoretical prediction that mutualisms should fall apart because of cheating (Bull & Rice 1991; Connor 1995; Brems 1996; Leimar 1997; Doebeli & Knowlton 1998; Roberts & Sherratt 1998; Schwartz & Hoeksema 1998).

Anti-cheating mechanisms such as retaliation (i.e. punishing partners who do not cooperate) alleviate the prisoner's dilemma (Bull & Rice 1991; Pellmyr & Huth 1994). Quantitatively regulating the resources or services in a mutualistic relationship and only making them available to the partner when the benefits of mutualism are high has also been proposed to increase stability in mutualisms (e.g. Leimar's (1997) state-dependent reciprocity; Roberts & Sherratt's (1998) 'raise the stakes' model; Doebeli & Knowlton 1998). Retaliation and adjustment of rewards in relation to need can have similar consequences, with the former being dependent on whether the partner cheats and the latter being dependent on what an individual obtains from the partner. In both cases, the theory is meeting observations: individuals have responses to mutualists that span the continuum between 'cooperate' and 'defect'. Empirically, such adjustments have been observed for the allocation of nectar rewards to defending ants and pollinating bees, which are inducible depending on the threat of predation and lack of previous pollination, respectively (Leimar & Axén 1993; Agrawal & Rutter 1998; Ladio & Aizen 1999). These examples exemplify environment-dependent or conditional mutualism (Bronstein 1994).

In this study, we examined indirect defence induced in the caterpillar of a lycaenid butterfly. In the mutualism between these caterpillars and ants, induced indirect defence is a mechanism for regulating the levels of resources (nectar rewards) invested by the caterpillar that facilitates ant tending. We examined how simulated attacks on larvae of the Acmon blue (*Plebejus acmon*) in a

\*Author for correspondence (agrawal@botany.utoronto.ca).

laboratory and field experiment affected activity of the eversible tubercles, production of nectar rewards and attendance by ants. We predicted that increasing the predation risk of the larvae would cause the larvae to employ higher levels of indirect defence. We further addressed whether tending of lycaenids by ants affected the feeding rate of the caterpillars. Here we tested the hypothesis that ant tending and consumption of nectar would affect the feeding rate of larvae. Previous studies have found positive, negative and neutral effects of ant tending on larval feeding and growth. We predicted that (i) defended (i.e. tended) larvae should be more likely to feed than untended larvae because of reduced predation risk (Cushman *et al.* 1994), and (ii) tended larvae may have to feed more than untended larvae in order to compensate for their investment in ant rewards (Pierce *et al.* 1987).

## 2. NATURAL HISTORY

The Acmon blue, *P.* (formerly *Icaricia*) *acmon*, is a eurytopic butterfly that is widely distributed in western North America. It is multivoltine at lower elevations, including our study area in northern California, with more than five broods between March and October. Adults feed on the nectar of various flowers and larvae feed on various legumes and polygonaceae, including species of buckwheats (*Eriogonum*), lupines (*Lupinus*), trefoils (*Lotus*) and milkvetches (*Astragalus*) (Tilden 1973; Opler *et al.* 1995). Larvae feed on leaves or flowers by chewing holes in the surface of the plant and inserting their heads in order to mine out internal tissues. *P. acmon* has four instars and its larvae have a single nectar-producing gland and a pair of eversible tubercles, structures that are associated with myrmecophily (Ballmer & Pratt 1988; A. A. Agrawal and J. A. Fordyce, personal observations). Several ant species tend the third- and fourth-instar larvae of *P. acmon*, but earlier instars are not tended (Peterson 1993; A. A. Agrawal and J. A. Fordyce, personal observations). Non-native Argentine ants (*Linepithema humile*) have invaded many of the habitats where *P. acmon* exists in northern California. Argentine ants tend various species of honeydew-producing insects, including Acmon larvae, although their relative effectiveness as mutualists compared to native species is unknown.

## 3. METHODS

### (a) *Induced responses in the laboratory*

All larvae used in the experiments were obtained from gravid females collected in Mix Canyon (Solano County, CA). Eggs were obtained by tightly enclosing butterflies with a common host plant (*Lotus purshianus*) in mesh bags in a greenhouse. In order to test for the responses of lycaenid larvae to a simulated predator attack, we introduced a pair of fourth-instar larvae on a sprig of *L. purshianus* to an 8-l plastic tub with a small colony of Argentine ants (*ca.* 100 workers, without the queen). Ants were collected from a single site in the field. They were given shelter and water via a test-tube half filled with water and plugged with cotton. Four such arenas were constructed and rotated for use for a total of 19 replicate pairs of larvae (each used only once). After the larvae had been allowed to acclimate to the leaves and arena (5 min), one larva was randomly selected to be pinched on the abdomen using soft insect-gripping

tweezers. The larva was pinched four times, simulating an attack by an invertebrate predator (Leimar & Axén 1993; Axén *et al.* 1996) and then the arena was examined with a dissection microscope. Although we did not observe predation or parasitism attempts on Acmon blue larvae in the field, our technique simulates the unsuccessful grasping of common generalist predators of lepidoptera (e.g. Vespidae) and several types of parasitoids. Four response variables were measured over the next 5 min: (i) time until first tending, (ii) total time tended (in ant min, i.e. two ants tending for 30 s each = 1 ant min), (iii) number of times the tubercles were everted, and (iv) number of nectar droplets produced by the gland. These data were highly non-normal and were analysed using Wilcoxon signed-ranks tests (non-parametric paired *t*-test) (control and disturbed larvae were paired from each arena). All statistical analyses were conducted using Systat v. 8.0 for Windows.

### (b) *Induced tending in the field*

In order to test for the effects of a simulated predator attack in a natural environment, we conducted a field experiment in Davis, CA (USA). The study site had a large natural population of *L. purshianus* and lycaenid larvae were seen feeding on the plants and being tended by ants. Argentine ants dominated the ant community at this site. We exposed experimental larvae to a simulated predator attack (see §3(a)) and observed the response of ants. We observed three control and three induced larvae (42 larvae in total) next to a foraging trail of Argentine ants in seven temporal blocks. Each temporal block simply consisted of a set of six larvae at different times of the day. The position of larvae within each block was randomized. The caterpillars were placed on sprigs of *L. purshianus*. The number of tending ants was recorded every 15 s, with nine observations before the simulated predator attack and 27 observations after the simulated attack. We analysed the effects of block, induction treatment and their interaction using two repeated-measures ANOVAs, one with data from before the treatment was imposed and one using data collected after the treatment was imposed. The residuals approximated a normal distribution.

### (c) *Effects of ant tending on caterpillar feeding*

In order to examine whether ant tending of lycaenid larvae affected larval feeding, we assayed how exclusion of ants affected the amount of feeding and feeding behaviour in a greenhouse experiment. Argentine ants were naturally established in the greenhouse and readily tended lycaenid larvae. *L. purshianus* plants were grown from seed and inoculated with nitrogen-fixing *Rhizobium* sp. in 800 ml plastic pots with greenhouse soil. A single newly emerged larva was placed onto each of 40 undamaged plants that had been growing for two weeks. No other herbivores were on the plants. Half of the pots were encircled with a ring of sticky tanglefoot (The Tanglefoot Company, Grand Rapids, MI, USA) in order to prevent ant visitation. None of the plants were caged. We censused the number of ants on the plants on each of the following seven days in order to verify that our ant exclusion treatment was effective. We summed the number of ant visitors for each replicate over the seven censuses and used a *t*-test in assessing the effects of our ant exclusion treatment on ant visitation. After three weeks of growth, when the larvae were beginning to pupate, the leaves of the plant were destructively harvested. Each leaf on each plant was examined for lycaenid damage and was scored as 0, 25, 50, 75 or 100% damaged by visual assessment. We summed these percentages for leaves for each plant in order to calculate the

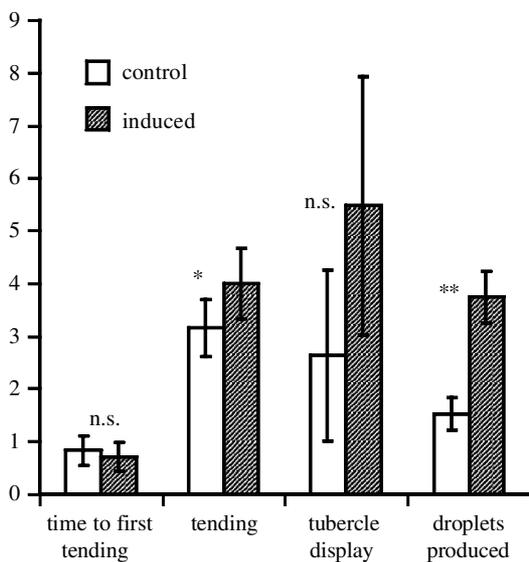


Figure 1. Effects of simulated predator attacks on lycaenid larvae on time to first attendance, total time tended (in ant min; two ants tending for 30 s each is equivalent to 1 ant min), number of times the tubercles were displayed and number of sugar droplets produced by the honey gland over 5 min of observation, as analysed by a non-parametric paired *t*-test (Wilcoxon signed-ranks test): \* $p < 0.05$ , \*\* $p < 0.001$  and  $n.s. \gg 0.05$ . Error bars are standard errors.

number of total leaves consumed (i.e. four leaves with 25% damage is equivalent to one leaf consumed). In addition, we counted the total number of leaves that had any damage in order to assess whether ant tending affected feeding behaviour and the pattern of damage. We used *t*-tests in examining the effects of ant tending on the total amount of plant damage and the number of leaves with damage. Our replication was reduced by a few plant deaths and lost larvae. We were unable to measure pupal weights because many of the larvae left the plant in the last few days in search of a pupation site.

#### 4. RESULTS AND DISCUSSION

##### (a) Induced tending

The simulated predator attack in the laboratory experiment did not influence the time until first tending of the caterpillars ( $Z = -0.900$  and  $p = 0.368$ ), but it resulted in 30% more time that caterpillars were tended by ants over the next 5 min ( $Z = 2.105$  and  $p = 0.035$ ) (figure 1). Two potential mechanisms of the induced increase in tending were examined, the first of which, displaying of the ever-visible tubercles, was unaffected by the induction treatment ( $Z = 1.123$  and  $p = 0.262$ ). However, the number of nectar droplets that were exuded by the caterpillars' gland more than doubled on disturbed larvae compared to controls. ( $Z = 3.188$  and  $p < 0.001$ ) (figure 1).

We found that the ant-tending levels in the field experiment examining the effects of unsuccessful predator attacks on caterpillars were twice as high on 'induced' caterpillars compared to control caterpillars (table 1 and figure 2). The only significant factor in this analysis was the effect of induction treatment after imposing the simulated attack. The effects of induction on ant attendance were immediate following the simulated attack and persisted for at least 7 min.

Induced indirect defence has been commonly observed in associations between plants and predators or parasites of herbivores. These associations can be mediated by several mechanisms, including the release of plant volatiles attractive to enemies of herbivores (Paré *et al.* 1999; Sabelis *et al.* 1999), the induction of extrafloral nectar (Agrawal & Rutter 1998) and other mechanisms (Agrawal & Dubin-Thaler 1999). Ant-lycaenid associations are parallel systems in which induction of indirect defence may mediate host-predator mutualism. The induction of nectar rewards from the glands of lycaenids was first demonstrated by Leimar & Axén (1993) in an elegant series of laboratory experiments with the European common blue *Polyommatus icarus*. In the current study we examined this phenomenon in a new system in a field setting. Indeed, simulated predator attacks on Acmon blue caterpillars doubled nectar production and ant attendance, which presumably confers increased protection from predators. Because we have not demonstrated that non-native Argentine ants are an effective defence for Acmon larvae, we note here that induction of ant attendance represents a potential defence for the caterpillars.

Although we observed eversion of the tubercles twice as often in disturbed larvae compared to controls, this difference between treatments was not statistically detectable. In general, tubercle display was very erratic and several of the larvae did not display them at all. Axén *et al.* (1996) showed a several-fold increase in tubercle display following simulated attack of the European common blue. Furthermore, they showed that inactivating the tubercles reduced ant tending, making a convincing link between tubercle display and ant attendance. Interactions between tubercle eversion and attraction of ants may be dependent on the ant species; it is unknown whether Argentine ants typically tend lycaenids in their native range. Many lycaenids also produce substrate-borne vibrations, which may increase tending of larvae by ants (DeVries 1990). Thus, induced nectar rewards may act together with other mechanisms in attracting ant protectors of lycaenids.

##### (b) Effects of ant tending on feeding

Our tanglefoot treatment successfully minimized ant visitation to plants and caterpillars in the ant exclusion experiment (mean  $\pm$  s.e., control =  $2.526 \pm 0.0498$  and ant exclusion =  $0.053 \pm 0.053$ ) (d.f. = 18.4, separate variance  $t = 4.942$  and  $p < 0.001$ ). However, after nearly three weeks of feeding, ant exclusion did not influence the amount of leaf tissue consumed by Acmon larvae (mean  $\pm$  s.e. number of leaves consumed, control =  $32.875 \pm 3.841$  and ant exclusion =  $33.183 \pm 3.917$ ) (d.f. = 27,  $t = 0.56$  and  $p = 0.56$ ). Ant attendance can strongly influence the feeding behaviour of larvae (Horvitz & Schemske 1984). However, in our experiment we found no evidence for this as the number of leaves with damage was not affected by ant tending (mean  $\pm$  s.e. number of leaves damaged, control =  $63.000 \pm 6.270$  and ant exclusion =  $62.467 \pm 4.744$ ) (d.f. = 27,  $t = 0.068$  and  $p = 0.946$ ). Thus, ant tending (and potential defence) does not appear to affect the feeding behaviour of Acmon larvae.

Ant defence can be costly for lycaenid larvae. Ant attendance to *Jalmenus evagoras* resulted in 13% lighter

Table 1. *Factorial repeated-measures ANOVA for effects of block and induction treatment on ant attendance of lycaenid caterpillars in the field before and after the induction treatment was imposed*

(Probabilities corrected for sphericity were estimated using the Greenhouse–Geisser (G–G) correction. SS, sum of squares; MS, mean squares.)

source	SS	d.f.	MS	F	p	G–G
before induction treatment						
block	15.349	6	2.558	1.604	0.183	—
induction	0.130	1	0.130	0.081	0.778	—
block × induction	11.519	6	1.920	1.203	0.334	—
error	44.667	28	1.595	—	—	—
time	3.974	8	0.497	1.545	0.143	0.187
time × block	13.175	48	0.274	0.854	0.739	0.673
time × induction	3.180	8	0.397	1.237	0.279	0.298
time × block × induction	18.339	48	0.382	1.189	0.204	0.259
error	72.000	224	0.321	—	—	—
after induction treatment						
block	60.956	6	10.159	1.787	0.139	—
induction	38.266	1	38.266	6.733	0.015	—
block × induction	35.590	6	5.932	1.044	0.420	—
error	153.457	27	5.684	—	—	—
time	8.670	26	0.333	0.787	0.767	0.626
time × block	49.093	156	0.315	0.742	0.989	0.902
time × induction	9.607	26	0.370	0.872	0.651	0.549
time × block × induction	51.890	156	0.333	0.785	0.968	0.853
error	297.543	702	0.424	—	—	—

pupae than untended larvae in a predator-free environment (Pierce *et al.* 1987). One benefit of inducible nectar production is that the costs associated with indirect defence are avoided unless it is needed. Inducible defences are generally thought to evolve as a strategy for saving the costs associated with defence when defence is not needed (Karban & Baldwin 1997; Agrawal 1998a; Agrawal *et al.* 1999b; Tollrian & Harvell 1999). However, ant attendance is not always costly. Cushman *et al.* (1994) found ant-tended *Paralucia aurifera* larvae to produce pupae that were 20% heavier than untended larvae (also in a predator-free environment). They hypothesized that tended larvae may feed more than untended larvae, which led us to test how ant tending affected larval feeding in our system. We were unable to detect an effect of tending on the amount of leaf area consumed. Similarly, Wagner & Martinez del Rio (1997) did not find an effect of ant tending on the leaf consumption or food assimilation ability of *Hemiargus isola*, which gained more weight when tended by ants compared to untended larvae (Wagner 1993). Wagner & Martinez del Rio (1997) hypothesized that tended larvae may expend less energy than untended larvae by not investing as much in risk avoidance mechanisms. Other costs associated with nectar production and tubercle eversion may favour inducibility of these defences. In addition to the necessary energetic input to these responses, parasitoids or other enemies of lycaenids may home in on cues such as nectar. For example, the defensive secretions of some leaf beetles are used as cues for predators, potentially having favoured inducible responses in the host (Kopf *et al.* 1997).

### (c) Conclusion

Our results support the predictions of recent models of mutualism (Leimar 1997; Doebeli & Knowlton 1998;

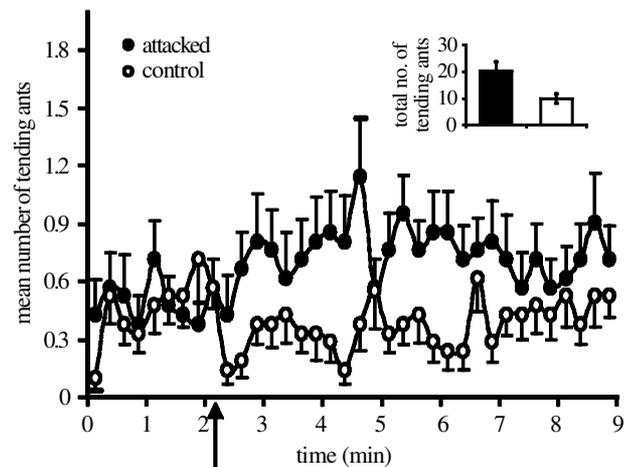


Figure 2. Ant attendance to lycaenid larvae in the field as influenced by a simulated predator attack. The arrow on the x-axis indicates the point at which the simulated attack was imposed. The inset graph shows the total number of ants tending induced (filled) and control (clear) caterpillars over the entire time-period following the simulated predator attack. Error bars are standard errors.

Roberts & Sherratt 1998). In particular, these models have suggested that, in the game between partners engaging in mutualism, there is the opportunity for partners to interact with responses that are intermediate to 'cooperate or defect'. Empirically, this seems obvious, as many organisms will vary the level of resources or services they provide depending on various biotic and abiotic factors. Such variation in quality may stabilize the relationship between partners and allow continued persistence of mutualism. Leimar's (1997) model was unique in

incorporating variation in investment based on an individual's need for a mutualistic partner. For lycaenids, many factors, including risk of predation, influence the rewards made available to mutualistic ants.

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## REFERENCES

- Addicott, J. F. & Bao, T. 1999 Limiting the costs of mutualism: multiple modes of interaction between yuccas and yucca moths. *Proc. R. Soc. Lond. B* **266**, 197–202.
- Agrawal, A. A. 1998a Induced responses to herbivory and increased plant performance. *Science* **279**, 1201–1202.
- Agrawal, A. A. 1998b Leaf damage and associated cues induced aggressive ant recruitment in a Neotropical ant–plant. *Ecology* **79**, 2100–2112.
- Agrawal, A. A. & Dubin-Thaler, B. J. 1999 Induced responses to herbivory in the Neotropical ant–plant association between *Azteca* ants and *Cecropia* trees: response of ants to potential inducing cues. *Behav. Ecol. Sociobiol.* **45**, 47–54.
- Agrawal, A. A. & Rutter, M. T. 1998 Dynamic anti-herbivore defense in ant–plants: the role of induced responses. *Oikos* **83**, 227–236.
- Agrawal, A. A., Tuzun, S. & Bent, E. 1999a *Induced plant defenses against pathogens and herbivores: biochemistry, ecology, and agriculture*. St Paul, MN: American Phytopathological Society.
- Agrawal, A. A., Strauss, S. Y. & Stout, M. J. 1999b Costs of induced responses and tolerance to herbivory in male and female fitness components of wild radish. *Evolution* **53**, 1093–1104.
- Axelrod, R. & Hamilton, W. D. 1981 The evolution of co-operation. *Science* **211**, 1390–1396.
- Axén, A. H., Leimar, O. & Hoffman, V. 1996 Signalling in a mutualistic interaction. *Anim. Behav.* **52**, 321–333.
- Ballmer, G. R. & Pratt, G. F. 1988 A survey of the last instar larvae of the Lycaenidae (Lepidoptera) of California. *J. Res. Lepidoptera* **27**, 1–81.
- Brembs, B. 1996 Chaos, cheating and cooperation: potential solutions to the prisoner's dilemma. *Oikos* **76**, 14–24.
- Bronstein, J. L. 1994 Conditional outcomes in mutualistic interactions. *Trends Ecol. Evol.* **9**, 214–217.
- Buckley, R. 1987 Ant–plant–homopteran interactions. *Adv. Ecol. Res.* **16**, 53–85.
- Bull, J. J. & Rice, W. R. 1991 Distinguishing mechanisms for the evolution of co-operation. *J. Theor. Biol.* **149**, 63–74.
- Clay, K., Marks, S. & Cheplick, G. P. 1993 Effects of insect herbivory and fungal endophyte infection on competitive interactions among grasses. *Ecology* **74**, 1767–1777.
- Connor, R. C. 1995 The benefits of mutualism: a conceptual framework. *Biol. Rev.* **70**, 427–457.
- Cushman, J. H., Rashbrook, V. K. & Beattie, A. J. 1994 Assessing benefits to both participants in a lycaenid–ant association. *Ecology* **75**, 1031–1041.
- Davidson, D. W. & McKey, D. 1993 Ant–plant symbioses: stalking the Chuyachaqui. *Trends Ecol. Evol.* **8**, 326–332.
- DeVries, P. J. 1990 Enhancement of symbioses between butterfly caterpillars and ants by vibrational communication. *Science* **248**, 1104–1106.
- Doebeli, M. & Knowlton, N. 1998 The evolution of interspecific mutualisms. *Proc. Natl Acad. Sci. USA* **95**, 8676–8680.
- Horvitz, C. C. & Schemske, D. W. 1984 Effects of ants and an ant-tended herbivore (*Eurybia elvina*) on seed production of a Neotropical herb (*Calathea ovandensis*). *Ecology* **65**, 1369–1378.
- Karban, R. & Baldwin, I. T. 1997 *Induced responses to herbivory*. University of Chicago Press.
- Kopf, A., Rank, N. E., Roininen, H. & Tahvanainen, J. 1997 Defensive larval secretions of leaf beetles attract a specialist predator *Parasymphus nigratarsis*. *Ecol. Entomol.* **22**, 176–183.
- Ladio, A. H. & Aizen, M. A. 1999 Early reproductive failure increases nectar production and pollination success of late flowers in south Andean *Alstroemeria aurea*. *Oecologia* **120**, 235–241.
- Leimar, O. 1997 Reciprocity and communication of partner quality. *Proc. R. Soc. Lond. B* **264**, 1209–1215.
- Leimar, O. & Axén, A. H. 1993 Strategic behaviour in an interspecific mutualism: interactions between lycaenid larvae and ants. *Anim. Behav.* **46**, 1177–1182.
- Opler, P. A., Pavulaan, H. & Stanford, R. E. 1995 *Butterflies of North America*. Jamestown, ND: Northern Prairie Wildlife Research Center Home Page.
- Paré, P. W., Lewis, W. J. & Tumlinson, J. H. 1999 Induced plant volatiles: biochemistry and effects on parasitoids. In *Inducible plant defenses against pathogens and herbivores: biochemistry, ecology, and agriculture* (ed. A. A. Agrawal, S. Tuzun & E. Bent), pp. 167–180. St Paul, MN: American Phytopathological Society Press.
- Pellmyr, O. & Huth, C. J. 1994 Evolutionary stability of mutualism between yuccas and yucca moths. *Nature* **372**, 257–260.
- Peterson, M. A. 1993 The nature of ant attendance and the survival of larval *Icaricia acmon* (Lycaenidae). *J. Lepidoptera Soc.* **47**, 8–16.
- Pierce, N. E., Kitching, R. L., Buckley, R. C., Taylor, M. F. J. & Benbow, K. F. 1987 The costs and benefits of cooperation between the Australian lycaenid butterfly, *Jalmenus evagoras*, and its attendant ants. *Behav. Ecol. Sociobiol.* **21**, 237–248.
- Roberts, G. & Sherratt, T. 1998 Development of cooperative relationships through increasing investment. *Nature* **394**, 175–179.
- Sabelis, M. W., Janssen, A., Pallini, A., Venzon, M., Bruin, J., Drukker, B. & Scutareanu, P. 1999 Behavioral responses of predatory and herbivorous arthropods to induced plant volatiles: from evolutionary ecology to agricultural applications. In *Inducible plant defenses against pathogens and herbivores: biochemistry, ecology, and agriculture* (ed. A. A. Agrawal, S. Tuzun & E. Bent), pp. 269–296. St Paul, MN: American Phytopathological Society Press.
- Schwartz, M. W. & Hoeksema, J. D. 1998 Specialization and resource trade: biological markers as a model of mutualisms. *Ecology* **79**, 1029–1038.
- Stachowicz, J. J. & Hay, M. E. 1996 Facultative mutualism between an herbivorous crab and a coralline alga: advantages of eating noxious seaweeds. *Oecologia* **105**, 377–387.
- Takabayashi, J. & Dicke, M. 1996 Plant–carnivore mutualism through herbivore-induced carnivore attractants. *Trends Plant Sci.* **1**, 109–113.
- Tilden, J. W. 1973 Specific entities of the subgenus *Icaricia* Nobakov (Lycaenidae). *J. Res. Lepidoptera* **12**, 11–20.
- Tollrian, R. & Harvell, C. D. 1999 *The ecology and evolution of inducible defenses*. Princeton University Press.
- Wagner, D. 1993 Species-specific effects of tending ants on the development of lycaenid butterfly larvae. *Oecologia* **96**, 276–281.
- Wagner, D. & Martinez Del Rio, C. 1997 Experimental tests of the mechanism for ant-enhanced growth in an ant-tended lycaenid butterfly. *Oecologia* **112**, 424–429.