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The influence of ants on host plant selection by *Jalmenus evagoras*, a myrmecophilous lycaenid butterfly

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Summary. (1) Females of the myrmecophilous lycaenid butterfly, *Jalmenus evagoras* are far more likely to lay eggs on plants that contain their attendant ants, *Iridomyrmex* sp. 25 than on plants without ants, although the clutch sizes of individual egg masses laid in either situation is the same. (2) Ovipositing females respond to the presence or absence of ants before they alight on a potential food plant. Once they have landed, they are equally likely to lay eggs whether or not they encounter ants. (3) Ovipositing females prefer to lay eggs on plants that contain ant tended homopterans than on plants that contain only a few foraging ants. The presence of ant tended homopterans can act as a strong stimulus to induce females to lay eggs on plant species that differ from their original host species. (4) Ant dependent oviposition behavior has been described or suggested in 46 species of lycaenid and one riodinid. In general, the more dependent a species is upon ants for either food or protection, the more likely it is to use ants as cues in oviposition. Prominent characteristics of lycaenids that have ant dependent oviposition are described and discussed. (5) Myrmecophilous lycaenids that may use ants as cues in oviposition feed on a significantly wider range of plants than non-myrmecophilous lycaenids. Possible reasons for this pattern and its ecological significance are discussed.

Introduction

A female butterfly's decision to lay an egg is made in two stages: during a pre-alighting phase she must search for a food plant upon which to land, and during a post-alighting phase she must assess the suitability of that food plant for the survival of her offspring. In making her choice, she may use visual or olfactory cues in her approach to a plant (e.g. Gilbert 1975; Benson 1978; Saxena and Goyal 1978; Rauscher 1978, 1979a, b, 1980; Stanton 1980, 1982; Williams 1981; Papaj and Rausher 1983). After landing, she may use any combination of visual, olfactory, gustatory and tactile cues (Dethier 1947, 1970; Thorsteinson 1960; David and Gardiner 1962; Downey 1962b; Ross 1966; Shoonhoven 1972; Abe et al. 1981; Feeny et al. 1983). Requirements for different species vary, but each female performs a complex set of tasks: she recognizes whether a plant is of the appropriate species and located in a desirable microhabitat; distinguishes special features of the plant that may render it unacceptable, such as low moisture content or the presence of conspecific eggs; and determines whether the requisite plant parts such as flower buds or young foliage are available to nurture her developing larvae. Not surprisingly, females have often been observed to make 'mistakes' by laying eggs on novel plant species that may not support larval growth (see Chew and Robbins 1984 for review of oviposition).

One of the most unusual cues that ovipositing females respond to is the presence or absence of ants (e.g. Bell 1915–1920, Fukuda et al. 1978; Atsatt 1981a; Henning 1983). As many as a third of the species in the family Lycaenidae associate with ants (Downey 1962b; see Hinton 1951; Cottrell 1984 for review). The larvae and occasionally the pupae secrete food in the form of carbohydrates and amino acids that their attendant ants harvest (Maschwitz et al. 1975; Pierce 1983; see also Kitching 1983). It has been demonstrated experimentally for several species that attendant ants protect larvae and pupae from predators and parasitoids (Pierce and Mead 1981; Pierce 1983). The larvae may also benefit from producing ant appeasement substances to deter those ants that might otherwise be threatening predators (Lenz 1917; Malicky 1970).

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Field observations of ovipositing females of the Australian lycaenid *Jalmenus evagoras* Donovan suggested to us that they are able to distinguish between plants with and without ants. In this paper, we report our findings from experiments designed to test whether females of *J. evagoras* detect and use ants as cues in oviposition, and whether this response occurs during both pre- and post-alighting phases. We examine experimentally how an ant tended homopteran can affect this ant/butterfly/host plant interaction. We review prominent characteristics exhibited by lycaenid species in which ant dependent oviposition has been suspected or reported. Finally, we make a comparative study of the host plant ranges of lycaenids that do and do not associate with ants, and discuss the results in terms of the ecological and evolutionary consequences of ant dependent oviposition.

Natural history of *J. evagoras*

J. evagoras is a widespread Australian species that ranges along the eastern coast and inland from Melbourne to just north of Gladstone (Common and Waterhouse 1981). It has been recorded to feed on at least 16 species of *Acacia* (Hawkeswood 1981; this study) and is tended by several species of *Iridomyrmex* ants. Our study site was on Mt. Nebo, Queensland, where we examined a dense and highly localized population of *J. evagoras*. On Mt. Nebo, the larvae feed predominantly on the foliage of short, young plants of *Acacia irrorata*. For example, in a 200 m by 200 m area in our study site, the mean height of trees colonized by *J. evagoras* was 152 ± 83 cm, which differed significantly from the mean height of *A. irrorata* trees in the same area (202 ± 134 cm; $t = 2.05$, 147 *df*, $P < 0.05$). We also found larvae on *A. spectabilis*, *A. fimbriata*, *A. macradenia* (new record), *A. penninervis* and *A. dealbata*.

Both the larvae and pupae are tended by myriad workers of the ant *Iridomyrmex* sp. 25 (Australian National Insect Collection) (*anceps* group). This ant is polygynous and polydomous, occurring in vast colonies with nest entrances established at the base of almost every plant bearing larvae of *J. evagoras*. Females of *J. evagoras* lay eggs in clusters, and the larvae and pupae also aggregate. In Queensland, there are as many as three broods a year, and females from the last brood lay eggs that overwinter until the following spring.

Materials and methods

Ants as cues in oviposition. Ant exclusion experiments with *J. evagoras* in 1980 and 1981 showed that larvae and pupae of *J. evagoras* cannot survive without attendant ants (Pierce 1983). During these experiments, we observed that females stopped laying eggs on plants from which ants had been excluded (Pierce 1983). For example, in the 1981 experiments, 175 egg masses were laid on plants with ants, whereas only 23 egg masses were laid on plants without ants. These results were suggestive, but did not control for the numbers of larvae and pupae (to which we will refer collectively as juveniles) found on each plant, or for any individual variation between plants or their positions that might have influenced the behavior of the butterflies. Such controls were particularly important because many juveniles disappeared due to predation when we excluded ants (Pierce 1983). Thus the choice available for ovipositing butterflies was essentially between plants with juveniles and ants, and plants without juveniles and ants. Since the juveniles of *J. evagoras* form highly visible aggregations that may attract ovipositing females, we wanted to control for their presence and determine whether females were responding to ants alone.

The oviposition experiments were conducted from January until March of 1981, in the middle of a cleared paddock where there were a number of young second growth trees of *A. irrorata* infested with natural colonies of *J. evagoras*. In an earlier set of observations, we found that females of *J. evagoras* confined in a bush house (2 m by 3 m by 3 m) could not distinguish between food plants with or without foraging ants, and oviposited indiscriminantly on all plants, and even on sticks, twigs, and other inert (non-host plant) objects (N.E. Pierce and R.L. Kitching, unpublished observations). Hence we have investigated the behavior of free-flying females from natural populations, rather than that of caged individuals.

We arranged ten potted plants of *A. irrorata*, each about 1 m high, in a circle approximately 3 m in diameter. To attract ants, six final instar larvae were placed on each plant. The number of larvae on each plant was kept constant throughout the experiment. We applied a sticky barricade of Tanglefoot (Tanglefoot Co., Grand Rapids, Mich., USA) around the base of all plants. Ant infested plants had twig bridges placed from the ground to the plant that allowed ants to forage on the plant. Similar twigs, ringed with a tanglefoot barrier to exclude ants were placed against ant free, experimental plants. Half our potted plants were designated ant-infested controls (Set A = juveniles with ants); the other half were ant free experimentals (Set B = juveniles without ants). To control for individual plant or position effects, the treatments were swapped after 4 days; ant infested plants became ant free plants (and vice versa). Eggs were counted and collected daily during the entire 8-day experimental period. Wind varied during these experiments, but it did not blow strongly or consistently in any given direction. Since the experiments spanned 8 days each and plant positions were swapped, we feel confident that wind direction was probably not an important feature in our experimental arena. During the second 8-day replicate, several larvae from each plant had pupated, and these pupae were counted as larval equivalents. Again, six juveniles (larvae and some pupae) were maintained on all plants during the course of the second experiment.

Pre-alighting phase. Approaches by butterflies to plants with and without ants were scored during the second oviposition experiment (see above). An 'approach' is a discrete, readily identifiable behavior in which a butterfly flies up to a plant (or branch of a plant) and flutters about it with a rapid, back and forth motion. Both males and females of *J. evagoras* show this behavior: males seek mates among female pupae that are about to eclose, and females search for oviposition sites.

The ten plants in the arena had been maintained with the same experimental treatment for 4 days. During the last 2 days (days −2 and −1), approaches of butterflies were scored for approximately 1 h each day (from 1000 to 1100 hours on

March 7, and from 1400 to 1500 hours on March 8). When a butterfly entered the oviposition arena, its approach behavior to plants in the arena was recorded until it landed on a food plant or until it left the arena. Only one butterfly at a time was followed, and as soon as it landed or left, the next butterfly to enter the arena was the next to be followed. On the 5th day, the experimental treatment was swapped. On the swap day (day 0), approaches of butterflies to plants were monitored for about $2^1/_2$ h (from 900 to 1130 hours on March 9). For the subsequent 2 days (day +1 and +2), approaches were scored for about 2 h each day (1015 to 1150 hours and 1400 to 1435 hours on March 10; 1015 to 1055 hours and 1300 to 1405 hours on March 11).

Post-alighting phase. Each ovipositing female was followed and her behavior recorded from the time she landed on a plant until she either laid an egg or flew away. Numbers of interactions with ants were also noted. Because we were interested primarily in the relationship between total ant encounters and number of eggs laid rather than in a comprehensive catalogue of all possible behaviors, our observations consisted of a series of continuous observations of oviposition sequences instead of a scanning point sample.

Associations with other ant tended homopterans. In order to examine the influence that ants tending other myrmecophilous insects might have on *J. evagoras,* we designed a slightly different oviposition test from that described above. Two common myrmecophilous insects in the Mt. Nebo area are homopterans: a large orange and white margarodid scale (unidentified), and the membracid, *Sextius virescens.* We allowed females to choose between trees with adults and nymphs of *S. virescens* and many foraging ants, and trees with only a few foraging ants. The choice provided in this test is one that females might often encounter in nature, especially early in the season when membracids have already become established on some trees, but *J. evagoras* is not yet fully active.

Results

Ants as cues in oviposition

Females of *J. evagoras* detect the presence or absence of attending ants and use them as cues in oviposition (Table 1). In both experiments, significantly more eggs and egg masses were laid on plants with ants than on plants without ants. However, the clutch size of egg masses laid on trees with ants did not differ significantly between the two treatments. Since numbers of juveniles and individual plants and plant positions were controlled for, the observed differences in female oviposition behavior were due solely to the presence or absence of ants.

Table 1. Oviposition by females of *J. evagoras* in response to ant tended and untended conspecific juveniles. Each experiment lasted 8 days, with treatments swapped after 4 days (see text). Experiment A took place between 21st and 28th February (inclusive) and Experiment B took place between 5th and 12 March (inclusive)

	Juveniles with ants	Juveniles without ants	Test statistic
Experiment A			
Number of eggs	618 (86%)	104 (14%)	
Number of egg masses	30 (88%)	4 (12%)	$\chi^2 = 19.9$, 1 *df*, $P < 0.005$
Mean no. eggs/mass	20.60 ±22.32	26.00 ±16.72	$t_s = 0.47$, 32 *df*, ns
Experiment B			
Number of eggs	548 (77%)	160 (23%)	
Number of egg masses	28 (85%)	5 (15%)	$\chi^2 = 16.0$, 1 *df*, $P < 0.005$
Mean no. eggs/mass	19.57 ±23.07	32.00 ±10.73	$t_s = 1.17$, 31 *df*, ns

Table 2. Approaches and landings of adult butterflies of *J. evagoras* to and on plants containing ant tended and untended conspecific juveniles. The data in the left hand column of the frequencies are from plants that had juveniles and ants on days −2 and −1, but ants excluded on the swap day and days +1 and +2 (vice versa for the right hand column)

Observation	Day	Frequencies (%)		Total number	Observation time (min)	χ^2
		Ants on day −2	No ants on day −2			
Approaches	−2	71	29	231	60	64.05**
	−1	73	27	111	60	
	Swap	53	47	349	150	1.15
	+1	37	63	203	70	33.61**
	+2	32	68	157	105	
Landings	−2	88	12	8	60	7.364*
	−1	100	0	3	60	
	Swap	50	50	34	150	0.000
	+1	36	64	14	70	8.33**
	+2	8	92	13	105	

* $P < 0.01$ ** $P < 0.005$

Pre-alighting phase

Butterflies of *J. evagoras* approach and land preferentially on plants with ants (Table 2). This corresponds well with observations of ovipositing females under natural circumstances in which 78% ($n = 27$) of landings were on colonized food plants (see Table 3). Hence, females of *J. evagoras* can detect the presence of ants before alighting on plants, and this influences their decision whether to land on that plant. On the swap day, the butterflies appeared to be confused, and approaches and landings were equally probable on plants with and without ants (see Discussion).

The approach behavior shown by males and females is indistinguishable. Since males and females are not sufficiently different morphologically to permit identification from a distance, the data for this approach experiment include both male and female behavior. We are not certain whether adults of *J. evagoras* use only visual and/or olfactory cues during the pre-alighting phase. Both males and females extend their antennae forward during approaches to plants and as they flutter back and forth, their antennae appear to occasionally tap against the tree they are investigating. In this way, butterflies still in flight may be able to taste a prospective food plant or a prospective mate.

The approach behavior exhibited by males is unusual for butterflies, and is related to the extraordinary mating habits of *J. evagoras*. When a female pupa of *J. evagoras* is about to eclose, the pupa attracts as many as 20 males. If an observer crushes one of these pupae in his or her fingers, the males still cluster around them, indicating that the signal the female emits to attract males is probably chemical. As soon as the female ecloses, there is a quick scramble amongst the males, and the female is mated before she has even expanded her wings. The pair usually remain *in copula* for as long as a day.

Post-alighting phase

We found no evidence that females respond to ants once they have landed on a tree. Of 21 observed arrivals by females on colonized trees, 11 (52.4%) of these finally resulted in oviposition, compared with three of the six females on uncolonized trees ($P = 0.28$, Fisher's Exact Test).

Ovipositing females exhibit seven main behaviors after landing on a plant. The most obvious of these, aside from laying eggs, is a 'testing' behavior, in which a female places the tip of her abdomen down and drags it along the substrate while walking up and down the branches of the food plant. Another predominant behavior is 'probing'. Females prefer to lay eggs either in cracks in the bark, or in hollows formed on the undersides of leaf petioles, and when they encounter a suitable crack or crevice, they stop and probe it with the tip of the abdomen.

Females occasionally make short flights from one branch to another during an oviposition sequence, usually to escape from ants. They may also sun, during which time they either open their wings, or rest with their wings closed at an angle to the sun, slowly rubbing their two hind wings together. An uncommon, but interesting behavior exhibited at this time is a slow unrolling and rolling of the proboscis.

Table 3. Observations of ovipositing females of *J. evagoras* on plants with and without ants. Mean values ±SD. Differences between samples tested using a Wilcoxon two sample test

	Plants with ants	Plants without ants	U	t_s
Total number of females observed	21	6		
Total observation time (min)	463	83		
Mean time taken to decide to lay eggs or leave (min)	12.38±11.07	6.33±5.01	78	0.8748
Number of females that laid eggs	11	3		
Number of eggs laid per min	3.02±1.19	2.35±1.02	88	1.458
Excluding time spent egg laying, mean proportion of time spent				
Testing	0.65±0.26	0.53±0.18	86	1.370
Probing	0.11±0.13	0.06±0.08	77	0.846
Flying	0.07±0.07	0.10±0.23	86	1.341
Resting/sunning	0.12±0.21	0.31±0.23	99	2.100*
Wing fluttering	0.03±0.08	0.0		
Other	0.02±0.07	0.0		

* $P < 0.05$

Although females of *J. evagoras* appear to mate only once, they spend a considerable amount of time resisting males that attempt to mate with them a second time. They do this by facing their opponent, lowering their antennae, and fluttering their wings vigorously. Males are persistent in pursuing females, and in three out of the 11 egg laying sequences we observed on trees with ants, males actually succeeded in disrupting females while they were laying eggs. The 'wing flutter' behavior shown by females is a general aggressive response: although usually displayed toward males, we have also seen it used when one ovipositing female uncountered another ovipositing female on the same branch.

Females on plants without ants spent more time resting and sunning then females on plants with ants, but there were no other differences in behavior patterns between the two groups (Table 3). On colonized trees, 18% ($n = 114$) of the flights made from one branch to another were in response to a sharp nip or bite from an ant. Without such disturbances from ants, females on uncolonized plants may fly less, and have more opportunity to rest and sun. The amount of time taken

Table 4. Oviposition by females of *J. evagoras* in response to the presence or absence of ant-tended membracids. The experiment lasted eight days (March 18th–29th inclusive), with treatments swapped after 4 days

	Trees with membracids and many ants	Trees with a few foraging ants	Test statistic
Mean no. membracids/tree			
Adults	2.6±1.51	0	
Juveniles	5.9±4.07	0	
Mean no. ants/tree	11.83±5.31	1.25±1.88	
Number of eggs	553	123	
Number of egg masses	26	10	$\chi^2=7.1$, 1 *df*, $P<0.025$
Mean no. eggs/mass	21.27±16.41	12.30±14.53	$t_s=1.53$, 34 *df*, ns

by each female to decide to either lay eggs or leave a food plant varied considerably, but there was no difference in this behavior between females on trees with and without ants (Table 3).

A more detailed analysis of females that landed on colonized trees and their interaction with ants reinforced the general observation that females did not respond to ants after landing. The behavior of workers of *Iridomyrmex* sp. 25 toward adults of *J. evagoras* is generally antagonistic. Tactile interactions include 'nips' to legs, 'bites' to the abdomen, 'holding legs down', and 'antennation' during oviposition. The latter two non-discrete behaviors were scored as either present or absent. Non-tactile interactions include 'gapes' in which an ant would rush toward a female as if to bite her, but then stop with its mandibles agape, apparently unable to bite (perhaps due to an appeasement substance secreted by the butterfly), and 'investigations' in which an ant would run up to an ovipositing female but then pass her without touching her.

For the 21 females that we observed on colonized plants, there was no correlation between the number of eggs laid and the number of tactile interactions with ants either before oviposition ($r=0.30$, 19 *df*, ns) or during oviposition ($r=-0.28$, 9 *df*, ns). The number of bites, nips or other tactile interactions also did not influence the rate at which eggs were laid (about 3 eggs per minute) ($r=0.21$, 9 *df*, ns).

Although the interaction rate varied considerably from one individual to the next, a female was bitten or nipped by an average of four ants per minute while she was looking for a place to lay her eggs, and she was bitten or nipped by four ants per minute while she was ovipositing. While laying eggs, 27% ($n=11$) of females had their legs pinioned by ants, and 18% ($n=11$) of them were antennated.

Associations with ant-attended homopterans

Females laid significantly more eggs and egg masses on trees with membracids *S. virescens* and many foraging ants, than on trees with only a few foraging ants (Table 4). On several occasions, eggs of *J. evagoras* were found beside *S. virescens* adults and their broods, and on two instances, eggs were laid directly on the female membracids. Again, there was no significant difference in clutch size between the two treatments.

Discussion

Pre-alighting behavior

Our analysis of pre-alighting behavior demonstrated that ants had a profound effect on the frequency with which females of *J. evagoras* investigated and landed on food plants, and that this behavior accounted for females ovipositing preferentially on plants with ants. This is the first experimental evidence of ant dependent pre-alighting oviposition behavior in the Lycaenidae, although many authors have suggested that other myrmecophilous species use ants as cues in selecting host plants (see Appendix).

There are at least two explanations for the butterflies' confusion in their pre-alighting behavior when the treatments were swapped on day 0. The first is that tending ants leave a residual chemical smell that the butterflies can identify, and that this smell lingered on the plants of Set A for at least a day after the treatment had been exchanged. Butterflies tapping against food plants with their antennae may even be able to taste chemical trails laid down by workers of the attendant ants species.

Alternatively, adults of *J. evagoras*, may be capable of learning, and simply remember the location of colonized trees. Gilbert (1975) has suggested that individual *Heliconius* butterflies that 'trap-line' abundant food resources in their habitats exhibit learning behavior. Rausher (1978) demonstrated that certain *Papilio* butterflies retain a search image for the leaf shapes of their food plants. Hence, individuals of *J. evagoras* may have become confused on the swap day because the positions of the trees bearing ant tended larvae had changed. This explanation is only possible if many of the butterflies we observed each day were the same individuals. Accordingly, we conducted a mark-release-recapture experiment for 4 days following the approach experiment (March 15–18). Of the original 18 butterflies marked on the first day of the census, we recaptured (in 10 min on each of the consecutive days) 10 (56%), 14 (78%) and 11 (61%) individuals respectively. We concluded that it was likely that many of the butterflies we observed approaching plants during our experiment were the same individuals, and that these individuals might have learned the positions of plants containing ant tended, conspecific juveniles.

Our observations of approach behavior point out another interesting phenomenon: males of *J. evagoras* are also able to recognize plants with and without ants. Since males approaching plants were actively searching for trees bearing female pupae, males must use ants as cues in finding the pupae. Males learning to trap-line trees containing conspecifics may have a better chance of finding females and mating than males that do not trap-line. Moreover, female pupae that are tended by ants and are highly visible may have a better chance of being discovered by trap-lining males than less visible, untended female pupae. Even though untended female pupae may still attract males by emitting a chemical attractant, they may not be discovered either as quickly or by as many competing males as their ant tended counterparts.

Post-alighting behavior

Our observations of females of *J. evagoras* in the field indicated that once a female had alighted upon a food plant, her oviposition behavior was no longer influenced by ants: she was equally likely to lay eggs whether or not the plant was occupied by ants, and there was no correlation between the number of eggs she laid and her encounter rate with ants. This post-alighting oviposition behavior appears to vary between different lycaenid species. Atsatt (1981a) found that when eight caged females of *Ogyris amaryllis* were offered branches of their food plants, they laid eggs on branches both with and without ants, but laid significantly larger clutch sizes if they encountered ants on these branches. The larger clutch sizes were apparently laid in response to tactile stimulation by ants (Atsatt 1981a). In other post-alighting oviposition experiments, Henning (1983) enclosed 10 females of *Lepidochrysops ignota* in a container with their food plant and workers of their attendant ants, and compared their behavior with that of ten females enclosed in a container with food plant alone. All ten females laid eggs in the container with ants, while none laid eggs in the container without ants. When Henning (1983) performed the same experiment with *Aloeides dentatis*, three females housed with ants laid eggs whereas none laid eggs in the container without ants.

Atsatt (1981a) and Henning's (1983) results indicate that females of some myrmecophilous lycaenids may respond to ants during the post-alighting phase of oviposition. Depending on the biology of the lycaenid, females may possess quite different ovipositional responses to ants. For example, the older larvae and pupae of *O. amaryllis* shelter during the day under the haustoria of the mistletoes they feed upon, as well as under loose bark of the host tree. As such, they do not create a large visual signal as do aggregations of *J. evagoras* juveniles that feed and pupate in the open on their food plants. Similarly, juveniles of both *A. dentatis* and *L. ignota* are sheltered from the third instar onwards the nests of their respective host ants (Henning 1983). Selection might have thus favored ant identification via direct tactile stimulation during the post-alighting phase for species such as *O. amaryllis, A. dentatis* and *L. ignota,* and visual identification during the pre-alighting phase for species such as *J. evagoras.*

Associations with ant tended homopterans

Females of *J. evagoras* occasionally lay eggs on plants that have not already been colonized by conspecifics. If newly colonized plants are near nests of the attendant ant *Iridomyrmex* sp. 25, as the plants in our experiment were, then newly hatched clusters of pioneer larvae may be able to attract a sufficient number of tending ants quickly enough to survive and thus establish a new food plant. This process may be facilitated in several ways. First, *A. irrorata,* like many other acacias, has extra-floral nectaries (three near the tip and one at the base of each leaf), and plants are patrolled regularly by nectar seeking ants, including workers of *Iridomyrmex* sp. 25. Larvae of *J. evagoras* that hatch out on these plants are thus likely to be discovered quickly by ants. Second, eggs of *J. evagoras* are laid in clusters that hatch synchronously, thereby creating an aggregation that is a potentially more attractive food source than only a single larva. Third, like many other social insects, workers of *Iridomyrmex* sp. 25 recruit nestmates to food resources in numbers commensurate with the quality of those resources (see Wilson 1971). A single worker discovering a cache of *J. evagoras* larvae may be able to recruit enough nestmates sufficiently quickly to tend the larvae and successfully protect them against predators.

Nevertheless, commencing life on a new food plant without the benefit of pre-existing conspecific juveniles that have attracted attendant ants involves considerable risk for young larvae of *J. evagoras.* Ant exclusion experiments performed in 1981 (Pierce 1983) revealed that the first and second instar larvae were preyed upon far more rapidly when they occurred on plants by themselves than when they occurred on plants that contained final instar larvae and pupae that had attracted large numbers of ants. One way *J. evagoras* may circumvent this problem is by ovipositing adjacent to ant tended homopterans. Atsatt (1981a) suggested a similar function for ant tended homopterans on food plants utilized by *Ogyris amaryllis*, although McCubbin (1971) and Das (1960) described situations in which myrmecophilous homopterans appeared to exclude lycaenids from potential host plants.

In addition to acquiring an immediately attentive ant guard, larvae of *J. evagoras* that hatch out beside myrmecophilous membracids gain a further advantage in the form of food. On numerous occasions, we observed larvae of *J. evagoras* feeding on the honeydew secretions of homopterans. The first and second instars sometimes even ride on the backs of adult membracids. This phenomenon of honeydew feeding has been described for several lycaenids (e.g. Hinton 1951). Although other lycaenids actually prey on homopterans (e.g. Cottrell 1984), we found no evidence of this in *J. evagoras.*

During the course of the 1981 field season, we noticed that females of *J. evagoras* laid eggs on several new species of *Acacia* in the garden adjoining our field site. These included *A. macradenia* (new record), *A. fimbriata, A. dealbata,* and *A. penninervis.* In each case, females laid eggs only on those trees that already contained membracids and attendant ants, and larvae of *J. evagoras* had no difficulty accepting these new food plants. These observations suggest the critical role that ant-tended homopterans may play in inducing *J. evagoras* to colonize new individual food plants. In addition, the propensity of female lycaenids to oviposit in response to myrmecophilous homopterans when they occur on a novel plants that are not the same species as the butterfly's original food plant could have important implications for the host plant range of species that use ants as well as plants as cues in oviposition (see final section of this discussion).

Characteristics of lycaenids suspected to have ant induced oviposition behavior

Although there is a substantial literature on interactions between ants and the juveniles of lycaenid butterflies, comparatively little mention has been made of associations between ovipositing female butterflies and ants (see Cottrell for discussion). We have tabulated every reference we could find in which ant induced oviposition has been specifically described or suggested (Appendix). The 46 lycaenid species cited in the Appendix comprise 29 genera in five subfamilies within the Lycaenidae (*sensu* Eliot 1973). There is a single record of ant induced oviposition for a riodinid from the neotropics (Callaghan 1981–1982). Among the lycaenids, the best represented subfamily is the Theclinae (30 species, with 10 of these in the *Aphnaeus* section of the Aphnaeini), followed by the Polyommatinae (10), Miletinae (4), Liphyrinae (2), and Lycaeninae (1). The attendant ants represent 12 genera in three subfamilies, predominantly *Crematogaster* (16 species), *Camponotus* (7), *Iridomyrmex* (7), and *Oecophylla* (6). Seven of the attendant ant genera are known from early Tertiary fossils (Wilson 1971).

A general conclusion that can be drawn from the Appendix, is that the more dependent a lycaenid species is upon its attendant ants either for food or for protection, the more likely it is to possess ant dependent oviposition behavior. Species considered to use ants as cues in oviposition exhibit the following prominent characteristics:

(1) The older instars of 92% of the species listed in the Appendix are never found without attendant ants.

(2a) During some portion of their life-time, the larvae and/or the pupae of 31% of the species live within the ant nest itself where they are thought to be parasitic upon the ants.

(2b) The juveniles of 40% of the species are sheltered in extensions of the attendant ant nest, or in byres or corrals constructed by the ants.

(3) 65% of the species lay their eggs in clusters and/or the juveniles aggregate, either in ant nests, ant shelter, or in the open on their food plants.

(4) 94% of the species have species or genera specific ant associations.

Characteristic (1) is probably a prerequisite for the possession of strongly ant dependent oviposition behavior. Clearly, lycaenids showing casual associations with several species of ants (as found in many North American and European species) would not use ants as necessary cues in oviposition. For example, Pierce (1983) experimentally demonstrated that females of the North American lycaenid, *Glaucopsyche lygdamus* do not use ants as cues in oviposition. Nevertheless, Funk's (1975) observation of *Lycaena rubidus*, and Bell's (1915–1920) description of *Freyeria trochilus,* neither of which are species with strong ant associations, indicate that females of casually tended species may be able to respond to ants while ovipositing, even though they may not specifically search for them.

Any lycaenid species possessing characteristic (2a) almost certainly uses ants as cues in oviposition. The majority of lycaenids that spend a portion of their life cycle in their host ant's nest are suspected to be parasitic, although actual observations of parasitism have been made for only a few species (Cottrell 1984). Parasitic lycaenids prey directly upon ant brood in the nest, or solicit trophallactic regurgitations from workers. Females of these species must be able to locate suitable ant nests to insure the survival of their offspring. A number of other aphytophagous lycaenids attack homopterans, and it has been suggested, primarily in the Japanese literature (e.g. Fukuda et al. 1978; also see Cottrell 1984) that these lycaenids use homopterans and sometimes homopterans and ants as cues in oviposition.

The juveniles of many species thought to have ant dependent oviposition live in shelters constructed by their attendant ants (characteristic 2b). In part, this may be because juveniles sheltered in byres are aggregated, and thus the species showing this behavior are particularly dependent upon attendant ants for defense (see below). Ant byres and similar structures are also highly visible and may serve as additional cues for ovipositing females. For example, juveniles of the Australian species *Hypochrysops ignitus* are housed in characteristic thatch byres constructed by workers of *Iridomyrmex nitidus* (see Fisher 1978, p. 210). This butterfly has been recorded to feed on at least 17 different plant families, but is always associated with the same ant species (Common and Waterhouse 1981).

A large number of the species cited in the Appendix lay eggs in clusters (see also Kitching 1981) and/or aggregate as juveniles (characteristic 3). In exclusion experiments with *J. evagoras*, Pierce (1983) found that young instars that aggregated on plants with old instars were tended by more ants and had a higher survivorship than early instars that occured on plants by themselves. However, when attendant ants were experimentally removed, larvae that aggregated suffered greater mortality: aggregation and predation rates were positively correlated on ant free plants (Pierce 1983). This experimental analysis indicated that while certain myrmecophilous lycaenids may benefit greatly from aggregating, by so doing they also increase their dependence upon ants for protection, and thus may be more likely to possess ant dependent oviposition.

Finally, the majority of species listed in the Appendix associate exclusively with only one species or genus of ant (characteristic 4). The nature of species specificity in lycaenid/ant interactions is poorly understood and it would be interesting to look at the relationship between degree of myrmecophily and the response of ovipositing females to specific ant taxa. Frohawk (1903) observed that females of the parasitic species, *Maculinea arion* laid eggs only on plants of *Thymus* that also had active ant nests in the ground below them. He noted, however, that the nests were not always those of the host ant. It is possible that females of *M. arion* can respond to the visual presence of ants but are unable to identify species. Similarly, *Maculinea teleius,* which in Japan associates with *Myrmica ruginodis* was recently found in the nest of *Lasius niger* (Fukuda et al. 1978).

The paucity of information available on attendant ants makes it difficult to quantify distinguishing characteristics of species eliciting oviposition by lycaenid butterflies. The predominant attendant ant genera involved (*Crematogaster, Camponotus, Iridomyrmex* and *Oecophylla*) are all agricultural, and possess extremely large colony sizes (Wilson 1971). With the exception of species of *Camponotus,* their nests tend to be polydomous, ameoboid-like structures with numerous entrances. All have impressive mass recruitment systems of defense (Wilson 1971). Both species of *Oecophylla* and many species of *Crematogaster* nest in trees, and this may have facilitated penetration by parasitic lycaenid species such as *Liphyra brassolis.*

One consequence of ant induced oviposition: host plant range

The characteristics of parasitic and other aphytophagous lycaenids have been reviewed at length by Cottrell (1984). In this section we will focus on herbivorous lycaenids and discuss how ant dependent oviposition may have influenced the diet of these species.

Bell (1915–20) was perhaps the first to recognize the role that ants played in the egg laying behavior of a number of phytophagous lycaenids. More importantly, he suggested an ecological and evolutionary consequence of this behavior: he maintained that particular lycaenids possessed an

Table 5. A comparison of the mean number of host plants of myrmecophilous and non-myrmecophilous lycaenid species in Australia, South Africa and North America

	Myrmecophilous lycaenids			Non-myrmecophilous lycaenids			F	P
	$\bar{x}$	SD	n	$\bar{x}$	SD	n		
Number of host plant species								
Australia	4.57	4.50	63	2.85	2.35	35	5.09	0.026
Number of host plant genera								
Australia	2.71	3.05	63	2.40	2.09	35	1.53	0.219
South Africa	2.83	3.25	42	1.78	1.45	50	4.56	0.036
North America								
Theclinae	16.00	25.18	3	1.76	1.61	46	21.68[a]	0.000
Polyommatinae	5.55	4.59	11	2.00	1.67	32		
Number of host plant families								
Australia	1.78	1.74	63	1.69	1.82	35	0.05	0.818
South Africa	1.90	1.53	42	1.10	0.32	50	12.96	0.001
North America								
Theclinae	7.67	11.55	3	1.50	1.01	46	12.65[b]	0.001
Polyommatinae	2.18	2.18	11	1.34	0.60	32		

[a] Sub-family interaction: $F=11.96$, $P<0.008$

[b] Sub-family interaction: $F=14.11$, $P<0.003$

unusually wide range of host plants because the females of these species laid eggs in response to attendant ants as well as to customary plant cues. Thus, plants may have been selected because of their proximity to ant nests in addition to their specific nutritive value. More recently, Gilbert and Singer (1975), Vane Wright (1978), Atsatt (1981a, b), Cottrell (1984) and Pierce (1984) have discussed similar ideas about ant induced host plant shifts and their possible evolutionary significance for the Lycaenidae. Several of these authors have also noted that with their mobile ant guard, myrmecophilous lycaenids may be able to shift hosts more readily than butterflies that rely upon chemical defenses obtained from their food plants (e.g. Brower and Brower 1964).

We investigated the possibility that ant association has amplified the host plant range of lycaenid butterflies by making a comparative survey of the plants consumed by different lycaenids. The number of host plant species, genera and families were tallied for individual lycaenids from Australia (Common and Waterhouse 1981; Symon 1980); and the number of host plant genera and families were counted for lycaenid species from South Africa (Clark and Dickson 1971) and North America (Klots 1951; Emmel and Emmel 1973; Howe 1975; Ferris and Brown 1981). Records of host plant species from the latter two regions were incomplete and omitted from the analysis. In the absence of a full knowledge about exactly which lycaenids possess ant induced oviposition, we took the broadest interpretation possible and simply compared the number of host plants consumed by lycaenids that do and do not associate with ants. We also analyzed the host plant ranges of lycaenids within the two main subfamilies represented in the data, the Theclinae and Polyommatinae (*sensu* Eliot 1973).

This comparative study of 282 species confirmed that in general, lycaenids that are tended by ants feed on a wider range of plants than lycaenids that are not tended by ants (Table 5). In both North America and South Africa, myrmecophilous lycaenids consumed a wider range of plant genera and families. A two-way ANOVA revealed that subfamily had a significant effect in the North American sample. This is probably the result of a small sample size rather than any intrinsic biological differences between the subfamilies in this region. In North America, only three species in the Theclinae ($n=49$) are myrmecophilous. Subfamily did not have an effect in either the Australian or South African fauna and hence the subfamily analysis is not included in Table 6. In Australia, myrmecophilous lycaenids fed on a significantly wider range of host plant species than non-myrmecophilous lycaenids, but not on a wider range of plant genera or families. This is probably because 21% ($n=167$) of the recordings of unique food plant species of myrmecophilous lycaenids in this region fell into only three out of 86 plant genera.

The overlap of species in plant genera utilized by myrmecophilous lycaenids in Australia is indicative of a general pattern that exists among the host plants of lycaenid butterflies. Although ant tended lycaenids feed on a greater number of plant species than their untended counterparts, most of these species are legumes (see Downey 1962a) and belong to only a few genera and families. This characteristic profile of host plant preference may again be the result of their myrmecophilous habits. Pierce (1984) showed a highly significant correlation between ant attendance and diet: myrmecophilous lycaenids usually feed on nitrogen-fixing, protein rich plants, whereas non-myrmecophilous lycaenids feed on other kinds of plants. The larvae of several myrmecophilous lycaenids have been shown to secrete concentrated amino acids in addition to carbohydrates as rewards for attendant ants (Pierce 1983). Therefore it seem likely that selection has favored specialization by myrmecophilous lycaenids on protein rich plants because these food plants enable them to produce the appropiate secretions to attract their attendant ants.

Two of the major trends apparent in host plant selection by phytophagous lycaenids may thus be explained in terms of freedoms and constraints that are ultimately the result of pressures exerted by the parasitoids and predators of these butterflies. For lycaenids that live in situations where the risk of predation or parasitism of juveniles is high, selection has often resulted in strong ant associations: attendant ants can act as a significant guard against parasitoids and predators (Pierce and Mead 1981; Pierce 1983). In species such as *J. evagoras*, ants are so important for the survival of offspring that females use them as cues in oviposition. Within their mobile ant guard and their higher chance of shifting onto novel plants that contain the appropiate attendant ant species, myrmecophilous lycaenids consume a wider range of hosts than non-myrmecophilous lycaenids. However, in order to attract their ant guards, these same lycaenids are constrained by the nutritional quality of their host plants.

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Appendix

Species of lycaenid butterflies in which ant induced oviposition has been described or suspected. See text for details of characteristics. *1* present; *0* absent; – unknown; *a* characteristic 2a; *b* characteristic 2b

Species	Ant associate	Food or food plant(s) cited in reference	Characteristics				Reference
			1	*2*	*3*	*4*	
Australian							
Acrodipsas cuprea	*Crematogaster* spp.	Ant brood? *Acacia baileyana* (Mimosaceae)	1	a	1	1	Common and Waterhouse 1981 (p. 427)
A. myrmecophila	*Iridomyrmex nitidus*	Ant brood? *Acacia pycnantha* (Mimosaceae)	1	a	1	1	McCubbin 1971 (p. 104) see also Common and Waterhouse 1981 (p. 428)
Arhopala centaurus	*Oecophylla smaragdina*	*Eucalyptus intermedia*, *Melaleuca quinquenervia* (Myrtaceae)	1	b	1	1	Common and Waterhouse 1981 (p. 468)
Hypochrysops delicia	Small black ants	*Acacia decurrens* (Mimosaceae)	1	b	1	1	Borch 1928 (p. 188)
H. ignitus	*Iridomyrmex nitidus*	Numerous (at least 17 families) (see Common and Waterhouse 1981, p. 446)	1	b	1	1	Burns 1931 (p. 135)
H. theon	*Iridomyrmex cordatus*	*Drynaria quercifolia* (Polypodiaceae)	1	b	1	1	Daniels 1976 (p. 199)
Jalmenus evagoras	*Iridomyrmex* sp. 25 (ANIC) (*anceps* group)	*Acacia irrorata* and others (16 species) (Mimosaceae)	1	0	1	1	This study
J. ictinus	*Iridomyrmex* sp. (*purpureus* group)	Acacia (9 species) (Mimosaceae) *Heterodendrum diversifolium* (Sapindaceae)	1	0	1	1	Atsatt 1981a (p. 63) see also Common and Waterhouse 1981 (p. 500)
J. pseudictinus	*Froggattella kirbyi*	*Acacia* (2 species) (Mimosaceae) *Heterodendrum diversifolium* (Sapindaceae)	1	0	1	1	Atsatt 1981a (p. 63) see also Common and Waterhouse 1981 (p. 501)
Liphyra brassolis	*Oecophylla smaragdina*	Ant brood	1	a	1	1	Dodd 1902 see also Common and Waterhouse 1981 (p. 422)
Ogyris amaryllis	*Iridomyrmex rufoniger*	*Amyema* (at least 10 species) (Loranthaceae)	1	b	1	1	Atsatt 1981a, see also Burns 1931 (p. 130)
O. barnardi	Small black ants	*Amyema quandang* (Loranthaceae)	1	b	1	1	Fisher 1978 (p. 16, p. 200) (implied)
O. genoeveva	*Camponotus* sp.	*Amyema miguelii* (Loranthaeceae)	1	b	1	1	Burns and Rotherham 1980 (p. 96) (implied)
O. g. araxes	*Camponotus perthianus*	*Amyema pendulum* (Loranthaceae) and on bark of host tree near ant nest	1	b	1	1	Burns 1931 (p. 129)
Ethiopian							
Aloeides dentatis	*Acantholepis capensis*	*Hermania depressa* (Sterculiaceae)	1	a	1	1	Henning 1983 (p. 73)
Apharitis acamas	*Crematogaster* sp.	Fed by ants? Oviposition on ant colony in date palm, *Phoenix dactylifera* (Avacaceae).	1	a	1	1	Larsen and Pittoway 1982 (p. 164)
Argiolaus alcibiades	*Crematogaster buchneri*	*Loranthus icanus* (Loranthaceae) growing on *Alstonia congensis* (Apocynaceae)	1	–	–	1	Farquharson 1921 (pp. 360–377)
A. iulus	*Crematogaster buchneri*	As above	1	–	–	1	Farquharson 1921 (pp. 360–377)

Species	Ant associate	Food or food plant(s) cited in reference	Characteristics				Reference
			1	*2*	*3*	*4*	
A. maesa	*Crematogaster buchneri*	As above	1	—	—	1	Farquharson 1921 (pp. 360–377)
Catochrysops phasma	*Camponotus maculatus*	*Solenostemon ocymoides* (Lamiaceae)	1	a	1	1	Farquharson 1921 (p. 400)
Euliphyra mirifica	*Oecophylla longinoda*	Fed by ants	1	a	1	1	Lamborn 1913 (p. 454) (implied)
Lachnocnema bibulus	*Camponotus* sp.	*Combretum sp.* (Combretaceae) *Vernonia sp.* (Asteraceae) secretions from membracids and jassids, and ant regurgitations. Sometimes membracids and jassids themselves	1	a	1	1	Cripps and Jackson 1940 (p. 449) also Lamborn 1913 (p. 470) and Farquharson 1921 (p. 388)
Lepidochrysops ignota	*Camponotus niveosetosus*	*Becium obovatum* (Lamiaceae)	1	a	—	1	Henning 1983 (p. 76)
Megalopalpus zymna	*Pheidole aurivilli*	*Musanga smithii* (Urticaceae) *Triumfetta cordifolia* (Tiliaceae) and membracids	1	b	—	1	Lamborn 1913 (pp. 458–470, esp. p. 466)
Poecilmitis aureus	*Crematogaster* spp.	*Clutia pulchella* (Euphorbiaceae)	1	b	1	1	Henning 1983 (p. 72)
P. lycegenes	*Crematogaster maculatus liengmei*	*Royena hirsuta* *Diospyros lycioides* (Ebenaceae) *Myrsine africana* (Myrsinaceae) *Rhus sp.* (Acacardiaceae)	1	b	1	1	Henning 1983 (p. 71)
P. palmus	*Crematogaster peringueyi*	*Berzelia intermedia* (Bruniaceae) *Chrysanthemoides monilifera, Osteospermum ciliatum* (Asteraceae) *Aspalathus sarcantha* (reared) (Fabaceae) *Anthospermum aethiopicum* (Rubiaceae) (oviposition record) and others	1	b	1	1	Claassens and Dickson 1980 (p. 60) see also Cottrell (1984)
Spindasis namaqua	*Crematogaster* sp.	*Zygophyllum refractum* (Zygophyllaceae)	1	b	1	1	Henning 1983 (p. 72)
S. phanes	*Crematogaster castanea*	*Ximenia caffra* (Olacaceae)	1	—	—	1	Henning 1983 (p. 73)
Thestor basutus	*Anoplolepis custodiens*	*Vernonia natalensis* (Asteraceae) and psyllids	1	a	1	1	Dickson (1954) also Clark and Dickson 1971 (p. 19, p. 262)
Nearctic							
Lycaena rubidus	*Formica altipetens*	*Rumex hymenosephalus* (Polygonaceae)	0	0	0	0	Funk (1975)
Neotropical							
Juditha molpe (Riodinidae)	*Camponotus* spp.	*Calliandra globerrima* (Mimosaceae) and oviposits on *Bauhinia pediolata* (Caesalpinaceae) with ants	1	0	0	1	Callaghan 1981–1982 (p. 46)
Oriental							
Anthene (Lycaenesthes) lycaenina	*Oecophylla smaragdina*	*Wagatea spicata* (Caesalpinaceae) *Buchanania latifolia* (Anacardiaceae)	1	0	0	1	Bell 1915–1920/ XXV (p. 659)

Species	Ant associate	Food or food plant(s) cited in reference	Characteristics				Reference
			1	*2*	*3*	*4*	
A. (L.) aemolus	*Oecophylla smaragdina*	*Combretum extensum,* *Terminalia paniculata* (Combretaceae) *Saraca indica* (Caesalpinaceae)	1	b	1	1	Bell 1915–1920/ XXV (p. 649)
Catapoecilma elegani	*Crematogaster* spp.	*Terminalia paniculata* (Combretaceae)	1	b	1	1	Bell 1915–1920/ XXVI (p. 761)
Freyeria trochilus	*Prenolepis* spp.	*Lotus corniculatus*	0	0	0	0	Bell 1915–1920/ XXV (p. 638)
Flos chinensis	*Polyrhachis dives*	Aphids	–	–	–	–	Kershaw 1905 cited in Lamborn 1913 (p. 463)
Spindasis (Aphnaeus) lohita	*Crematogaster* spp.	Terminalia paniculata (Combretaceae) *Dioscorea pentaphylla* (Dioscoraceae)	1	b	1	1	Bell 1915–1920/ XXVI (p. 479) see also Cottrell 1984
S. vulcanus	*Crematogaster* sp.	*Canthium parviflorum* (Rutaceae) *Zizyphus rugosa, Z. jujuba* (Rhamnaceae) *Allophyllus cobbe* (Sapindaceae) *Clerodendrum siphonanthus* (Verbenaceae)	1	b	1	1	Bell 1915–1920/ XXVI (p. 477) see also Cottrell 1984
Surendra quercetorum	Unidentified	*Acacia pennata* (Mimosaceae)	1	0	0	–	Bell 1915–1920/ XXVI (p. 442)
Tarucus (Castalius) ananda	*Crematogaster* spp.	*Loranthus sp.* (Loranthaceae) *Zizyphus* sp. (Rhamnaceae)	1	b	1	1	Bell 1915–1920/ XXVI (p. 122)
T. (C.) plinius	*Crematogaster* spp.	*Sesbania aculeata* (Fabaceae) *Plumbago capensis* (Plumbaginaceae)	0	0	0	1	Bell 1915–1920/ XXVI (p. 121)
Zezius chrysomallus	*Oecophylla smaragdina*	*Terminalia paniculata* (Combretaceae) *Pterocarpus marsupium* (Fabaceae) *Dioscorea* (Dioscoriaceae)	1	b	–	1	Bell 1915–1920/ XXVI (p. 456)
Palearctic							
Maculinea arion	*Myrmica scabrinodis* *M. rubra* *M. sabuleti*	*Thymus drucei* (UK) *Origanum vulgare* (UK) *Thymus serphyllum* (Japan) (Lamiaceae)	1	a	0	1	Frohawk 1903 see also Fukuda et al. 1978 (p. 60)
M. teleius	*Myrmica ruginodis* (UK) *M. rubra* (Japan)	*Sanguisorba officionalis* (France) "Waremoko" (Japan) (Rosaceae)	1	a	0	1	Fukuda et al. 1978 (p. 60)
Niphanda fusca	*Camponotus japonicus*	*Quercus serrata* (Fagaceae) and the secretions of the aphid, *Greenidea spp.* and ant regurgitation	1	a	1	1	Nagayama 1950 Fukuda et al. 1978 (plate 30) see also Iwase 1952
Shirozua jonasi	*Lasius spathepus*	"Buna" tree (Fagaceae) and secretions of aphids	1	a	–	1	Fukuda et al. 1978 (p. 64)
Spindasis takanomis	*Crematogaster* spp.	*Pinus* sp. (Pinaceae) and ant larvae and ant regurgitation	1	a	1	1	Shirozu and Hara 1962 (p. 68) see also Cottrell 1984, Iwase 1955, Fukuda et al. 1978 (p. 58)