

Local distribution of the lycaenid butterfly, *Jalmenus evagoras*, in response to host ants and plants

John T. Smiley^{1,*}, Peter R. Atsatt¹, and Naomi E. Pierce²

¹ Department of Ecology and Evolutionary Biology University of California, Irvine, CA 92717, USA

² Department of Biology, Princeton University, Princeton, NJ 08544, USA

Summary. The caterpillars of *Jalmenus evagoras* are tended by ants as they feed upon *Acacia* trees. In the area of Brisbane, Australia, *J. evagoras* require ants of the *Iridomyrmex anceps* species group; predation and parasitism are so intense that larvae and pupae deprived of attendant ants cannot survive (Pierce 1983). We investigated the efficiency with which *J. evagoras* locate and exploit the “host ant” resource by sampling 737 quadrats in 30 sampling grids and six study sites containing appropriate host plants; ants were collected at baits located in the center of each quadrat. *J. evagoras* was found in all habitats where *I. anceps* co-occurred with host *Acacia*. Nine of the ten sampling grids which had three or more *I. anceps*/*Acacia* “host” quadrats also had colonies of *J. evagoras* present (or immediately adjacent), including sites as far as 35 km apart. Of 19 sampling grids on which “host” quadrats were rare (i.e., less than three quadrats), none had *J. evagoras* ($P < 0.001$). Within sample grids, *I. anceps* was distributed independently from *Acacia* trees, suggesting that they are not dependent for their survival on either *Acacia* or on *J. evagoras*. Within montane pasture habitats, *I. anceps* and at least one other ground-dwelling *Iridomyrmex* species were distributed in mutually exclusive “ant mosaic” territories which were stable during a one month period. *I. anceps* did not colonize or tend pupae of *J. evagoras* experimentally placed in adjacent territories of a different, nontending species of *Iridomyrmex*, demonstrating the integrity of territory boundaries. Sampling of ants in *Acacia* trees revealed that, in the absence of *J. evagoras*, *Iridomyrmex* workers are not common above ground level, and that their numbers decline in larger trees ($P = 0.02$). In *I. anceps* territories, eight of nine *J. evagoras* pupae placed in trees over 3.0 m tall were not found after 24 h whereas all ten controls placed in low trees were found and tended ($P = 0.00012$). This may explain why *J. evagoras* tends to oviposit in trees less than 2.0 m tall. An alternative hypothesis, that smaller trees have higher content of total nitrogen, and are therefore more nutritious, was not supported. We conclude that the local distribution and host tree selection by *J. evagoras* is dependent upon the distribution, patchiness, and foraging behavior of the host ant, *I. anceps*, and its spatial overlap with a number of species of host *Acacia*.

The distribution and abundance of insect herbivores is known to be a function of the distribution of host plants in most habitats (Strong et al. 1984). However, there is increasing evidence that the distribution and behavior of natural enemies is also a major factor (Price et al. 1981), suggesting that the presence of “enemy-free space” may be just as important as host plant in determining the distribution of herbivores (Atsatt 1981b; Jeffries and Lawton 1984). For example, Pierce and Mead (1981), Pierce (1983) and Pierce and Eastal (1986) have shown that several species of lycaenid butterflies (Lepidoptera: Lycaenidae) are dependent on protective ants for their survival, and will not oviposit unless the correct ants are physically present at the oviposition sites (Atsatt 1981a; Pierce and Elgar 1985). Pierce (1984) has suggested that the patchy distribution and low vagility characteristic of lycaenid populations is caused by the patchy distribution of habitats which contain the requisite species of plants and ants. Ants have also been found to affect the distribution of many other types of insect herbivores (Buckley 1982).

In the area of Brisbane, Australia, larvae of *Jalmenus evagoras* (Lepidoptera: Lycaenidae) feed upon small host trees of *Acacia irrorata* and *A. melanoxylon* and are tended by ants of the *Iridomyrmex anceps* species group (Pierce 1983, 1984; Pierce and Elgar 1985; Elgar and Pierce, in prep., Kitching 1983). This lycaenid has an extremely patchy distribution (Pierce 1983), and females frequently oviposit on the same host tree from which they eclosed as pupae. “Colonies” of aggregated larvae and pupae are extremely vulnerable to predation by other invertebrates and cannot survive unless they are protected by a “guard” of *I. anceps*, which obtain food rewards of nectar and amino acids secreted by glands on the juveniles of *J. evagoras* (Pierce et al. 1987). The selection of nitrogen-fixing *Acacia* by *J. evagoras* may be strongly dependent on the need for a rich source of amino acids with which to feed ants (Pierce 1985), and *I. anceps* may be attracted to the extrafloral nectaries or nectar-secreting homopterans found on *Acacia* (Pierce 1983). Since the butterflies, host plants, and host ants can be surveyed with certainty, the *J. evagoras* system provides an opportunity to examine how enemy free space and food availability affect the distribution of this insect herbivore.

In this paper we examine the co-distribution of ants, *Acacia* spp, and *J. evagoras* by (1) comparing different sites and habitats within a 50 km radius of Brisbane, (2) sam-

* Present address: University of California Big Creek Reserve, Big Creek, CA 93920, USA

Offprint requests to: P.R. Atsatt

pling from grids at each site, and (3) sampling individual trees. For each case we analyze (1) how often host ants and host plants occur together, and (2) how often host ants/plants are colonized by *J. evagoras*. We also evaluate the stability of ant distributions by repeated sampling, and experimentally determine the potential for *J. evagoras* to "attract" *I. anceps* out of its territory. We sample *Acacia* trees of different height to determine if the preference of *J. evagoras* for small host trees is correlated to (1) increased likelihood of encountering ants, or (2) increased nutritive value as indicated by total nitrogen content. Tests of the effects that different host ants and plants have on *J. evagoras* oviposition behavior will be described elsewhere.

Methods

We investigated *Acacia* spp., *Iridomyrmex* spp. and *J. evagoras* near the city of Brisbane, Queensland, Australia during the middle of the summer flight season of *J. evagoras* (January 24 to March 12, 1984). Study sites were located on the ridge and slopes of Mt Nebo ("MN" in Table 1; 152 47'E/27 23'S), Mt Glorious ("MG"; 152 46'E/27 20'S), and Mt Coot-tha ("MC"; 152 58'E/27 28'S), on the nature reserve on the campus of Griffiths University ("GU"; 152 4'E/27 35'S), near the Lone Pine Koala Sanctuary ("LP"; 153 0'E/27 30'S), and in hills near Coomera about 50 km south of the city of Brisbane ("CO"; 153 51'E/27 50'S). Principal habitats included (1) Eucalyptus-*Acacia* woodland ("Mt Nebo woodland," "Lowland woodland"), (2) pastures located in rainforest ("Mt Nebo pasture," "Mt Glorious pasture") and (3) pastures located in Eucalyptus-*Acacia* woodland ("Lowland pasture"). These habitats contained diverse species of *Iridomyrmex* ants and numerous small *Acacia* trees, the principal resources required by *J. evagoras*, and include most habitats in the Brisbane area which potentially contain populations of *J. evagoras*. The region around Mt Nebo was specifically chosen because many colonies of *J. evagoras* were known to be present.

Sampling grids

Acacia, *Iridomyrmex*, and *J. evagoras* were surveyed on 30 sampling grids, each consisting of about 25 quadrats (Table 1). Grids were situated on the ground away from dense vegetation and heavily shaded understory. Most sampling grids were purposely located in areas with numerous small *Acacia* trees, but grid 'R' was selected because it had an unusual species of *Iridomyrmex* (*I. nitidus*). Two grids ('E' and 'S') were located at sites where small colonies of *J. evagoras* were previously known to be present, and grid 'O' was located around another colony tended by a species of *Iridomyrmex* only rarely associated with *J. evagoras*. The remaining 27 sampling grids were located without prior knowledge of the presence of *J. evagoras*.

Each quadrat was approximately 5.0 m on a side, and quadrats were usually arranged in a square or rectangular array. Each sampling grid was mapped and the position and height of *Acacia* trees and saplings recorded. *Acacia* were searched for the presence of *J. evagoras* eggs, larvae and pupae. Ants were baited with 1–2 g of canned tuna fish placed on a white 8 × 13 cm card located in the center of each quadrat. Ants of all species were collected from baits by placing a sample of the workers in 80% alcohol,

and sorted to species by comparison with voucher specimens. Some voucher specimens were obtained from colonies of known identity (R.W. Taylor, personal communication). The identifications of *Iridomyrmex* are tentative since many species have not been formally described.

Distribution of *I. anceps* and *Acacia* within grids

Within sampling grids, the co-occurrence of *I. anceps* ants and *Acacia* trees was determined by counting the number of quadrats on each grid which contained both. The observed number of such "host" quadrats was compared to that expected if ants and trees were independently distributed. The expected number was calculated as $p(I)p(A)N$, where $p(I)$ and $p(A)$ are the proportion of quadrats with *I. anceps* and *Acacia* trees under 3.0 m tall, respectively, and N is the total number of quadrats on the grid.

To determine whether spatial distributions of ants, as assayed by the above methods, remain stable or fluctuate from one month to the next, sampling grids A, B, and F (Mt Nebo pasture) were sampled 21 January and again on 24 February. These sampling grids principally contained *I. anceps* and another *Iridomyrmex* which we labelled species "B". Quadrats with the same ant species on both sample days were designated as "core" territories.

The integrity of *Iridomyrmex* sp. "B" core territories, against intrusion by *I. anceps*, was tested by placing "bait" pupae of *J. evagoras* in small (<1.5 m tall) plants of *A. irrorata* within the core areas of both species. Pupae were pinned to stems by passing an insect pin through a small piece of tape attached to the cremaster. The pupae are highly attractive to *I. anceps*, but are not tended by *Iridomyrmex* sp. "B". We reasoned that if *I. anceps* workers began tending these pupal "baits" it would indicate that they are capable of rapidly locating and exploiting *J. evagoras* within the core territory of other species of ants, and that the distribution of *J. evagoras* colonies within grids would not be strongly constrained by the boundaries of the ant territories.

Distribution of *I. anceps* in trees of different height

Since *J. evagoras* usually colonizes *Acacia* trees under 3 m tall, we investigated the abundance of *I. anceps* on trees of different height. We also experimentally placed bait pupae of *J. evagoras* in trees of different height within core territories of *I. anceps* to see if pupae in taller trees would be less likely to be found and tended. We additionally determined the nitrogen content of foliage of three species of *Acacia*, comparing trees <1 m tall, 2 m tall trees, and 4–5 m tall trees, to see if smaller trees were more nutritious and might therefore be preferred by *J. evagoras*. Three samples were taken from each size class of each species, dried in the field, and sent to the University of California Agricultural Extension Laboratory for determination of total nitrogen content.

Results

Sampling grids

Acacia sp. were found in a large proportion of quadrats in all habitats sampled (Table 1). Species found include *A. irrorata*, a pinnate-leaved species which is the preferred host

Table 1. Number of quadrats containing *Acacia* sp., *Iridomyrmex* sp., and *J. evagoras* (in parenthesis) in 30 grids in five habitats and six sites near Brisbane, Australia: PN=Mt Nebo pasture, WN=Mt Nebo woodland, PG=Mt Glorious pasture, PL=lowland woodland; see text for site designations.

GRD	HAB	SITE	no QUAD	<i>Acacia</i> species			<i>Iridomyrmex</i> species				other ants
				IR	ME	FI	<i>anceps</i>	"A"	"B"	"D"	
A	PN	MN	27	23	0	0	16 (3)	1	8	0	2
B	PN	MN	25	15	0	0	6	1	13	0	6
C	PN	MN	25	19	7	0	8 (1)	1	16	0	1
D	PN	MN	25	1	1	0	14	0	7	0	4
E	PN	MN	25	17	1	0	6 (2)	9 (2 ^b)	4	3	3
F	PN	MN	20	12	0	0	10 (1)	0	10	0	0
I	PN	MN	25	7	3	0	0	0	3	0	22
J	PN	MN	25	4	17	0	6	0	1	0	18
R	PN	MN	25	0	0	0	8	0	5	0	12
G	WN	MN	25	17	3	0	7 (2)	8	0	0	10
H	WN	MN	30	17	0	20	2	14	2	0	12
K	WN	MN	20	8	0	9	10	0	0	9	1
L	WN	MN	25	2	0	15	5	3	0	2	15
M	WN	MN	20	4	1	0	6	0	10	0	4
N	WN	MN	25	4	4	0	0	7	0	0	18
O	WN	MN	20	2	1	0	0	19 (2)	0	0	1
P	WN	MN	25	18	1	3	0	0	3	0	22
Q	WN	MN	25	6	3	0	4	0	1	8	12
S	PG	MG	25	0	4	0	12 (2)	0	4	0	10
T	PG	MG	25	0	10	1	2	1	0	8	14
U	PG	MG	20	5	11	0	0	6	0	2	13
V	PG	MG	25	11	6	0	3	3	5	6	8
Y	PL	CO	25	0	23 ^{ab}	0	0	0	24 ^e	0	1
Z	PL	CO	25	0	14 ^{ab}	0	0	0	14 ^e	10	1
AD	PL	LP	37	0	2 ^d	0	0	0	6	6 ^f	25
W	WL	MC	25	0	2 ^a	8	0	1	2	0	22
X	WL	MC	25	0	17 ^a	5	9 ^g (1)	0	1	0	15
AA	WL	GU	25	0	4 ^{ac}	0	2 ^g	0	7	0	17
AB	WL	GU	25	0	11 ^{ac}	0	0	0	2	0	23
AC	WL	LP	18	0	0	0	0	0	0	0	18

^a *A. aulacocarpa*,

^b *A. penninervis*

^c *A. falcata*,

^d species similar to *A. aulacocarpa*,

^e similar to *Iridomyrmex* species "B",

^f similar to *Iridomyrmex* species 'D',

^g similar to *I. anceps*,

^h *J. evagoras* tended by *I. anceps*

of *J. evagoras* in the region, and several species with broad "leaves" (phyllodes) such as *L. melanoxylon*, *A. aulacocarpa*, *A. penninervis*, and *A. falcata*. Most of these species are acceptable as host plants by *Jalmenus* species (Common and Waterhouse 1972; N. Pierce, personal observation). Of the species of *Acacia* sampled, only *A. fimbriata* appeared to be generally unacceptable as a host, although *J. evagoras* was observed to feed on this species once (N. Pierce, personal observation). In the present analysis of host availability we have treated *A. fimbriata* as a non-host.

The ant baits were found to be extremely attractive to all species of *Iridomyrmex* known to be present, as well as to certain other species of ant (Table 1). Within an hour of placement, 58% of all baits were colonized by dense aggregations of *Iridomyrmex* belonging to 6 species, and 39% were colonized by other genera of ants, including species of *Nononcus*, *Pheidole*, *Crematogaster*, and *Paratrichina*. *I. anceps* and morphospecies "A", "B", and "D"

were the most common species of *Iridomyrmex* found at baits. *I. nitidus* and *Iridomyrmex* species "C" (a large purple ant similar to *I. detectus*) were collected infrequently (6 quadrats on grid 'R' and 26 quadrats on grids 'H' and 'P', respectively). *I. anceps* was found on 63% of all sampling grids ($N=30$), and in all habitats except lowland pasture. It was present on 77% of the sampling grids in montane habitats ($N=22$), while *Iridomyrmex* species "A", "B" and "D" were present on 55%, 68%, and 32% of these grids, respectively. Thus, the host ant *I. anceps* shared montane habitats about equally with three other species of *Iridomyrmex*, but was much less common in lowland habitats (Table 1).

Eggs, larvae, and pupae of *J. evagoras* were found in eight of the sampling grids, in four of the five habitats (Table 1). The only habitat lacking *J. evagoras* was the lowland pasture, which also lacked *I. anceps* in our samples. We intentionally placed grid 'O' around a colony of *J.*

evagoras tended by *Iridomyrmex* sp. "A"; this was the only instance of tending by any species other than *I. anceps* that we observed. Preliminary data suggest that the survivorship of these *J. evagoras* was reduced in comparison with nearby colonies tended by *I. anceps*. The majority of *J. evagoras* juveniles were found on *Acacia* plants under 2.0 m tall, but on grid X they were found on a sapling of *A. aulacocarpa* which was 3.0 m tall. Thus, colonies of *J. evagoras* were found in all habitats which contained *I. anceps*, using several species of *Acacia* hostplants.

Of the 13 sampling grids which contained "host" quadrats (those with *I. anceps* and host *Acacia*), seven contained *J. evagoras*. Among the 27 grids located without prior knowledge that *J. evagoras* was present, five out of eleven grids with "host" quadrats had colonies of *J. evagoras* while none of the remaining 15 did (Fisher's exact probability $P=0.007$). Of the six grids with host quadrats but no *J. evagoras*, two (Grids B and J) had colonies within 5 m of the boundary of the grid.

Distribution within sampling grids

Repeated sampling of grids A, B and F indicated that 47 of 72 quadrats had the same species of ants present at the end of February as were present in mid-January; i.e. that 63% of the pasture habitat was occupied by "core" territories of *Iridomyrmex* sp. (Fig. 1). The great majority (36/47) of these core quadrats belonged to four distinct areas ranging between 150–250 m², minimum area. The other 12 core quadrats (except one quadrat in grid B) bordered on edges and may have belonged to extensive core areas off the sampling grid.

Placement of *J. evagoras* pupae, six on core areas of *Iridomyrmex* sp. "B" and six on core areas of *I. anceps*, revealed that workers of *I. anceps* located and began tending all six pupae within their core territory within 24 h, but did not tend any of the pupae 5 m away located in core areas of *Iridomyrmex* sp. "B" (Fig. 1; Fisher's exact probability, $P<0.001$). These latter pupae remained untended by ants for the duration of the experiment (48 h).

Within sampling grids, *I. anceps* was commonly observed in grass, litter, and vegetation away from *Acacia* trees. The observed frequency of occurrence of *I. anceps* on quadrats containing *A. irrorata* was approximately equal to the expected frequency based on the product of the separate probabilities (Table 2), suggesting that *I. anceps* does not significantly associate with *Acacia* trees at this scale of measurement.

Distribution in trees of different height

A survey of *I. anceps* found in 30 *Acacia* trees revealed 0 to 5 workers at any given time, unless larvae or pupae of *J. evagoras* were present, in which case numbers ranged from 20 into the hundreds. This suggests that the trees were not a significant resource for the ants in the absence of *J. evagoras*, and that colonies of *I. anceps* are commonly found in sites where they do not come into contact with mutualist lycaenids.

Between 6% and 34% of small (<3.0 m tall) *Acacia* trees in six montane sites had workers of *I. anceps* present (Table 3), and 27% to 56% of *I. anceps*-occupied trees (excluding *A. fimbriata*) had eggs, larvae, or pupae of *J. evagoras* present. These data suggest that within suitable habi-

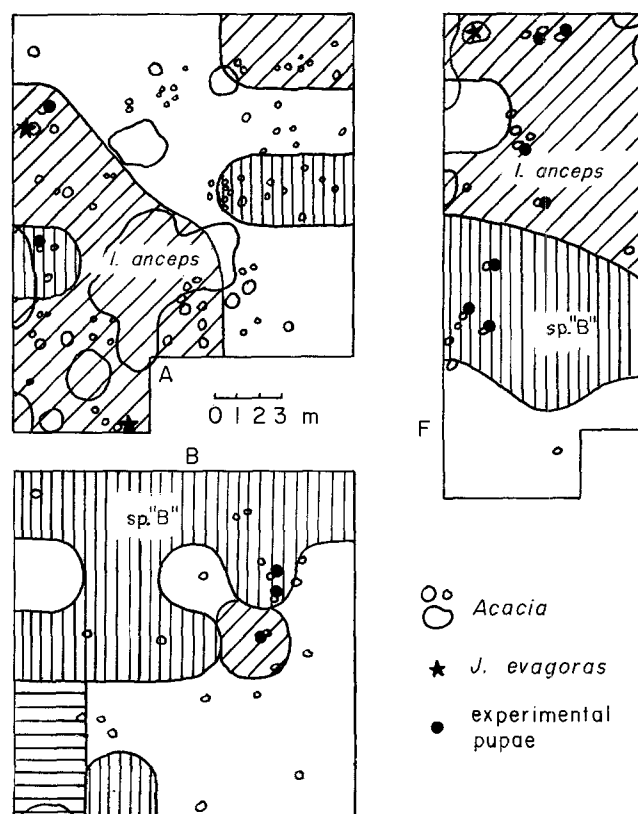


Fig. 1. Distribution of *Acacia* plants, *Iridomyrmex* "core territories," and *J. evagoras* colonies in late February, 1984, on three grids in pasture habitat at Mt Nebo, Queensland. "Core territories" were determined by bait sampling before and after a one-month interval; *I. anceps* core territories are indicated by diagonal bars, *Iridomyrmex* sp. "B" by vertical bars, and *Iridomyrmex* sp. "A" by horizontal bars. Location of experimental pupae indicated by solid dots. Pupae placed in *I. anceps* territories were colonized by *I. anceps* workers within 24 h, but none of the others were colonized by 48 h (see text)

tat, between one fourth and one half of all host *Acacia* bearing *I. anceps* received eggs from *J. evagoras*. However, few of these events are likely to result in successful reproduction by *J. evagoras*, which are usually successful only in large colonies tended by hundreds of ants.

The numbers of *I. anceps* per tree declined as tree height increased (linear regression: ants = height (m) \times 0.39 + 1.5; analysis of variance: df = 61, $f = 5.6$, $P = 0.02$). Ant density expressed as ants per vertical meter of tree height declined even more as tree height increased (Fig. 2), suggesting that *I. anceps* may be rare in taller trees. Of the nine pupae of *J. evagoras* placed in *I. anceps* "core territory" trees over 2.0 m tall, only one was colonized during 48 h. All 10 control pupae placed in 1.0 m tall plants were colonized, indicating that *I. anceps* is much less likely to locate and tend *J. evagoras* on larger trees in their territory (Fisher's exact probability, $P = 0.0001$).

Two way analysis of variance of nitrogen content of foliage from *A. irrorata* and *A. melanoxylon* (Table 4) indicated (1) *A. irrorata* foliage contained a higher percentage of nitrogen than *A. melanoxylon* ($F = 7.1$, $P < 0.02$), (2) percent nitrogen did not consistently decline as trees became taller ($F = 0.2$, $P > 0.50$), and (3) the two species of *Acacia* differed in the relationship between height and percent nitrogen ($F = 5.9$, $P < 0.02$). There was no suggestion in the

Table 2. Co-occurrence of *I. anceps*, *A. irrorata*, and *J. evagoras* in quadrats on sampling grids.

Grid no	no quadrats	w/ <i>I. anceps</i>	w/host <i>Acacia</i>	expected w/both	observed w/both	with colonies <i>J. evagoras</i>
A	27	16	23	14.7	16	3
B	25	6	15	3.6	4	0
C	25	8	19	6.1	6	2
D	25	14	2	1.1	1	0
E*	25	6	17	4.1	4	5
F	20	10	12	7.5	8	1
I	25	0	7	0	0	0
J	25	6	17	4.0	4	0
R	25	8	0	0	0	0
G	25	7	20	2.4	3	2
H	30	2	17	0.9	2	0
K	20	10	8	5.0	6	0
L	25	5	2	0.4	0	0
M	20	6	5	1.9	0	0
N	25	0	7	0	0	0
O*	20	0	3	0	0	3
P	25	0	19	0	0	0
Q	25	4	3	0.5	0	0
S*	25	12	4	1.9	4	2
T	25	2	10	0.8	1	0
U	20	0	16	0	0	0
V	25	3	15	0	0	0
Y	25	0	23	0	0	0
Z	25	0	14	0	0	0
AD	37	0	2	0	0	0
W	25	0	2	0	0	0
X	25	9	17	6.1	6	1
AA	25	2	4	0.3	0	0
AB	25	0	11	0	0	0
AC	18	0	0	0	0	0

* Grid intentionally placed around *J. evagoras* colony. The observed number of "host" quadrats containing *Acacia* and *I. anceps* was similar to the expected product of the independent abundances within grids ("goodness of fit" $G=11.0$, d.f.=17, $P=0.90$; Sokal and Rohlf 1981)

Table 3. Frequency of foraging ants on *Acacia* species at four sites between Mt Nebo and Mt Glorious, Queensland. Site 1: disturbed pasture at Mt Nebo. Site 2: roadside forest at Mt Glorious. Site 3: roadside forest between Mt Nebo and Mt Glorious. Site 4: roadside forest at Mt Nebo. Other ants: at site 2, other=6% *Iridomyrmex* species "A"; at site 3, other=18% *Iridomyrmex* species "A" and 48% *Iridomyrmex* species "D"; at site 4, other=59% *Iridomyrmex* species "A" and 30% *Notoncus* sp.

Site	<i>Acacia</i> species	Percent trees with:			N	
		<i>I. anceps</i>	<i>anceps</i> trees w/ <i>Jalmenus</i>	other ants		no ants
1a	<i>irrorata</i>	15	56	2	83	107
1b	<i>irrorata</i>	34	28	5	61	116
1c	<i>melanoxydon</i>	10	27	3	87	115
2	<i>melanoxydon</i>	31	30	42	27	84
3	<i>fimbriata</i>	6	0	40	54	100
4	<i>irrorata</i>	20	27	48	32	112

data that percent nitrogen declined among taller trees of *A. irrorata*, the preferred host of *J. evagoras* (analysis of variance, $F=1.7$, $P>0.2$).

Discussion

Among 27 sampling grids chosen without prior knowledge of the presence of *J. evagoras*, eight had three or more "host" quadrats (with host ants and host plants present).

Of these eight, five were colonized by *J. evagoras*. Two of the remainders (B and J) had *J. evagoras* colonies within 5 m of the boundary of the grid, while grid K may have been unsuitable for *J. evagoras*, with most host plants over 2.0 m tall. None of the remaining 19 grids (with two or fewer "host" quadrats) had *J. evagoras* (Fisher's exact probability, $P=0.002$). The high frequency of colonization of *I. anceps*/*Acacia* "host" grids, which were scattered over a considerable distance, leads us to conclude that *J. evagor-*

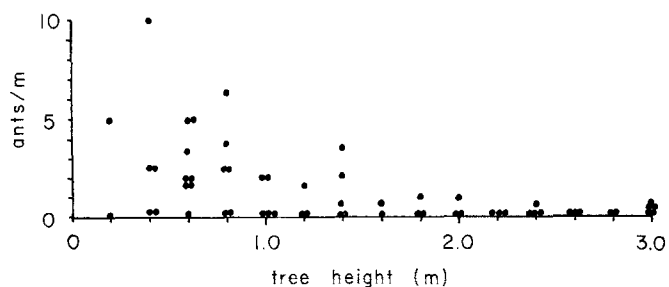


Fig. 2. Abundance of *I. anceps* per meter of tree height (ant density) on *Acacia* trees with no *J. evagoras* present. Trees with colonies of *J. evagoras* had 20–100 times as many ants. Trees were sampled in pasture habitat at Mt. Nebo, Queensland

Table 4. Percent nitrogen in dried foliage of *Acacia* trees of different height. Standard deviation in parenthesis; $N=3$ for each sample. Nitrogen content of *A. irrorata* and *A. melanoxyton* did not decline significantly as trees became larger (analysis of variance for each species: $F=1.7$, $P>0.2$ and $F=4.1$, $P>0.05$, respectively). See text for two way analysis of variance

tree height	<i>Acacia</i> species		<i>fimbriata</i> ^b
	<i>irrorata</i> ^a	<i>melanoxyton</i> ^a	
Under 1.0 m	3.0 (0.41) 3.0 (0.40) ^b	3.1 (0.73)	3.0 (0.11)
2.0 m	3.3 (0.64)	2.0 (0.13)	2.5 (0.29)
4.0 m	3.2 (0.10)	2.5 (0.29)	

^a Mt Nebo pasture

^b Mt Nebo woodland

as sample their environment thoroughly for *I. anceps*, and exploit most patches of suitable habitat. This supports the hypothesis that the scattered, patchy distribution of lycaenids such as *J. evagoras* is a direct consequence of the relative scarcity of sites with suitable ant-plant combinations.

I. anceps and *Iridomyrmex* sp. “B” occurred in relatively stable “core territories,” and *I. anceps* apparently does not invade the territory of *Iridomyrmex* sp. “B” in order to reach pupae of *J. evagoras*. This supports the interpretation that these ants are distributed in an “ant mosaic” (Leston 1978), although we have no information about the long-term stability of these mosaics. *I. anceps* and *Iridomyrmex* sp. “B” construct complex systems of tunnels and chambers at or just below the ground surface throughout their core territories, as predicted for ground-dwelling ants which form a mosaic (Jackson 1984).

The lack of positive co-occurrence of host *Acacia* and *I. anceps* on sampling grids suggested that the ant colonies were distributed independently of *Acacia* and therefore of *J. evagoras*. Since *I. anceps* colonies were common in pasture away from *Acacia*, where they presumably feed upon live prey, and were seen ascending large *Eucalyptus* trees on grid K, where they presumably were tending animal or plant nectar sources, we suspect that *J. evagoras* are one of several resources enabling *I. anceps* to survive and reproduce. However, because larvae of *J. evagoras* provide ants with a rich food source, it is possible that colony survival and reproduction are enhanced when tending large colonies of *J. evagoras*, and that the colonies we observed away from *J. evagoras* contribute relatively little reproduction

during mating flights. More data on the biology of *I. anceps* is needed to resolve this and related questions.

Our data suggest that the preference of *J. evagoras* for small host plants may be a response to the increased probability of detecting *I. anceps* on smaller plants. The alternative hypothesis, that *J. evagoras* obtains more nutritive foliage from smaller *A. irrorata*, was not supported by our data on nitrogen content. It is possible, however, that young plants contain fewer or less toxic secondary compounds than older plants, or that measurement of total nitrogen content is not a relevant assay of plant nutritive quality. Direct tests of the effects of tree height and foliage composition on the ability of larvae and pupae to attract and retain ants are needed to resolve this question.

Overall, the distribution of sites with numerous host “ant plants” (small host *Acacia* plants in territories of *I. anceps*) was found to be a very strong predictor of the distribution of *J. evagoras*. Except for a common requirement for open ground or short grass, the two host organisms were not strongly associated with each other, indicating that *J. evagoras* may depend on their chance co-occurrence for reproductive success. Apparently, the frequency of patches with both “hosts” is quite low, causing *J. evagoras* to have a scattered, patchy distribution. *J. evagoras* is efficient in locating such patches, and hence may have greater vagility than earlier suspected (Pierce 1984). Thus, in spite of many potentially conflicting factors (such as host plant quality and butterfly adult resources), the availability of enemy free space appears to be a major determinant of the distribution of these insect herbivores.

Acknowledgements. We thank K. Miller for careful and critical field assistance, G. Snell for kindly letting us use his horsepasture as a field site, and R.L. Kitching for his hospitality at the Australian School of Environmental Science, Griffith University. Support for this research was provided by National Science Foundation grant #DEB82-03520.

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Received October 10, 1987