own brood. The glandular origin of this secretion produced by *L. ignota* is most likely the perforated cupolas as these were the only glands common to both areas of cuticle under study.

4.2.3 *Euchrysops dolorosa* (Trimen)

4.2.3.1 Field observations

(I) Egg

In the study area the foodplant is *Becium obovatum* (Benth) N.E.Br. (Labiatae) which flowers from September to November. The eggs are laid singly among the buds on which the larvae are later to feed. The eggs take about six days to hatch.

(II) Larvae

The larvae feed on the buds and flowers of the foodplant. The flowers of the plant are often frequented by *Camponotus niveosetosus* Mayr workers, but they were only observed (3 instances) to give a brief examination of the larvae with their antennae before passing on.

(III) Pupae

The light green pupae are secured to dead leaves by the cremastral hooks and a silk girdle.

(IV) Egg laying behaviour of female

In the study area *E. dolorosa* is widely distributed being found on the rocky ridges and adjacent grassland, wherever the foodplant is present. The female appears to lay on the flowers throughout the area. They can often be observed circling around the foodplants in a slow erratic flight. The female would land briefly on an inflorescence and curve her abdomen around to lay a single egg on a bud.

To see if the presence of ants was necessary for the female to lay as in *A. dentatis* and *L. ignota* several specimens were captured and placed in separate containers with their foodplant. The females laid readily without the presence of ants.

4.2.3.2 Formicarium observations

A. Description of early stages

For a full description of the egg, larval and pupal stages of *E. dolorosa* see Appendix V.

B. Interaction between *E. dolorosa* and ants

Colonies of three species of ants were available from the study area all of which were known to be lycaenid associated. These three species were *Acantholepis capensis* Mayr, *Camponotus niveosetosus* Mayr and *Camponotus maculatus* (Fabricius).

(I) Interaction between *E. dolorosa* and *A. capensis*

The larvae placed directly on the floor of the arena were completely ignored by the *A. capensis* workers. When a *Becium obovatum* inflorescence with *E. dolorosa* larvae feeding on the flowers was placed in the arena, the ants investigated the flowers, but again ignored the larvae.

An *E. dolorosa* larva was placed directly into the nest to test the ants reaction. Placing the larva in the nest disturbed the ants and they started running wildly around. Several worker ants initially investigated the *E. dolorosa* larva, but after the activity died down due to the opening of the nest, the lycaenid was again ignored. The odd worker ant would quickly investigate the larva with its antennae as it passed it in the nest.

(II) Interaction between *E. dolorosa* and *C. niveosetosus*

The larvae placed directly on the floor of the arena were investigated by worker ants with their antennae when discovered. The ant would stroke and touch the larvae, usually in the vicinity of the honey-gland, but also on the thoracic region. After about 30-60 seconds the worker ants usually lost interest and wandered off. The larvae found on an inflorescence placed in the arena were treated in a similar manner by the ants. They would touch and stroke them with their antennae but would soon wander off.

A final instar *E. dolorosa* larva placed directly in the *C. niveosetosus* nest was investigated by a worker ant with its antennae for approximately

two minutes, then was picked up and carried towards the ant brood, but the larva started moving and appeared to be injured. The ant dropped the larva near the brood, but the cuticle was punctured and it was bleeding in two places. The larva was consumed by the ants. In another two instances *E. dolorosa* larvae placed in the nest were investigated by the ants off and on for over an hour. The larvae were left in the nest and when checked about three hours later there was no trace of the caterpillars. The larvae were most likely consumed by the ants as was observed with the first individual.

(III) Interaction between *E. dolorosa* and *C. maculatus*

The larvae placed directly on the floor of the arena were investigated by the *C. maculatus* workers with their antennae. The worker ants would stroke and touch them mainly in the vicinity of the honey-gland but also on the thoracic region. The ants were fairly persistent and one individual investigated a larva for approximately 5 minutes. It could not be seen whether the lycaenid responded to this treatment by exuding liquid from the honey-gland. When found on an inflorescence the *E. dolorosa* larvae were treated in a similar manner to the above. The extrusion of the tubercles by the larvae elicited no response in the ants.

Three *E. dolorosa* were placed directly into the *C. maculatus* nest. These larvae were investigated by both worker and soldier ants off and on for about an hour. No individual investigated the lycaenid larvae for more than a minute. The larvae were left in the nest and after 24 hours two still remained, the third having vanished. The missing larva may have died or been killed and eaten by the ants. The two larvae were generally ignored by the ants during a 30 minute observation period after they had been in the nest 24 hours. The two larvae were then removed from the nest as they would have died without food.

4.2.3.3 Reaction of the ants to the glandular extracts of *E. dolorosa* absorbed on to corn cob grits

The following behavioural responses were observed in the worker ants of the three species investigated.

A. *Acantholepis capensis* response to the extract from whole *E. dolorosa* larvae (Table 11)

The grits were placed in the arena near the entrance to the nest and were completely ignored by the workers of *A. capensis*.

B. *Camponotus niveosetosus* response to the extract from whole *E. dolorosa* larvae (Table 11)

The grits were placed in the arena near the entrance to the nest and when discovered by the worker ants were investigated by them. The ants passed their antennae over the surface and two workers investigated a grit for three minutes. After about an hour the grits were being ignored or had been removed to the refuse pile.

C. *Camponotus maculatus* response to the extract from a whole *E. dolorosa* larva (Table 11)

The grits were placed in the arena near the entrance to the nest and when discovered by the worker ants were investigated by them. The ants passed their antennae over the surface, and some grits were investigated for as long as five minutes at a time. After about an hour the grits were being ignored.

4.2.3.4 Gas chromatography of the volatile secretions of *E. dolorosa*

The peaks on the chromatogram from the extract of *E. dolorosa* were compared using relative retention times with those of the brood extracts of *A. capensis*, *C. niveosetosus* and *C. maculatus* (Table 12). The relative amounts of each component were also compared by taking the areas under the peaks and calculating the percentage of each (Table 13)

The retention times and the areas of the peaks as given by the Autolab Minigrator and the calculations for the tables can be found in in Appendix VI

Comparison of the chromatograms showed that four peaks were common to all extracts, these are peaks 6, 15, 16 and 17 (Table 12)

A. Comparison of the *E. dolorosa* chromatogram with the brood extract chromatogram of *A. capensis*

The comparison with the brood extract chromatogram of *A. capensis*

Table 11. The reactions of worker ants to the extracts of *Euchryeops dolorosa* larvae and their own brood.

Ant species and Extracts on grits	n	Reactions of worker ants			
		no reaction	Alarm Behaviour	Investigation	Carrying & brood tending behaviour
A. capensis					
A. capensis brood	30	1		1	28
E. dolorosa	30	30			
C. niveosetosus					
C. niveosetosus brood	30			1	29
E. dolorosa	30	4		26	
C. maculatus					
C. maculatus brood	30	1		2	27
E. dolorosa	30	1		29	

n = number of individual grits

Table 12. Gas chromatographic peaks with relative retention times for the brood extracts of *A. capensis*, *C. niveosetosus* and *C. maculatus*, and whole *E. dolorosa* larvae run on a Carbowax 20M column.

Peaks	Extracts			
	A. capensis brood	*C. niveosetosus* brood	*C. maculatus* brood	*E. dolorosa*
1	0.386			
2	0.560			
3			0.585	
4			0.664	
5	0.670			
6	0.710	0.706	0.704	0.704
7	0.750		0.750	
8			0.810	0.812
9	0.856		0.857	0.857
10			0.876	
11	0.893	0.891		
12		0.908		0.908
13			0.924	
14	0.958		0.960	0.963
15	1.000	1.000	1.000	1.000
16	1.025			1.025
17	1.060	1.069	1.060	1.058
18		1.090	1.090	1.089
19	1.108			1.111
20			1.139	1.140
21			1.161	
22	1.175			
23			1.193	1.190
24	1.210			
25	1.248			

Table 13. The area of each peak on the chromatograms of the brood extract of *A. capensis*, *C. niveosetosus* and *C. maculatus*, and *E. dolorosa* larvae expressed as a percentage.

Peaks	Extracts			
	A. capensis brood	*C. niveosetosus* brood	*C. maculatus* brood	*E. dolorosa*
1	7.4			
2	7.5			
3			1.0	
4			0.4	
5	1.3			
6	1.2	1.6	2.0	1.1
7	7.3		0.7	
8			2.8	2.0
9	5.2		1.9	1.6
10			1.6	
11	3.3	7.5		
12		6.7		6.6
13			10.0	
14	6		4.7	10.2
15	7.	16.3	7.0	8.2
16	5.			4.5
17	7.5	47.8	16.7	17.1
18		19.6	10.7	9.6
19	7.8			10.0
20			16.9	13.3
21			8.5	
22	12.1			
23			14.9	15.8
24	4.4			
25	13.5			
Total	100.0	100.0	100.0	100.0

(fig. 25) shows that 8 of its 15 peaks do not occur on the *E. dolorosa* chromatogram (fig. 34), which in turn has 5 of its 12 peaks not occuring in *A. capensis*. There are in fact only 7 peaks in common between the two chromatograms (Table 12). These results and the fact that *A. capensis* ants completely ignored the larvae and extracts indicates that they are never likely to tend *E. dolorosa*.

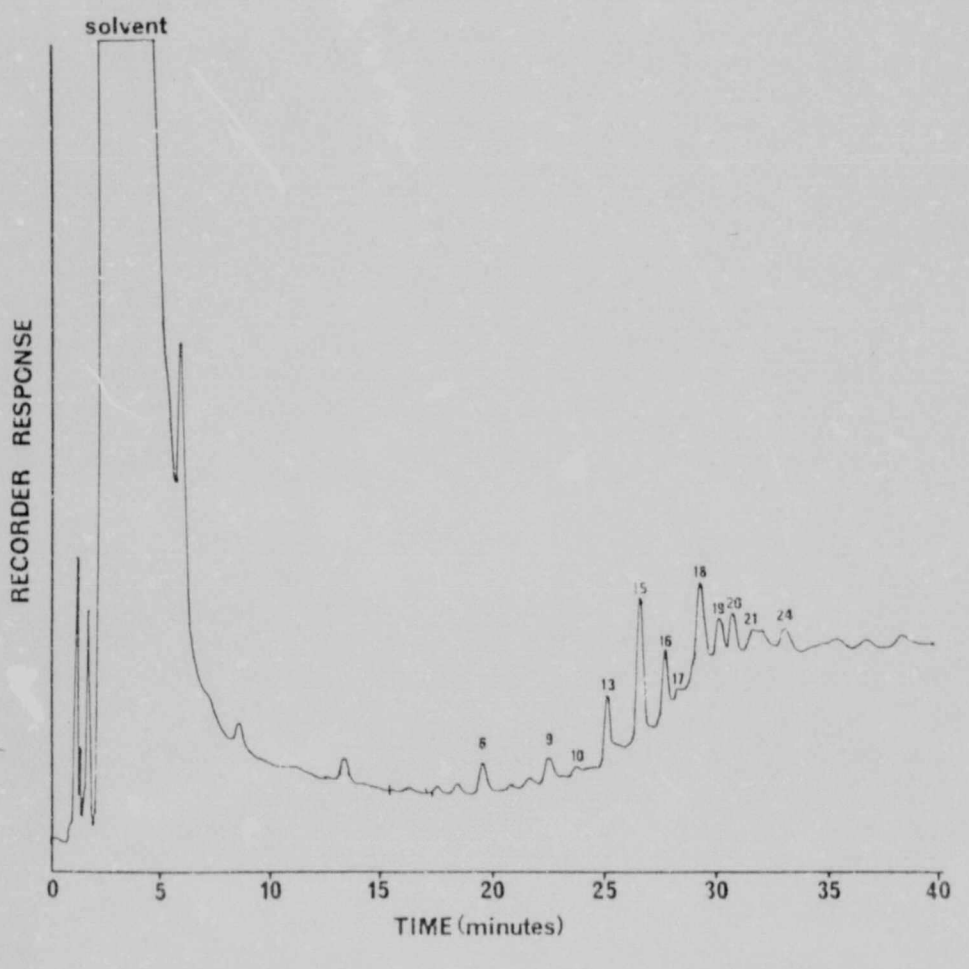

Fig. 34. Gas chromatogram of the volatile material extracted from whole *E. dolorosa* larvae.

B. Comparison of the *E. dolorosa* chromatogram with the brood extract chromatogram of *C. niveosetosus*.

The *E. dolorosa* chromatogram (fig. 34) has all but one of the peaks found in the brood extract chromatogram of *C. niveosetosus* (fig. 31), the only one missing being peak 10 (Table 12). The relative proportions of these chemicals in the two chromatograms is not very similar. The chromatogram of *C. niveosetosus* shows that peak 17 makes up 47.8% of the volatile chemical substance extracted from the brood, while in

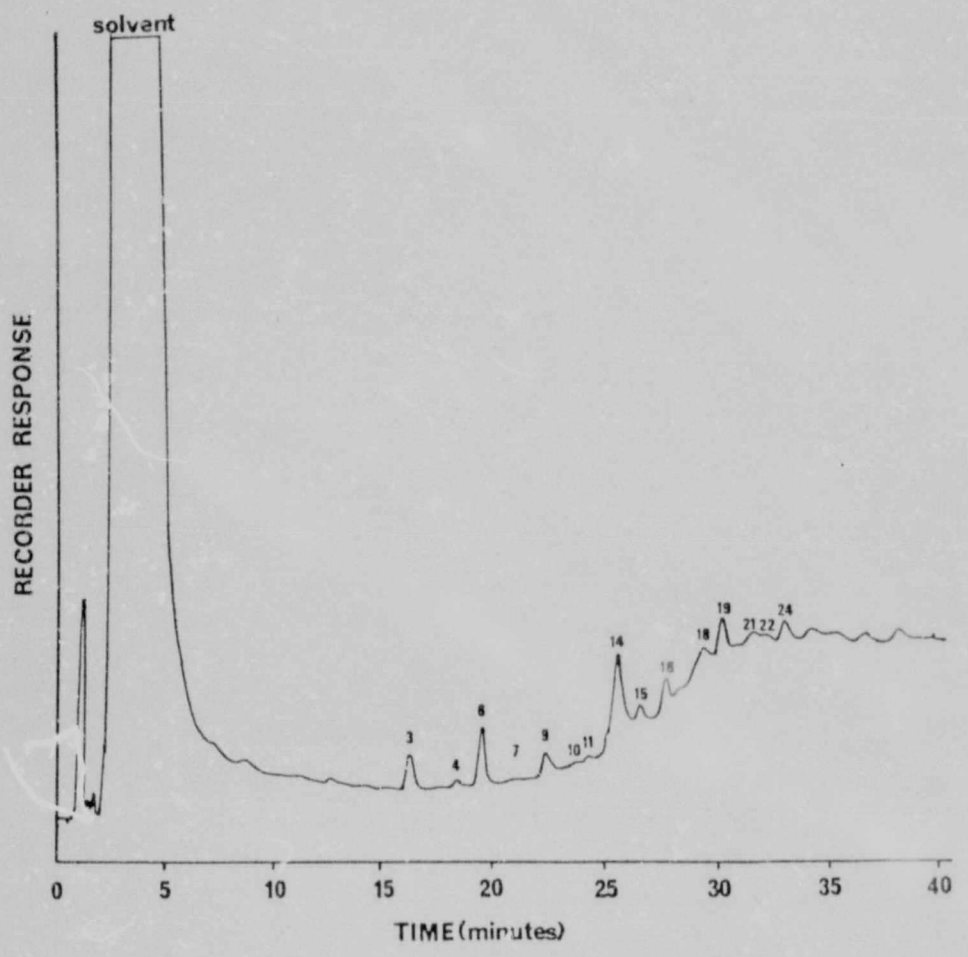

Fig. 35. Gas chromatogram of the volatile material extracted from the brood of *C. maculatus*.

E. dolorosa it only constitutes 17.1% (Table 13).

C. Comparison of the *E. dolorosa* chromatogram with the brood extract of *C. maculatus*

A comparison of the *E. dolorosa* chromatogram (fig. 34) with that of *C. maculatus* (fig. 35) shows that they are quite similar. From Table 12 it can be seen that 9 of the 12 peaks on the *E. dolorosa* chromatogram are to be found on that of *C. maculatus*. The relative amounts of the chemicals represented by the peaks are also very similar (Table 13). This indicates that *E. dolorosa* larvae are very likely to be tended by *C. maculatus* ants if they are present as was found by behavioral experiments.

D. Comparison of the *E. dolorosa* results with those of the two myrmecophilous associations

From Table 14 it can be seen that *E. dolorosa* has 58% of its peaks in common with the chromatogram of *A. capensis*, 42% with *C. niveosetosus* and 75% with *C. maculatus*. In the two myrmecophilous relationships it can be seen that *A. dentatis* has 92% of its peaks in common with its host ant *A. capensis*, while the percentages of peaks in common with its non host ants, *C. niveosetosus* and *C. maculatus*, are much lower, being 38% and 69% respectively. The same can be seen with *L. ignota* which has 63% of its peaks in common with its host ant *C. niveosetosus*, but only

Table 14. Percentage of peaks on the chromatograms of the lycaenid larvae corresponding to those on the chromatograms of the three ant species investigated (see Appendix VII for calculation)

Lycaenid species	Ant Species		
	A. capensis	*C. niveosetosus*	*C. maculatus*
A. dentatis	92	38	69
L. ignota	50	63	38
E. dolorosa	58	42	75

50% and 38% respectively for the non hosts *A. capensis* and *C. maculatus*. Therefore it appears that the more peaks the lycaenid larvae have in common with the ants the more likely they are to be associated with them. Using this as a criterion it can be seen that *C. maculatus* with 75% of the peaks corresponding to the *E. dolorosa* chromatogram is more likely to associate with this larva than the other species of ant.

With the two myrmecophilous lycaenid species the relative amounts of the chemical represented by the peaks on their chromatograms are very similar to those found in the brood extract chromatograms of their host ants (see Tables 7 & 10). Also the relative amounts of chemical on the *E. dolorosa* chromatogram broadly corresponds to the brood extract chromatogram of *C. maculatus* (Table 13) again indicating that this ant species could associate with it.

4.2.3.5 Conclusion

From this study it appears that *E. dolorosa* produces a volatile secretion that can attract certain ant species. The chromatogram of this secretion appears to be most similar to the chromatogram of the brood extract of *C. maculatus*. The chromatogram was also found to resemble that *C. niveosetosus*, but the proportions of the various chemical constituents were different. Although there are some common peaks in the chromatograms of *E. dolorosa* and the two ant species mentioned above, the actual chemical concerned with carrying must be absent, as the extracts on the corn cob grits only caused them to be investigated and not carried. The chromatogram of the brood extract of *A. capensis* did not resemble that of *E. dolorosa* at all and the larvae and extracts were completely ignored by the ants.

So it appears that *E. dolorosa* produces a volatile secretion that will attract ants belonging to the genus *Camponotus* to varying extents, but which is not found to be attractive at all to *Acantholepis*. The ability of the secretion to attract the ants appears to depend on how closely the secretion resembles that of the brood pheromone of the ants. From the behavioural studies *C. maculatus* workers were attracted more often to the *E. dolorosa* extracts and larvae than were the workers of *C. niveosetosus*. The brood extract chromatogram of *C. maculatus* resembled that of *E. dolorosa* more closely than the brood extract chromatogram of *C. niveosetosus*.

5. DISCUSSION

This study has established that chemical communication plays an important part in the relationships between some lycaenid species and their host ants. This work supports the conclusions reached by several authors from their behavioural studies (Ehrhardt, 1914; Malicky, 1969, 1970; Claassens, 1974, 1976).

In the studies undertaken here it was found that a volatile lycaenid larval secretion appeared to mimic the brood pheromone of the host ant. This volatile secretion of *L. ignota* caused the ants, *C. niveosetosus* to carry the lycaenid larvae into the nest. In the case of *A. denta* the larvae are too large to be carried by their host ant *A. capensis*, but they do appear to be groomed and generally tended as the workers would do their own brood. Small corn cob grits soaked in extracts of *A. dentatis* larvae were carried by their host ant, indicating that a similar chemical signal was being employed as in the case of *L. ignota* However, size may not only be the reason that some lycaenid larvae are not carried by ants, since, *L. ignota* larvae are not carried into the nest until the third instar. Ants have been observed to try to pick up *Lepidochrysops* larvae of all stages (Claassens, 1976), but they are unable to do so until the larvae themselves release their hold on the substrate. It was found during the course of this study that third instar *L. ignota* larvae could be induced to release their hold on the substrate and roll up into a sphere by gentle stroking with a paint brush, indicating this was a response to a tactile stimulus. First and second instar *L. ignota* larvae when stroked with a paint brush just tightened their grip on the substrate. Claassens (1976) observed that an ant before attempting to pick up a *Lepidochrysops* larva would investigate it with its antennae, thus possibly producing a tactile stimulus similar to the one obtained with the paint brush, so causing the third instar larvae to release their hold. In this study it was also observed that third instar *L. ignota* larvae were always investigated by the ant with their antennae before they released their hold on the substrate. So it appears that both the chemical attraction of the ant and the tactile stimulus of the larva may be needed before the ant can carry the lycaenid larvae.

In the case of *E. dolorosa*, which is not dependent on ants the

situation is not quite so clear. The chromatogram of the volatile secretion of the larva resembles most closely that of the brood extract of *Camponotus maculatus*, having several peaks in common. This ant was not observed to tend *E. dolorosa* larvae in the field. In the laboratory *E. dolorosa* was only investigated by *C. maculatus* and not carried into the nest. Corn cob grits soaked in extracts of *E. dolorosa* larvae were also only investigated by the ants. Therefore it appears that although there are several peaks in common between the chromatograms of *C. maculatus* brood and *E. dolorosa* larvae, the chemical actually concerned with carrying must be absent in the lycaenid. The peaks in common to both chromatograms may represent chemicals involved in attraction, grooming and general attention of the ant to the brood.

and Tschinkel (1974) and Brain (1975) found that the brood of the ants they were studying was of low volatility and transmitted mainly by contact (see p. 14). Referring to the first chemical on the gas chromatogram of the brood of *C. niveos* took some twenty minutes to pass through the column showing that the secretion is not as volatile as, for example, its alarm pheromone (fig. 30) which first appeared after eleven minutes. *L. ignota* had several chemicals passing through the column, all corresponding with peaks in the head extract, before the first chemicals passed through from the brood extract of *C. niveosetosus* (Table 9). If, as Walsh and Tschinkel (1974) and Brain (1975) suggest, the brood pheromone is a contact or short range pheromone it would be advantagous to a lycaenid larva to produce in addition a more volatile chemical to attract ants from a distance. As about half of the chemicals produced by the *L. ignota* larvae are more volatile than the bulk of the *C. niveosetosus* brood pheromone this could be the case (see Tables 9 & 10). As these chemicals also all correspond to those on the head extract chromatogram it suggests that they may be mimicking certain components of the alarm pheromone, possibly those involved in attraction. Although this hypothesis works with *L. ignota* and *C. niveosetosus*, it does not fit the situation with *A. dentatis* and its host ant *A. capensis* (see Table 7). In this latter association the brood pheromone is actually more volatile than the alarm pheromone.

The discovery that the tubercles of *A. dentatis* produced a volatile secretion that appeared to mimic the alarm pheromone of the host ants

may be a remarkable example of co-evolution. From the observations it appears that only certain components of the alarm pheromone are actually involved. As was pointed out in the introduction (see p. 9) the term alarm pheromone is rather misleading. The behaviour encompassed by this term includes alerting, attraction and biting. The volatile secretion of the tubercles of *A. dentatis* appeared to be involved only in alerting and attraction.

Claassens and Dickson (1977) in their study of the closely related *Aloeides thyra* (L.) also discussed the possible function of the tubercles. They suggested that the function of the tubercles in this case might be to render the ants aggressive so that they would attack insects or spiders when these approached the larvae. To try to demonstrate this they placed small spiders, beetles, bugs, flies and other insects individually in containers together with the lycaenid larvae and the host ants. The ants reacted, upon the extension of the tubercles, in the usual manner, but did not show increased aggressiveness or molest the 'intruders' in any way. It must be remembered though that ant alarm behaviour is highly context specific, i.e. the very unnaturalness of these experiments may well have effected the results obtained. However from the results of my study with *A. dentatis* it appears that the volatile secretion of the tubercles releases only alerting and attraction in the host ants, and there is nothing in the observations of Claassens and Dickson to indicate that a different situation exists in *A. thyra*. The presence of the ants themselves may possibly act as a deterrent to potential predators.

The results obtained with the symphilic *L. ignota* show that the volatile secretions produced by lycaenid larvae can be very specific. Third instar *L. ignota* larvae that had stopped feeding on plant material were offered to seven different species of ant (Henning, unpublished work) but it was only their host ant, *Camponotus niveosetosus*, that was attracted to them and carried them into their nest, the other six species completely ignoring them. The six species that ignored them were *Camponotus maculatus*, *Camponotus* sp., *Acantholepis capensis*, *Anoplolepis custodiens* and two species of *Crematogaster*, all species found in association with other lycaenid species.

This is also supported by the work on *A. dentatis*. Although *A. capensis* and *C. maculatus* shared the same formicarium, the *A. dentatis*

larvae only followed the pheromone trails of the former. The *A. dentatis* larvae, when they everted their tubercles and released the volatile secretion, also only elicited a response in *A. capensis*. In all the hours of observation not once was *C. maculatus* seen to pay any attention to the *A. dentatis* larvae. Although there were two nests in the formicarium the *A. dentatis* larvae were found only in the one occupied by *A. capensis*, and were never observed in the nest occupied by *C. maculatus*. These two ant species shared the same formicarium for 18 months with no adverse effects to either colony. On several occasions they were found nesting under the same stone in the wild. In the study area at Witpoortjie, *A. dentatis* larvae were found only in the nests of *A. capensis* although at least ten other species of ant occurred in the area.

The results with *E. dolorosa* show that the volatile secretions produced by trophobiont lycaenid larvae not dependent on ants are able to attract some species. It was found that the secretions produced by *E. dolorosa* were able to attract two species of ants from the same genus *Camponotus*, i.e. *C. maculatus* and *C. niveosetosus*, but were completely ignored by *Acantholepis capensis*. The volatile secretion of *E. dolorosa* resembled the brood extracts of both *C. maculatus* and *C. niveosetosus*, which in turn had a number of peaks in common on their chromatograms. The *A. capensis* ants presumably ignored the *E. dolorosa* larvae as the volatile secretions produced by them (as indicated in the chromatograms) did not resemble that of the brood pheromone of the ant at all.

The extrusion of the tubercles of *E. dolorosa* elicited no response in the ants investigating them during the course of this study. The tubercles are of a different type to those of *A. dentatis*, being shorter, not curving towards the honey-gland and having short setae. It appears likely that the tubercles of *E. dolorosa* have no communicatory function. The tubercles in the Lampidinae are often lost (Table 4) and possibly where present are non-functional, or serve no observable function as in *E. dolorosa*, and are still undergoing reduction.

The secretion of the honey-gland of the lycaenid larvae is generally considered to be a sugar-rich liquid similar to the honeydew excreted by sap-feeding homopterans. The gas chromatograms of the thoracic area and the honey-gland and surrounding cuticle of *L. ignota* were

virtually identical. This indicates that the actual honey-gland secretion was not particularly volatile as the peaks obtained appear to have emanated from the perforated cupolas which were common to both extracts. To determine the actual chemical composition of the 'honey-dew' secreted by the lycaenid larvae further chemical analysis will have to be done on the glands.

Comparing the secretion of the honey-gland to the honeydew excreted by aphids is probably misleading. To me the honey-gland appears to be more analogous to the appeasement gland of myrmecophilous staphylinid beetles (see p. 17). I say this because the excretion of the aphid is a waste product, while the secretions of both the honey-gland and the appeasement gland have a glandular origin, The function of the secretions of both the honey-gland and appeasement gland is similar, i.e. to gain acceptance by the ants. The chemical composition of the secretions of both these glands is still not known nor whether or not they are simple nutrients, secondary phagostimulants or mimics of the pheromones of the host ants, although this last point seems unlikely in the lycaenids.

There is another striking difference between *E. dolorosa* and the two dependent myrmecophilous species investigated in this study. This is the duration of the larval stages. The larval stages of *E. dolorosa* only last a total of 19 days, while those of *A. dentatis* may last six months or even a year if diapause takes place. In *L. ignota* the larval stages last some 10-11 months.

To explain the above differences in the duration of the larval stages is most difficult because such factors as size, weight, type of food, dependence on ants etc., all have to be taken into consideration. To discover whether the dependence on ants has anything to do with the duration of the instars one would have to eliminate some of the other possible influencing factors. To do this one would need to select closely related species of similar size feeding on the same foodplant at the same time of the year at the same locality, with the only major difference being their dependency on ants.

E. dolorosa and *L. ignota* appear to fill the above requirements. These two species belong to closely related genera, are about the same size and feed on the flowers of *Becium obovatum* during the months September to November at Witpoortjie in the Transvaal. The only major

differences between them is that from the third instar onwards *L. ignota* becomes carnivorous and dependent on ants. The duration of the larval stages differs considerably, that of *E. dolorosa* lasting a total of 19 days and that of *L. ignota* 10-11 months. The duration of the first two instars of *L. ignota*, while they are feeding on the flowers of *B. obovatum*, is equivalent to those of *E. dolorosa*, lasting 8 days. Thus it appears that it is from the 3rd instar onward, when *L. ignota* becomes carnivorous and dependent on its host ant, that factors influencing the duration of the instar come into play. Before discussing the implications of this let us look at another example.

Another two species to fill the requirements mentioned above are *Aloeides trimeni* Tite and Dickson and *A. dentatis*. These two species are closely related, belonging to the same genus, are the same size and feed on the leaves of the plant *Hermania depressa* during the months September to January at Witpoortjie in the Transvaal. The only major difference between them is that the larvae of *A. dentatis* shelter during the day in the nest of their host ant, while the larvae of *A. trimeni* never leave the foodplant. The duration of the larval stages of these two species differs considerably, that of *A. trimeni* lasting some 3 months, and that of *A. dentatis*, dependent on ants, lasting 6-12 months.

The above two examples suggest that there may be some correlation between dependence on ants and the duration of the larval stages. Change in diet does not appear to be a major factor as *A. dentatis* feeds on the same plant throughout its larval stages as does *A. trimeni*. To check that the above observations were not atypical a survey of the literature was made. The most important works consulted were those of Clark and Dickson (1971), Jackson (1937), Hinton (1951). Lamborn (1914) and Farquharson (1922). All these authors described the lycaenid life histories in great detail so that all possible factors influencing the duration of the instars could be taken into consideration. From this literature survey (see Table 4) it does appear that lycaenids associated with ants tend to have much longer larval period than those not dependent on them.

The larval stages of the Aphaeinae, which are nearly all dependent on ants, are all relatively long, lasting from 3-6 months or even more and going through some six instars. In the subfamilies Plebejinae,

Everinae, Brephidinae, Zizeerinae, which are not usually dependent on ants, the larval stages are very short, lasting only 18-34 days, and passing through four instars. The Theclinae and the Lycaeninae also are not dependent on ants, but they have four or five instars lasting some 18-45 days. In the Lampidinae there are four or five instars and those species not dependent on ants have larval stages lasting only 20-40 days, but in the *Lepidochrysops*, which are dependent on ants, the larval stages last some 10-11 months.

I think it can be assumed that the ant associated species evolved from free living forms. If this is the case it appears that it is possibly the relaxation of certain selective pressures caused by the presence of the ants that has resulted in the longer larval period. Most authors appear to agree that the presence of the ants afford the lycaenid larvae some protection from predation and parasitism. It is possibly this protection that led to the increased duration of the larval stages of ant associated species.

The increased larval period in some ant associated lycaenid species is due to the fact that the larvae will undergo diapause when food becomes scarce. Some larvae, even if on the verge of pupation, will undergo diapause if the conditions become unfavourable. Only with the return of favourable conditions will they pupate (see p. 64). This ability to undergo diapause and remain in the larval stage for considerable periods of time appears to be an adaptation to life within an ants nest. If the ants happened to move their nest for some reason the lycaenid caterpillars can follow or be carried while pupae would be left behind. Claassens and Dickson (1977) found that lifting stones while searching for *Aloeides thyra* (L.) larvae often led to the ants deserting their nests and leaving the lycaenid pupae behind. These pupae would be in danger in the deserted nest as the tunnels and exit holes may become filled without the ants constant maintenance, thus newly emerged adults may not be able to leave the nest. Claassens and Dickson (1977) found that the larvae of *A. thyra* would follow their host ant, *Acantholepis capensis*, if they deserted their nest.

It would appear from the above that some lycaenid larvae may have even developed slightly more extended larval stages as an adaptation to life within an ants nest. The whole question of life history

strategies is a complex story and only a thorough ecological study would provide the necessary evidence to identify the selection pressures which could have effected the early stages of the lycaenids.

Based on his studies of the anatomy and histology of lycaenid larvae, Malicky (1970) suggested that they originated from a kind which differed from other lepidopterous larvae by their voluminous cuticle. He suggested that larvae such as *Nemeobius lucina*, a species without perforated cupolas and unable to induce an ant association, may derive directly from this stage.

From the evidence provided by adult morphology and life histories it appears that quite early on the Lycaenidae began to exploit at least three different niches. In the one group the larvae fed on lichens (Thallophyta) and possibly developed long hairs as protection against ants they came into contact with. The second group fed on Angiosperns (Embryophyta) and developed the honey-glands and tubercles. The third group became carnivorous, at first preying on Homoptera and later on the brood of the ants which attended the Homoptera.

It is the group feeding on Angiosperms plants which concerns us in our study on the chemical communication between lycaenid larvae and ants, because it is here that the association has undergone its greatest development. It is this group, with its honey-glands and tubercles, that occupies the centre of all evolutionary arguments on the family Lycaenidae.

The latest theory has come from Malicky (1970) who suggests that the earliest development in the group was of big and eversible glandular equipment similar to the honey-gland, which he presumed to have been serial in their earliest ancestral stage. On this evolutionary line he believed the perforated cupolas developed whose secretion proved to be more effective than the big glands in attracting ants. The big glands were subsequently modified and reduced. He suggests the result of this evolution is a caterpillar which is provided only with perforated cupolas, as demonstrated by several species of the Lycaeninae and the Theclinae.

However, from the available evidence it appears more likely that the perforated cupolas evolved before the more complex honey-gland as they appear to be common to all the evolutionary lines. Malicky (1969, 1970) in his histological study of the lycaenid larval organs

found that both these glands appear to have a common origin, i.e. they both originated from epidermal gland cells that normally produce setae In both cases each gland consists of an outer duct homologous to the tormogen cell and an inner secreting chamber homologous to the trichogen cell (see Chap. 2). I suggest that the honey-gland may well be an epidermal gland (or glands) modified to produce large amounts of secretion so that the ants encountering a larva are 'rewarded' by finding a food resource.

At the same time as the honey-gland developed the tubercles must have evolved, possibly as a mechanical deterrent to unwanted insects visiting the honey-gland (see p. 34).

This group became very successful and spread rapidly, occupying new regions with different habitats and climate, leading to some sections of the population occupying habitats where they seldom, if ever, came into contact with ants. The honey-gland and tubercles in these species became modified and reduced, resulting in the caterpillar which is provided only with perforated cupolas. Other members of the population, though, developed even more intimate associations with the ants, entering their nests and exploiting them as a food resource.

Several factors indicate that myrmecophily in this group of lycaenids might well have had its roots in 'trophobiosis'. I say this because myrmecophily in this group appears to be analagous with the situation in homopterans in some ways.

Wilson (1971) says trophobionts differ from other ectosymbionts in a basic way: they obtain their own food and pass some of it on to their hosts. He describes the ideal trophobiont as one which feeds on a single species of foodplant and whose life cycle is not tightly synchronized, so that stages capable of producing honeydew are available throughout the year. He says the evidence shows that not only do taxa possessing these properties as original traits become trophobiotic more frequently, but some species acquire or enhance them secondarily in evolution after the association with ants has begun.

In discussing trophobiosis in the homopterans Wilson (1971) points out that both the insect partners have evolved special adaptations with the apparent sole function of implementing the mutualism. For example, some myrmecophilous aphids have acquired a new trophobiotic organ, a