INTERACTIONS BETWEEN ANTS, HERBIVOROUS INSECTS AND BRACKEN (*PTERIDIUM AQUILINUM*), A FERN WITH EXTRAFLORAL NECTARIES

Thesis submitted in fulfilment of the requirements
for the degree of MASTER OF SCIENCE
of Rhodes University

by

VANESSA KARIN RASHBROOK

FEBRUARY 1989

CONTENTS

ACKNOWLEDGEMENTS

To my supervisor, Dr. Steve Compton, I owe immeasurable thanks for many valuable suggestions and discussions, for help with the fieldwork and for the constructive comments leading to substantial improvements in the manuscript. I am also deeply grateful for his advice, encouragement and good-humour, which were so generously given throughout this study.

I am indebted to Professor John Lawton for introducing me to the world of bracken, and for providing the opportunity for me to study in South Africa. His perceptive comments and discussions of the work, and his interest and enthusiasm were always invaluable.

Dr. Amy Jacot Guillarmod provided hospitality and access to the most scenically situated bracken patch in the eastern Cape on her farm "Faraway", and was indispensible in identifying the flora. Mr. Pat Grant also kindly allowed me to work on the bracken at Glenthorpe farm, and Rob Palmer offered hospitality and assistance.

My sincere thanks are also due to Professor Patrick Hulley and Mr. David Bunyan for helpful comments on the manuscript, Dr. Hamish Robertson and Mr. B. Bolton for ant identifications and Dr. John Scott for useful discussions. Casper de Villiers, Kathy Holton, Tony Ware and Stephanie Vincent all contributed their skills towards the preparation of the manuscript.

I am very grateful to the National Collection of Insects, Pretoria, and the Commonwealth Institute of Entomology, British Museum (Natural History) London, for the insect identifications.

ABSTRACT

Bracken (*Pteridium aquilinum*) is a cosmopolitan species of fern which possesses extrafloral nectaries. A survey of the arthropod fauna associated with the plant throughout its range in South Africa identified the most widespread and damaging bracken herbivores and those species most likely to be influenced by ants visiting the extrafloral nectaries.

Seventeen herbivorous arthropods were found to be definitely feeding on bracken and a further thirteen species with a less certain status were recorded. In addition, several species of ants were observed on the fronds and feeding at the extrafloral nectaries.

On the basis of their widespread distribution and abundance, four bracken herbivores emerged as being particularly detrimental to the plant in South Africa. They were an eriophyid gall mite, a leafhopper and two moths. The biology of the two lepidopterans, *Appana cinisigna* and *Panotima* sp., suggested that they were potentially vulnerable to ants at various stages of their life histories.

Laboratory experiments were undertaken to observe ant-lepidopteran interactions under controlled conditions. The ant *Crematogaster peringueyi* rapidly removed exposed *A. cinisigna* eggs, but did not appear to regard *Panotima* eggs as food items. Small instar larvae of both species proved vulnerable, but the larger larvae appeared capable of escaping ant predation.

Ant exclusion experiments in the field, using natural and artificially augmented ant densities, were carried out at two sites near Grahamstown. The dominant ant species was *C. peringueyi*. Neither the numbers of lepidopterans nor levels of herbivory were significantly reduced by the presence of ants.

Despite the implications of the laboratory tests, the results of these field experiments did not support the hypothesis that ants which visit bracken extrafloral nectaries benefit the plant. Ant-bracken field studies on other continents also reported no significant ant-related

effects, though marginal reductions in the abundance of certain herbivores have been noted at one site in the U.K.

Since ant protection does not appear to be an inevitable consequence of having extrafloral nectaries, their value to bracken is in some doubt. The most likely situation where effective protection will occur is when high densities of vulnerable herbivores are preyed upon by large numbers of aggressive ants. However, even under these conditions, enhancement of plant fitness is not inevitable. This raises the question of why extrafloral nectaries have been retained in a plant that is as successful and widespread as bracken.

1. INTRODUCTION

1.1 The role of ants and extrafloral nectaries in plant defence.

Relationships between species in which the participants obtain reciprocal benefits are termed mutualistic. Plants and ants are involved in a wide variety of direct and indirect mutualistic interactions (as reviewed by Buckley 1982 and Beattie 1985). Ants may aid plant reproduction by assisting in pollination or in fruit and seed dispersal. Some epiphytes may also gain nutrients from ants nesting among their roots (Thompson 1982). Ants tending lepidopteran larvae for their sugary secretions (Atsatt 1981; Pierce & Mead 1981), or more commonly Homoptera for their honeydew (reviewed by Way 1963), are usually detrimental to the plant (Dixon 1971; Bristow 1984). They may however also contribute indirectly to plant defence where, for example, they reduce levels of other herbivore damage (Messina 1981; Compton & Robertson 1988). Features of plants which have been shown to entice ants include specialized nesting sites (domatia), food bodies (Beltian bodies), and nectar other than that produced by the flower (extrafloral nectar).

Although the occurrence of extrafloral nectaries (EFNs) has long been known (Belt 1874; Delpino 1874, cited in F. Darwin 1877), the relationships between ants and plants with EFNs are of particular interest, because their functional significance has been in some dispute (reviewed by Bentley 1977a; Beattie 1985). The two main views either ascribe a physiological function to EFNs, where surplus sugars are "excreted" from the plant, or maintain that plants produce nectar specifically to attract ants and other insects that will defend the plant from herbivores. Delpino is noted to have said that EFN secretions "attract ants to keep other creatures away", whereas Darwin (1877) took bracken fern (*Pteridium aquilinum* (L.) Kuhn) to illustrate the opposing view, because the plant did not appear to suffer from herbivore attack in any case. Von Wettstein (1889, cited in Beattie 1985) performed some of the earliest exclusion experiments and showed that ants, attracted to the EFNs of two Compositae species, reduced seed damage levels.

A number of studies confirming the "protectionist" view have taken place since then, commencing with Janzen's (1966) work. He demonstrated that an obligate mutualism occurred between ants (*Pseudomyrmex* spp.) and the swollen-thorn acacia (*Acacia cornigera* L.) whereby ants effectively protected the plant from herbivorous insects and mammals, being attracted to the plant by extrafloral nectar, food bodies and nesting sites in specialized swollen thorns. Recent studies have also described facultative mutualisms in a wide range of plant taxa and ant species. These interactions may involve a number of component species which are not exclusively dependent upon each other. For example, Koptur (1979) showed that a mutualism can occur between an introduced plant and a non-native ant (both from different countries of origin), while Bentley (1976) obtained a mutualistic response by creating experimental "nectaries" on plants normally lacking EFNs, demonstrating the ease with which such relationships between plants and ants can arise.

The effects of ants visiting EFNs have often been determined by correlating differences in herbivore damage between plants which show a natural variation in ant abundance (Bentley 1977b; Tilman 1978; Koptur & Lawton 1988). Other studies have excluded ants experimentally from plants and have compared aspects such as herbivore damage to leaves (Bentley 1976; Keeler 1977; Stephenson 1982; Temple 1983; Whalen & Mackay 1988), flowers, ovules and developing seeds (Inouye & Taylor 1979; Pickett & Clark 1979; Keeler 1980, 1981a; Schemske 1980; Beckmann & Stucky 1981; Stephenson 1982; Barton 1986) or herbivore population densities and survival (Pickett & Clark 1979; Heads & Lawton 1984; Heads 1986; Smiley 1986; Whalen & Mackay 1988).

EFNs are usually situated outside the reproductive structures of the flower and are not normally directly involved in pollination. However, there are exceptions; for example, the large EFNs of *Poinsettia* species (Vansell 1940) and *Acacia terminalis* (Salisb.) Macb. (Knox et al. 1985) serve to attract bird pollinators to the flowers. The structure of EFNs shows many diverse forms, from simple groups of cells to complex glandular structures. The composition and concentration of the nectar produced is equally variable, and dependent on plant species, age, habitat, altitude and season (Bentley 1977a). Extrafloral nectar consists principally of sugars (sucrose, glucose and fructose, in varying proportions), together with low concentrations of amino acids, lipids and other organic compounds (Bentley 1977a).

Since metabolic energy is required for nectar secretion (Luttge 1971), control in the timing of nectar production is one means by which costs to the plant can be reduced. If the presence of ants enhances plant fitness, and such adjustments on the part of the plant are possible, then the production of nectar might be expected to coincide with critical periods of development when protection is most required. Intensive field studies by Tilman (1978) provided information on the relationships between the North American black cherry, *Prunus serotina* Ehrh., the ant *Formica obscuripes* Forel, and the main defoliator, *Malacosoma americanum* Fabricius, the eastern tent caterpillar. Timing proved to be crucial in this association, as later instars of the herbivore were capable of extreme defoliation and were large enough to escape ant predation. Tilman (1978) suggested that the high production of nectar over a relatively short period was responsible for attracting large numbers of *F. obscuripes* which successfully predated small *M. americanum* larvae. Supporting surveys showed that caterpillar survival and distance from ant colonies were positively correlated. Bentley (1977b) also found that high nectar flow rates in *Bixa orellana* L. were correlated with high ant activity, and occurred specifically at a time when the shrub was most susceptible to flower bud damage.

Stephenson (1982) measured extrafloral nectar production on undamaged leaves of *Catalapa speciosa* (Warder ex Barney) Englm. and compared secretion rates with those from leaves damaged by *Ceratomia catalpae* (Boisduval) larvae. It appeared that herbivore damage increased EFN secretion. Trees produced nectar after the young leaves were fully expanded, but before the first generation of moth eggs were laid. This suggests that in this species extrafloral nectar was not an excretory secretion associated with actively growing tissue, and supports the view that EFNs have a protective rather than a physiological function. Exclusion experiments indicated that the reproductive output of *C. speciosa* was significantly increased by visiting ants. Ants showed aggressive behaviour by removing *C. catalpae* eggs and larvae, decreased foliage herbivory and caused a corresponding increase in fruit production. Koptur (1987) tested the hypothesis that extrafloral nectar can be "induced" in response to defoliation. Nectar production in *Vicia* *sativa* L. increased after experimental defoliations, but that of *Ipomoea carnea* Jacq. showed no change, indicating that nectar induction is not a general phenomenon.

Effective ant exclusion may not be possible with plants such as vines or vetches because of their inter-twining growth with neighbouring vegetation. An alternative experimental technique is to remove the sugar source, either by blocking or excising the nectaries. The latter technique was used by Koptur (1979) to determine the effect of the Argentine ant *Iridomyrmex lumilis* Mayr. on herbivores of two *Vicia* species in California (where neither the plants nor the ants are native). By comparing leaf damage between plants with excised nectaries and control plants, Koptur found that the ants did in fact protect the foliage from herbivores (but see Koptur & Lawton 1988). McLain (1983) also removed the EFNs from paired *Passiflora incarnata* L. vines in order to compare differences in herbivory levels and number of fruits produced. Not only did intact plants attract more ants and suffer less leaf tissue and fruit loss, but the number of ants per plant was positively correlated with the number of EFNs present and negatively correlated with herbivory.

Ant densities are clearly important, and there is a strong correlation between the distribution of some EFN-bearing plant species and areas of high ant foraging activity (Bentley 1976). In order to demonstrate that it is the nectaries, and not other resources, which are central to the ant-plant relationship, Bentley (1976) simulated the presence of EFNs on bean seedlings (*Phaseolus vulgaris* L.) in habitats with varying ant densities. Measurements of plant dry weight were taken after 10 days and any differences were attributable to the removal of plant tissue by chewing insects. In habitats where ant activity was low, dry weights were not significantly different. Where ant activity was high, the experimental plants (with "nectaries" and ants) weighed significantly more than the control plants, indicating that even in artificial situations, ants attracted by sugar sources can reduce herbivore damage

Other studies have reported instances where EFN-plants have received no protection from their visiting ants. O'Dowd & Catchpole (1983) tested the protectionist's hypothesis by excluding ants from the flower heads of two *Helichrysum* species. In the presence of ants, they obtained a statistically significant decrease in the absolute numbers of other insects, but no corresponding decrease in seed damage. Ants appeared to selectively reduce insect visitors to the flower heads, but none of the seed predators were negatively influenced. The abundance of adults of the most numerous seed predator, a tephritid fly, was hardly affected, although its position on the plant was changed; it was more likely to be found on the flower stalks than on the flower heads. Thus the predictions of the ant protection hypothesis were not fulfilled, despite the presence of abundant ants which reduced the overall number of insects on the flower heads. At one site during one season, herbivore damage was actually higher on plants that allowed access to ants than on those where ants were excluded.

It is not only ants which attend the EFNs of plants. Other insects such as parasitic and predatory wasps, bees, flies and beetles, may also be attracted to the nectar. Interference between ants and parasitoids attending sugar sources has been demonstrated. An inverse relationship was obtained between the ants and parasitic wasps attending the EFNs of *V. sativa*, causing increased seed damage by *Cydia* caterpillars at some sites with high ant densities (Koptur & Lawton 1988). Washburn (1984) found that ants, attracted by the sugar secreted by galls of a cynipid wasp on Californian oaks, increased cynipid survival by "guarding" them from their parasitoid enemies. Pierce & Mead (1981) also documented reduced parasitism of lycaenid larvae tended by ants. In these studies, the specialist herbivores benefitted from the parasitoid exclusion behaviour shown by ants, but ant-parasitoid interactions are not always antagonistic. O'Dowd & Catchpole (1983) obtained no differences in percentage parasitism of tephritid fly larvae between ant excluded and control plants.

Koptur (1985) recorded the presence of hymenopteran and dipteran parasitoids (as well as ants) at the EFNs of two species of *Inga*. She found that at high elevations (where ants were less common), parasitoids were more abundant at EFNs and caterpillar parasitization was significantly higher than at low elevations. This result suggests that parasitoids attracted to EFNs may also confer a degree of protection upon plants, but since no independent measure of parasitoid abundance was made at low or high elevations, the effects of EFNs *per se* on parasitism rates cannot be established. For instance, the high levels of parasitism observed at high elevations may have been a direct result of increased parasitoid densities, in which EFNs played no significant part. Moreover, since many parasitized caterpillars continue to feed, the link between parasitoid visits to EFNs and benefits to the plant via reduced herbivore numbers are much less clear than in the case of direct predation by ants.

Hespenheide (1985) studied the insect visitors to EFNs of *Byttneria aculeata* Jacq. He argued that ants probably did not protect the plant to any great extent as they spent approximately 80% of their time at the nectaries and little time foraging on other parts of the plant, and suggested that parasitoids were equally, if not better, suited to a mutualistic relationship with *Byttneria*. He found that the total numbers of ants, parasitoids and flies at the EFNs were similar. Flies present at the nectaries were probably "nectar thieves", removing nectar, but providing no benefit to the plant in return. Even though 57 species of parasitoids were collected at the EFNs, only one of these was found parasitizing any of the herbivores, suggesting that their overall effect on the herbivore population was minimal. A large variety of ant species accounted for most of the nectar removed and despite Hespenheide's doubts, could collectively have had a significant effect on the herbivores of *Byttneria*. Since exclusion experiments were not performed, it is difficult to apportion the effects of ants and parasitoids in this system. Certainly his concern that recent studies have placed too much emphasis on the effects of ants in the EFN-plant mutualism to the exclusion of other contributing factors such as parasitoids, should be taken into consideration, but his study did not demonstrate a lack of importance of ants in the *Byttneria*-insect system, nor in EFN plant-ant systems in general.

EFNs do not only occur in angiosperms and are also found in a few fern genera. A casual association was noted between *Drynaria sparsisora* (Desv.) Moore, and *Crematogaster* and *Iridomyrmex* species in the rainforests of Borneo (Paterson 1982). Both ant species nested in the soil within the fern's "basket" leaves, but no mention of them visiting EFNs was made. Analyses of secretion from EFNs of several ferns have been carried out for *Polypodium* and *Drynaria* species (Koptur et al. 1982), but it is bracken (*P. aquilinum*) which has been most extensively studied.

1.2 The ant-bracken extrafloral nectary system.

In the past, bracken (Dennstaedtiaceae) was mistakenly assumed to be relatively immune to herbivory and thought to possess a scant arthropod fauna (F. Darwin 1877). The plant does in fact contain an array of secondary plant compounds (Lawton 1976; Cooper-Driver et al. 1977) as well as possessing EFNs, but it is by no means under-exploited by insect herbivores in comparison with other common plant species (Lawton 1976). Records of bracken EFNs and their ant associations date back to the observations of F. Darwin (1877) and Lloyd (1901), yet it is only recently that the functional significance of the EFNs has been studied (Douglas 1983; Temple 1983; Lawton & Heads 1984; Heads & Lawton 1984, 1985; Heads 1986). A comprehensive account of the structure, distribution, activity and variation of bracken nectaries is given by Page (1982). Chemical analysis of bracken extrafloral nectar showed that it mainly consists of the sugars glucose and fructose, with small amounts of sucrose and low concentrations of amino acids (Lawton & Heads 1984).

Douglas (1983) studied bracken in Michigan (U.S.A.) and noted that the plant suffered heavily from insect herbivory with up to 30% of the frond biomass destroyed. Several species of ants (and also spiders) were attracted to the EFNs of croziers in particular. He noted that ants systematically patrolled the plant, during which time "intruding" arthropods were driven off or killed, but it is not clear whether these intruders were experimentally introduced or natural bracken herbivores. Spiders were also observed to ambush or search for prey on the fronds, but whether they were utilizing the extrafloral nectar was uncertain. Douglas stated that "the croziers are protected (to an unknown extent) from adapted and non-adapted herbivores during this most susceptible stage of growth" by a "mobile, predaceous arthropod defense community". Experimental data to confirm such claims was lacking, but these observations were suggestive of a mutualistic interaction between bracken and nectar-feeding ants.

Tempel (1983), looking at bracken in New Jersey (U.S.A.), concluded that although ant activity was correlated with seasonal availability of nectar, the ant-plant interaction was non-mutualistic. She conducted experiments comparing herbivore damage to fronds with ants excluded versus controls to which ants had normal access. No differences were found between them, but insect densities appeared to be very low, with 89% of the fronds examined being unoccupied by either ants or herbivores. Less than 1% of the observed fronds yielded ants and herbivores present together, suggesting that there was little scope for significant interaction between the two. Tempel also observed no foraging by ants on the fronds or any suggestion of aggressive behaviour between ants and herbivores, even though two of the ant species involved in this study had been noted to systematically patrol the plant by Douglas (1983). It seems that a combination of low ant and herbivore densities with non-aggressive ant behaviour provided the basis for the non-mutualistic interaction recorded by Tempel (1983).

Results of exclusion experiments on British bracken (Heads & Lawton 1984) also showed that ants had no effect on bracken-specific herbivores, either on their densities or on the number of species found per frond. They discussed possible explanations as to why bracken appeared to offer a free source of food for no predictable gain. The ants may be "uninvited guests" with the EFNs specifically designed to attract other herbivore enemies, or the EFNs may merely serve an excretory function for the plant. Conversely, the ants may only be effective against some herbivores for some of the time, or in parts of the geographical range of bracken not studied by them. An additional hypothesis was put forward after an experimentally introduced non-adapted moth species was found to suffer heavy mortalities from nectar-visiting ants (Lawton & Heads 1984). They argued that the major bracken specific insects either already possessed "exaptations" (sensu Gould & Vrba 1982) or had evolved adaptations to minimize ant predation (for example, gall formers and leaf miners hidden within plant tissues, or sawflies with distasteful haemolymph) thus placing them in "enemy free space" (Jeffries & Lawton 1984). In contrast, generalist species would fall prey to ants foraging on the plants. Thus the bracken-ant association was potentially mutualistic at times when non-adapted or potential colonists were affected.

Heads (1986) later obtained data suggesting that ants may have an impact, albeit weak, on common bracken herbivores in Britain. He carried out exclusion experiments at sites with large, aggressive wood ants, *Formica lugubris* Zett., but again found no significant changes in herbivore abundancies. However, short-term introduction experiments using a range of external bracken feeders plus one non-adapted folivore indicated that wood ants were effective at finding and removing most external herbivores, though a species of highly distasteful sawfly remained immune. It is therefore possible for certain ant species to influence populations of specific bracken herbivores in some places for some of the time.

1.3 Summary and prospectus.

Studies of ant-EFN plant relationships have generally supported the "protectionist" view, that ants are capable of defending plants against herbivores in return for nectar. However, additional variables such as altitude, plant morphological differences, alternative defense mechanisms and the presence of parasitoids affect the interaction, and it would be unwise to assume that herbivores are important to all plants, let alone that ants automatically protect plants with EFNs. It is perhaps not surprising that the degree of mutual interdependence between ants and plants differs considerably, given the large number of different EFN-plant and ant species involved (as well as a host of environmental variables). The effectiveness of ants as protective agents will depend upon a number of factors, including:

1) the timing of ant activity patterns on the EFN-plants;
2) the ant species present and their differential effects as predators (determined by their aggressiveness and willingness to forage over the whole plant);
3) ant densities on the EFN-plants;
4) herbivore community structure (particularly any ant-related specializations exhibited by herbivores);
5) herbivore density.

Bracken is probably unique in that it is an EFN-bearing plant which is native in many regions of the world (Page 1976). Various parts of its range support different herbivore faunas (Lawton 1984) and attract different species of ants (Lawton & Heads 1984), providing the opportunity to study and compare the same plant under a variety of conditions. Because factors 1 - 5 are likely to vary from region to region, details of the relationship may change accordingly. There is some evidence to support this assumption. Ants visiting bracken EFNs in New Jersey (U.S.A.) and part of the U.K. appeared to be exploiting the plant without providing any reward. Bracken studied in areas of the U.K. where a more aggressive ant species was present may be gaining slight protection, while observations on bracken in another part of the U.S.A. (Michigan) suggested that the plant may be benefitting from its EFN-arthropod visitors.

The aim of this investigation was to assess whether a mutualism exists between bracken and the insects attending its EFNs in South Africa. It was therefore necessary to:

1) determine the herbivorous arthropod community structure and the major visitors to bracken EFNs (chapter 2);

2) investigate the interactions between bracken-specific herbivores and EFN-visiting ants in the laboratory in order to determine whether ants could potentially protect the plant (chapter 3); and

3) carry out experimental manipulations to establish whether ants did confer protection on the plant under natural conditions (chapter 4).

2. BRACKEN AND ITS ASSOCIATED ARTHROPOD FAUNA IN SOUTH AFRICA

Bracken is a ubiquitous plant, occurring naturally worldwide including South Africa (Page 1976). Although considered to be a single species (Tryon 1941), the taxon is morphologically very variable and can be divided into a dozen geographical varieties, classified into two subspecies. Chemotaxonomic studies (on the flavonoids and simple phenolic compounds) support the view that *Pteridium* is a monospecific genus (Cooper-Driver 1976).

Bracken is thought to have originated in the tropics, though its distribution was already widespread by the Tertiary, as shown by fossil records in both Australia and Europe (Page 1976). Bracken's cosmopolitan status suggests that it is an extremely vigorous plant, able to adapt to a wide range of environmental conditions. It can establish in new areas by means of spores, or can reproduce vegetatively by highly resistant rhizomes. Part of bracken's success can also be attributable to man's interference with natural habitats. A classic opportunist species, it rapidly colonizes marginal, burnt or deforested land and is more dominant in open situations (often forming dense monocultures) than in the woodlands where it is believed to have originated (Page 1976; Rymer 1976). Its dramatic rate of increase in recent years has led to the plant becoming a major agricultural weed species in countries such as the U.K., New Zealand and Japan.

Several studies made worldwide indicate that a large and varied arthropod fauna exists in different parts of bracken's range. Areas surveyed include Europe (Simmonds 1967), the U.K. (Lawton 1976), Papua New Guinea (P.N.G.) (Kirk 1977, 1982), south west U.S.A. (Lawton 1982), Hawaii (Pimm, in Lawton 1982), and New Zealand (Winterbourn 1987). As bracken's distribution is cosmopolitan, much of its range still remains to be investigated.

An examination of the South African bracken fauna provided the opportunity to compare insect communities in South Africa with those on the same plant in other parts of the world. This allowed comparisons to be made of the numbers of herbivore species (in terms of the species-area relationship) and community structure (for example, guild composition). To this end, a sampling programme was initiated to survey bracken throughout its range south of the Limpopo River. The objectives were to determine the arthropod fauna associated with the plant and to identify the ants (and any parasitoid species) attending the EFNs. More detailed studies of the major herbivores were then undertaken to assess whether these species were vulnerable to, or likely to be influenced by, ant activity on the plant.

2.1 Methods.

2.1.1 Distribution of bracken in South Africa.

A distribution map for the plant was compiled from various sources. Records were obtained from the Botanical Research Institute (Gibbs Russell 1985), national herbaria and museums (Albany Museum, Grahamstown; Bolus Herbarium and Compton Herbarium, Capetown; Drakensberg National Botanic Garden; University of Natal; Potchefstroom University), W. B. G. Jacobsen (pers. comm.) and supplemented by personal observations. Bracken records were assigned grid references and transferred to the corresponding "quarter degree" square (so called because the sides of each square are a quarter of a degree in length) used for vegetation mapping by the South African National Herbarium. As bracken is so common, its presence is often ignored and consequently records are unlikely to be complete.

In addition to indicating bracken's distribution, the grid reference system can be used to provide an estimate of the total area potentially occupied by the plant. The area of each quarter degree square varies slightly with latitude, becoming larger towards the equator. The areas of squares in different regions of South Africa were calculated and the average value of 660 km^2 taken.

2.1.2 Study sites.

Samples of the bracken fauna were made throughout the range of the plant in the Cape, Natal and Transvaal Provinces. The Cape was further divided into the western Cape (areas to the west of 20°E longitude), the southern Cape (between 20°E and 26°E longitude) and eastern Cape (areas to the east of 26°E longitude). Sample sites were also chosen to ensure that all the habitats occupied by the fern were investigated. More intensive surveys were carried out at "Faraway" (33° 20'E/26° 29'S, grid reference 3326AD), a site 6km south west of Grahamstown in the eastern Cape Province.

2.1.3 Plant phenology.

In order to give an overall picture of the pattern of bracken development throughout the year, the phenology of the plant was studied at "Faraway". Fronds were scored as belonging to four discrete developmental stages (figure 2.1). The crozier stage applied to the young emerging fronds, commonly termed fiddle-heads. Unfurling fronds referred to the stage when the rachis ("stem") was upright, but the pinnae ("leaves") remained unopened (see figure 2.2 for a diagrammatic representation of a frond at the unfurling stage). Mature fronds had fully opened pinnae, and a frond was considered senescing if at least a third was brown or dead. The developmental stage of fronds within eight permanent 1m^2 quadrats was recorded at monthly intervals for one year from March 1986 to February 1987.

2.1.4 Sampling procedure.

Sampling followed the procedure described by Lawton (1976). At each of the sample sites, 20 fronds representing the range of growth stages from young crozier to mature plant were uprooted and carefully examined in the field for the presence of herbivorous arthropods and feeding damage. Approximate numbers of each herbivore species were recorded. A general visual search and sweep netting was also carried out in case rare species had been overlooked. Specimens were sent to the National Collection of Insects (Pretoria) and the Commonwealth Institute of Entomology (London) for identification.

Figure 2.1. The developmental stages of a bracken frond. (A) crozier; (B) unfurling; (C) mature; (D) senescing.

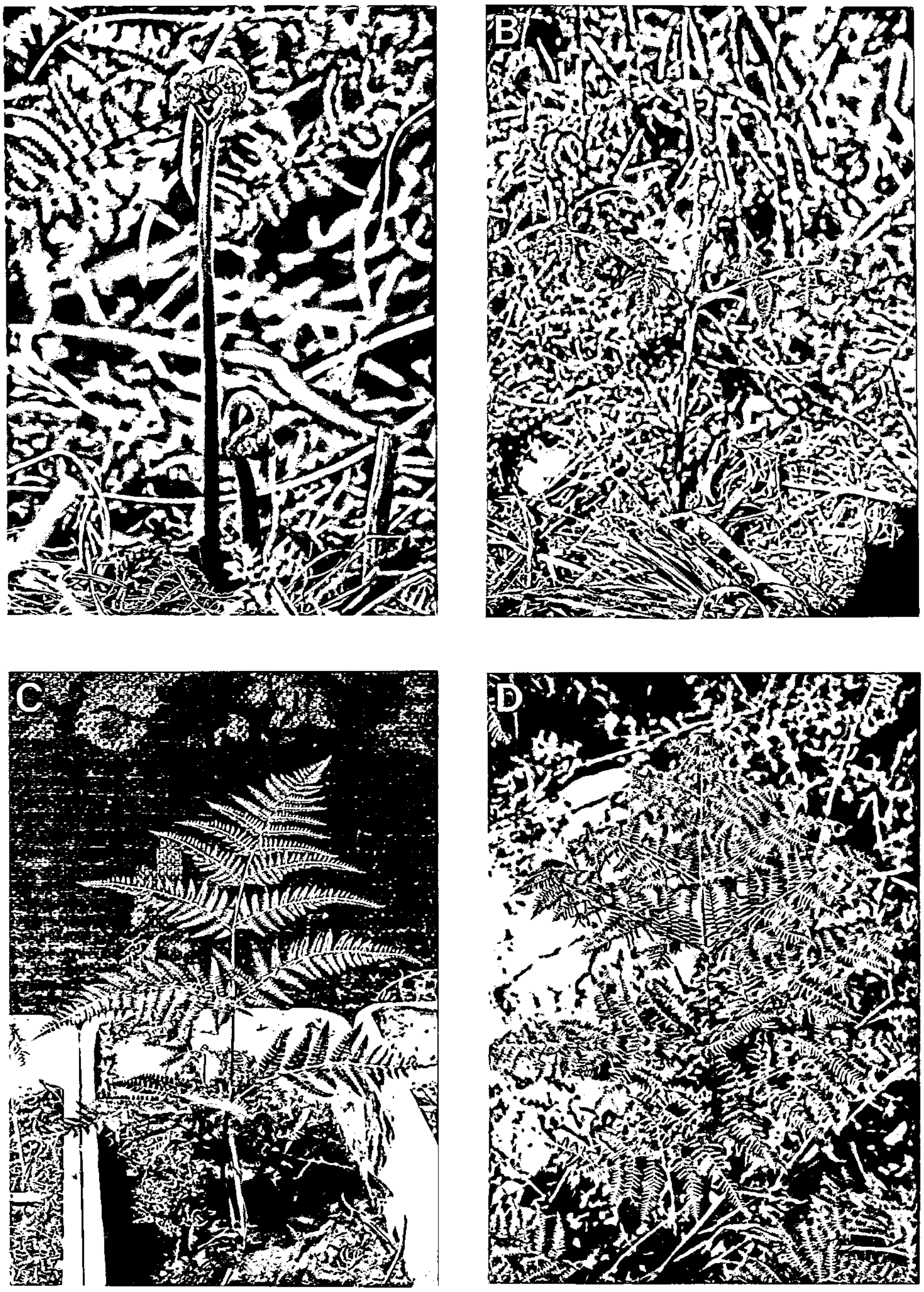
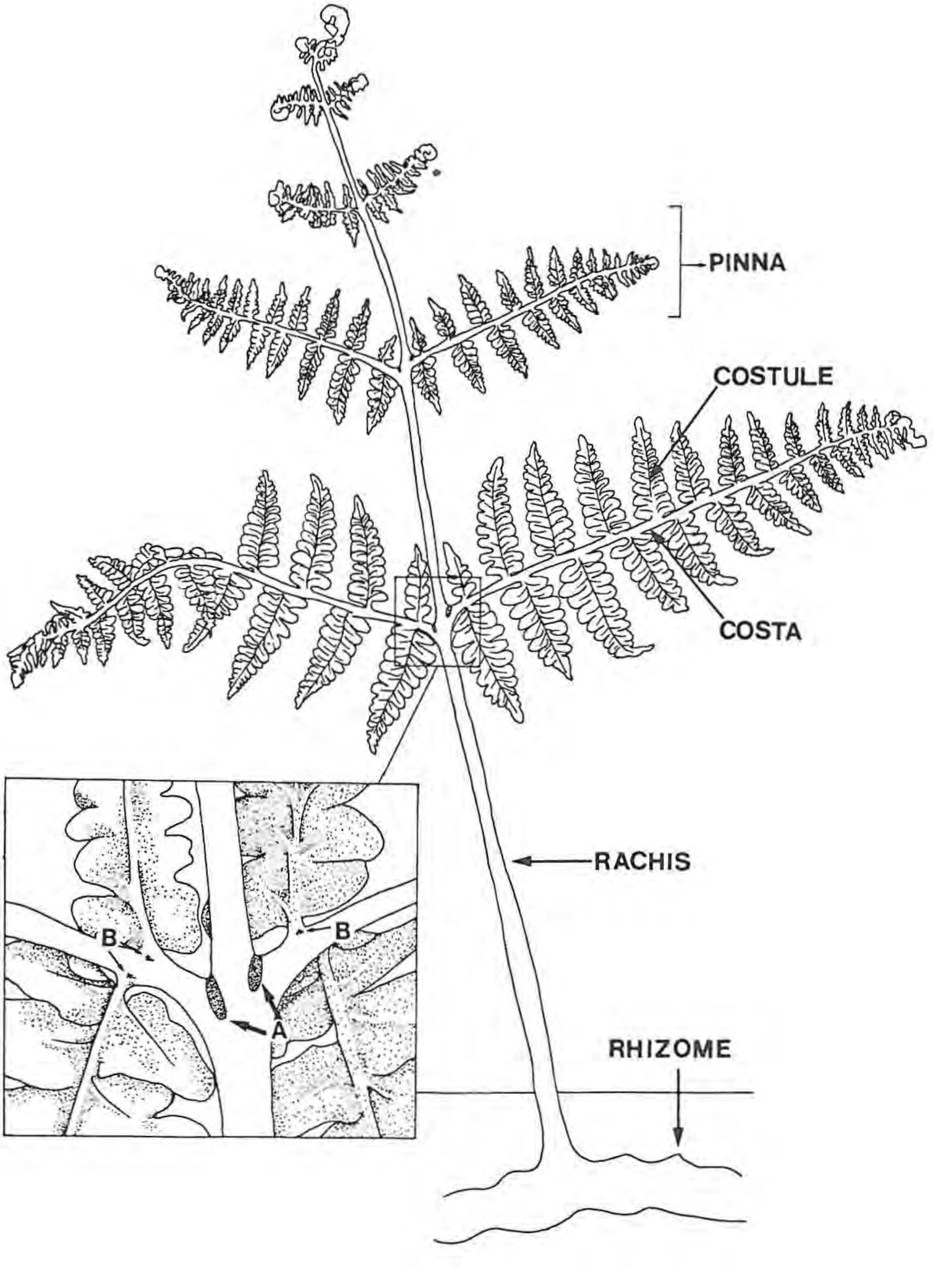


Figure 2.2. Diagram of an unfurling bracken frond showing the position of the extrafloral nectaries (EFNs). A = major EFNs; B = minor EFNs.



An advantage of using the same sampling method as Lawton (1976, 1982) is that direct comparisons can be made between this study and those made on other continents. The cumulative frequency curve obtained from a bracken site in northern England (Lawton 1976) suggested that the vast majority of herbivore species (at any one site at any one time) would be uncovered by examining 20 "haphazardly" selected fronds. Recruitment curves, indicating the number of species obtained in a 20 frond sample, were constructed for four sites in the Cape province. An overall recruitment curve for the South African region was also constructed, incorporating the effects of increased geographical range.

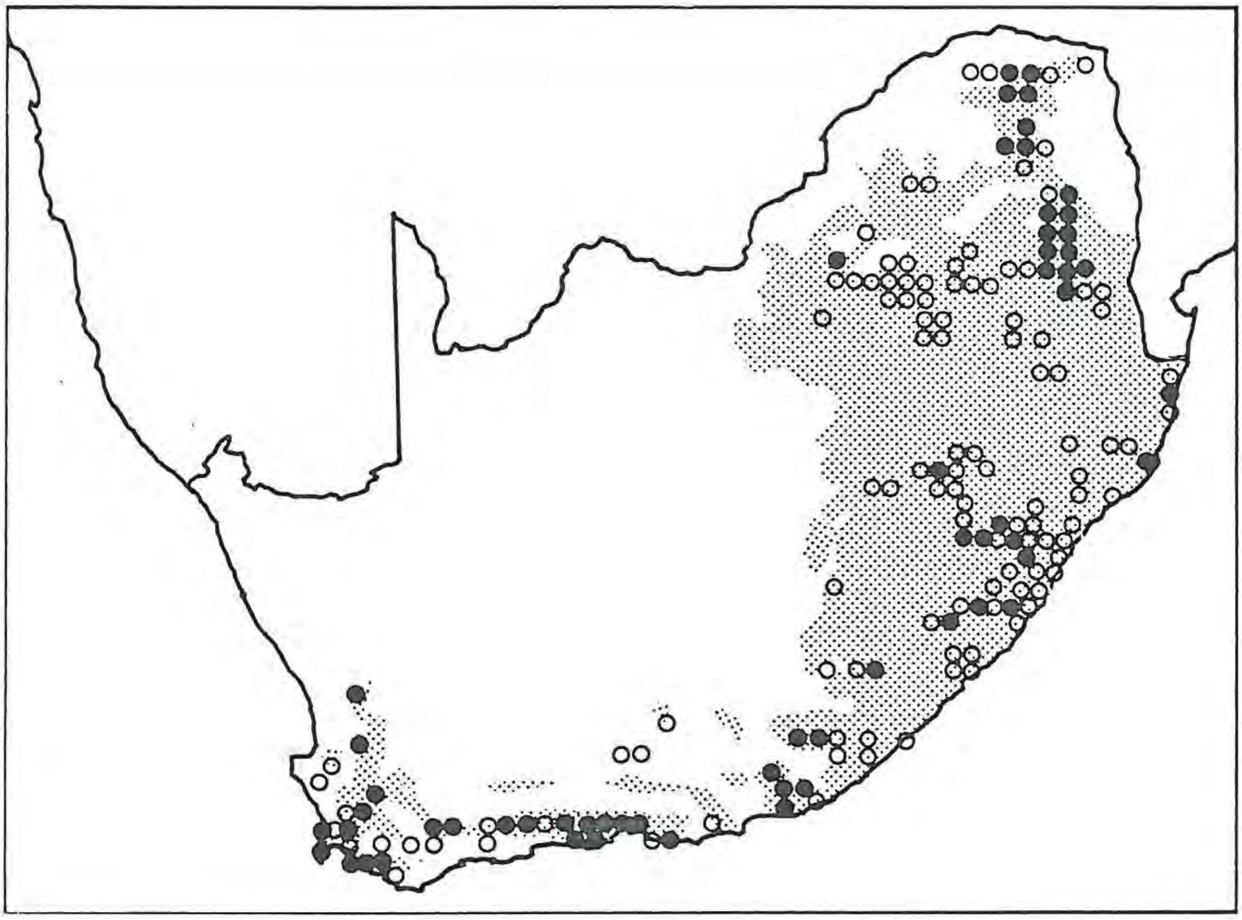
2.2 Results.

2.2.1 Distribution of bracken in South Africa.

Available records indicate that bracken in South Africa has a well defined distribution, being confined to the coastal regions and to higher altitudes further inland, especially in the subtropical north-east of the country. Figure 2.3 (open and solid circles) illustrates this distribution. Also indicated are areas of the country which receive greater than 500mm rain per annum. In general, bracken's occurrence corresponds closely with the moister areas of South Africa: Jacobsen (1983) remarked that the plant is unlikely to survive in areas where annual rainfall is less than 400mm per annum and is well established in parts where 600mm and above is received. Exceptions to this are in Lesotho and parts of the Orange Free State where the plant is almost completely absent despite a relatively high rainfall.

As bracken has been been recorded in 171 quarter degree squares, the area over which it occurs in suitable habitats in South Africa can be estimated as 112,860 km^2.

Figure 2.3. The distribution of bracken in South Africa. Quarter degree squares where bracken has been recorded are represented by solid and open circles. Those squares where faunal samples were taken are indicated by solid circles. Bracken is restricted to areas where annual rainfall exceeds 500mm (stippling).



2.2.2 Study sites.

Eighty sites (in 59 quarter degree squares) were sampled at least once between September 1985 and January 1987. The plant grows in a variety of habitats which can be loosely defined as being "open", "understory" or "roadside". In open situations, such as fynbos (heathland), bracken tends to form discrete monocultures. Occasionally it forms part of the understory in pine plantations and is often found growing along roadside verges.

A total of 102 samples were made, of which 82 were from bracken in open situations (including most roadside sites) and 10 were from woodland understory areas. The remaining sites were of an indeterminate nature consisting of, for example, bracken patches on roadside verges adjacent to forest. A list of all the study sites, together with the quarter degree square reference codes and sampling dates, is given in appendix I. Figure 2.3 illustrates the distribution of these sites (solid circles), which were spread throughout the range of the plant. It was not possible to sample throughout every province during each season of the year, but all areas were sampled at least once during the spring and summer months when insect activity was at its maximum. However, more continuous sampling was possible in the eastern Cape. Table 2.1 provides a summary of the number of sample sites in each region, together with the habitat types covered.

2.2.3 Plant phenology.

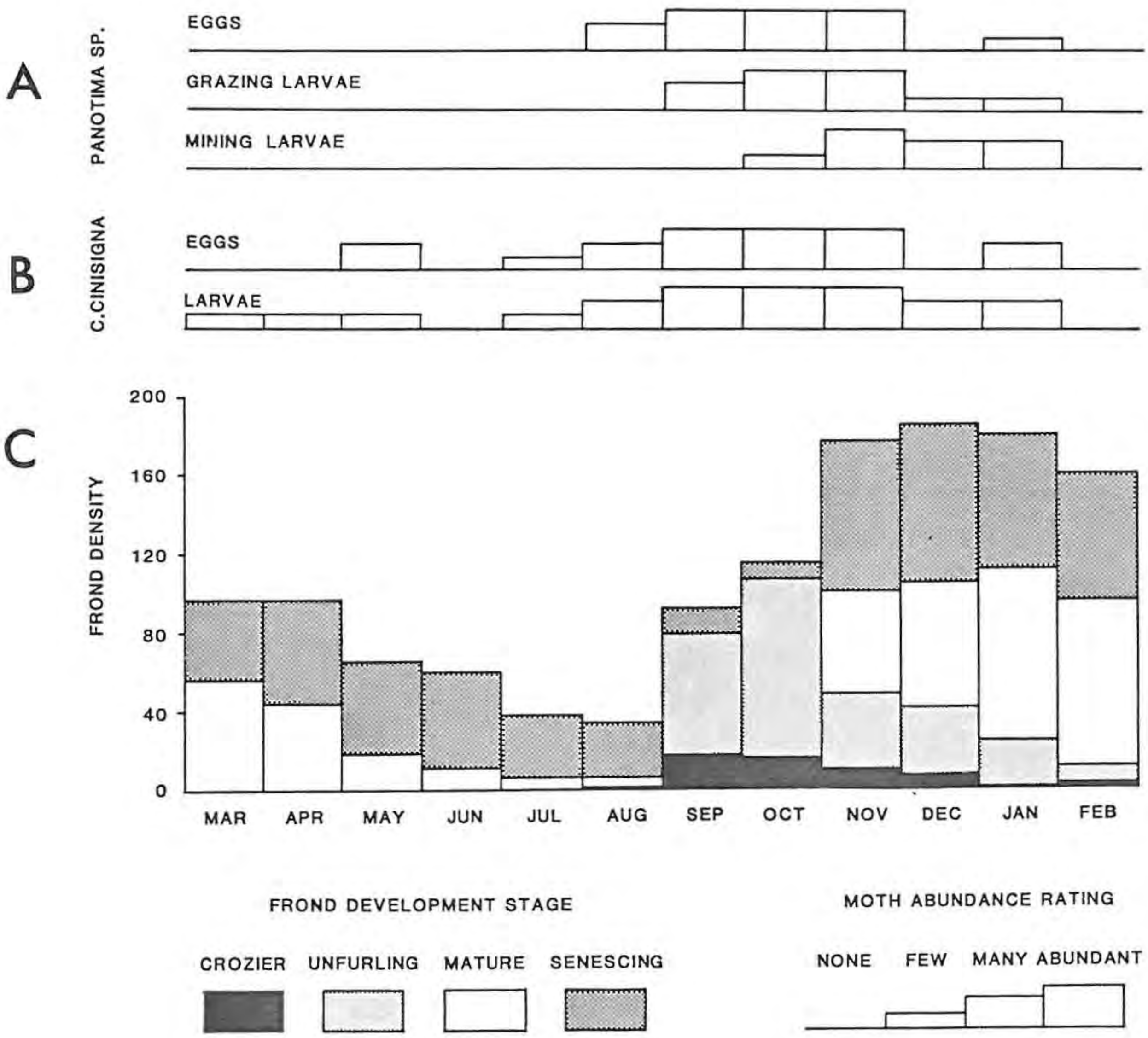
Monthly assessments of plant development at "Faraway" are displayed in figure 2.4C. A distinct seasonal trend was observed, with consistently higher frond densities obtained during the summer (December-February) and lower densities being recorded in winter (June-August). Spring (September-November) was characterised by an increase in frond numbers and conversely, autumn (March-May) showed a steady decline.

New growth was concentrated in the spring. Croziers first emerged in August, but reached maximum production during September and October. Unfurling fronds also reached a peak during these months, whereas

Table 2.1. The regional distribution of sample sites in South Africa divided according to habitat type.

REGION	OPEN	ROADSIDE (OPEN)	WOODLAND UNDERSTORY	INDETER-MINATE	TOTAL NO. OF SITES
W. CAPE PROVINCE	7	3	2	0	12
S. CAPE PROVINCE	4	6	1	2	13
E. CAPE PROVINCE	9	3	2	3	17
NATAL (INCLUDING TRANSKEI)	7	8	1	2	18
TRANSVAAL	6	10	2	2	20
TOTAL	33	30	8	9	80

Figure 2.4. The relationship between (A) *Panotima* and (B) *Appana cinisigna* life histories and (C) bracken phenology. Plant development stages (ignoring dead fronds) were measured at "Faraway" (near Grahamstown, eastern Cape Province) during 1986 and 1987. Moth abundances were gathered at a number of sites in the eastern Cape during 1985 and 1986. Few = 1-5, many = 6-20, abundant = >20 individuals per 20 frond sample.



mature fronds were completely absent. The latter only appeared from November onwards, becoming the most common developmental stage during summer. Senescing fronds were found every month, but in very low numbers in spring compared with the rest of the year. In autumn and winter, mature and senescing fronds predominated, although some new growth was noted to occur outside the sample quadrats. The decrease in overall frond density during this period could be attributed to the absence of new growth and the die-back of the above ground parts of the majority of the fronds (which were ignored for the purposes of the phenology survey).

2.2.4 Validity of the sampling procedure.

Cumulative herbivore frequency data from four sites in the Cape Province (figure 2.5) show the acceptability in South Africa of the sampling procedure utilized by Lawton (1976). The curves reach an asymptote well before 20 fronds are reached, indicating that all the herbivore species present were routinely recorded within the 20 frond samples. Subsequent searching by eye and sweep netting did not uncover additional species.

2.2.5 The bracken arthropods.

The faunal samples yielded 17 herbivorous arthropod species closely associated with bracken and 13 other species which may possibly feed on the plant (table 2.2). It was sometimes difficult to confirm whether the species found were true bracken feeders, predators or merely "tourists", present on the plant by chance. Thrips and bugs for example could not always be observed feeding in the laboratory and rearing to the adult stage was often difficult on cut plant material. Thus, for these groups was a direct association between that species and bracken assumed only if nymphs of a particular species were found on the plant (as well as eggs and/or adults). Secondary phytophages, such as psocids and a fungal-feeding dipteran, were ignored. Brief details of the biology of each species are given in appendix 2.

Figure 2.5. Cumulative frequency curve for the herbivores of bracken at four sites in South Africa.

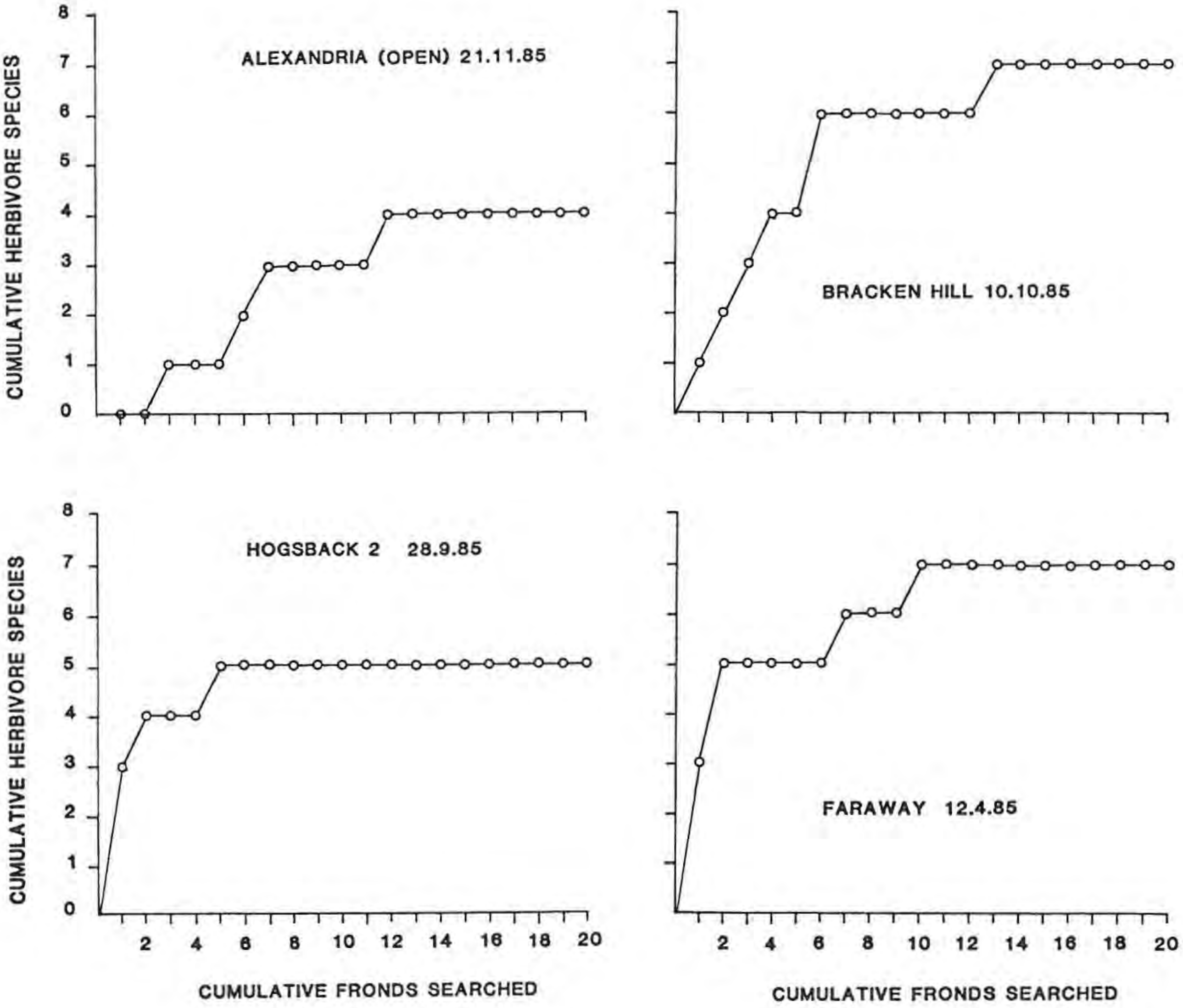


Table 2.2. Herbivorous arthropods recorded from bracken in South Africa. (A) Species definitely feeding on the plant. (B) Species whose association with the plant is more uncertain. Lepidopteran species after Vari & Kroon (1986).

(A.)

ACARI

Prostigmata
1. *Eriophyes* sp. near *helicantyx*(Keifer)

HEMIPTERA: HOMOPTERA

Cicadellidae
2. *Eupteryx maigudoi* Dworakowska

Coccoidea
3. *Coccid* sp.

Pseudococcidae
4. *Pseudococcus* sp.

HEMIPTERA: HETEROPTERA

Pentatomidae
5. *Erachtheus spinosus* (Signoret)

THYSANOPTERA

Thripidae
6. *Mycterothrips* sp.

COLEOPTERA

Curculionidae
7. *Holcolaccus* sp.

LEPIDOPTERA

Pyralidae
8. *Panotima* sp. near *angularis* (Hampson)

Geometridae
9. *Idiodes saxaria* (Guenee)
10. *Epigynopteryx maeviaria* (Guenee)

Lasiocampidae
11. *Pachypasa* sp.

Arctiidae
12. *Rhodogastria amasis* (Cramer)
13. *Leucaloa eugraphica* (Walker)

Lymantriidae
14. *Knappetra fasciata* (Walker)

Noctuidae
15. *Appana cinisigna* (de Joannis)
16. *Appana minor* (Holland)
17. Hadeninae gen. et sp. indet.

(B.)

COLLEMBOLA

1. *Sminthurid* sp.

HEMIPTERA: HOMOPTERA

2. *Fulgorid* sp.
3. *Cicadellid* sp./?spp.

4-9. *Aphid* spp.

HEMIPTERA: HETEROPTERA

Anthocoridae
10. *Orius* sp.

Miridae
11. *Taylorilygus ?pallidulus* (Blanchard)

THYSANOPTERA

Thripidae
12. *Chirothrips pretorianus* Hood

Phlaeothripidae
13. *Haplothrips nigricornis* (Bagnell)

2.2.6 The distribution of the bracken arthropods.

Not all the species uncovered in the survey occurred at each site (figure 2.6). A sample generally revealed between 2 and 5 species, with a maximum of 7. Regular sampling and observations at "Faraway" throughout the year indicated that this site had a typical compliment of six species. Figure 2.7 illustrates a "feeding niche matrix" based on the feeding site and methods by which each of the six insects at "Faraway" utilized the plant (after Lawton 1982). Bracken feeding sites can be categorized as being the rachis, pinnae, costae ("petioles") and costules ("main leaf veins"). Forms of insect attack consist of external chewing, sucking (of cell contents or the vascular system), internal mining and tissue galling. Each dot on the matrix represents an arthropod species, and dots joined by lines indicate the same arthropod exploiting the plant in more than one way; for example, *Panotima* larvae graze the pinnae and mine the costae and rachis.

Figure 2.8 displays the species accumulation curve for the 102 samples, divided so as to show the effects of extending the geographical regions visited. The flattening out of the curve indicates that the survey was successful in discovering most of the bracken-feeding arthropods of the subcontinent. The majority of species were comparatively rare, occurring in less than half the 80 sites sampled (figure 2.9). However, most had a widespread geographic range, the exceptions being the pentatomid *Erachtheus spinosus* (Signoret) which was restricted to Natal and Transvaal, and four of the lepidoptera species, which were found only in the eastern Cape Province.

The number of species per sample was greatest in the Transvaal (mean 4.45 species/sample, number of samples = 20) and Natal (mean 4.40, n = 18), with other areas all lower (E. Cape 3.20, n = 34, S. Cape 3.33, n = 15, W. Cape 3.20, n = 15). Mean number of species per sample differed significantly between the five regions ($P < 0.001$, Kruskal-Wallis). Sampling date had no significant effect on the number of species found per sample ($P > 0.05$, Kruskal-Wallis). All the more frequently found herbivore species apparently showed no preference for bracken growing in the open or in the shade (table 2.3). Other species occurred too rarely for distinctions to have been detected.

Figure 2.6. Frequency distribution for the number of species of bracken-feeding arthropods found in single samples at bracken sites throughout South Africa.

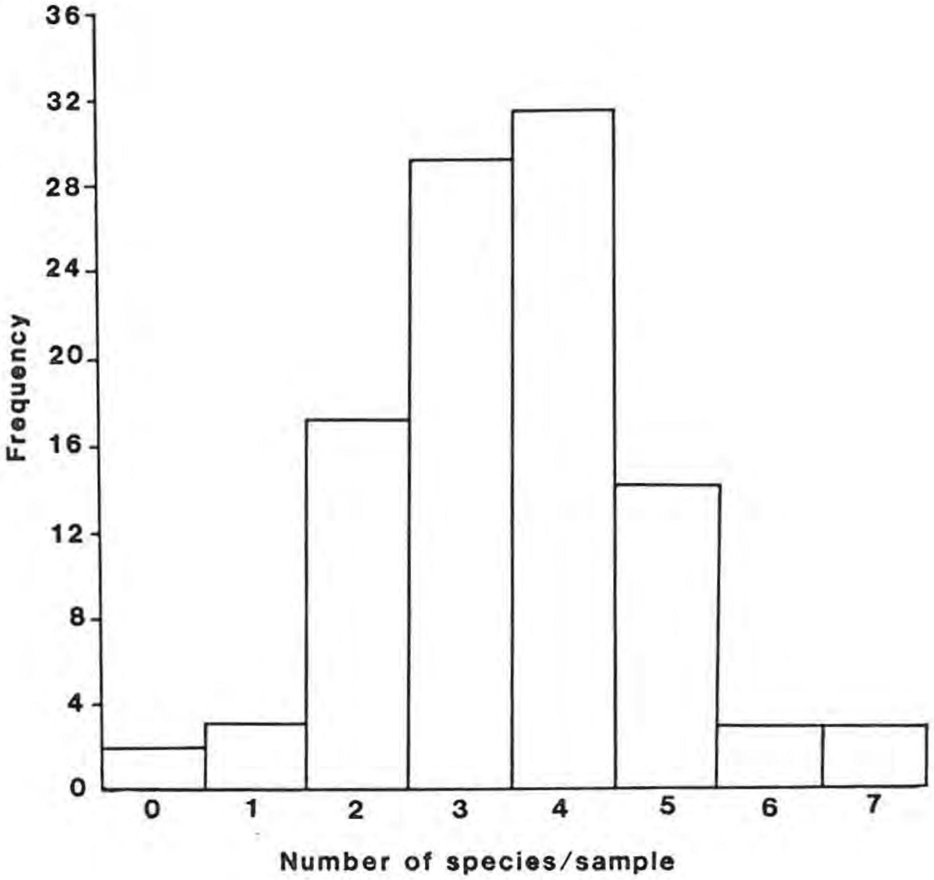


Figure 2.7. Feeding niches (sites on the frond and method of feeding) for six species of herbivorous arthropods (five insects and one mite) at "Faraway". Feeding sites of species exploiting more than one part of the frond are joined by lines. The parts of the frond are: rachis (main stem), pinnae ("leaves"), costae (main stalks of the pinnae, arising from the rachis) and costules (main "leaf veins" of the pinnae). The arthropods at "Faraway" are: the gall-forming mite *Eriophyes* sp., the cicadellid *Eupteryx maigudoi*, three pinnae-chewing lepidopteran caterpillars (*Appana cinisigna*, *A. minor* and *Idiodes saxaria*), and caterpillars of *Panotima* sp. that chew and mine.

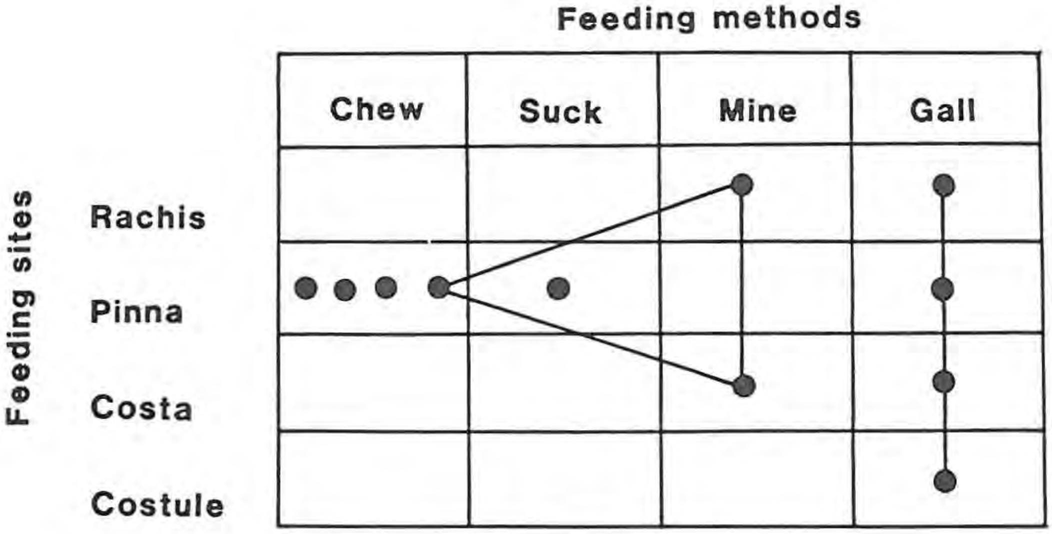


Figure 2.8. The cumulative number of species of bracken-feeding arthropods found with increasing number of samples in different regions of South Africa. A sample consists of at least 20 fronds examined at one site (see text).

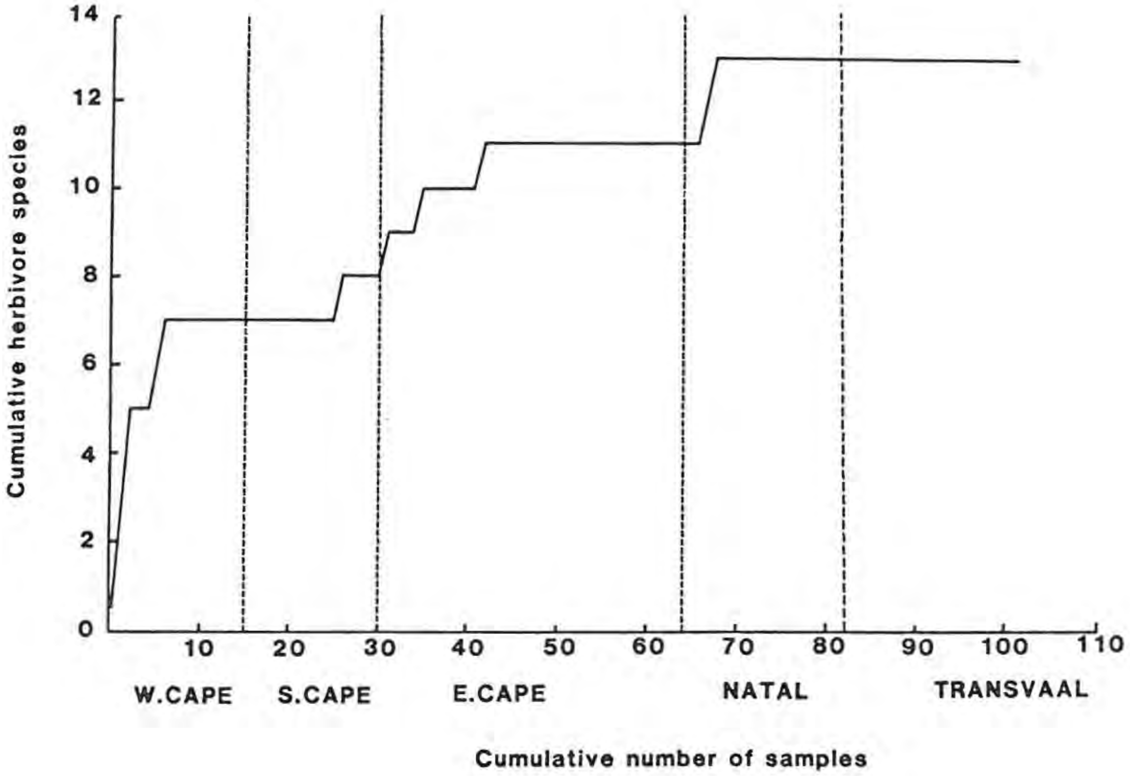


Figure 2.9. Frequency of occurrence of bracken herbivores (arranged in order of abundance). Eighty bracken sites were sampled in total.

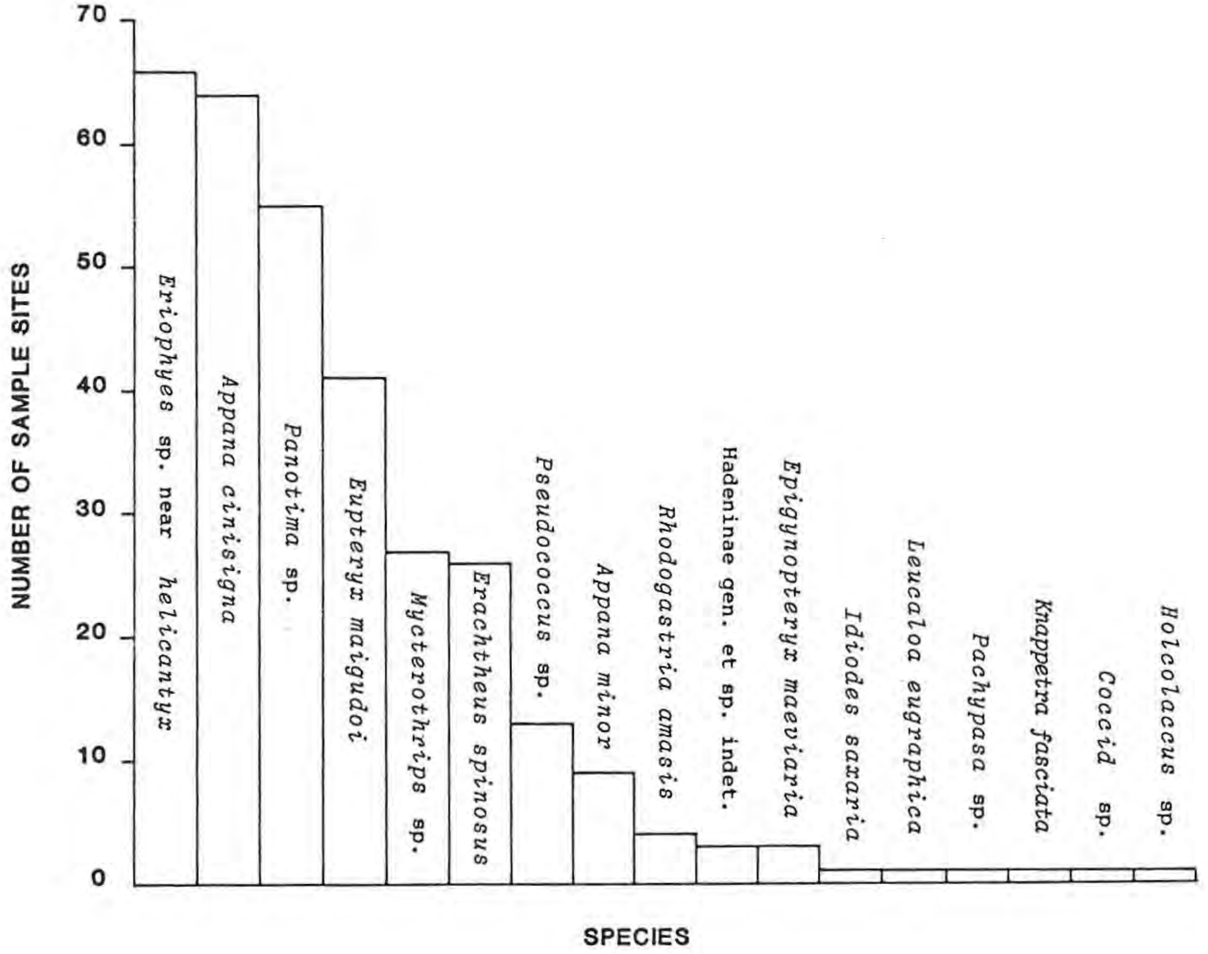


Table 2.3. Comparison of the habitats occupied by the more frequently found bracken herbivores. None of them show significant preferences for bracken growing in the open or shade (critical value for chi-squared with 1 d.f. = 3.84).

SPECIES	TOTAL NUMBER OF SITES WITH SPECIES PRESENT:		CHI²
	IN OPEN	IN WOODLAND	
Eriophyes sp.	61	5	2.62
Eupteryx maigudoi	40	4	0.28
Pseudococcus sp.	9	2	0.69
Erachtheus spinosus	21	3	0.09
Mycterothrips sp.	23	2	1.06
Panotima sp.	52	9	2.82
Appana cinisigna	62	7	0.15
Appana minor	6	1	0.09
Total number of samples in each habitat	82	10	

It was possible to identify the most important bracken herbivores by applying the following criteria: a) extent of geographical range; b) extent of habitat range; c) level of abundance where present; d) degree of visible damage inflicted on the plant. On the basis of these characteristics, four herbivorous arthropods emerged as the ones most likely to be damaging to the plant. They were:

1) *Eriophyes* sp. nr *helicantyx* (Keifer)	(Eriophyidae)
2) *Eupteryx maigudoi* (Dworakowska)	(Cicadellidae)
3) *Appana cinisigna* (de Joannis)	(Noctuidae)
4) *Panotima* sp. nr. *angularis* (Hampson)	(Pyralidae)

All four herbivores were distributed throughout the geographical range and habitat range occupied by bracken (table 2.4). The 20 frond samples indicated that high levels of abundance were often attained by each, resulting in correspondingly high damage levels. Detailed investigations of the life histories of the two lepidopteran species carried out, while preliminary observations of the biology of the eriophyid and the cicadellid were made.

2.2.7 The major bracken herbivores.

Eriophyes* sp. near *helicantyx

A feature of eriophyid gall mites is their tiny size; individuals of this species measured approximately 0.1mm in length. For this reason, abundance measurements were not attempted, and presence/absence was scored according to the distinctive galling produced by their feeding. Degree of frond damage ranged from slight thickening of the pinnule edges, to gross distortion of the entire frond. Scanning electron micrographs indicated that eggs, nymphs and adults were found protected within the galled tissue of younger fronds. Details such as timing and mode of dispersal are unknown, but it is likely that adults are wind dispersed. Under shade house conditions, newly galled fronds appeared during the summer months of December and January.

Table 2.4. Distribution of the four major bracken herbivores in terms of (A) geographical region and (B) type of habitat.

(A) Geographical region

HERBIVORE SPECIES	NUMBER OF SITES W. CAPE n=12	S. CAPE n=13	E. CAPE n=17	NATAL n=18	TRANSVAAL n=20	TOTAL n=80
Panotima sp.	8	8	16	13	10	55
A. cinisigna	11	8	17	17	11	64
E. maigudoi	7	9	11	5	9	41
Eriophyes sp.	10	11	14	11	20	66

(B) Type of habitat

HERBIVORE SPECIES	NUMBER OF SITES OPEN n=33	ROADSIDE (OPEN) n=30	WOODLAND UNDERSTORY n=8	INDETERMINATE n=9	TOTAL NO. OF SITES n=80
Panotima sp.	24	17	8	6	55
A. cinisigna	27	23	5	9	64
E. maigudoi	17	15	5	4	41
Eriophyes sp.	29	24	5	8	66

Eupteryx maigudoi

This species had pale cream, typical cicadellid banana-shaped eggs that were placed between the epidermal layers of the pinnae (laid from the underside) or in the costules (S. Fowler, pers. comm.). Low numbers of both nymphs and adults occurred on bracken throughout the year, though abundances were noticeably higher during the autumn months. Because new frond growth at this time is limited, this species was usually found on older fronds. Uncharacteristically high densities were noted at sites in the Katberg Mountains (eastern Cape) in May 1986 and June 1988. It was only at these densities that any appreciable damage to the plant could be seen, with mottled white patches on the pinna undersurface indicating areas of cell-sucking activities by nymphs and adults.

Appana cinisigna

Taxonomy.

A. cinisigna was originally described as *Conservula cinisigna* by de Joannis (1906), and is known in English as the "Pink Angle Shades" (Pinhey 1975).

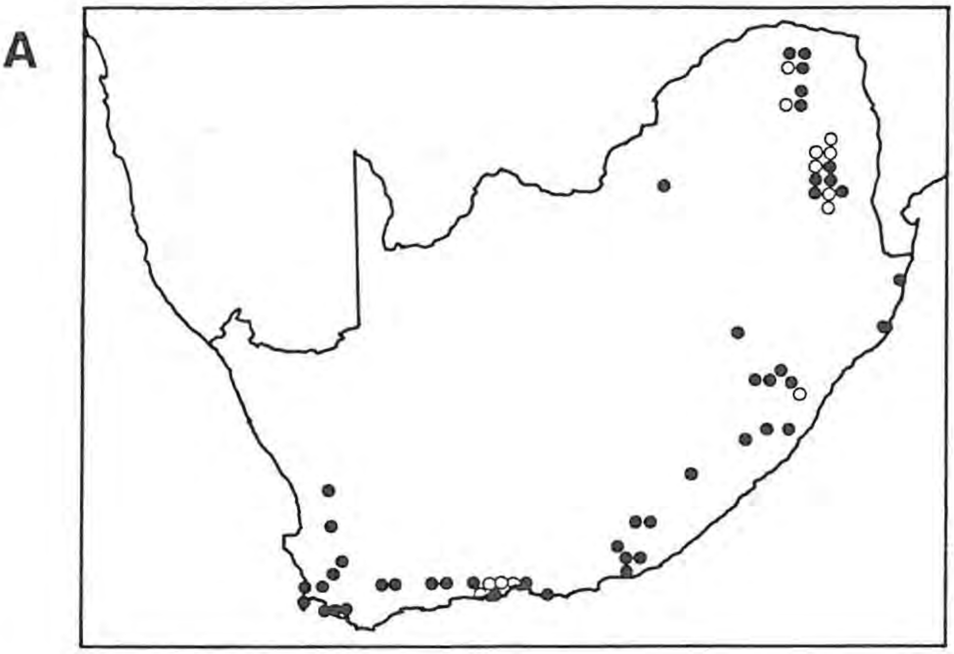
Distribution.

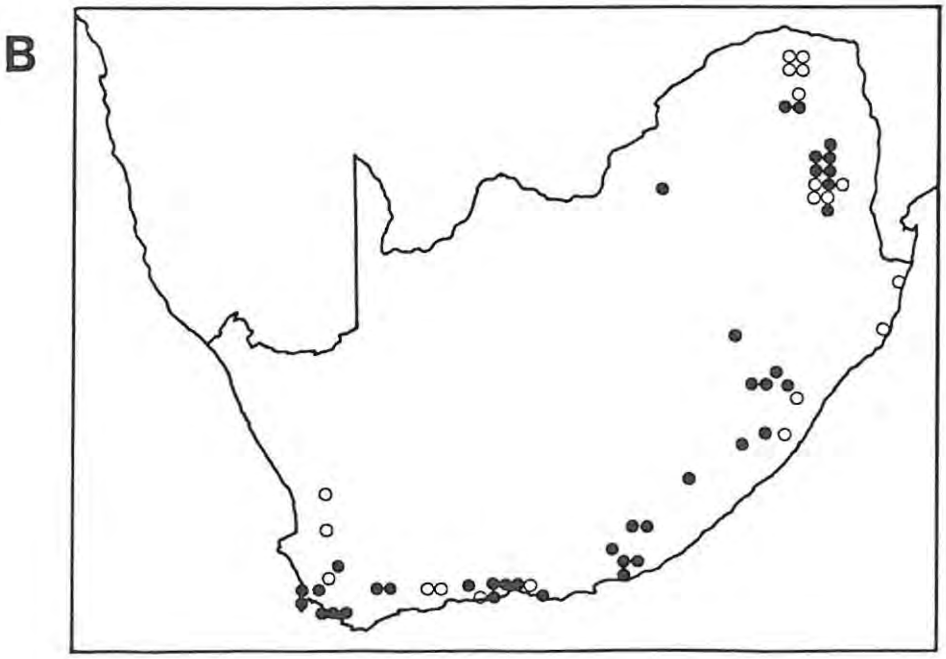
A. cinisigna has been recorded from Mauritius, Malawi to Uganda and other parts of tropical Africa (Pinhey 1975). The bracken faunal surveys indicated that it is widely distributed in South Africa (figure 2.10A).

Life History.

Measurements of *A. cinisigna* abundance during 1985-6 were obtained from the E. Cape surveys, the results of which are displayed in figure 2.4B. Data from all the sites sampled in this region are included, though the sites varied considerably in their climatic and altitudinal conditions as well as in habitat type. The following estimates of herbivore abundance were used: "none" = no individuals per 20 frond sample, "few" = 1-5, "many" = 6-19, "abundant" = >20. Abundance of each life history stage is indicated per month.

Figure 2.10. The distribution of (A) *Appana cinisigna* and (B) *Panotima* sp. in South Africa. Samples were taken from bracken throughout its geographical distribution and from a variety of habitats. ● indicates a quarter degree square where the moth species were present, o indicates their absence.



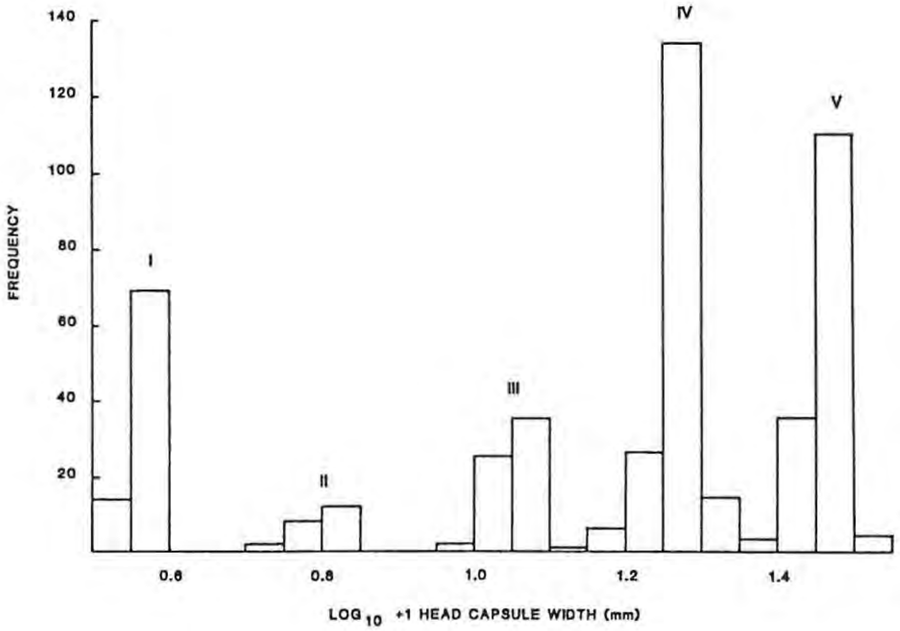


The main period of egg laying and larval development coincided with the emergence of bracken croziers in the spring and early summer (figure 2.4B & C). Batches of one to nine spherical pink eggs (mean ± S.D. = 3.4 ± 1.8, no. batches = 148) were laid in the unfurling frond tips. They were glued tightly together and to the surrounding plant tissue and were coated with a light covering of scales. Head capsule measurements indicated that there were five larval instars (fig. 2.11A). The newly hatched larvae fed within the curled frond tips. Later instars moved around the plant to graze on the underside of open fronds. Their colour at this stage varied from pale green to dark brown; the significance and genetic basis of this variation is unknown. All instars were external chewing folivores and the larger instars were voracious feeders, capable of causing extensive damage to the fronds. Pupation occurred in the soil. In addition to the main spring generation there was a partial second generation and low numbers of eggs and larvae were found throughout the year. Since the oviposition sites were determined by the frond growth stage, egg laying was restricted to times when young unfurling fronds were available. In South Africa such new growth appeared year round, but was not abundant outside of the spring months (figure 2.4C). Field observations and laboratory starvation trials using other ferns showed that *A. cinisigna* is probably bracken specific (Lawton et al. 1988).

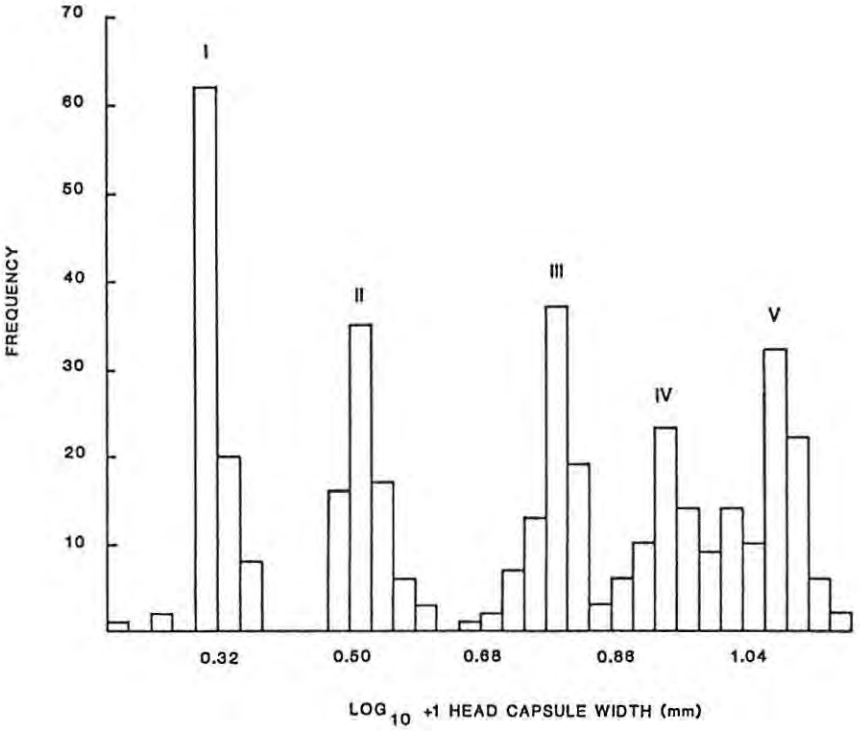
The most widespread parasite of *A. cinisigna* was *Euplectrus ?epiblemae* Ferriere (Hymenoptera: Eulophidae), a colonial ectoparasite which attacked the grazing larvae. Parasitism by this chalcid reached high levels at certain sites affecting, for example, 87% of the 62 larvae collected at "Mountain Drive" near Grahamstown in January 1986. A solitary, endoparasitic braconid was also fairly common, as was an egg parasite (Trichogrammatidae). Of lesser importance were another unidentified braconid and three ichneumonids, all of which were rare. At one site ("Hogsback 4", October-December 1988), spider mites were commonly found attached to *A. cinisigna* larvae. Up to five mites on a single larvae were found and larvae usually, though not always, died as a consequence.

Figure 2.11. Frequency distribution of (A) *Appana cinisigna* and (B) *Panotima* sp. larval head capsule widths.

(A) *Appana cinisigna* (n = 500).



(B) *Panotima* sp. (n = 400).



Panotima* sp. near *angularis

Taxonomy.

There is still some question as to the taxonomic status of this moth. It has been referred to as *Parthenodes angularis* Hampson (Lawton 1986a, b; Heads & Lawton 1986), but was recently transferred to the genus *Panotima*, with the possibility that more than one species is present in South Africa (M. Schaeffer, pers. comm.).

Distribution.

Panotima has been recorded from Madagascar and is widely distributed in South Africa (figure 2.10B), but its absence from a few of the hotter and drier sites suggests an inability to tolerate these conditions. Additional sampling is needed to confirm the absence of *Panotima* from these areas.

Life History.

Measurements of *Panotima* egg and larval abundance at all eastern Cape sites for the period of one year were obtained using the same rating scale as for *A. cinisigna* (figure 2.4A).

Panotima had one major generation each spring. The white, oval eggs were laid singly on the underside of open pinnae, preferred sites being towards the rachis. Eggs were probably also laid on the young unfurling fronds because young larvae (which were unlikely to travel up the plant at such an early stage) were found in these areas. Egg densities varied greatly, with as many as 50 per frond recorded ("Faraway", September 1985). There are five larval instars (fig. 2.11B). The newly hatched larvae exhibited several different feeding modes. Most grazed small sections of the under-surface of the pinnae and were often covered with a shelter formed by a mixture of silk and frass. They also fed in the uncurling tips, sometimes with *A. cinisigna* larvae, and occasionally mined in the unopened terminal pinna where they destroyed the growing point.

Irrespective of their previous feeding pattern, all third instar larvae migrated down the plant and tunnelled into the rachis. Here they completed their larval development. One larva was found per mine, but small larvae were occasionally discovered in old mines suggesting that tunnels may be re-utilized. Several mines per stem could occur, the presence of larvae being detectable by frass expelled through the entrance hole as the rachis tissue was mined. Larvae left their mines towards the end of the fifth instar to pupate in the soil. In the laboratory, adults either emerged within a month (n = 16), or in the following spring (pupation time = 11-13 months, n = 7). In the field, the presence of a partial second generation was indicated by January records of small numbers of eggs and larvae, well after the initial spring peak (fig. 2.4A).

The parasitoid *Trichogrammatoidae lutea* Girault (Hymenoptera: Trichogrammatidae) parasitized *Panotima* eggs. The young grazing larvae were subject to attack by an ectoparasitic parasite, *Elachertus* sp. (Hymenoptera: Eulophidae) and an unidentified ichneumonid. Two unidentified species of braconid, one colonial and the other solitary, developed on larvae mining in the rachis.

2.2.8 Extrafloral nectary visitors.

The visual search which accompanied each 20 frond sample was useful in obtaining a qualitative record of the insects attracted to the extrafloral nectaries (EFNs).

Bracken EFNs have two groups of location sites (see figure 2.2). The larger nectaries, here termed major EFNs, consist of a pair of tear-shaped glands found on the rachis at the junction with the costae. The largest pair correspond with the lowest, largest pinnae, while progressively smaller pairs occur at junctions further up the rachis. Even smaller, minor EFNs occur in pairs along the pinnae undersurface where the costules join the costae. This network of EFNs ensures a supply of nectar over the entire frond and provides a readily available source of food to insects.

Miscellaneous Diptera and Coleoptera were occasionally found, but parasitic Hymenoptera were never noted at the nectaries. However, ants were observed on bracken at just under half the sites, with many different species recorded. Table 2.5 lists the species found at a selection of the sites, but this is without doubt an underestimate of the variety of species utilizing the extrafloral nectar. Rather than providing a complete list of the ant species composition on bracken, table 2.5 serves to show the diversity of ants attracted to the EFNs.

2.3 Discussion.

The species-area phenomenon characterizes a wide range of insect-plant associations, usually comparing different species of plants within one geographic region (Strong et al. 1984). The worldwide bracken studies are probably unique in enabling a comparison of the fauna on the same species of host plant in different geographical regions. The species-area relationship for the herbivorous arthropods found on bracken in the U.K., U.S.A., P.N.G. and Hawaii was given by Lawton (1982, 1984). The relationship incorporating the new South African data is also highly statistically significant (figure 2.12): $\log_{10}(S+1) = 0.70 \log_{10} A - 2.35$ ($F_{1,3} = 109.7$, $r^2 = 0.97$ $P = 0.002$), where S is the number of species and A is the area in km^2 over which bracken grows in each region. S+1 has been used in the regression because there were no definite records of bracken feeding insects in Hawaii (see Lawton 1984).

The three main hypotheses proposed to account for the species-area relationship, that is, the larger the area occupied by the plant, the higher the number of species recorded as being associated with it, can be summarized as follows (Strong et al. 1984):

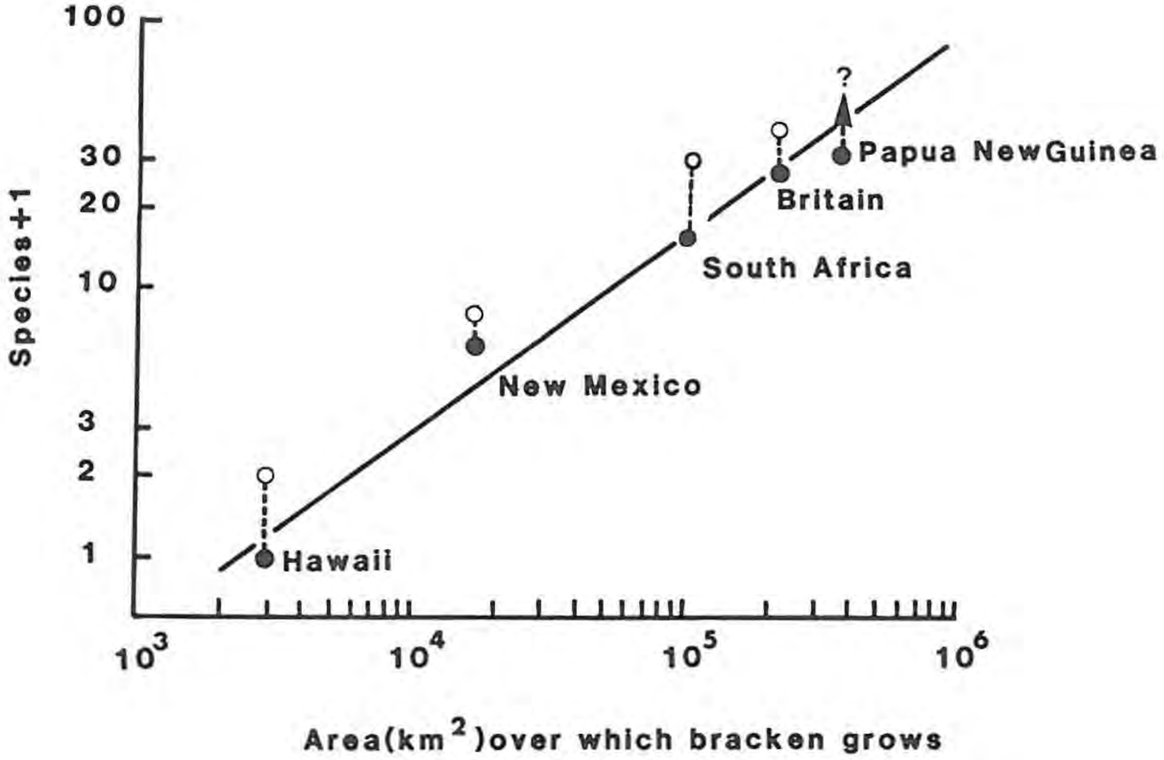
1) Large areas of plants will be colonized by more species as they **passively sample** a greater proportion of the total number of arthropod species available.

2) If small areas of plants support small populations which are more

Table 2.5. Ant species associated with bracken in South Africa.

SPECIES	SITE(S)	COLLECTION DATES
Crematogaster spp.	Featherstone Kloof	15.11.85
	Mapelane	04.12.86
	Bongwan	13.12.86
	Brondal	20.01.87
	Hendriksdal	21.01.87
C. peringueyi	Hogsback	14.04.86
	"Faraway"	26.01.86
		19.06.86
C. liengmei	Scarborough	21.04.86
Acantholepis spp.	Featherstone Kloof	15.11.85
	Bongwan	13.12.86
A. capensis	"Faraway"	30.05.85
		19.03.86
A. spinosior	"Faraway"	-.10.86
Camponotus spp.	Betty's Bay	26.04.86
	Bracken Hill	14.09.86
	Sugarbush	14.12.86
	Lorna Doone 2	02.12.86
	Bongwan	13.12.86
C. niveosetosus	"Faraway"	26.11.86
Tetraponera spp.	Herbertsdale	14.09.86
	Mapelane	04.12.86
T. emeryi	Richmond	07.06.86
Iridomyrmex humilis	Paarl Mountain	23.04.86
	Kirstenbosch	22.04.86
	Kleinmond	16.09.86
	Cape Peninsula	19.09.86
Plagiolepis spp.	Hogsback	14.04.86
	Bainskloof Pass	23.04.86
P. demeti	Richmond	07.06.86
Meranoplus peringueyi	Featherstone Kloof	15.11.85
	Paarl Mountain	19.09.86
Monomorium rhopalocerum	Bracken Hill	14.09.86
	Hogsback	22.10.86
M. tchelichofi	Clanwilliam	20.09.86
Tetramorium frigidum	"Faraway"	18.10.86
T. erectum	"Glenthorpe"	12.11.88
Polyrhachis sp.	Mapelane	04.12.86
Pheidole sp. 1	"Faraway"	29.09.86
Pheidole sp. 2	Tsitsikamma forest	13.09.86
Myrmicaria natalensis	Kosi Bay	02.12.88

Figure 2.12. Species-area relation for the number of species of herbivorous arthropods definitely (o) feeding on the plant in different parts of the world, from previously published data in Lawton (1984), with the addition of the new data for South Africa. Also shown (o) are total numbers of species including possible, occasional and uncertain records for each region (the arrow on the data for Papua New Guinea indicates that the number of species may be an underestimate; see Lawton 1984). Species + 1 has been used as the dependent variable to allow the inclusion of a zero count for definite species in Hawaii. The regression line has been fitted to the definite records only.



vulnerable to extinction, the equilibrium number of species will depend on the **area per se.**

3) Large areas of plants have a greater potential for **heterogeneity** in terms of **habitat** and can therefore support a wider variety and number of species.

Rigby & Lawton (1981) proposed that "habitat" structure, specifically the effect of plant size, was the most important component in the species-area relationship obtained from arthropods on varying sized bracken patches on the North York Moors. On a global scale, historical factors, the climate, types of habitats, frond density, size and other morphological features (as well as the area colonized by the plant) will vary markedly within and between continents and will certainly influence the number of species that an area can maintain.

In South Africa, many of the herbivore species are rare on the plant and are unlikely to be bracken specific. Passive sampling may play a major part in "picking-up" these infrequent, polyphagous species. There is also no doubt that sampling intensity must play a role, certain regions yielding a greater proportion of species than expected due to intensive surveying. Indeed, 14 of the 17 species associated with bracken in South Africa were collected in the eastern Cape, and yet the 6 quarter degree squares sampled in this section of the province represent only a small proportion of the 59 squares sampled countrywide. There is little evidence that local communities of bracken herbivores are more diverse in the subtropics compared with temperate regions. Average richness per sample was only about one species higher in the subtropical Natal and Transvaal, and was probably due to the absence of *E. spinosus* from the temperate Cape.

As well as a quantitative comparison of species numbers between regional herbivore communities, differences in community structure can be analysed qualitatively in terms of the taxa present and by comparison of guild composition. Table 2.6 divides the bracken insect faunas of the U.K., U.S.A., P.N.G. and South Africa into component orders. It is clear that different arthropod groups predominate according to the region. Kirk (1977, 1982) noted the dominance of beetles on bracken in P.N.G., while in contrast, the South African community comprises bugs and moths almost entirely.

Table 2.6. Comparison of bracken arthropod orders between South Africa and three other countries. Data for the U.K. and U.S.A. in Lawton (1982) and for Papua New Guinea (P.N.G.) in Kirk (1982).

ARTHROPOD ORDER	U.K.	U.S.A.	P.N.G.	R.S.A.
ACARI	0	0	0	1
COLEMBOLA	1	0	0	0
ORTHOPTERA	0	0	1	0
HEMIPTERA	4	1	5	6
THYSANOPTERA	0	1	0	1
COLEOPTERA	0	0	16	1
DIPTERA	8	1	1	0
LEPIDOPTERA	7	2	7	8
HYMENOPTERA	7	2	0	0
TOTAL	27	7	30	17

The inter-continental differences between bracken communities are also marked when viewed in terms of guilds. Lawton's (1982) classification of guilds using a "feeding niche-matrix" can be used to contrast the species found at a typical site in South Africa ("Faraway") with existing faunal studies (figure 6.3 in Lawton 1984). Vacant niches (unused parts of the plant) appear to be a feature of the bracken system. It is perhaps not unexpected that the pinnae are a commonly exploited resource in every region. However, in South Africa the dominant pinnae chewers are Lepidoptera, whereas in the U.K. this niche is largely filled by the Symphyta (sawflies), a group which is poorly represented in South Africa (Southwood et al. 1982). In P.N.G. it is the rachis which is under heavy assault from chewing and mining insects, while in the U.S.A. many of the guilds are not represented. Gall formers are rare on all continents, the only representative in South Africa being the eriophyid mite. Clearly, the number of herbivores and their methods of frond exploitation varies markedly.

Comparison of species number and composition in open and woodland communities also revealed differences between the continents. In South Africa there was no significant difference between open and woodland habitats, whereas in the U.K. and U.S.A. distinct preferences were evident, with more species found in open habitats in the U.K. and marginally more in woodland habitats in the U.S.A. (Lawton 1982; MacGarvin et al. 1986). No distinction between habitat type was made for sites in P.N.G.

At the species level it is interesting to note that the worldwide regional pools studied to date have no bracken herbivores in common, although congeneric *Eriophyes* occur on bracken in South Africa and Europe (Simmonds 1967; Lawton 1976, 1988), congeneric *Eupteryx* are found on bracken in South Africa and the U.K. (S. Fowler, pers. comm.) and different species of *Idiodes* feed on bracken in South Africa and Australia (Holloway 1987). With the possible exceptions of the above species, it appears that the bracken herbivore communities in different parts of the world have evolved independently of each other. Presumably as bracken colonized the globe, it recruited herbivores from the locally available species. The results of the South African bracken faunal survey lend further support to Lawton's (1982) conclusion that bracken herbivores show no convergence in community structure, insects in the South African region varying considerably in type and mode of resource utilization compared with those on other continents.

In addition to the herbivores recorded on bracken during the South African general survey, the other major group of insects found on the plant were ants. A variety of ant species were attracted (though ants were not present at every site examined), providing the potential for an effective herbivore deterrent. Tempel (1983) and Lawton & Heads (1984) also reported ants as being the main visitors to the EFNs of bracken in the U.S.A. and U.K. respectively, and ants were seen at bracken EFNs in P.N.G. (A.A. Kirk, pers. comm.)

Of the South African bracken fauna, the two moths *A. cinisigna* and *Panotima* appear to be the most abundant and damaging herbivores. Furthermore, their life histories include periods when they could be subject to intense ant predation. Active removal of lepidopteran eggs and larvae by ants has been previously noted on other plants (Tilman 1978; Stephenson 1982; Jones 1987). *Panotima* eggs are laid exposed on the frond undersurface, and although grazing larvae are sometimes covered by a layer of silk and frass, it was not certain whether this would offer adequate protection. The larvae must venture onto the rachis directly in the path of EFN-foraging ants on two occasions, during the third instar stage in order to mine into the rachis and again as fifth instar caterpillars when they leave their mines to pupate in the soil. *A. cinisigna* eggs seem to be relatively well protected, but the exposed larvae grazing on the frond undersurface are potentially vulnerable to ant attack.

Both lepidopterans were present on bracken throughout the main growing season, providing an extended period over which ant predation could take place. Eriophyid mite damage also occurred at all times of the year, but individuals were so minute that ants appeared to overlook them. Similarly, *E. maigudoi* was less likely to come into contact with ants, as this species was generally found on older fronds where ant activity was at a minimum (see chapter 4), and adults were capable of jumping or flying off the frond should the need arise. For these reasons the investigation into the role of ants and EFNs in bracken defense was confined to interactions involving the two moth species.

3. INTERACTIONS BETWEEN BRACKEN HERBIVORES AND ANTS: LABORATORY EXPERIMENTS

Previous studies of ant-EFN plant mutualisms have concentrated on investigating the systems in situ, with little attempt being made to reproduce natural systems in the laboratory. This alternative was employed to determine the effects of ants on the herbivores of bracken, an approach which enabled the observation and testing of various ant-herbivore confrontations under controlled conditions, and the detection of any specialized behaviour for ant avoidance.

The laboratory investigations focussed on the bracken herbivores considered most susceptible to ant attack, *A. cinisigna* and *Panotima* sp. The aim was to examine aspects of the bracken herbivore-ant interaction which could not easily be observed in the field; in particular, the fate of the moths during the life history stages when they appeared most vulnerable. For example, it was necessary to know whether their eggs were palatable to ants. It was also important to discover whether larvae were capable of avoiding ants, and if so, whether different sized larvae had different escape mechanisms. In the laboratory it was relatively easy to determine the reaction of specific larval instars to potential ant predation and to test the effectiveness of any ant avoidance behaviour.

3.1 Materials and Methods.

3.1.1 The maintenance of laboratory colonies of *Crematogaster peringueyi*.

The ant species used in the laboratory investigations was *Crematogaster peringueyi* Emery, a species widespread throughout South Africa and locally abundant on bracken at several sites around Grahamstown. Also known as the black cocktail ant, it is arboreal and nests in hollow stems and tree trunks, but also constructs carton nests from vegetable fibres glued together with maxillary gland secretions (Skaife 1961).

These carton nests are built in small trees and shrubs and were easily transferred to the laboratory.

Three colonies were obtained from different sites in the eastern Cape. One was acquired from "Faraway" and another from the Katberg Mountains in 1986, and a third carton nest was obtained in 1988 from Glenthorpe farm. The colonies differed in size, with the "Katberg" nest having the fewest occupants and the "Faraway" nest the most. The main branch supporting each nest was placed into a jar of soil and kept on a table, 50 x 30cm in size. The legs of the table stood in talcum-powder which acted as an escape-proof barrier (the design is modified from Skaife 1961). The colonies were kept on separate tables and once installed, were largely self-maintaining on a diet of water, sugar solution and chopped flour beetle larvae (*Tribolium* sp., Tenebrionidae).

After two weeks in the laboratory the colonies were considered to have acclimatized sufficiently for experiments to commence. A pot containing young bracken fronds was placed adjacent to one or other of the colonies (with the same precautions taken to prevent escape as before), and a connecting bridge made between the two. No attempt was made to regulate the numbers of ants passing across the bridge. The colonies were starved during the experiments to encourage ants to forage on the fronds. The experimental design is shown in figure 3.1. Experiments were conducted using ants from the three colonies as indicated in the relevant tables of results.

3.1.2 Egg palatability tests.

The palatability of eggs of *A. cinisigna* and *Panotima* to *C. peringueyi* was tested by removing eggs from the frond tissue (and in the case of *A. cinisigna*, separating them from each other) and placing them singly on moist filter paper. This precaution was taken to ensure that the eggs did not desiccate and in addition, the moisture served to attract ants to the area. Three replicates of five *A. cinisigna* eggs and four replicates of five *Panotima* eggs were left "exposed" to ants on the table. *A. cinisigna* eggs were scored after a maximum of 5 hours, but because of lower predation rates, *Panotima* were scored after 24-36 hrs.

Figure 3.1. A carton nest of *Crematogaster peringueyi* with access to a potted bracken plant.

The tests were repeated using eggs still attached to the plant tissue and presented on moist filter paper as before. Since *A. cinisigna* oviposits in the curled frond tips, small pieces of bracken containing an egg batch were used. Variously sized pieces of frond with *Panotima* eggs laid on the undersurface were offered with eggs uppermost. Five replicates of three *A. cinisigna* batches and four replicates of ten *Panotima* eggs were tested and scored 12-24 hours after being offered to the ants.

3.1.3 Ant-larval confrontations.

A. cinisigna

Direct observations.

Confrontations between *A. cinisigna* larvae and *C. peringueyi* were staged by placing larvae on potted bracken fronds to which the ants were allowed access. Ten individuals of each larval instar were tested to ascertain whether different sized larvae behaved similarly.

Field simulation experiments.

Short-term experiments were conducted to assess the effectiveness of the escape strategies of *A. cinisigna* larvae that were observed during confrontations with ants. Although measurements of ant density were not made during the course of the experiments, ants were regularly present at the EFNs and on the fronds of experimental plants.

First instar caterpillars were tested by placing 15 larvae on the young unfurling tips of each of two pots of bracken fronds, after which they were allowed a few hours to settle. The "Faraway" ant colony was then connected to one of the bracken pots, leaving the other (with no ants) as a control. The experiment was repeated on four occasions with durations ranging from four to seven days, after which time the number of larvae remaining on the control and experimental plants was compared.

Second and third instar larvae were tested using a similar method. In this set of experiments, 10 II or III instar caterpillars were placed on control fronds (no ants) and a further 10 on experimental fronds (with ants). After four days (in the case of II instar larvae) or six days (using III instar caterpillars), the number of larvae on each was counted. Each experiment was replicated three times. IV and V instar larvae were not tested in this way since any disappearances could have been due to larvae leaving the plant to pupate in the soil rather than as a direct consequence of ant activity. "Faraway" and "Glenthorpe" colonies of *C. peringueyi* were used.

***Panotima* sp.**

Direct observations.

It was extremely difficult to simulate, or to observe, encounters between I and II instar *Panotima* larvae and ants on the fronds of potted bracken, as the small, delicate larvae were easily overlooked or simply lost. Encounters between III-V instar larvae were induced by removing them from their mines and placing single larvae directly on to the ant table.

Field simulation experiments.

Pieces of bracken with a mixture of different sized grazing caterpillars (I-III instars) were collected in the field. The fronds, with the larvae left undisturbed on the undersurface, were positioned on the ant table in damp blocks of "Oasis" (a water-retaining material) so as to simulate natural conditions. Some of the larvae were grazing under a covering of silk and frass, others were not. The larvae were exposed to the "Faraway" ants for varying periods. Daytime replicates were left for half an hour only, whereas replicates left overnight were exposed for up to 18 hours.

Larvae at the III instar stage were also tested by placing them on the rachis in the path of oncoming ants. This simulated the period at which the transition from frond grazing to stem mining occurred. Ten larvae were used and several observations made with each until individuals succumbed to ant attack. The *C. peringueyi* colony used was from "Glenthorpe". V instar larvae, also susceptible to ants on the rachis when leaving their mines to pupate in the soil, were not tested due to a shortage of suitable material. It was not necessary to simulate field confrontations between IV instars and ants, since this stage remains hidden inside the rachis mines (see chapter 2).

3.2 Results.

3.2.1 Egg palatability tests.

The results of the egg palatability tests are given in table 3.1. All the exposed eggs of *A. cinisigna* were removed within 5 hours (table 3.1a). When eggs of *A. cinisigna* that were still in the curled pinnae tips were offered, 28% of the batches were removed (table 3.1b).

In contrast, only 25% of the exposed *Panotima* eggs were removed, even after ten times the period of exposure to ants of *A. cinisigna* (table 3.1a). None of the 40 *Panotima* eggs attached to the fronds were removed by *C. peringueyi* (table 3.1b).

3.2.2 Ant - larval confrontations.

A. cinisigna

Direct observations.

Confrontations between *C. peringueyi* and *A. cinisigna* on potted bracken are summarized in table 3.2. Encounters invariably involved a single ant at a time investigating one larva. Ants did not inevitably attack larvae and often either ignored or did not detect them. However, on occasions when ants approached and antennated larvae, a range of escape responses were invoked, (although no particular sequence was noted). The most striking of these consisted of the larva immediately

Table 3.1. Tests of moth egg palatability to ants.

(A) "Exposed" eggs, removed from plant

ANT COLONY	*A. cinisigna* t=1.5-5h		*Panotima* sp. t=24-36h	
	INITIAL NUMBER OF EGGS	NUMBER OF EGGS REMAINING	INITIAL NUMBER OF EGGS	NUMBER OF EGGS REMAINING
F	5	0	5	5
K	5	0	5	5
F	5	0	5	1
K	-	-	5	4
TOTAL	15	0	20	15

(B) Eggs still attached to plant

ANT COLONY	*A. cinisigna* t=12-24h		*Panotima* sp. t=12-24h	
	INITIAL NUMBER OF BATCHES	NUMBER OF BATCHES REMAINING	INITIAL NUMBER OF EGGS	NUMBER OF EGGS REMAINING
F	3	2	10	10
K	3	3	10	10
F	3	2	10	10
K	3	1	10	10
F	3	2	-	-
K	3	3	-	-
TOTAL	18	13	40	40

F = "Faraway" ant colony; K = "Katberg" ant colony;

t = duration of test in hours

Table 3.2. Laboratory confrontations between *A. cinisigna* larvae and *C. peringueyi* ants. Ten individuals of each larval instar were used, and the ant colonies used were from "Faraway" and "Glenthorpe".

INSTAR	TAKEN BY ANT	NOT NOTICED BY ANT	LARVAL RESPONSES							TOTAL NO. OF OBSERVATIONS
			NO RESPONSE	TWITCH	FLICK	MOVE AWAY	THRASH & FLUID	SILK THREAD	FALLS OFF FROND	
I	4	7	0	0	0	0	4	16	0	31
II	2	0	0	0	16	1	5	19	7	50
III	0	1	0	0	36	6	4	11	18	76
IV	0	2	3	15	70	3	0	3	3	99
V	0	3	13	40	50	17	1	0	1	125

Definitions:

'taken by ant' = larva killed by ant

'not noticed by ant'= ant did not antennate larva or initiate attack

'no response' = larva did not respond to being antennated by ant

'twitch' = quick jerk of anterior or posterior part of larva away from ant

'flick' = more violent movement than twitch

'move away' = larva walked onto another part of frond after persistant antennating by ant

'thrash and fluid' = violent twisting and writhing of body accompanied by regurgitated fluid which repelled ant

'silk thread' = larva dropped off frond, suspended on short length of thread

'falls off frond' = usually occurred after persistant antennating by ant dropping off the frond and hanging suspended on a length of silk 20mm or so in length. After a few minutes the larva would hoist itself back up, unless an ant was in the vicinity whereupon it would re-suspend itself. I-IV larval instars were all observed using this silk thread escape technique, though it was favoured by the smaller instar sizes.

Larvae were also capable of shaking off attackers by writhing and twisting violently - the "thrash reflex" - usually accompanied by the regurgitation of a green fluid which caused ants to retreat in an apparently dazed and disoriented manner. Larger larvae were less likely to respond to antennating ants and if repeatedly disturbed, simply flicked their body away or walked quickly to another part of the frond (here, size undoubtedly proved an advantage). Occasionally, larvae would fall completely off the frond. In all, 381 observations using 50 larvae (10 of each instar) were made, but in only six cases, involving I and II instar larvae, did *A. cinisigna* individuals succumb to ant attack.

Field simulation experiments.

The results of the short-term experiments with I instar larvae are shown in table 3.3. Larval disappearances on the control (ant-free) fronds were generally trivial compared with losses when ants were present. The number of I instar larvae remaining on the experimental plants was significantly lower than that on the controls in each replicate, indicating that I instars were vulnerable to increased disturbance or predation by ants (total $chi^2_{[1]} = 70.53$, $P < 0.001$).

The results of the individual experiments with II instar larvae were not as clear-cut (table 3.4). However, pooling the replicates indicated that ants had a significant effect on larval disappearances (total $chi^2_{[1]} = 7.95$, $P < 0.01$, heterogeneity $chi^2_{[2]} = 2.60$, N.S.). There was an absence of any general statistical trend in the numbers of disappearing III instar larvae (table 3.5, total $chi^2_{[1]} = 1.67$, N.S.).

Table 3.3. Comparison of I instar *A. cinisigna* larval disappearences on fronds with and without attending ants from the "Faraway" colony.

DURATION (DAYS)	NO. OF LARVAE REMAINING FROM INITIAL FIFTEEN		CHI^2 d.f.=1
	EXPERIMENTAL (+ ANTS)	CONTROL (- ANTS)	
4	1	13	19.3, $P < 0.001$
5	2	14	19.3, $P < 0.001$
6	4	14	13.9, $P < 0.001$
7	0	12	20.0, $P < 0.001$

Table 3.4. Susceptibility of II instar *A. cinisigna* larvae to ants under laboratory conditions. The duration of each experiment was four days. F = "Faraway" ant colony; G = "Glenthorpe" ant colony.

C. peringueyi COLONY	NO. OF LARVAE REMAINING FROM INITIAL TEN		CHI^2 d.f.=1
	EXPERIMENTAL (+ ANTS)	CONTROL (- ANTS)	
F	2	8	7.2, $P < 0.01$
G	7	10	3.53, N.S.
G	10	10	0, N.S.

Table 3.5. Susceptibility of III instar *A. cinisigna* larvae to ants under laboratory conditions. The duration of each experiment was six days. F = "Faraway" ant colony; G = "Glenthorpe" ant colony.

C. peringueyi COLONY	NO. OF LARVAE REMAINING FROM INITIAL TEN		CHI² d.f.=1
	EXPERIMENTAL (+ ANTS)	CONTROL (- ANTS)	
F	7	8	0.27, N.S.
F	0	5	6.67, $P < 0.01$
G	6	5	0.2, N.S.

***Panotima* sp.**

Direct observations.

The results of confrontations between *C. peringueyi* and different larval instars of *Panotima* placed directly on the ant table are shown in table 3.6. Larvae that were killed can be subdivided into those that nonetheless exhibited some defense and those that did not. Although the III instar larvae often attempted some defense, they proved extremely vulnerable to ants, which simply picked them up from the table and carried them off to the nest. It was only the IV and V instar larvae which possessed effective defense mechanisms. In response to ant attack they would writhe furiously and strike at the ants with their heads. A greenish or yellowish liquid would usually be exuded from the mouth, which on contact caused the ants to retreat, wiping their antennae and mandibles. Often a semi-solid faecal pellet was produced which also appeared distasteful to the ants.

The results of repeated confrontations on the rachis between ants and III instar *Panotima* larvae are given in table 3.7. All ten individuals tested attempted some form of defense before they eventually succumbed to ant attack. Larvae occasionally used the silk thread technique, similar to *A. cinisigna*. However, the most frequently observed response was the "thrash reflex", often used in conjunction with the apparent production of a repellent fluid. If an ant held a larvae mid-way along or at the posterior end of the body, the larva would arch back and attempt to touch the ant with its mouth. If the movement was successful, the attacker would retreat, wiping its mandibles and antennae. Later, the same ant might try again, or a new ant would continue the attack. However, despite attempts to writhe, a larva would invariably fall prey to a determined ant if grabbed immediately behind the head capsule. Although no active recruitment behaviour was observed, the first aggressor would often be joined by a second and they would hold the larva between them until it ceased to struggle.

Table 3.6. Summary of laboratory confrontations between *Panotima* larvae and ants from "Faraway" and "Katberg".

LARVAL INSTAR	NUMBER OF LARVAE USED	FATE OF LARVAE				
		ESCAPED		SUCCUMBED		TOTAL NUMBER OF OBSERVATIONS
		THRASH REFLEX	THRASH + REPELLENT FLUID	SOME DEFENSE ATTEMPTED	NO APPARENT DEFENSE	
III	5	0	2	3	2	7
IV	5	3	4	3	0	10
V	5	1	13	2	0	16

Definitions:

'thrash reflex' = vigorous writhing by larva

'thrash + repellent fluid' = larva writhed and produced a repellent fluid

'some defense attempted' = some writhing occurred but ant was undeterred

'no apparent defense' = larva made no apparent effort to escape

Table 3.7. Confrontations on the bracken rachis between III instar *Panotima* larvae and ants from "Glenthorpe". Ten larvae were used and observations continued until larvae eventually succumbed.

CONFRONTATIONS WHERE LARVAE ESCAPED			CONFRONTATIONS WHERE LARVAE SUCCUMBED	
NO ANT ATTACK	SILK THREAD	THRASH + REPELLENT	SOME DEFENSE ATTEMPTED	NO APPARENT DEFENSE
1	4	23	5	5

Definitions:

'no ant attack' = ant antennaed larva, but did not attempt to attack

'silk thread' = larva dropped from rachis, suspended on short length of thread

'thrash and repellent' = larva writhed and apparently produced a repellent fluid

'some defense attempted' = larva made some attempt to writhe and thrash, but was captured nonetheless

'no apparent defense' = larva made no apparent attempt to escape

Field simulation experiments.

Ants were undeterred by the "protective" covering of silk and frass produced by I, II and III instar *Panotima* grazing larvae and did not restrict their foraging to the upper frond surface only. As a result, larvae were rapidly removed by ants (table 3.8).

3.3 Discussion.

The results of these laboratory investigations can only be extrapolated to the situation in the field with caution. They reveal which life history stages are vulnerable to ant predation, but they do not reflect natural predation rates in the field. Densities of ants on the table, and to a lesser extent on the potted bracken, exceeded anything found in the field (see chapter 4). Consequently, larvae that might have escaped attack by a single ant were soon overpowered by several ants acting together, particularly in the more artificial table experiments. However, the table experiments were valuable in showing that *A. cinisigna* eggs and young *Panotima* larvae are palatable to ants, and that the larger *Panotima* larvae are capable, even under these conditions, of self defense. It is conceivable that the ants used from the three colonies may have differed in their behavioural characteristics, but any differences, for example in their degree of aggressiveness, were not noted during the observations.

The results of the egg palatability experiments can be interpreted in terms of the different life histories of the two moths. *A. cinisigna* eggs, glued firmly together in the tightly curled pinnae tips, were extremely palatable, but gained protection from their carefully selected oviposition sites. With hindsight, the experiment testing the degree of protection conferred by the plant tissue did not mimic the field situation adequately. The eggs were left for between 12 and 24 hours, during which time the bracken lost its turgidity and became dry and brittle. The success shown by ants in removing some of the egg

Table 3.8. Removal of grazing *Panotima* (I-III instar larvae on pieces of frond) by ants from "Faraway".

NO. OF LARVAE ON FROND (I - III INSTARS)	NO. OF LARVAE REMAINING AFTER EXPOSURE TO ANTS	DURATION (HOURS)	
3	0	18	(night)
10	0	12	(night)
7	0	0.5	(day)
2	0	0.5	(day)

batches appeared to vary according to the extent to which the plant tissue was dehydrated. The longer the tissue was left, the drier and less springy it became, making it easier for the ants to prize it apart in order to reach the eggs. Since, in the field, the plant tissue would not be subject to changes due to desiccation, *A. cinisigna* eggs would normally be immune from ant predation. Conversely, the *Panotima* eggs, which appeared relatively exposed to potential predation on the pinna undersurface, were almost invariably ignored by foraging ants in laboratory tests. There was no indication that the eggs were overlooked, since they were slightly larger than those of *A. cinisigna* and ants were observed investigating them with their antennae. This suggests that *Panotima* eggs were unpalatable or were simply not recognised as edible, making concealment unnecessary.

Ant-larval confrontations indicated that small and large *A. cinisigna* showed preferences for different escape mechanisms. Although I instar larvae appeared to be relatively protected when feeding in the curled pinnae tips and were often undetected or ignored, when confronted by ants, both I and II instars were frequently observed using the silk thread escape technique. III instar larvae seemed to carry this response a stage further, often falling off the frond completely if flicking failed to deter persistent ants. In the natural state this might not be such a drastic "last resort" method of escape, since the chances of landing on a lower frond away from ants, and not on the ground, would be high. The larger IV and V instar larvae successfully dissuaded ants by quick, flicking movements and were less likely to leave the frond in order to escape ant attack, moving away only if persistently disturbed. Early instars tended to use the "thrash reflex" in combination with a distasteful repellent to a lesser degree than the other escape techniques, while later instars appeared to forgo this escape mechanism, perhaps because they were relatively immune from attack.

The removal of I and II instar larvae by foraging ants in the field simulation experiments indicated that these escape methods were not completely effective. It was also noted that the larvae surviving in the II and III instar experiments were considerably smaller than their counterparts on the controls, suggesting that their grazing had been disrupted. In this way, ants may contribute to a reduction in levels of herbivory by harassing *A. cinisigna* larvae. The disappearance of some *A. cinisigna* larvae from the control fronds is puzzling and may be a laboratory artifact. However, in the field experiments discussed in chapter 4, *A. cinisigna* also disappeared occasionally from fronds and appeared on previously unoccupied fronds. Presumably reasons such as food quality or disturbance contributed to this larval movement between fronds.

The results of the ant-*Panotima* field simulation experiments suggest that grazing larvae (instars I-III) do not exercise any detectable escape mechanisms and are potential prey for *C. peringueyi*. This was particularly interesting, since it is while grazing that larvae are exposed to foraging ants. It was also surprising that III instar larvae do not, apparently, have any effective means of evading ant predation, since they are necessarily exposed to attack during descent of the stem. Nor do they appear to reduce the risk of attack by mining at night; *Panotima* caterpillars have often been observed burrowing into the stem during the day - a process which takes several hours. Only the IV and V instar larvae, removed from their mines, appeared capable of effective self defense, presumably as a consequence of their larger size.

Since bracken generally contains the precursors and enzymes necessary for benzaldehyde and hydrogen cyanide (HCN) synthesis (Cooper-Driver & Swain 1976), and South African bracken is polymorphic for HCN production (Compton & Rashbrook, unpublished data), the fluid regurgitated by *A. cinisigna* and *Panotima* larvae when attacked may have contained HCN and benzaldehyde. In experiments with eastern tent caterpillars, the fluid of larvae fed cyanogenic black cherry foliage was more repellent to ants than that produced after they had fed on less cyanogenic leaves (Peterson et al. 1987). Both HCN and benzaldehyde were present in the regurgitates, but Peterson et al. found that the odour of benzaldehyde proved to be the component responsible for ant repellency. They concluded that the use of plant-derived compounds in fluid discharges may be a valuable caterpillar defense mechanism.

The observations and experiments undertaken in the laboratory provide an indication of the defensive capabilities of the two herbivore species, and demonstrate the potential vulnerability of the various life history stages to attack by at least one species of ant. The following chapter describes field experiments which determined whether this susceptibility is important for natural populations of the moths.

4. INTERACTIONS BETWEEN BRACKEN HERBIVORES AND ANTS: FIELD EXPERIMENTS

The techniques used to test the ant-bracken mutualism hypothesis in the field were similar to those employed in studies in the U.K. (Heads & Lawton 1984; Heads 1986). First, seasonal and diurnal ant activity was monitored, since ant density on the plant is a critical variable. Analysis of nectar content or measurements of nectar secretion rates were not attempted, as quantities of nectar produced by South African bracken were often low and secretion rates very variable, as in the U.K. (see Lawton & Heads 1984). Then, to determine whether ants were instrumental in removing herbivores on bracken, thereby "protecting" the plant, ants were excluded from experimental fronds. Any disparity between the numbers of herbivores on ant-excluded and control plants could be attributable to the presence of visiting ants. In addition, ant densities were enhanced in an endeavour to bias conditions in favour of detecting any effects of ants on the herbivores of bracken.

In addition to attracting ants, another possible benefit of having extrafloral nectaries is that they may attract adult parasitoids, which then parasitize herbivores on the plant (Koptur 1985). Although experiments were not specifically designed with this alternative in mind, data that addressed this problem were gathered wherever possible.

4.1 Study sites.

Field studies were carried out at two farms near Grahamstown in the eastern Cape Province. The farms are at an altitude of approximately 700m and receive an average annual rainfall of 681mm (Anon 1986).

At "Faraway" (see chapter 2), two study areas, both in open situations, were used. Site A was positioned on a south-facing slope where bracken covered about 400m^2. The bracken patch was surrounded by grassy fynbos (heathland) characterized by the Grahamstown endemic *Erica chamissonis* kl. ex Benth. At site B, the patch used was of a similar size, but on level ground and among different vegetation, notably *Pelagonium* species and *Tephrosia grandiflora* (Ait.) Pers.

The second farm, "Glenthorpe", was situated about 10 km south of Grahamstown (quarter degree grid reference 3326BC). The experimental site consisted of a 650m^2 open stand of dense bracken on a south-facing slope, surrounded by fynbos type vegetation.

4.2 Ant activity: Methods.

Seasonal Variation.

Day-time ant activity was monitored on a monthly basis throughout the year (from March 1986 to February 1987) at "Faraway". At each of the two sites (sites A and B), haphazardly chosen fronds representing each developmental stage (crozier, unfurling, mature and senescing) were examined at times between mid-morning and mid-afternoon for the presence of ants. A maximum of 120 fronds at each stage was inspected, but often fewer were available, especially during the winter months when mature and senescing fronds predominated (chapter 2). The species, number and position of ants found on the fronds were noted.

Diurnal Variation.

Measurements of diurnal variation in ant activity were undertaken on two occasions at "Glenthorpe". The first assessment, in November 1988, used 50 fronds, but on the second occasion in January 1989 the sample size was only 20, because ant activity on bracken was generally lower at this time of year. The fronds were selected on the basis of having at least one *C. peringueyi* ant at the start of the observations (12h00 and 08h00). These were subsequently examined at four hourly intervals during a 24 hour period. Maximum and minimum air temperatures were obtained from the local weather station, situated in Grahamstown.

4.3 Ant activity: Results.

Ant Community Composition.

Table 4.1 records the ant species found commonly on bracken at "Faraway" and "Glenthorpe" and compares the approximate lengths of the workers visiting the EFNs. Three species occurred at all the study sites; they were *Crematogaster peringueyi* Emery, *Acantholepis capensis* Mayr and *Camponotus niveosetosus* Mayr. A fourth species, *Tetramorium erectum* Emery, was only found during nocturnal sampling at "Glenthorpe". Other, "casual" species were very seldom seen and are not included in the table.

Seasonal Variation in Ant Activity.

A comparison of total ant activity on bracken at sites A and B at "Faraway" revealed similar fluctuations at both sites (figure 4.1). Ant densities were low (a mean of 0.5 ants/frond or less) for most of the year (February-August), but rose during the spring months reaching a peak in November. This peak was especially marked at site A (a mean of 2.16 ants/frond compared with 0.7 ants/frond at site B).

During the period of peak activity in November the numbers of ants foraging on a frond ranged between 0 and 13. Approximately half of the total fronds examined in November (127 from 240) were being visited by ants, and most fronds with ants had between 1 and 5 individuals present (figure 4.2). The observed numbers of ants per frond were significantly different from a poisson distribution, with more fronds than expected being ant-free (mean = 1.96 ants/frond; $\chi^2_{[3]} = 93.32$, $P < 0.001$).

Monthly monitoring of the ant species visiting bracken indicated that *C. peringueyi* and *A. capensis* were by far the most common ants present on fronds at site A, where both showed a similar trend in abundance (figure 4.3). At site B, however, ant activity was almost entirely due to *A. capensis*, with other species present in very low numbers (figure 4.4).

Table 4.1. The ant species found commonly on bracken at the "Faraway" and "Glenthorpe" study sites during 1986-7. Approximate lengths of the visiting workers are also given.

SPECIES	SUB-FAMILY	LENGTH (mm)
Crematogaster peringueyi Emery	Myrmicinae	4.0
Acantholepis capensis Mayr	Camponotinae	2.0
Camponotus niveosetosus Mayr	Camponotinae	6.0
Tetramorium erectum * Emery	Myrmicinae	4.0

* Found only during nocturnal sampling at "Glenthorpe"

Figure 4.1. Seasonal variations in ant activity (all species), (means and standard errors), on bracken at "Faraway", sites A and B, in 1986-7. The durations of experiment 1 at sites A and B, and experiment 2 at site A are indicated. The numbers of fronds examined are shown under the appropriate month.

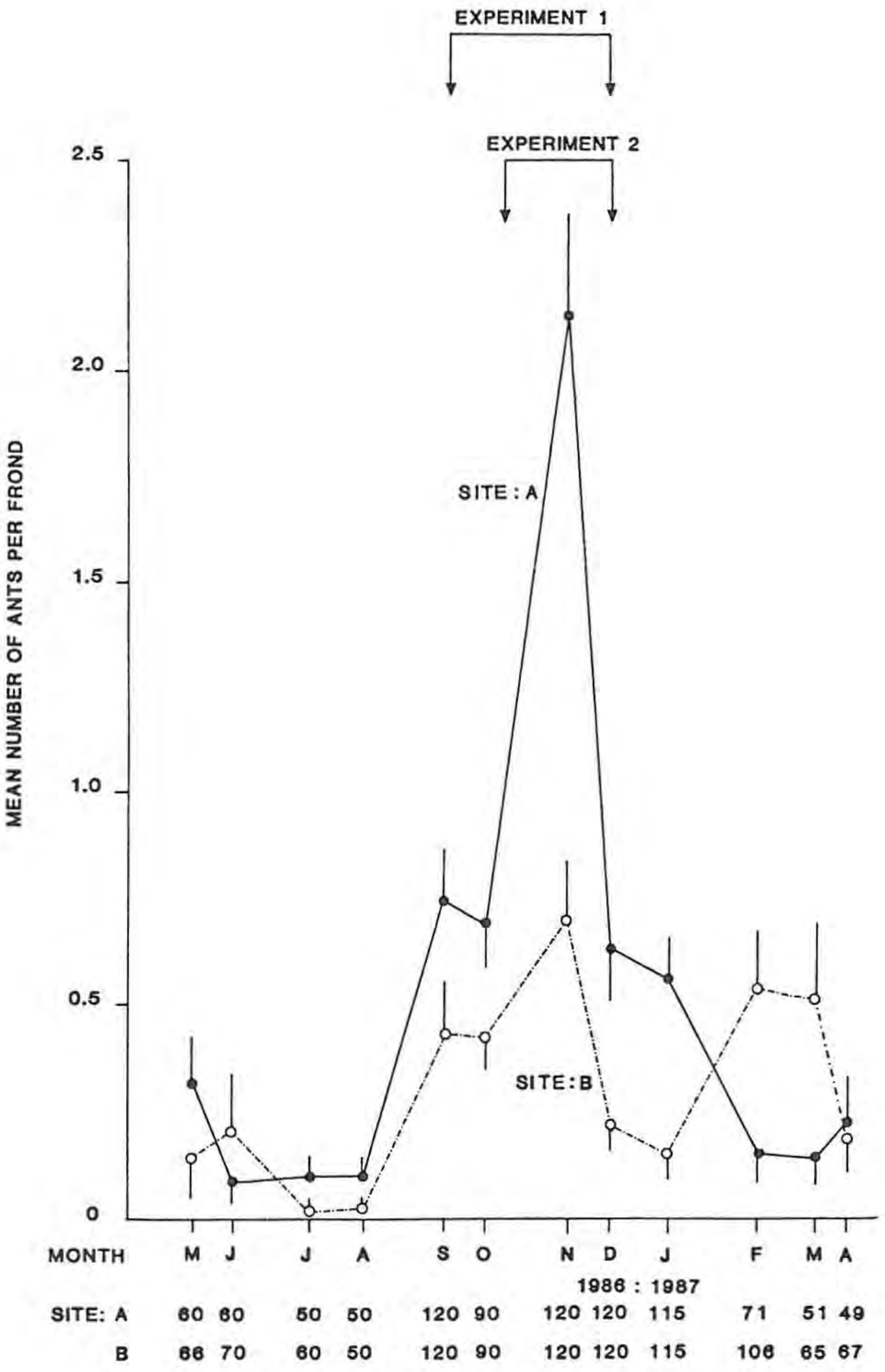


Figure 4.2. Observed numbers (histogram) of ants per frond at "Faraway" sites A and B, on 26.11.86, compared with a poisson distribution with the same mean (1.96 ants/frond).

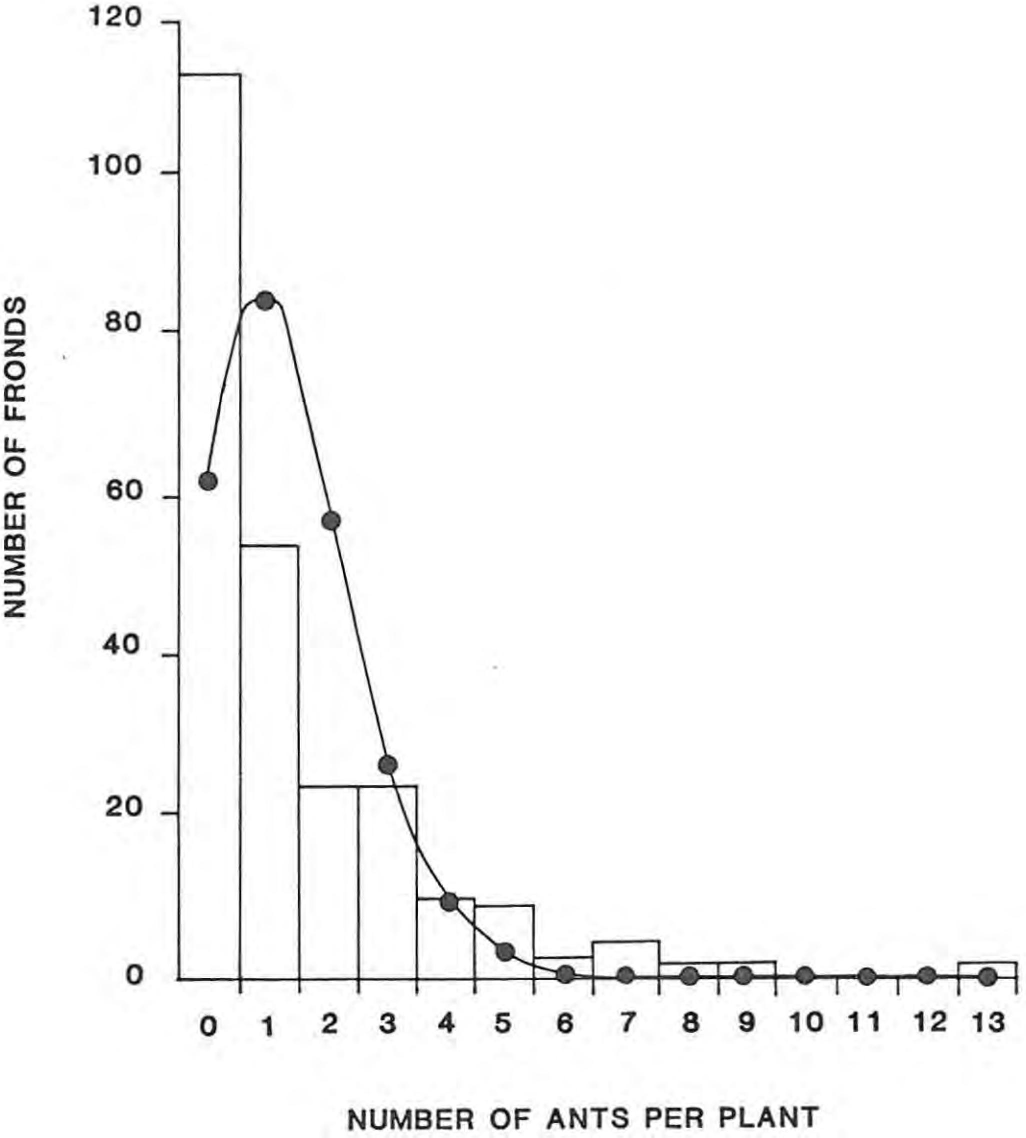


Figure 4.3. Seasonal variations in the abundance of different ant species on bracken at "Faraway" site A in 1986-7. Fronds were examined between 11h30 and 16h00.

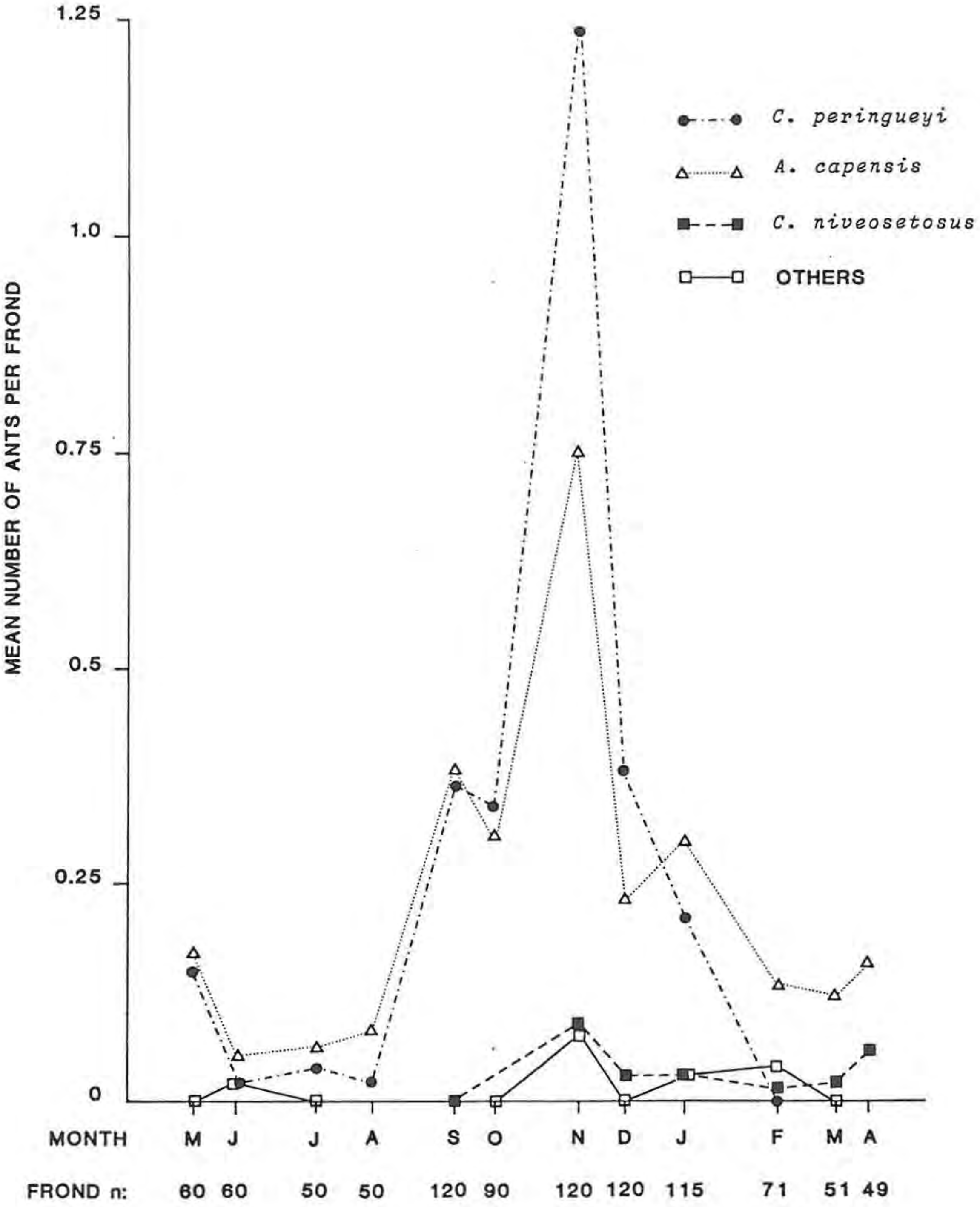
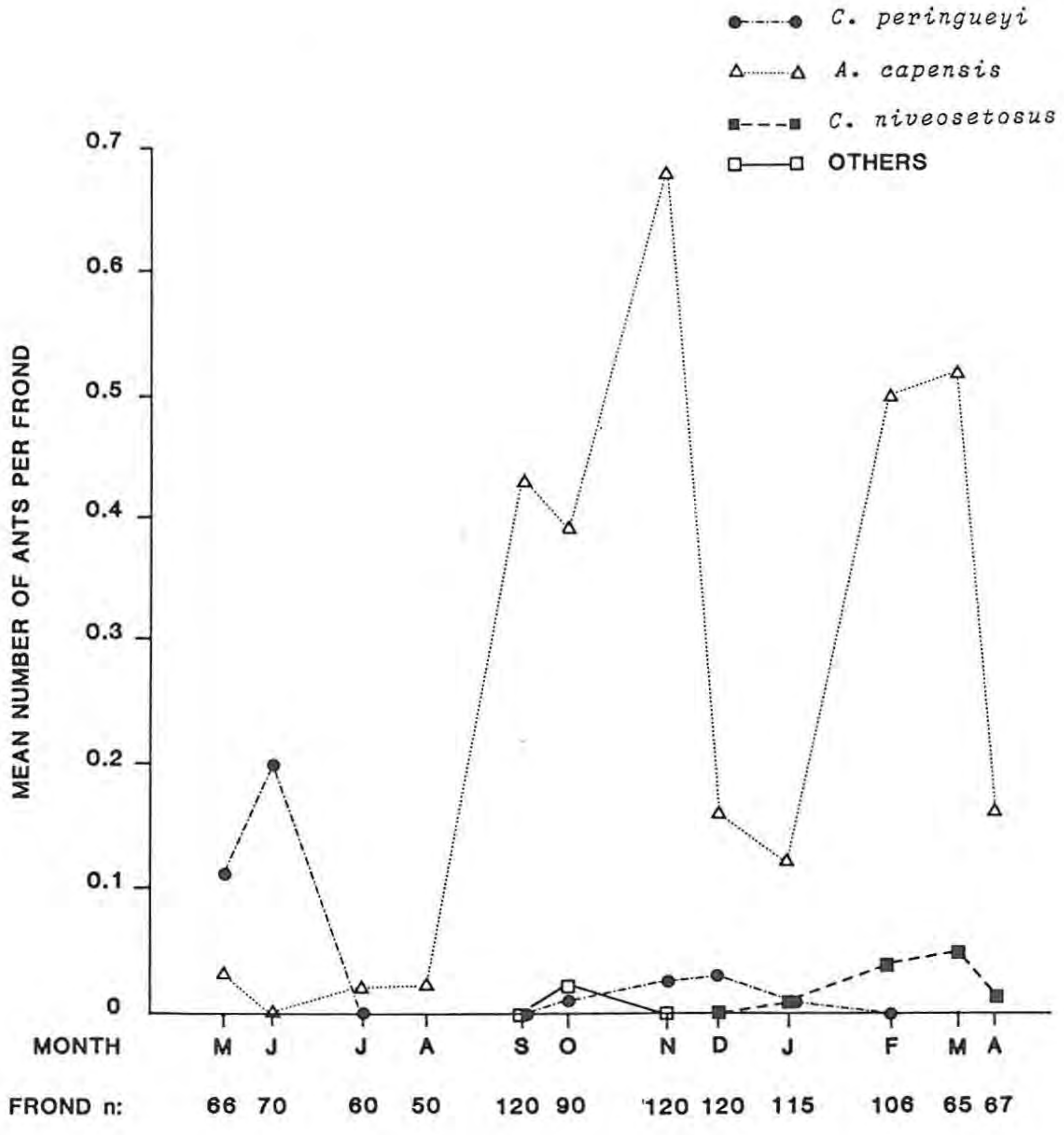


Figure 4.4. Seasonal variations in the abundance of different ant species on bracken at "Faraway" site B in 1986-7. Fronds were examined between 11h30 and 16h30.



The positions of ants found on the plant were recorded and are shown in table 4.2. It is apparent that the major EFNs are the preferred feeding sites with four times as many ants seen here than at the smaller, minor EFNs. However, a large proportion of the ants were also found searching the pinnae (both the upper and lower surfaces) and on the stem, presumably either moving between nectaries or actively foraging for other food items. *A. capensis* distributed its activities evenly between the EFNs, pinnae and rachis, whereas *C. peringueyi* was more likely to be feeding at the EFNs. *C. niveosetosus*, though considerably rarer on bracken compared with the other two species, showed the highest preference for the pinnae. The numbers of ants at the EFNs compared with other parts of the frond was highly significantly different between the three species ($chi^2[2] = 217.45$, $P < 0.001$). No aggressive interactions at EFNs were observed between ants of the same or different species. Since counts of different ant species were accumulated over the whole sample, tests for exclusion or aggregation between species could not be made.

Comparisons of the presence of ants on different plant developmental stages in each month are summarized in figure 4.5 (site A) and figure 4.6 (site B). At both sites the unfurling and mature fronds had the highest densities of ants, with lower numbers being recorded on croziers and the senescing fronds. Table 4.3 shows the seasonal pattern of ant activity. Ants were generally more active on all the frond developmental stages during the spring and summer.

Diurnal Variation in Ant Activity.

Considerable diurnal variations in ant activity on bracken at "Glenthorpe" were recorded (figures 4.7 and 4.8). The foraging times of *C. peringueyi*, *A. capensis* and *C. niveosetosus* clearly emerged as being largely confined to daylight hours; during the night their activity was reduced to almost zero. In contrast, *T. erectum* was only active nocturnally, although numbers present were relatively low. Maximum and minimum temperatures for each sampling period are given in the figures.

Table 4.2. Position of ants on bracken plants. Data were collected at monthly intervals between mid-morning and mid-afternoon at "Faraway" sites A and B during 1986-7.

ANT SPECIES	PROPORTION OF ANTS FOUND TO BE ON THE:				TOTAL NUMBER OF ANTS SCORED
	MAJOR EFNS	MINOR EFNS	PINNAE	RACHIS	
Crematogaster peringueyi	0.58	0.13	0.16	0.13	337
Acantholepis capensis	0.33	0.08	0.28	0.31	566
Camponotus niveosetosus	0.285	0	0.685	0.03	35
Others	0.61	0.055	0.055	0.28	18
Total	0.42	0.10	0.25	0.24	956

Figure 4.5. Seasonal variations in ant activity (all species), with frond development (crozier, unfurling, mature and senescing stages) at "Faraway" site A in 1986-7. The number of fronds examined are shown next to each data point (mean and standard error).

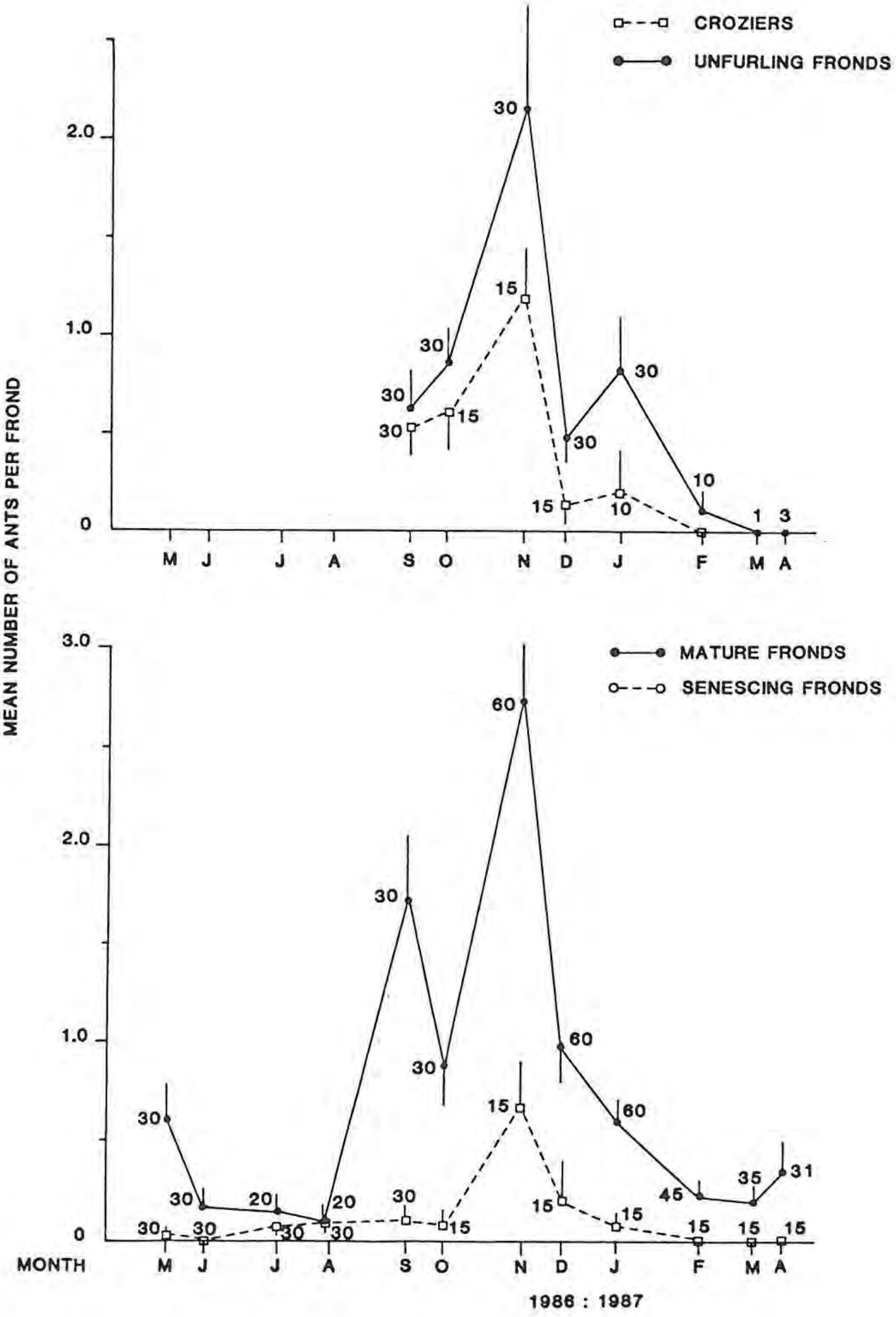


Figure 4.6. Seasonal variations in ant activity (all species), with frond development (crozier, unfurling, mature and senescing stages) at "Faraway" site B in 1986-7. The numbers of fronds examined are shown next to each data point (mean and standard error).

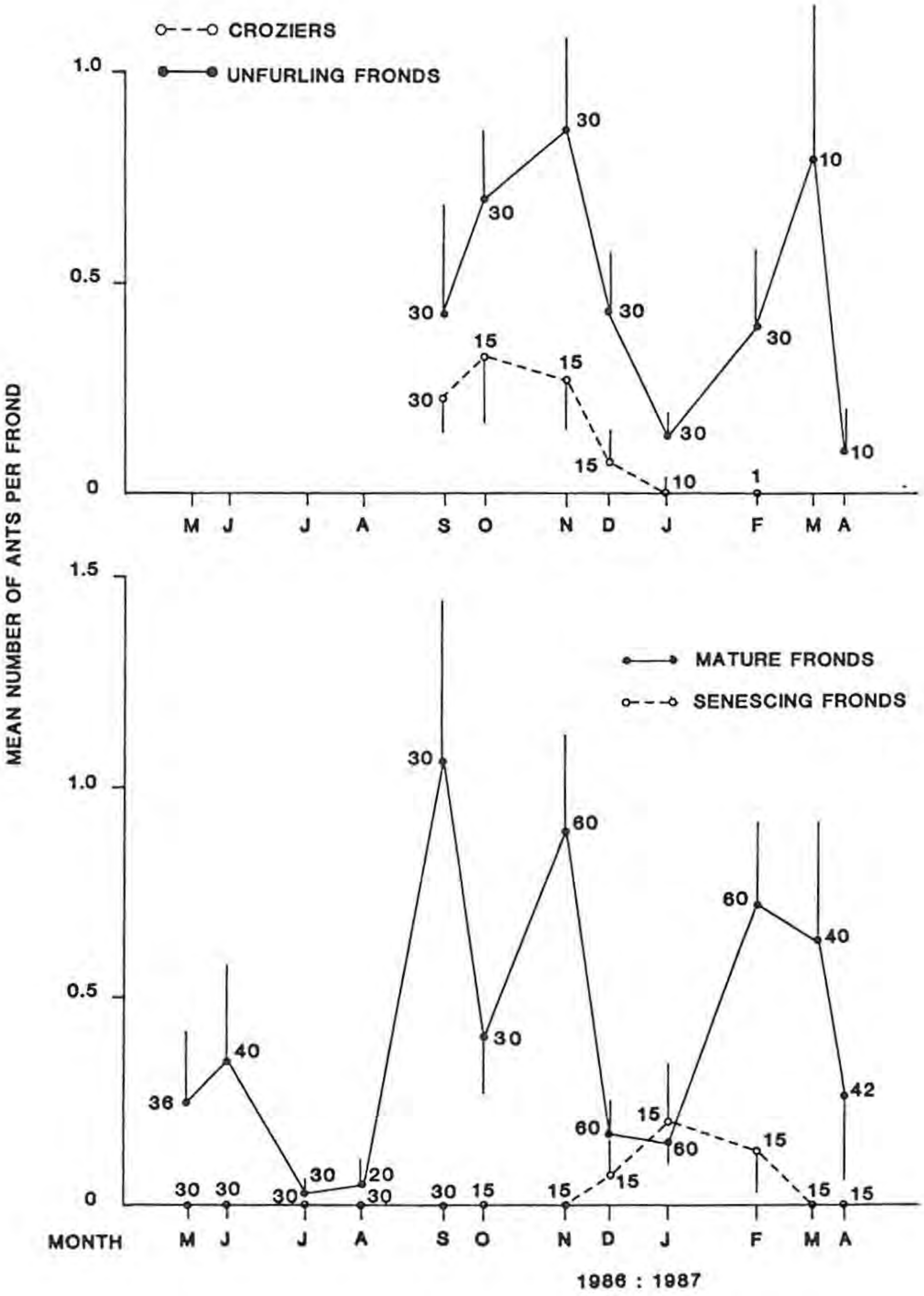


Table 4.3. Ant activity on bracken in relation to season and plant development stage. Data collected monthly at "Faraway" sites A and B, 1986-7. The number of fronds examined are shown in parentheses.

SITE	SEASON *	MEAN NUMBER OF ANTS/FROND			
		PLANT STAGE			
		CROZIER	UNFURLING	MATURE	SENESCING
A	Spring	0.72 (60)	1.22 (90)	2.03 (120)	0.17 (60)
	Summer	0.15 (26)	0.57 (70)	0.63 (165)	0.09 (45)
	Autumn	-	0 (4)	0.38 (96)	0.02 (60)
	Winter	-	-	0.14 (70)	0.06 (90)
B	Spring	0.27 (60)	0.67 (90)	0.82 (120)	0 (60)
	Summer	0.04 (26)	0.29 (90)	0.34 (180)	0.13 (45)
	Autumn	-	0.45 (20)	0.38 (118)	0 (60)
	Winter	-	-	0.19 (90)	0 (90)

* Spring = September - November

Summer = December - February

Autumn = March - May

Winter = June - August

Figure 4.7. Diurnal variations (mean and standard error) in ant activity at "Glenthorpe". The same 50 fronds were examined at each time period. The maximum and minimum air temperatures on the 12/13.11.88 were 35.3o and 9.0oC. Note the different scales.

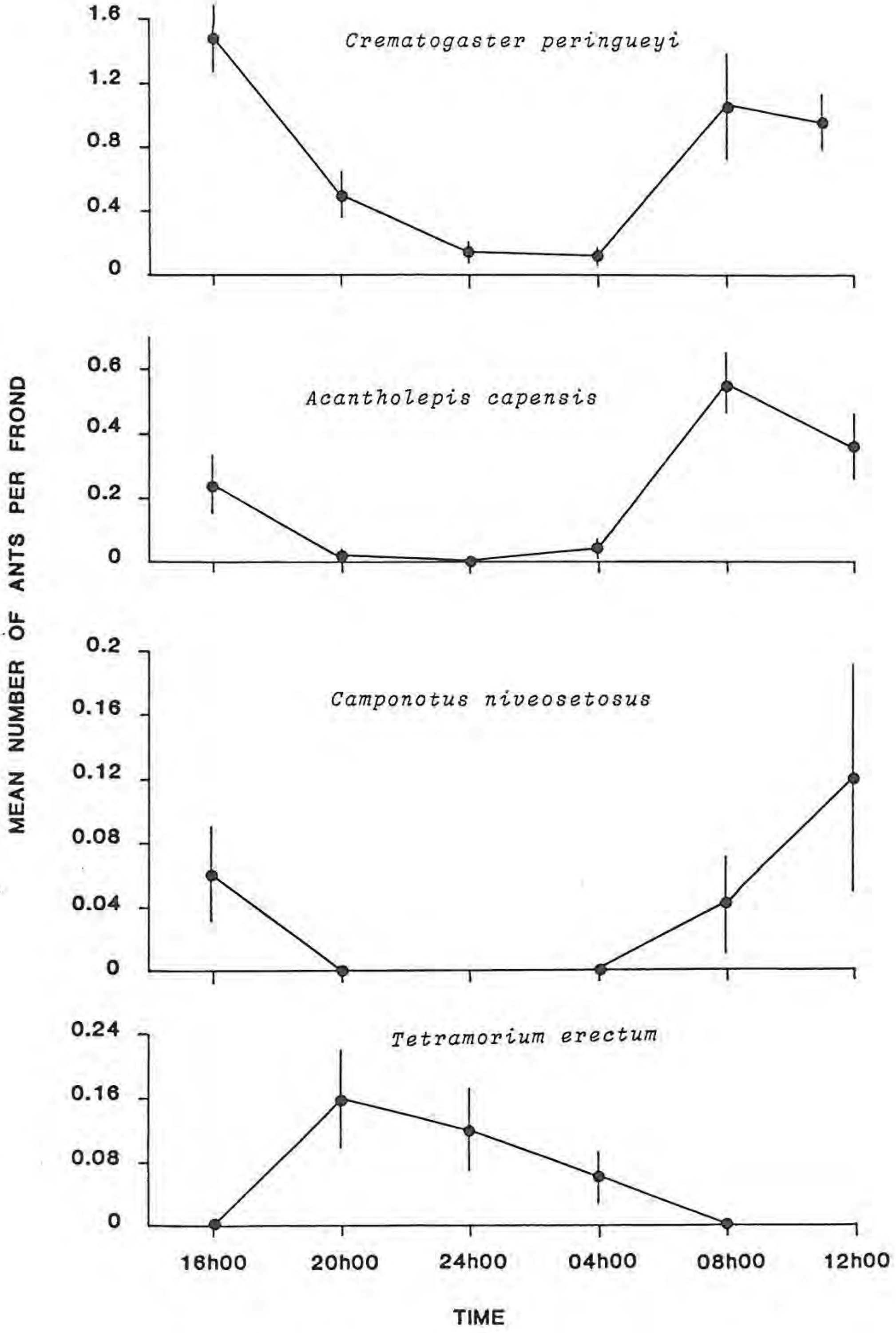
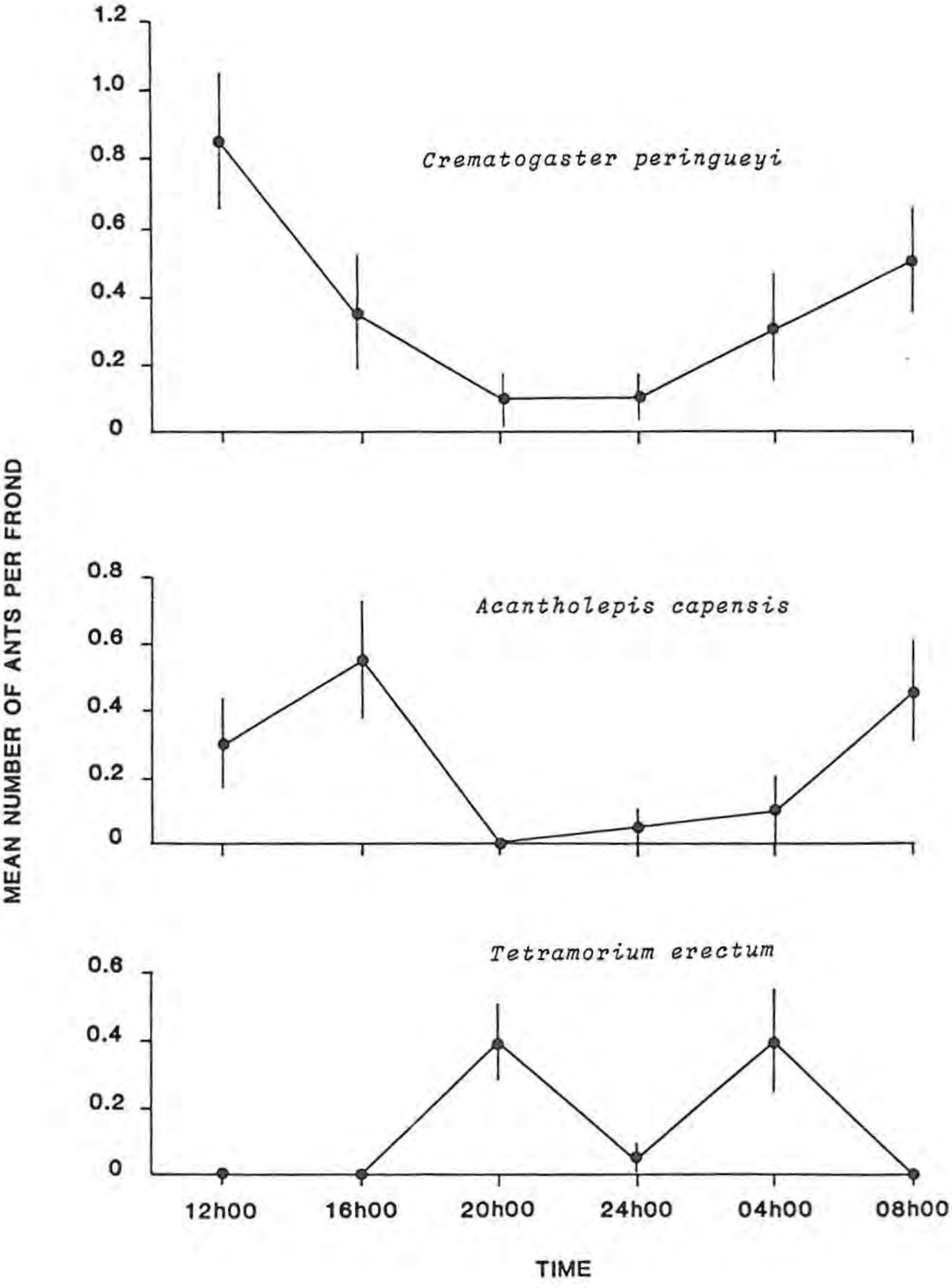


Figure 4.8. Diurnal variations (mean and standard error) in ant activity at "Glenthorpe". The same 20 fronds were examined at each time period. The maximum and minimum air temperatures on the 13/14.01.88 were 33.0° and 17.5°C. *C. niveosetosus* is not shown, since only one individual was found at 08h00.



4.4 Ant exclusion experiments.

A series of four ant-exclusion experiments, designed to assess the effects of ants on the herbivores of bracken, were carried out at "Faraway" in 1986 and 1987, and at "Glenthorpe" in 1987. In each experiment, pairs of fronds were matched as closely as possible, with selections based on either size, stage of development, proximity to each other or, if eggs had already been laid, initial number of herbivores.

In experiments 1-3, ants were excluded from experimental fronds in order to compare the survival of *A. cinisigna* and *Panotima* with ant-accessible control fronds. Two types of exclusion methods were used and the differences and merits of each were compared. Experiment 4 was a modification of the basic technique employed in experiments 1-3 and involved increasing the density of ants visiting control fronds by means of honey baits and by manipulating the position of ant nests. The methods and results of experiments 1-3 and experiment 4 are described separately, because of the slightly different techniques involved.

Differences between experimental and control fronds in each set of experiments were analysed using the Mann-Whitney U test, because sample sizes did not exceed 30 and the data were not normally distributed (Campbell 1974). Contingency tables were used for the analysis of discrete data sets.

4.5 Exclusion Experiments 1-3: <u>Materials</u> <u>and</u> <u>Methods</u>.

Experiment 1.

The first ant-exclusion experiments at "Faraway" were initiated at site A on 2.10.86 and at site B a day later. At each site, 20 matched pairs of young fronds were selected on the basis of their similarity in size and stage of development, since insufficient numbers of lepidopteran eggs had been laid at this time. As far as possible, neighbouring fronds were chosen in the hope of minimizing the effects of variables such as proximity to ant nests. The vegetation surrounding each frond was cleared away and "exclusion tubes" placed around the base of one from each of the matched pairs. The tubes consisted of a rubber cylinder, 6cm in length and 2.5cm in internal diameter, slit longitudinally so as to allow placement around the stem base (figure 4.9A). They were designed to exclude ants while still allowing *Panotima* larvae to mine unhampered at the base of the stem. Each tube was liberally smeared with a sticky ant repellent (Formex; Ciba Geigy (Pty) Ltd.) to exclude ants from the experimental fronds. Formex was re-applied as required and the vegetation periodically cleared to prevent ants from gaining access to the experimental fronds.

The fronds were examined at weekly intervals, when the numbers of ants, *A. cinisigna* and *Panotima* eggs and larvae, and parasitized larvae were counted. Occasionally ants were found on the experimental plants. This happened if the growing fronds had either touched neighbouring vegetation or had blown over, or if ants had gained entry beneath the exclusion tubes. When this occurred, the ants were removed and action was taken to prevent them returning. When the bracken died back at the end of November, the fronds were collected in order to assess *Panotima* larval grazing damage on the pinnae, and mines in the rachis. Chewing damage by *A. cinisigna* larvae could not be identified with confidence on senescent fronds, and was not scored.

Experiment 2.

A second set of experiments was started at "Faraway" site A on 29.10.86., using 10 pairs of plants. Site A only was used because observations during experiment 1 indicated that ant activity on fronds at site B was negligible. Since this experiment began later in the season when eggs of the two moth species were more abundant, plants were matched as closely as possible according to the initial number of *A. cinisigna* and *Panotima* eggs present. A different exclusion technique was also utilized, as the tube method used in experiment 1 had not proved entirely successful at excluding ants. Formex was applied to tape placed around the base of experimental plants (Heads & Lawton 1984; Heads 1986), (figure 4.9B). As before, numbers of herbivores and ants were monitored at weekly intervals, and estimates of *Panotima* damage (larval grazing areas and rachis mines) were made at the end of the season.

Figure 4.9. The ant-exclusion experimental design using Formex, a sticky ant repellent, and A) "exclusion tubes", B) "exclusion tape".

(A)

(B)

Experiment 3.

The procedure used in experiment 2 was repeated at "Faraway" site A in spring 1987 in order to re-examine the effects of ants on populations of *Panotima*. *A. cinisigna* was not monitored in this experiment, because the species was too scarce. Ten pairs of fronds were matched according to the number of *Panotima* eggs present. Ants were excluded from one of each frond pair using the exclusion tape method. Fronds were scored for ants and herbivores once a week on five occasions during November and December, and final counts of larval grazing-damage areas and stem mines were made after harvesting.

A summary of the experimental design (location, date, duration, exclusion techniques, method of frond pairing and number of fronds used) of each experiment is given in table 4.4.

4.6 Exclusion Experiments 1-3: <u>Results</u>.

Experiments 1 and 2.

At site B, where the ant densities were generally very low, ants were entirely absent from all the plants during the times when they were monitored. This site therefore acted as a test for whether or not the exclusion methods, independent of ants, influenced the herbivore populations. Table 4.5 gives the numbers of ants found on experimental and control fronds at site A over the experimental periods. Ant densities on the fronds were low during experiment 1, but had increased when experiment 2 was initiated a few weeks later. The timing of each experiment was responsible; during the peak of ant activity in November (see figure 4.1), many experiment 1 fronds were beginning to senesce and were not attractive. By then, experiment 2 fronds had reached the mature stage and were producing more nectar and therefore attracting more ants. A second major difference between the two experiments at site A was in the ant species composition. Only *A. capensis* and *C. niveosetosus* were recorded on fronds during experiment 1, but *C. peringueyi* became the second most abundant species in experiment 2.

Table 4.4. Experiments 1-3: summary of ant-exclusion experimental designs. Details of the exclusion methods are given in the text.

EXPERIMENT	LOCATION	DATE OF COMMENCEMENT	DURATION (WEEKS)	EXCLUSION METHOD	FRONDS PAIRED ON THE BASIS OF:	NO. OF FRONDS	
						EXPT. (- ANTS)	CONTROL (+ ANTS)
1	"Faraway" Site A	02.10.86	8	Tube and formex	Size and development	20	20
	"Faraway" Site B	03.10.86	11	Tube and formex		20	20
2	"Faraway" Site A	29.10.86	7	Tape and formex	Initial no. of *A. cinisigna* & *Panotima* eggs	10	10
3	"Faraway" Site A	09.11.87	5	Tape and formex	Initial no. of *Panotima* eggs	10	10

Table 4.5. Experiments 1 - 3: distribution of ants on experimental and control fronds at "Faraway", Site A, 1986.

ANT SPECIES	MEAN NUMBER OF ANTS/FROND (RANGES GIVEN IN PARENTHESES)					
	EXPERIMENT 1		EXPERIMENT 2		EXPERIMENT 3	
	EXPERIMENT (- ANTS)	CONTROL (+ ANTS)	EXPERIMENT (- ANTS)	CONTROL (+ ANTS)	EXPERIMENT (- ANTS)	CONTROL (+ ANTS)
Number of observations	135	138	50	50	40	40
Crematogaster peringueyi	0	0	0.04 (0-1)	0.58 (0-5)	0.025 (0-1)	0.075 (0-3)
Acantholepis capensis	0.03 (0-1)	0.14 (0-3)	0.1 (0-2)	0.88 (0-5)	0	0.05 (0-1)
Camponotus niveosetosus	0.007 (0-1)	0.02 (0-2)	0.06 (0-3)	0.26 (0-1)	0.05 (0-1)	0.25 (0-1)
Total	0.037	0.16	0.2	1.72	0.075	0.375
Mann-Whitney U test	U = 127 U1 = 251.5 U2 = 148.5	N.S.	U = 23 U1 = 91 U2 = 9	P < 0.05	U = 23 U1 = 78 U2 = 22	P < 0.05

The exclusion tube method was not effective in excluding ants from experiment 1 plants at site A, with the result that although the mean number of ants was less on experimental than control fronds, the two treatments were not significantly different. The exclusion tape method used in experiment 2 proved more effective at preventing ants from gaining access to the experimental fronds (Mann-Whitney U test, $P < 0.05$). However, the main drawback with this technique was that the Formex interfered with *Panotima*'s attempts to mine the rachis. When this happened, larvae were seen to be stuck in the Formex and were counted as having reached the mining stage. Despite this drawback, the exclusion tape method was adopted for the remaining exclusion experiments.

The number of *A. cinisigna* egg batches counted on ant-excluded and control fronds in experiments 1 and 2 are given in table 4.6. Although fronds in experiment 1 had been selected on the basis of their similarity in size and stage of development, eggs were found on some of the fronds prior to the exclusions. Oviposition by *A. cinisigna* continued after experiment 1 commenced, but at neither site A or site B were significantly different numbers of new batches laid, suggesting that oviposition was not affected by the presence of ants. In experiment 2, where fronds had been chosen on the basis of herbivore egg densities, the initial number of *A. cinisigna* egg batches laid on ant-excluded and control fronds was identical and additional batches were not found (table 4.6). *Panotima* eggs were more difficult to count than those of *A. cinisigna* and, in a few cases, larvae were discovered on fronds where eggs had not been previously seen. Either eggs had been laid and hatched in the period between samples, or the eggs had been overlooked. *Panotima* activity on experimental and control plants was therefore compared by scoring fronds for the presence of *Panotima* eggs and/or larvae. An equal number of control and experimental fronds at sites A and B (experiment 1) showed evidence of *Panotima* activity, while the difference obtained in experiment 2 was negligible (table 4.6). *Panotima* activity on experimental and control fronds was thus comparable.

Numbers of herbivore larvae and damage scores on fronds in the presence and absence of ants were compared (table 4.7). Since herbivore

Table 4.6. Experiments 1 and 2: herbivore densities at "Faraway" (1986).

	EXPERIMENT 1				EXPERIMENT 2	
	SITE A		SITE B		SITE A	
	E n=20	C n=20	E n=20	C n=20	E n=10	C n=10
Mean no. of *A. cinisigna* egg batches at beginning of exclusion experiment (ranges in parentheses)	0.40 (0-2)	0.55 (0-4)	0.65 (0-3)	0.45 (0-3)	0.9 (0-2)	0.9 (0-2)
Mean no. of *A. cinisigna* egg batches laid during exclusion experiment (ranges in parentheses)	0.90 (0-3)	0.75 (0-3)	0.2 (0-2)	0.35 (0-2)	-	-
Mann-Whitney U test (new *A. cinisigna* batches only)	U1 = 191 U2 = 209	N.S.	U1 = 220.5 U2 = 179.5	N.S.		
Proportion of fronds with evidence of *Panotima* activity	0.95	0.95	0.70	0.70	0.90	0.80

E = experimental fronds (ants excluded)

C = control fronds (ant accessible)

Table 4.7. Experiments 1 and 2 ("Faraway" 1986) : comparison of *A. cinisigna* and *Panotima* larvae and damage on fronds in the presence or absence of ants. Ranges are given in parentheses. No significant differences were found between treatments (Mann-Whitney U test).

		EXPERIMENT 1				EXPERIMENT 2	
		SITE A		SITE B		SITE A	
		E n=20	C n=20	E n=20	C n=20	E n=10	C n=10
A. cinisigna	Mean cumulative no. of larvae/frond	3.5 (0-9)	2.7 (0-10)	2.5 (0-8)	2.7 (0-7)	1.8 (0-5)	3.3 (0-14)
	Mean peak no. of larvae/frond	2.05 (0-6)	1.7 (0-5)	1.2 (0-5)	1.55 (0-4)	1.5 (0-3)	2.2 (0-7)
Panotima sp.	Mean cumulative no. of grazing larvae/frond	5.05 (0-26)	3.95 (0-12)	0.8 (0-6)	1.4 (0-5)	2.6 (0-11)	3.3 (0-13)
	Mean peak no. of grazing larvae/frond	2.35 (0-11)	2.0 (0-6)	0.55 (0-3)	0.75 (0-3)	1.8 (0-7)	1.5 (0-5)
	Mean no. of grazing damage areas/frond	29.4 (0-126)	24.05 (0-100)	4.8 (0-20)	6.2 (0-28)	10.5 (0-40)	18.1 (0-70)
	Mean no. of stem mines/frond	1.3 (0-5)	0.9 (0-3)	0.35 (0-2)	0.55 (0-2)	1.1 (0-5)	0.8 (0-2)

E = experimental fronds (ants excluded)

C = control fronds (ant accessible)

n = number of fronds

populations were low, the cumulative number of larvae counted on the ant-excluded fronds from each experiment was compared with the cumulative total obtained on the control fronds. However, repeated counts over the experimental period were not independent, so comparisons of the peak number of larvae recorded on each plant over the whole sampling period were also made. No significant differences were obtained between herbivore populations or damage scores on experimental and control fronds in the experiments. Although numbers of larvae and damage scores were all consistently higher on experiment 1 ant-excluded fronds at site A, none was significant. This pattern was not repeated at site B nor at site A in experiment 2. Ants therefore did not influence the numbers of herbivores on the fronds, nor did they reduce the amount of damage they caused.

Experiment 3.

The numbers of ants were significantly higher on control than on ant-excluded fronds (table 4.5). The densities of *C. peringueyi* and *A. capensis* were low compared with those recorded during the same month the previous year, but the numbers of *C. niveosetosus* were comparable with those recorded in experiment 2 that year.

Table 4.8 compares the *Panotima* data between treatment fronds. The pairing of fronds at the start of the experiment ensured that the mean numbers of eggs on experimental and control fronds were not statistically different. Examination of the fronds after harvesting showed that pinna grazing damage on the experimental and control fronds was not statistically significant. A comparison of the peak numbers of grazing larvae also indicated no difference between treatments. Finally, no significant difference was obtained in the number of stem mines present. Ants therefore made no significant impact on the abundance of *Panotima*, nor on the levels of their grazing or mining damage.

The results of larval parasitism obtained during exclusion experiments 1-3 are given in section 4.9.

Table 4.8. Experiment 3 ("Faraway" 1987) : comparison of *Panotima* abundancies in the presence or absence of ants. Ranges are given in parentheses.

TREATMENT	MEAN NUMBER OF:			
	EGGS/FROND	PEAK GRAZING LARVAE/FROND	LARVAL-DAMAGE AREAS ON PINNAE	STEM MINES PER FROND
Experimental fronds (- ants) n = 10	3.8 (1-11)	1.9 (0-5)	37.8 (3-96)	0.7 (0-3)
Control fronds (+ ants) n = 10	3.4 (1-10)	2.1 (0-4)	24.7 (3-60)	1.0 (0-3)
Mann-Whitney U test	U1 = 58.5 U2 = 41.5 N.S.	U1 = 46.5 U2 = 53.5 N.S.	U1 = 64.5 U2 = 35.5 N.S.	U1 = 38.5 U2 = 61.5 N.S.

4.7 Exclusion Experiment 4: Materials and Methods.

Ant-exclusion experiments were repeated at the "Glenthorpe" study site in November 1987, and incorporated attempts to artificially increase the numbers of ants visiting the control fronds. This was achieved by physically moving ant colonies into the experimental area and attracting ants to the fronds using honey baits. In this way it was hoped to maximize the impact of ants on the herbivores.

A track through the bracken stand was used to arbitrarily divide the "Glenthorpe" site into two parts. 17 *C. peringueyi* carton nests were collected from one half of the site and the surrounding area, and relocated amongst 150m^2 of bracken on the other side of the path (figure 4.10). This part of the site is referred to as the "high ant density" area (HAD). Bracken in the corresponding "low ant density" area (LAD) also had some ants visiting the EFNs, because not all the *C. peringueyi* colonies had been detected and removed, and other species such as *A. capensis* were also present. Four days after the transfers had been made, 5 of the colonies had deserted the cartons, but the remaining 12 nests were occupied at the commencement of the observations. Prior to setting-up the exclusions, ant densities in the two areas were assessed by making a count of ants on haphazardly chosen fronds.

20 pairs of ant-excluded (experimental) and control fronds, paired according to the number of *A. cinisigna* egg batches present, were set-up on each half of the site using the exclusion tape method, making 20 HAD experimental fronds, 20 HAD control fronds, 20 LAD experimental fronds and 20 LAD control fronds in all. To attract even further numbers of ants to the control fronds in the HAD area, pieces of unused cigarette filter soaked in honey were pinned close to the EFNs to act as baits. The fronds were scored twice a week for the presence of ants, *A. cinisigna* and *Panotima* eggs and larvae. This procedure continued until the larvae pupated, mined the stem, were parasitized or disappeared, whereupon the fronds were harvested and checked for damage.

Figure 4.10. A relocated *Crematogaster peringueyi* carton nest at "Glenthorpe" HAD area.

4.8 Exclusion Experiment 4: Results.

As expected, measurements of ant activity in the HAD and LAD areas of the site prior to commencement of the exclusion experiments showed that higher densities of ants were present in the region to which the ant nests had been transferred (figure 4.11 and table 4.9). However, even with the augmentation there were fewer than two ants per frond at the start of the experiment. Of the ant species present, *C. peringueyi* was six times more abundant than *A. capensis* in the HAD area, while the latter species was the more common in the LAD area. *C. niveosetosus* was not seen in either area at that time.

Ants were often found at the honey baits of HAD control fronds (figure 4.12). The total number of ants scored on control plants over the three week experimental period is given in table 4.10 (the number of counts totalled 100, since each of the 20 fronds were scored on five occasions). Although many of the fronds were invariably attended by ants some, especially in the LAD area, were never visited. More control fronds were visited in the HAD area and ant densities on them were higher, the dominant species present being *C. peringueyi*. No ants were ever detected on the experimental fronds, although both *C. peringueyi* and *C. niveosetosus* were discovered caught in the formex.

As fronds had been selectively paired according to the number of *A. cinisigna* egg batches present, differences in initial egg densities between experimental and control fronds were negligible (table 4.11). Additional batches were occasionally laid during the monitoring period, but the numbers counted on experimental and control fronds were not significantly different (table 4.11). The presence of ants, as in earlier experiments, did not therefore reduce the number of additional eggs laid.

The cumulative number of *A. cinisigna* larvae scored on experimental fronds was compared with the cumulative number found on controls. Peak numbers of *A. cinisigna* larvae at any sampling date were also compared. No significant difference was found between experimental and control fronds in either the high or low ant density areas (table 4.12), and there was no evidence that the presence of ants affected the larval abundance of this species.

Figure 4.11. A comparison of *C. peringueyi* densities between HAD and LAD areas at "Glenthorpe" after relocation of the nests, but prior to ant-exclusion experiments.

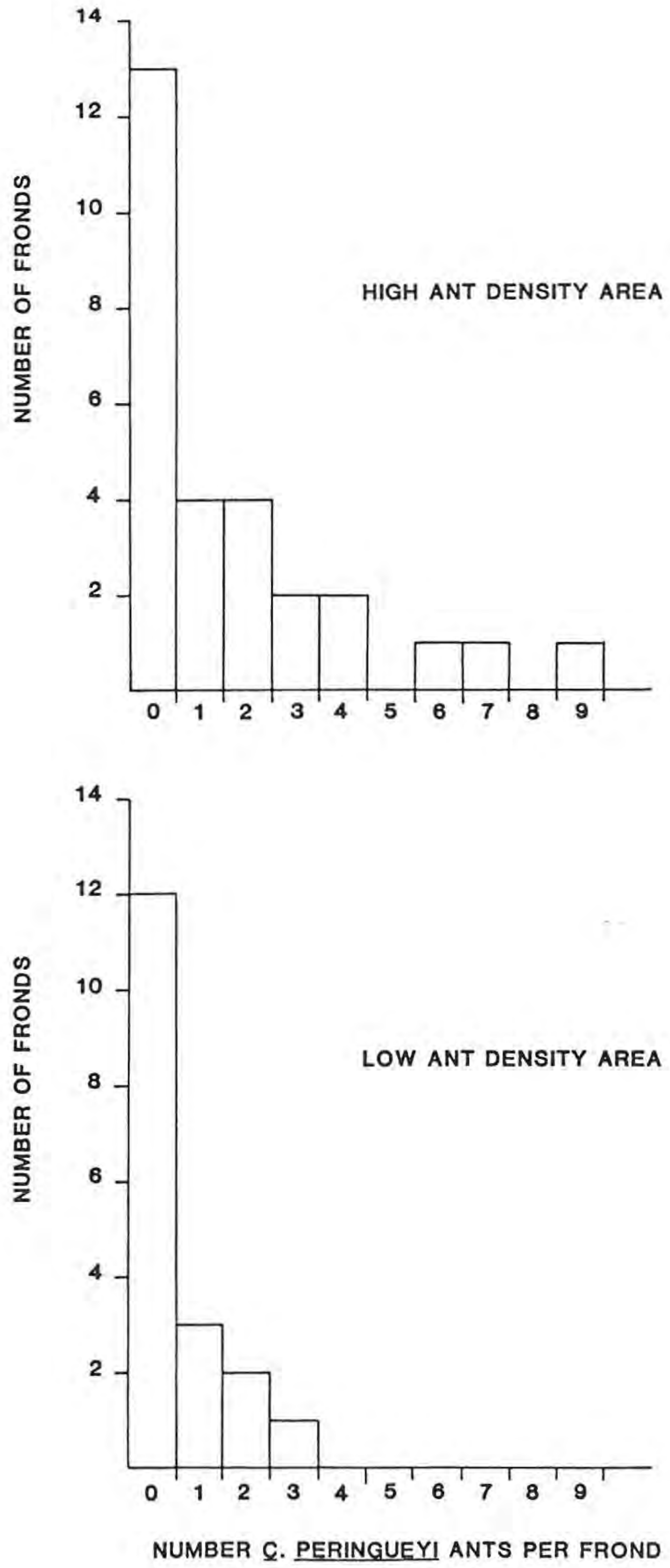


Table 4.9. Comparison of ant densities between HAD and LAD areas at "Glenthorpe". Fronds were sampled on 21.10.87., prior to the exclusion experiments.

	MEAN NUMBER OF ANTS/FROND (RANGES GIVEN IN PARENTHESES)		
	C. peringueyi	*A. capensis*	TOTAL: BOTH SPECIES
HAD No. fronds sampled = 33	1.45 (0-9)	0.24 (0-2)	1.69
LAD No. fronds sampled = 32	0.31 (0-3)	0.53 (0-2)	0.84

HAD = high ant density area

LAD = low ant density area

Figure 4.12. *C. peringueyi* ants visiting a bracken extrafloral nectary (left) and a honey bait (right).

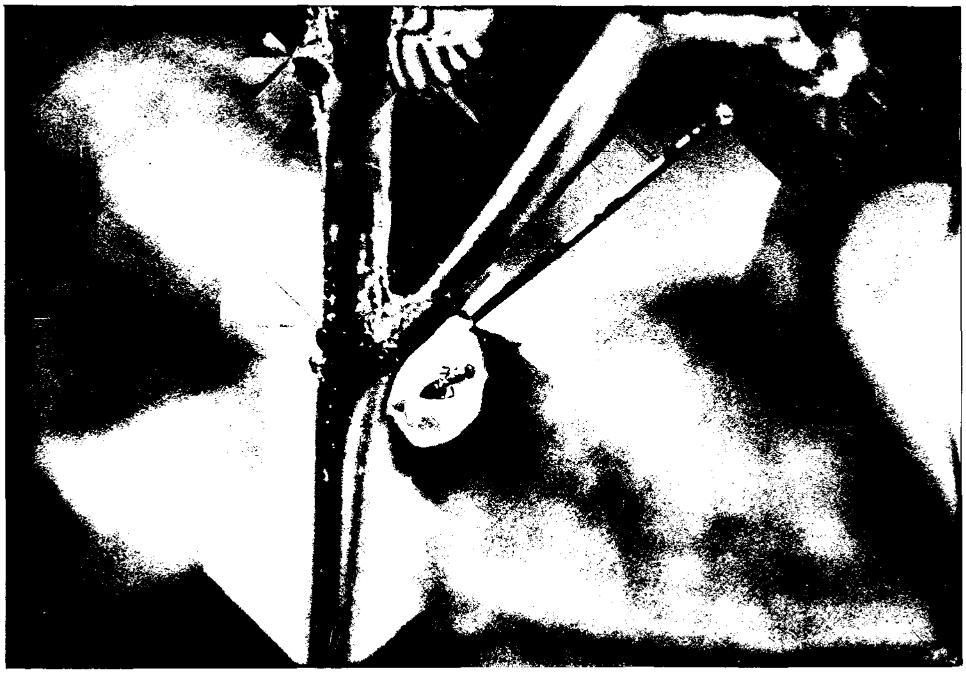


Table 4.10. Experiment 4 ("Glenthorpe", 1987) : comparison of ant species and numbers on HAD and LAD control fronds.

ANT SPECIES	MEAN NUMBER OF ANTS/FROND (RANGES GIVEN IN PARENTHESES)	
	HAD n = 100 counts	LAD n = 100 counts
Crematogaster peringueyi	0.35 (0-8)	0.03 (0-1)
Acantholepis capensis	0.18 (0-4)	0.1 (0-2)
Camponotus niveosetosus	0.01 (0-1)	0
Total	0.54	0.13
No. of control plants regularly visited by ants (n = 20)	12	8

HAD = high ant density area

LAD = low ant density area

Table 4.11. Experiment 4 ("Glenthorpe", 1987) : comparison of *A. cinisigna* egg batches on HAD and LAD ant-excluded (experimental) and control fronds.

	HAD		LAD	
	E	C	E	C
Total number of egg batches at beginning of exclusion experiment (ranges in parentheses)	37 (1-5)	39 (1-5)	36 (1-4)	31 (1-3)
Additional egg batches laid during exclusion experiment (ranges in parentheses)	2 (0-1)	4 (0-1)	5 (0-1)	7 (0-2)
Mann-Whitney U test (new batches only)	U1 = 220 U2 = 180	N.S.	U1 = 212.5 U2 = 187.5	N.S.

E = experimental fronds (ants excluded); n = 20

C = control fronds (ant accessible); n = 20

HAD = high ant density area

LAD = low ant density area

Table 4.12. Experiment 4 ("Glenthorpe", 1987) : comparison of *A. cinisigna* larvae on HAD and LAD ant-excluded and control fronds. Counts were taken over the whole experimental period.

TREATMENT		MEAN CUMULATIVE NO. OF LARVAE/FROND (RANGES SHOWN IN PARENTHESES)	MEAN PEAK NO. OF LARVAE/FROND (RANGES SHOWN IN PARENTHESES)
HAD	E	5.9 (1-12)	3.2 (1-8)
	C	7.1 (0-17)	3.7 (0-8)
MANN-WHITNEY U TEST		U1 = 216 U2 = 184 N.S.	U1 = 194 U2 = 206 N.S.
LAD	E	7.6 (0-28)	3.5 (0-9)
	C	6.2 (0-14)	3.35 (0-6)
MANN-WHITNEY U TEST		U1 = 181 U2 = 219 N.S.	U1 = 201 U2 = 199 N.S.

E = experimental fronds (ants excluded); n = 20

C = control fronds (ant accessible); n = 20

HAD = high ant density area

LAD = low ant density area

The data collected on *Panotima* damage were summed within each 20 frond category and are summarized in table 4.13. Only fronds which had evidence of larval grazing (column 1) were used in the comparisons of rachis mining damage (columns 2-5). Differences between experimental and control fronds were examined for the HAD and LAD areas separately. The total numbers of fronds with rachis mines (column 2) were not significantly different between treatments within either the HAD or LAD area (HAD $chi^2[1] = 0.29$ N.S.; LAD $chi^2[1] = 1.3$ N.S.), showing that neither *C. peringueyi* in the HAD area or *A. capensis* in the LAD area significantly affected the mining activities of *Panotima* larvae.

Comparisons were also made between the HAD and LAD control fronds. Interestingly, significantly fewer mined fronds were found among the HAD controls than the LAD controls (3 from 15 compared with 12 from 19, $chi^2[1] = 6.33$, $P < 0.05$). However, ant-accessible fronds in the HAD area had more mines per mined frond than the LAD controls (column 4); in other words fewer stems were mined in the HAD area, but those that were sustained more damage. These results therefore indicate that the patterns of *Panotima* damage varied between the two control groups. Both experimental and control grazed fronds were more likely to be mined by *Panotima* in the HAD area than in the LAD area (column 5), and so clearly this difference could not be attributable to ant related effects.

4.9 Parasitoids (exclusion experiments 1-4).

Euplectrus ?epiblemae, a larval parasite of *A. cinisigna*, was extremely rare at "Faraway". An *Elachertus* sp. which parasitized *Panotima* grazing larvae was active at all sites, while the colonial braconid sp. A, which attacked the mining stage of *Panotima*, was restricted to "Glenthorpe". Despite many hours in the field spent examining bracken fronds, no parasitoids were ever seen visiting the EFNs, either on control fronds, or on experimental fronds with ants excluded.

At both the "Faraway" and "Glenthorpe" study sites levels of larval parasitism were very low. It was not possible to calculate the percentage parasitism due to the cumulative nature of the unparasitized larval counts, but any parasitized larvae found during the course of

Table 4.13. Experiment 4 ("Glenthorpe", 1987) : comparison of *Panotima* damage on ant-excluded and control fronds.

		1	2	3	4	5
TREATMENT		NO. OF FRONDS WITH EVIDENCE OF LARVAL GRAZING DAMAGE	NO. OF FRONDS WITH RACHIS MINES	NO. OF RACHIS MINES	MINES/ MINED FROND	% OF FRONDS (WITH GRAZING DAMAGE) SUCCESSFULLY MINED
HAD	E	14	4	9	2.25	29%
	C	15	3	14	4.66	20%
LAD	E	16	7*	12*	1.7	44%
	C	19	12	19	1.58	63%

E = experimental fronds (ants excluded); n = 20

C = control fronds (ant accessible); n = 20

HAD = high ant density area

LAD = low ant density area

* also includes fronds where larvae were found trapped in formex

the exclusion experiments were removed (table 4.14). Comparisons between levels of parasitism on ant-attended and ant-excluded fronds of limited value, because larval parasitism was so seldom encountered.

4.10 Discussion.

Boecklen (1984) suggested that high density stands constituted a superabundant resource to ants, whereas at low densities, a higher proportion of the plants would be visited and hence ant activity would be increased. Lawton and Heads (1984) noted considerable variability in ant activity at the EFNs of bracken in different habitats in the U.K., and showed that more ants were found on bracken growing amongst grass than on bracken in pure stands. This parallels the situation at "Faraway" where the more ant-rich site A was in a grassy heathland, whereas site B was a more dense bracken patch. Lawton & Heads also noted that ant densities on bracken varied markedly between different years at the same site. Regular observations of ant activity at "Faraway" were only made once a month for a period of a year; it is therefore not possible to comment fully on between-year differences in ant visitation rates on South African bracken. However, the ant densities monitored at "Faraway" over two consecutive seasons during exclusion experiments 1-3 indicated that, like in the U.K., ant activity was extremely variable.

Statistical differences between treatment fronds were only achieved during experiment 2 and 3 ("Faraway" site A) and experiment 4 ("Glenthorpe" HAD area). Significant changes in herbivore densities would therefore not have been expected during the remaining experiments, or if any differences had been recorded, they could not have been attributable to the presence of ants. Despite attempts to augment ant densities at "Glenthorpe", the increased numbers of *C. peringueyi* obtained prior to the exclusion experiment were not maintained for long. Although ant activity on control fronds in the HAD area was high relative to the nearby LAD area, it did not reach the

Table 4.14. Lepidopteran larval parasitism during exclusion experiments 1-4.

SITE	TREATMENT	NO. OF *A. cinisigna* PARASITIZED BY *E. ?epiblemae*	NO. OF GRAZING *Panotima* PARASITIZED BY *Elachertus* sp.	NO. OF MINING *Panotima* PARASITIZED BY *Brachonid* sp. A.
"FARAWAY" EXPERIMENTS 1-3	EXPERIMENTAL (- ANTS)	0	2	0
	CONTROL (+ ANTS)	1	3	0
"GLENTHORPE" EXPERIMENT 4	EXPERIMENTAL (- ANTS)	3	5	3
	CONTROL (+ ANTS)	3	1	1

intensity recorded during experiment 2 ("Faraway" site A), which relied on natural densities. This suggests that the site at "Glenthorpe" was incapable of sustaining high ant densities, or alternatively that ants deserted the bracken for a better quality resource such as Homopteran honeydew (Sudd & Sudd 1985).

At "Faraway", not only were higher densities of ants recorded at site A than site B (especially during the spring months), but a greater number of species also occurred there. Herbivores present on bracken at site A were therefore potentially subject to the influence of a range of ant species, particularly *C. peringueyi*, whereas only *A. capensis* was important at site B. However, whether *A. capensis* can have an impact on bracken herbivores is debatable. Individuals are smaller in size than *C. peringueyi* or *C. niveosetosus*, a factor which could limit their effectiveness in attacking the larger larval instars. They also exhibited a more "nervous" behaviour than the other ant species. For example, in *A. capensis*, but not the other species, disturbance to the fronds would frequently cause individuals to leave the nectaries and run down the rachis.

Ants were not confined to feeding at the EFNs and were seen foraging over the entire fronds, although the most common species, *C. peringueyi*, was more frequently found at the EFNs than elsewhere. However, in general, ants were as likely to be found searching the rest of the frond as feeding at the EFNs, thus providing the potential for interactions between ants and herbivores to take place. This is a prerequisite for any defensive mutualism to be operating.

The "defense hypothesis" also requires that ants are present on the fronds at the "correct" time of year (Keeler 1981b). Ant activity on bracken was low for most of the year, but larger numbers of ants were attracted to the bracken patch at a time when frond density, and hence nectar availability, was at a maximum. This period also coincided with the time when the populations of both species of lepidopterans were at a peak (chapter 2). The potential for ants and moths to interact was therefore high, and was favoured by the timing of the EFN activity.

The nectaries on senescing fronds ceased to function and ants were rarely found on them. Relatively few ants were seen on the croziers, which may have been a function of plant architecture, croziers being smaller and having fewer EFNs than fully opened fronds. Of note was the high number of ants found on mature fronds, which was about the same as recorded from unfurling fronds. The lower pairs of EFNs on mature fronds had often ceased activity, but mature fronds may still have produced more total nectar than younger fronds, where sugars were only secreted from the lower EFNs. Ants were therefore present on bracken at the developmental stages when lepidopteran larvae were feeding.

Lawton & Heads (1984) obtained a positive correlation between the number of active EFNs per frond and the number of ants visiting the fronds, and suggested that the non-random distribution of ants across fronds was a function of a non-random distribution of rewards (ie. nectar). However, they did not distinguish between the frond development stages in their assessment of ant activity. Tempel (1983) also correlated high ant activity on bracken with high nectar availability, but found that the "percentage ant occupancy" (cf. Bentley 1977b) of mature fronds was significantly lower than that of croziers and unfurling plants. The highest ant activity was observed in "stage 2 fiddleheads" (when the major pinnae, but not the pinnules, were beginning to unfurl), corresponding to the crozier stage in the present study. Hence patterns of ant activity on South African bracken are rather different to those observed by Tempel in North America. It is unclear whether these differences reflect different patterns and quantities of nectar secretion, and/or species-specific differences in foraging behaviour by ants.

Despite high temporal and spatial overlap between ants and the two species of lepidopterans on South African bracken, and despite laboratory results (chapter 3) which clearly showed the vulnerability of both *A. cinisigna* and *Panotima* to attack by *C. peringueyi* at various stages during their life history, the ant exclusion experiments made at two sites over a period of three years yielded no evidence that ants significantly influenced either species of herbivore in the field. Firstly, the number of eggs laid by the moths did not vary between ant-excluded and control fronds. However, since adult moths are nocturnal while the three main ant species involved are mainly active during the day, it appears that ovipositing moths may have largely avoided any contact with ants.

The experiments also failed to detect ant effects on the numbers of grazing larvae on the fronds, although there is no doubt that mortalities due to ants did occur in the field. For example, on one occasion, a grazing *Panotima* larva was witnessed being carried from the pinna by *C. peringueyi*. Several *C. peringueyi* ants were also seen attacking a *Panotima* larva in the process of tunnelling into the rachis. At other times, *A. cinisigna* larvae were observed hanging beneath the frond as if they had been disturbed by ants (the silk-thread escape technique, see chapter 3).

The effectiveness of the bracken EFNs in attracting herbivore parasitoids was also not substantiated by the exclusion experiments. No parasitic wasps were ever detected at the nectaries during routine monitoring, either at control fronds or on fronds from which ants had been excluded, suggesting that the lack of parasitoids at the nectaries was not due to aggression by ants (Pierce & Mead 1981; Washburn 1984; Koptur 1985). The low incidence of parasitism confirmed that at these study sites, bracken EFNs were not important in attracting parasitoids to the plant.

The lack of ant effects in the field cannot be due to the effective escape responses of the larger larvae, since individuals counted in the field were predominantly small, early instar larvae. The most likely explanation is that ant and herbivore densities in the field were too low for encounters between them to be detected in "noisy" field experiments. At best this suggests the impact of ants on either *A. cinisigna* or *Panotima* populations is weak. Possible reasons for the generally negative results obtained in this and other bracken-ant studies will be explored in the following chapter.

5. DISCUSSION

Extrafloral nectaries are a feature of numerous plant species (Bentley 1977a; Elias 1983). Since EFNs occur on plants in many types of habitat which are subjected to widely differing environmental conditions, some variation in their function might be expected. As a result, hypotheses proposed to account for their presence may apply under certain circumstances, but not others. However, the proposal that EFNs merely act as sugar excreting organs has not been confirmed for any species, while evidence accumulated over the last two decades leaves little doubt that ants are attracted to the nectar and are capable of reducing herbivory on many EFN-bearing plants (Bentley 1977a; Beattie 1985). Since other predators (for example, vespid wasps and adult beetles) and parasitoids often feed on the extrafloral nectar, the potential for their mutualistic interaction with plants has also been recognised (Koptur 1985). However, no conclusive results have been obtained to support this view and plant protection soley by ants remains the only substantiated explanation for the occurrence of EFNs.

5.1 Factors influencing the ant-EFN plant defense mutualism.

The mutualism between ants and EFN-bearing plants has been described as facultative. In contrast to an obligate mutualism where both parties are physiologically and/or ecologically committed to the other for survival, facultative mutualisms are less likely to be the result of co-evolved responses (Schemske 1982). While EFNs provide ants with a readily available source of sugars and amino acids to supplement their diet of insect protein, ants are also likely to utilize alternative, more lucrative sources of liquid nutrients, such as homopteran honeydew, at certain times of the year (Sudd & Sudd 1985). The extrafloral nectar produced by plants such as bracken may not regularly feature in the foraging patterns of the majority of workers, and therefore be less likely to constitute a large fraction of the needs of a colony. Nevertheless, the interaction between plant and ant clearly benefits the latter, although the importance of EFNs to a particular colony may be minimal. In contrast, benefits to the plant may not be an inevitable consequence of ant attendance at the EFNs.

As Bentley (1977a) pointed out, no mutualism exists between ants and plants unless the plants are actually vulnerable to their herbivores and ants constitute a meaningful defensive force. Jermy (1984) questioned the generally accepted principle that herbivores are instrumental in reducing plant fitness and argued that there is no conclusive evidence that insects have generally exerted significant selection pressures on plants. However, herbivores have been shown to significantly limit the distribution and abundance of some plants (Parker & Root 1981; Compton et al. 1983); reduced growth rates (Dixon 1971; Whittaker & Warrington 1985) together with increased mortality (Rausher & Feeny 1980) have also been directly attributed to the effects of herbivory. Moreover, the success of weed biological control using phytophagous arthropods relies upon the susceptibility of plants to their specific herbivores (Andres & Goeden 1971).

Testing the importance of herbivory is most readily achieved in plants for which an accurate measurement of sexual reproductive output can be made (Rockwood 1973; Waloff & Richards 1977; Whitham & Mopper 1985). However, in a fern such as bracken which spreads vegetatively as well as by spores, changes in herbivore abundance or levels of herbivory will necessarily continue to be used as an indication of possible ant protection, although the extrapolation of these measurements to the costs or benefits to the plant must be made with caution. Due to the vegetative mode of reproduction of bracken, an entire patch can consist of a single clone (Wolf et al. 1988), and even though individual fronds may not directly sustain damage from herbivores or benefit from ants, the combined effects on the plant's overall fitness might still be appreciable.

Several studies have reported no measurable benefits to plants by ants (O'Dowd & Catchpole 1983; Tempel 1983; Boecklen 1984; Whalen & Mackay 1988). Boecklen (1984), for example, concluded that reproductive output of the annual legume *Cassia fasciculata* Michx. on the Florida/Georgia (USA) border was not affected by ants. Similarly, Kelly (1986) found that ants did not influence seed set on the same plant in eastern Iowa even though ant presence or absence produced significant differences in the number of herbivores, leaf damage and growth. However, Barton (1986) investigated *C. fasciculata* in northern Florida and in contrast to Boecklen (1984) and Kelly (1986), obtained strong evidence for the existence of an ant-plant defense mutualism. Ants on control plants attacked larvae of the major seed pod predators, consequently lowering seed pod damage and increasing reproductive output. These studies of *C. fasciculata* show that ant exclusion experiments on the same plant in different areas of its range can yield contrasting results.

The bracken-ant system has also been studied in different regions of its geographical range, with varying results (Douglas 1983; Tempel 1983; Heads & Lawton 1984; Heads 1986). The aim of this study was to investigate the same system in South Africa. Assuming that the two sites used in the eastern Cape Province are representative of other bracken patches in South Africa, the experiments detailed in chapter 4 provide evidence for a non-mutualistic interaction between bracken and ants, since ants did not substantially reduce herbivory or increase mortalities of two of the most damaging, and apparently most ant-susceptible, bracken herbivores. This result is in agreement with some of the experimental studies made on bracken in other continents. Tempel (1983) found no differences in the levels of herbivory between control fronds and those with ants excluded. Similarly, Heads and Lawton (1984) detected no difference in the abundance of herbivores on ant-attended and ant-excluded fronds. Only Heads (1986) recorded a significant effect due to ants in short-term herbivore introduction experiments, but in "classic" ant exclusion experiments, he again found no significant differences in herbivore densities or in species richness.

As outlined in the introduction, effective plant defence by ants depends on a number of factors, including the species of ants that are present and their densities on the plants. If, for example, the ant species attracted to an EFN-bearing plant do not exhibit predatory behaviour, they are in effect acting as nectar thieves. Of equal importance are the ant visitation rates; occasional activity may lead only to few encounters with herbivores and produce negligible effects. Also important are the composition and densities of the herbivore fauna. If herbivores are rare, or possess behavioural adaptations to avoid ants, protection may be insignificant. Under certain circumstances, ant activity may actually prove highly detrimental to EFN-plants if honeydew-producing homopterans and lepidopteran larvae are present and tended (and thus protected) by ants. An examination of these variables which influence ant-EFN mutualisms in general may provide an understanding of the conditions under which bracken EFNs are most likely to function to the plants advantage.

5.2 Ant activity patterns on bracken.

Bracken has a seasonal pattern of development in many areas of its worldwide range, for example Hawaii, south west U.S.A. and the U.K. (Lawton 1982), although not in others, for example P.N.G. (A. A. Kirk pers. comm). Lepidopteran larvae (both generalists and specialists) associated with bracken in the U.K. do not feed in the early spring when the plant is most nutritious (Lawton 1976). Heads and Lawton (1985) attributed this to the influence of ants, as the greatest ant densities occurred on the plant at this time (Lawton & Heads 1984). In contrast, the two major lepidopteran larvae in South Africa were abundant on young fronds from early spring to late summer, during the peak period of ant activity. The only other reasonably common lepidopteran, *Appana minor*, and the leafhopper, *Eupteryx maigudoi*, appeared mainly on older fronds in late summer, thus reducing to a minimum spatial and temporal overlap with ants. The dispersal phase(s) of the eriophyid mite, *Eriophyes* sp., may coincide with times when ants are active, but its tiny size (approximately 0.1mm long) probably means it is ignored by these predators.

Diurnal patterns in ant activity are also important considerations when assessing the likelihood of effective plant defence. Most ant species on South African bracken would come into contact with grazing lepidopteran larvae, but would not have disrupted oviposition since adult moths were nocturnal. However, one nocturnally active ant, *Tetramorium erectum*, was observed and may have been widespread. In the U.S.A., Tempel (1983) found no nocturnal ant species on bracken, while Lawton and Heads (1984) did not sample at night.

5.3 Between-species differences in ant protective ability.

Nectar-collecting ants vary in their degree of aggressiveness (Bentley 1977a, 1977b). *Camponotus niveosetosus*, one of the largest ants recorded on bracken in South Africa and therefore possibly the most capable of effectively tackling the larger lepidopteran larvae, was only present at low densities at the two study sites. The crematogastrines have been frequently recorded gathering extrafloral nectar and providing corresponding plant protection (Bentley 1977b; Pickett & Clark 1979; Keeler 1980; Beckmann & Stucky 1981; Barton 1986; Kelly 1986; Whalen & Mackay 1988). In laboratory tests with bracken herbivores, *Crematogaster peringueyi* proved a most aggressive ant, readily removing eggs and young caterpillars. Although, under natural conditions, foragers were more likely to be found feeding at the EFNs than patrolling the fronds, they did initiate attacks on herbivores and were observed removing grazing and tunnelling *Panotima* larvae. Ants also appeared to be responsible for dislodging *A. cinisigna* larvae, and in so doing could reduce plant damage by disrupting herbivore feeding (Bentley 1977a).

Large size and overt aggressiveness are not essential characteristics for a reduction in herbivory, if ants act as passive aggressors. For example, the *Pheidole* ants inhabiting *Piper* plants were described as "small and sluggish", and yet Letourneau (1983) showed that they played an important defensive role by removing herbivore eggs. Thus, a protective role for *A. capensis* could not be dismissed. *T. erectum* has also been noted at the EFNs of *Opuntia* species where it was responsible for the predation of *Cactoblastis cactorum* (Berg) eggs (H.G. Robertson, pers. comm.). Presumably eggs of the bracken lepidopterans may also have been under threat from this species.

5.4 Ant density.

A third influence on the potential for effective plant defense is the densities of ants on the EFN plants. High ant densities have been linked directly with increased plant growth (Messina 1981) and reproductive success (Schemske 1980) and with providing a more effective herbivore deterrent (Compton & Robertson 1988).

Ant densities obtained on control bracken fronds during exclusion experiments in South Africa, the U.S.A. and U.K. are compared in table 5.1. Data from the U.S.A. were expressed as ant occupancy (proportion of fronds with ants), while those from the U.K. were expressed as the

Table 5.1. Comparison of ant densities on fronds during exclusion experiments at sites in South Africa, the U.S.A. (Tempel 1983) and the U.K. (Heads & Lawton 1984; Heads 1986). Data for the U.K. were calculated from published graphs and are approximate values only. The only significant ant-related effects were reported in the herbivore introduction experiments at Hazel Head Wood*.

	MEAN ANT OCCUPANCY (PROPORTION OF FRONDS WITH ANTS)		MEAN ANTS/FROND	
SITE	OVER WHOLE SAMPLING PERIOD	MAX. AT ANY ONE SAMPLE	OVER WHOLE SAMPLING PERIOD	MAX. AT ANY ONE SAMPLE
SOUTH AFRICA (E. CAPE)				
FARAWAY EXPT. 1	0.12	0.15	0.16	0.80
FARAWAY EXPT. 2	0.62	0.80	1.72	2.40
FARAWAY EXPT. 3	0.325	0.50	0.375	0.70
GLENTHORPE HAD	0.27	0.40	0.54	0.95
GLENTHORPE LAD	0.11	0.25	0.13	0.30
U.S.A. (NEW JERSEY)				
EXPERIMENTAL STATION	0.156	0.35	-	-
STATE PARK	0.075	0.167	-	-
U.K. (N. YORKSHIRE)				
SKIPWITH COMMON	-	-	2.50	3.14
HAZEL HEAD WOOD	-	-	0.71	2.14
HAZEL HEAD WOOD*	-	-	2.36	-

mean number of ants per frond. Although average values do not necessarily give the complete picture, because of considerable interplant variation, mean ant occupancy was generally higher during experiments in South Africa than in the U.S.A., while ant densities in the U.K. were generally greater than those obtained in South Africa. However, even the relatively high ant densities in the U.K. did not inevitably affect numbers of bracken herbivores. Only at Hazel Head Wood (where a particularly pugnacious ant species was present) were significant differences reported in short-term herbivore introduction experiments (Heads 1986). Comparisons between ant densities on bracken and other EFN-bearing plants are not easy because of differences in plant morphology and it is difficult to comment on whether or not the general absence of protection for bracken is due to it having fewer ants.

5.4 Herbivore community composition.

Herbivore community structure is another important variable linked with the value of EFNs. If ants fail to interact with the most damaging phytophages because, for example, they are endophages and therefore largely immune, the plant is less likely to receive any reciprocal benefit.

Lawton and Heads (1984) proposed that the U.K. bracken herbivores either possessed life history characteristics (exaptations) or had adaptations which gave them immunity from ants. The major South African bracken herbivores also appear to possess features which reduce their susceptibility to predators such as ants. The life history of the *Eriophyes* sp. in combination with its tiny size means that contact with predators on the frond surface is avoided, and *E. maigudoi* is capable of escape by running, jumping or flying. The two moths have been shown to employ specific anti-predator adaptations involving physical and chemical means of defense. In addition, fifth instar *A. cinisigna* larvae, which reach approximately 30mm in length, appear to be immune to *C. peringueyi* by virtue of their size. On other plants, ants did not attack lepidopteran larvae larger than 10mm (Tilman 1978; Barton 1986), but where very large, aggressive ants are present this may not always be the case. Even taking the escape strategies demonstrated by *Panotima* into account, the vulnerability of third instar larvae when mining into the rachis appears to be a potentially weak link in the life history of this moth. No obvious attempts to avoid ants during the transition from grazing to mining were made; tunnelling took place by day when most ants were foraging, and the process was not a fast one. Since larvae obviously burrowed head first, there was no question of them being able to use their repellent (regurgitated) fluid against attack from the rear. This suggests that if large numbers of aggressive ants were patrolling the fronds, *Panotima* populations could be reduced.

Interestingly, the four common herbivores on South African bracken are effectively monophagous, while the known polyphagous species were generally very rare. There is evidence that generalist herbivores are more susceptible to predation than specialists (Bernays 1988), and Lawton and Heads (1985) suggest that the bracken herbivore fauna in the U.K. may have been shaped by ant predation. However, the majority of the "bracken-feeding insects" they tested were highly polyphagous and fed on a variety of other plants with no EFNs, and it is not certain whether bracken is (or ever was) the major food plant of these species. Thus, the contention that the U.K. bracken-feeding insects possess adaptations in response to selection from ant predation on bracken seems unlikely. These generalists may equally well have been influenced by ants on other plants, and the link between their immunity to ants and the bracken EFNs may be purely coincidental. Certainly not only the South African bracken specialists, but also many of the generalists appear capable of self defence. For example, the polyphagous arctiids, lymantriid and lasiocampid larvae were covered with long, dense irritating hairs, while in the special case of the scale insect, the sugar secretions it produced were more attractive to the ants than the extrafloral nectar. Thus it appears that the generalists which colonize bracken in South Africa are not likely to suffer more than the specialists from predation by ants.

5.6 The effects of herbivore density.

Fluctuations in the densities of herbivores will also cause variation in the potential advantages conferred by EFNs. If herbivore populations are low, the likelihood of ant predation producing a beneficial effect is less than if populations were large. Thus, EFNs may be most valuable when herbivore densities reach high levels.

The importance for plant protection of spatial fluctuations in the densities of both ants and herbivores was demonstrated by Barton (1986). *C. fasciculata* was studied at three sites where the rates of ant visitation and herbivore pressure ranged from low to high. The effects of ants on the reproductive success of plants at these sites varied accordingly; no measurable effect was obtained where both ant and herbivore densities were low, at intermediate levels a small, but significant increase in seed set was detected, while at the site with the highest ant and herbivore densities, ants caused a marked increase in reproductive success.

Inouye and Taylor (1979) claimed that ants were less efficient at deterring species feeding on sunflower seeds in situations where both ants and herbivores were abundant, because seed predators per flower head were only significantly reduced where numbers of ants and herbivores were low. However, significant decreases in seed predation were only measured under high density conditions, again supporting the contention that herbivory *per se* is more likely to be reduced when ant and herbivore densities are high.

The densities of herbivores on South African bracken appears to have been intermediate between those recorded in the U.S.A. and U.K. (Tempel 1983; Heads 1986). Bracken herbivores may have been at lower than average abundance during times when the South African studies were carried out. A preliminary investigation at Faraway in 1985 showed that lepidopteran populations were considerably higher in that year than at the same site in 1986 and 1987 when the experiments took place. For example, up to 50 *Panotima* eggs per frond were found in 1985, compared with maximum densities of 7 eggs/frond in 1986 and 11 eggs/frond in 1987. In the laboratory, the numbers of ants patrolling the potted bracken fronds were considerably higher than field densities, and the experimentally placed *A. cinisigna* larvae were at substantially higher densities than those in the field. Thus, the low insect densities in the field would clearly lead to fewer confrontations.

5.6 The South African bracken-ant system.

Summing up, the bracken-ant system studied at two sites in South Africa appeared to satisfy three of the five conditions suggested as being conducive for ants to benefit the plant. Firstly, the availability of extrafloral nectar coincided with the period when two of the most damaging bracken herbivores were abundant, so ensuring that ant activity on the plant was maximized at the time when protection was most required. Secondly, at least one of the dominant ant species was aggressive and capable of effective predation in laboratory experiments. Thirdly, the two major herbivores, although able to employ a variety of defences against ants, were not invulnerable to ant attack. In contrast, the other two conditions, those of high ant and herbivore densities, were not satisfied; densities of ants and herbivores were not comparable with those obtained in the U.K. for example (Heads 1986).

Both Tempel (1983) and Lawton & Heads (1984) remarked on the presence of parasitic Hymenoptera at the EFNs of bracken in the U.S.A and U.K. respectively, although it was not known whether these parasitoids utilized bracken herbivores as hosts. The failure to observe parasitic wasps at the EFNs of bracken in South Africa suggests that here, bracken EFNs were unimportant for attracting parasitoids and since larval parasitism rates were consistently low on both ant-excluded and control fronds, interference between ants and parasitoids is unlikely to have occurred.

Future work on the South African bracken-ant system could test the effects of herbivore density by seeding fronds at a site showing naturally high densities of *C. peringueyi* with large numbers of the two specialist lepidopteran larvae and leafhopper nymphs, plus any of the generalist bracken-feeders. This would also enable a comparison of the survival of specialist versus generalist herbivores on a plant which has the capacity to attract generalist predators. The interactions between ants and parasitoids should also be investigated further. Since colonies of *C. peringueyi* are relatively easy to transfer, ants could be introduced into sites where herbivore parasitism was high, but where ant activity was previously low or absent. Only short-term experiments are likely to be possible however, unless high ant densities are maintained by continual re-location of active colonies to the site.

5.7 The bracken-ant system worldwide.

Studies of bracken worldwide have generally failed to establish that EFNs have a protective effect. Several explanations may account for this. Trelease (1879, in Yokoyama 1978) suggested that the extrafloral nectar produced by cotton plants provided predators with an alternative food source when suitable prey was absent. The aphid-tending ants on *Betula* sp. switched to predating caterpillars when densities of these defoliators became exceptionally high (Laine & Niemela 1980). Similarly, bracken EFNs may ensure that ants are available to protect the plant at times when herbivores multiply. For a long-lived plant such as bracken, EFNs could therefore function as a "latent defense mechanism", only valuable in years when herbivore outbreaks occur.

Lawton and Heads (1984) drew upon evolutionary history to account for the apparent lack of mutualistic effects in the bracken-ant system. Their "ghost of predation past" hypothesis emphasized the evolution of ant avoidance strategies by bracken herbivores, such that EFNs provided no protection against specialist herbivores in present times. EFNs were viewed as being retained as a preventative measure against casual, non-adapted species. Punctuated equilibrium (Gould & Eldredge 1977) and Janzen's (1985) line of thought on "ecological fitting" may provide another evolutionary alternative. If it is accepted that EFNs have a defensive function, then selection favouring their presence must have occurred at some time. However, this does not mean that EFNs must significantly reduce herbivore pressure to be still retained today. Bracken EFNs may be present not because they are still effective, but because of evolutionary stability in a widespread, successful species.

It has been speculated that bracken speciated in the tropics (Page 1976). During speciation, an initially small bracken population in the tropical forests may have acquired or retained the genotype for EFNs, because of selective advantages gained from the locally available ants acting on the herbivores that were present at that time. Sometime before the Tertiary, bracken increased its distribution, encountering many different habitats and environments as it extended into its present worldwide range. During this phase of expansion, EFNs were retained perhaps because there was never sufficient selection against the possession of EFNs (see below). Once bracken was widespread, in Janzen's terms it was now "evolutionarily static" and only populations that returned to a reduced state could be "evolutionarily labile".

Hawaii, for example, lacks native ants and bracken occurs in the absence of potential ant mutualists. Furthermore, no bracken feeding herbivores have definitely been reported on the island (Lawton 1982). If the EFNs in these populations had disappeared, it could have been argued that the redundant EFNs were too costly to maintain and, in accordance with the optimal defense hypothesis (Rhoades 1979), had been selected against. However, as bracken on Hawaii has retained its EFNs despite the lack of ant mutualists and herbivore pressure (J.H. Lawton, pers. comm.), this supports the idea of stasis, at least in this respect. In spite of the ferns' clonal properties, continental bracken populations are of average genetic variability (Wolf et al. 1988), suggesting that the retention of EFNs is not a reflection of a limited gene pool (although studies of island populations would be necessary to confirm this).

The question of whether bracken is currently in a phase of stasis can be addressed by extending studies of the plant and its ant-herbivore interactions elsewhere, particularly in areas where bracken has been isolated for long periods such as on tropical mountain peaks or on islands. The retention of active EFNs on oceanic islands with no native ants, or in places with feeble herbivore pressures would provide support for the punctuated equilibrium hypothesis (Gould & Eldredge 1977) and would strengthen the argument that bracken EFNs no longer serve a protective function at most times over most of its present range.

6. REFERENCES

Andres, L.A. & Goeden, R.D. (1971). The biological control of weeds by introduced natural enemies. *Biological Control. Proceedings of an AAAS Symposium on Biological Control, Boston, Massachusetts, December 30-31 1969.* (Ed. by C.B. Huffaker), pp. 143-164. Plenum Press, New York.

Anon. (1986). Climate of South Africa (1986). *Climate Statistics up to 1984*. Weather Bureau, Department of Environmental Affairs, Government Printer, Pretoria.

Atsatt, P.R. (1981). Lycaenid butterflies and ants: Selection for enemy free space. *The American Naturalist*, **118**, 638-654.

Barton, A.M. (1986). Spatial variation in the effect of ants on an extrafloral nectary plant. *Ecology*, **67**, 495-504.

Beattie, A.J. (1985). *The Evolutionary Ecology of Ant-Plant Mutualisms*. Cambridge University Press.

Beckmann, R.L. & Stucky, J.M. (1981). Extrafloral nectaries and plant guarding in *Ipomoea pandurata* (L.) G.F.W. Mey. (Convolvulaceae). *American Journal of Botany*, **68**, 72-79.

Belt, T. (1874). *The Naturalist in Nicaragua*. Dent & Sons: London.

Bentley, B.L. (1976). Plants bearing extrafloral nectaries and the associated ant community: interhabitat differences in the reduction of herbivore damage. *Ecology*, **57**, 815-820.

Bentley, B.L. (1977a). Extrafloral nectaries and protection by pugnacious bodyguards. *Annual Review of Ecology and Systematics*, **8**, 407-427.

Bentley, B.L. (1977b). The protective function of ants visiting the extrafloral nectaries of *Bixa orellana* (Bixaceae). *Journal of Ecology*, **65**, 27-38.

Bernays, E.A. (1988). Host specificity in phytophagous insects: selection pressure from generalist predators. *Entomologia experimentalis et applicata*, **49**, 131-140.

Boecklen, W.J. (1984). The role of extrafloral nectaries in the herbivore defense of *Cassia fasciculata*. *Ecological Entomology*, **9**, 243-249.

Botha, J.H., Van Ark, H. & Scholtz, A.J. (1986). The effect of bollworm control with regard to populations of spider mites and some of their natural enemies on cotton. *Phytophylactica*, **18**, 141-150.

Bristow, C.M. (1984). Differential benefits from ant attendance to two species of Homoptera on New York ironweed. *Journal of Animal Ecology*, **53**, 715-726.

Buckley, R.C. (1982). Ant-plant interactions: a world review. *Ant-Plant Interactions in Australia* (Ed. by R.C. Buckley), pp. 111-162. Junk, The Hague.

Campbell, R.C. (1974). *Statistics for Biologists.* (Second edition). Cambridge University press.

Compton, S.G., Beesley, S.G. & Jones, D.A. (1983). On the polymorphism of cyanogenesis in *Lotus corniculatus* L. IX. Selective herbivory in natural populations at Porthdafarch, Anglesey. *Heredity*, **51**, 537-548.

Compton, S.G. & Robertson, H. G. (1988). Complex interactions between mutualisms: ants tending homopterans protect fig seeds and pollinators. *Ecology*, **69**, 1302-1305.

Cooper-Driver, G. (1976). Chemotaxonomy and phytochemical ecology of bracken. *Botanical Journal of the Linnean Society*, **73**, 35-46.

Cooper-Driver, G.A. & Swain, T. (1976). Cyanogenic polymorphism in bracken in relation to herbivore predation. *Nature*, **260**, 604.

Cooper-Driver, G., Finch, S., Swain, T. & Bernays, E. (1977). Seasonal variation in secondary plant compounds in relation to the palatability of *Pteridium aquilinum*. *Biochemical Systematics and Ecology*, **5**, 177-183.

Darwin, F. (1877). On the glandular bodies of *Acacia sphaerocephala* and *Cecropia peltata* serving as food for ants. With an appendix on the nectar-glands of the common brake fern, *Pteris aquilina*. *Botanical Journal of the Linnean Society*, **15**, 398-409.

Dixon, A.F.G. (1971). The role of aphids in wood formation. I. The effects of the Sycamore aphid *Drepanosiphum platanoides* (Schr.) (Aphididae), on the growth of Sycamore, (*Acer pseudoplantanus* L.). *Journal of Applied Ecology*, **8**, 165-179.

Douglas, M.M. (1983). Defense of bracken fern by arthropods attracted to axillary nectaries. *Psyche*, **90**, 313-320.

Elias, T.S. (1983). Extrafloral nectaries: their structure and distribution. *The Biology of Nectaries* (Ed. by B. Bentley & T. Elias), pp.174-203. Columbia University Press, New York.

Fritz, R.S. (1983). Ant protection of a host plant's defoliator: consequence of an ant-membracid mutualism. *Ecology*, **64**, 789-797.

Gibbs Russell, G.E. (1985). Precis: The National Herbarium's computerised information system. *South African Journal of Science*, **3**, 62-65.

Gould, S.J. & Eldredge, N. (1977). Punctuated equilibria: the tempo and mode of evolution reconsidered. *Paleobiology*, **3**, 115-151.

Gould, S.J. & Vrba, E.S. (1982). Exaptation - a missing term in the science of form. *Paleobiology*, **8**, 4-15.

Heads, P.A. (1986). Bracken, ants and extrafloral nectaries. IV. Do wood ants (*Formica lugubris*) protect the plant against insect herbivores? *Journal of Animal Ecology*, **55**, 795-809.

Heads, P.A. & Lawton, J.H. (1984). Bracken, ants and extrafloral nectaries. II. The effect of ants on the insect herbivores of bracken. *Journal of Animal Ecology*, **53**, 1015-1031.

Heads, P.A. & Lawton, J.H. (1985). Bracken, ants and extrafloral nectaries. III. How insect herbivores avoid ant predation. *Ecological Entomology*, **10**, 29-42.

Heads, P.A. & Lawton, J.H. (1986). Beat back bracken biologically. *New Scientist*, **111**, 41-43.

Hespenheide, H.A. (1985). Insect visitors to extrafloral nectaries of *Byttneria aculeata* (Sterculiaceae): relative importance and roles. *Ecological Entomology*, **10**, 191-204.

Holloway, J.D. (1987). Bracken-feeding Geometridae in the genus *Idiodes* Guenee, 1857, and allied taxa in the tribe Lithinini (Lepidoptera). *Tinea*, **12**, 242-248.

Inouye, D.W. & Taylor, O.R. (1979). A temperate region plant-ant-seed predator system: consequences of extrafloral nectar secretion by *Helianthella quinquenervis*. *Ecology*, **60**, 1-7.

Jacobsen, W.B.G. (1983). *The ferns and fern allies of Southern Africa*. Butterworths, Durban.

Janzen, D.H. (1966). Coevolution of mutualism between ants and acacias in Central America. *Evolution*, **20**, 249-275.

Janzen, D.H. (1985). Dan Janzen's thoughts from the tropics. I. On ecological fitting. *Oikos*, **45**, 308-310.

Jeffries, M.J. & Lawton J.H. (1984). Enemy free space and the structure of ecological communities. *Biological Journal of the Linnean Society*, **23**, 269-286.

Jermy, T. (1984). Evolution of insect/host plant relationships. *The American Naturalist*, **124**, 609-630.

Jones, R.E. (1987). Ants, parasitoids and the cabbage butterfly, *Pieris rapae*. *Journal of Animal Ecology*, **56**, 739-749.

Keeler, K.H. (1977). The extrafloral nectaries of *Ipomoea carnea* (Convolvulaceae). *American Journal of Botany*, **64**, 1182-1188.

Keeler, K.H. (1980). The extrafloral nectaries of *Ipomoea leptophylla* (Convolvulaceae). *American Journal of Botany*, **67**, 216-222.

Keeler, K.H. (1981a). Function of *Mentzelia nuda* (Loasaceae) postfloral nectaries in seed defense. *American Journal of Botany*, **68**, 295-299.

Keeler, K.H. (1981b). A model of selection for facultative nonsymbiotic mutualism. *The American Naturalist*, **118**, 488-498

Kelly, C.A. (1986). Extrafloral nectaries: ants, herbivores and fecundity in *Cassia fasciculata*. *Oecologia*, **69**, 600-605.

Kirk, A.A. (1977). The insect fauna of the weed *Pteridium aquilinum* (L.) Kuhn (Polypodiaceae) in Papua New Guinea: a potential source of biological control agents. *Journal of the Australian Entomological Society*, **16**, 403-409.

Kirk, A.A. (1982). Insects associated with bracken fern *Pteridium aquilinum* (Polypodiaceae) in Papua New Guinea and their possible use in biological control. *Acta Oecologica/Oecologia Applicata*, **3**, 343-359.

Knox, R.B., Kenrick, J., Bernhardt, P., Marginson, R., Beresford, I., Baker, I., & Baker, H.G. (1985). Extrafloral nectaries as adaptations for bird pollination in *Acacia terminalis*. *American Journal of Botany*, **72**, 1185-1196.

Koptur, S. (1979). Facultative mutualism between weedy vetches bearing extrafloral nectaries and weedy ants in California. *American Journal of Botany*, **66**, 1016-1020.

Koptur, S. (1985). Alternative defenses against herbivores in *Inga* (Fabaceae: Mimosoideae) over an elevational gradient. *Ecology*, **66**, 1639-1650.

Koptur, S. (1987). Is extrafloral nectar production an inducible antiherbivore defense? *Fourth Annual Meeting of the International Society of Chemical Ecology. University of Hull, England. 13th - 17th July, 1987.* (Abstract, p.29)

Koptur, S., Smith, A.R. & Baker, I. (1982). Nectaries in some neotropical species of *Polypodium* (Polypodiaceae): preliminary observations and analyses. *Biotropica*, **14**, 108-113.

Kopton, S. & Lawton, J.H. (1988). Interactions among vetches bearing extrafloral nectaries, their biotic protective agents and herbivores. *Ecology*, **69**, 278-283.

Laine, K.J. & Niemela, P. (1980). The influence of ants on the survival of mountain birches during an *Oporinia autumnata* (Lep., Geometridae) outbreak. *Oceologica*, **47**, 39-42.

Lawton, J.H. (1976). The structure of the arthropod community on bracken. *Botanical Journal of the Linnean Society*, **73**, 187-216.

Lawton, J.H. (1982). Vacant niches and unsaturated communities: a comparison of bracken herbivores at sites on two continents. *Journal of Animal Ecology*, **51**, 573-595.

Lawton, J.H. (1984). Non-competitive populations, non-convergent communities, and vacant niches: the herbivores of bracken. *Ecological Communities: Conceptual Issues and the Evidence.* (Ed. by D.R. Strong, D. Simberloff and L.G. Abele), pp.67-100. Princeton University Press, Princeton N.J.

Lawton, J.H. (1986a). Biological control of bracken: plans and possibilities. *Bracken, Ecology, land use and control technology* (Ed. by R.T. Smith & J.A. Taylor), pp.445-452. Carnforth: Parthenon Publishing.

Lawton, J.H. (1986b). Ecological theory and choice of biological control agents. *Proceedings of the VIth International Symposium on the Biological Control of Weeds, August 1984, Vancouver, Canada* (Ed. by E.S. Delfosse), pp. 13-26. Ottawa: Agriculture Canada.

Lawton, J.H. (1988). Biological control of bracken in Britain: constraints and opportunities. *Philosophical Transactions of the Royal Society of London B*, **318**, 335-355.

Lawton, J.H. & Heads, P.A. (1984). Bracken, ants and extrafloral nectaries. I. The components of the system. *Journal of Animal Ecology*, **53**, 995-1014.

Lawton, J.H., Rashbrook, V.K. & Compton, S.G. (1988). Biocontrol of British bracken: the potential of two moths from Southern Africa. *Annals of Applied Biology*, **112**, 479-490.

Letourneau, D.K. (1983). Passive aggression: an alternative hypothesis for the *Piper-Pheidole* association. *Oecologia*, **60**, 122-126.

Lloyd, F.E. (1901). The extra-nuptial nectaries in the common brake, *Pteridium aquilinum*. *Science*, **13**, 885-890.

Lüttge, U. (1971). Structure and function of plant glands. *Annual Review of Plant Physiology*, **22**, 23-44.

MacGarvin, M., Lawton, J.H. & Heads, P.A. (1986). The herbivorous insect communities of open and woodland bracken: observations, experiments and habitat manipulations. *Oikos*, **47**, 135-148.

Messina, F.J. (1981). Plant protection as a consequence of an ant-membracid mutualism: interactions on goldenrod (*Solidago* sp.). *Ecology*, **62**, 1433-1440.

McLain, D.K. (1983). Ants, extrafloral nectaries and herbivory on the passion vine, *Passiflora incarnata*. *The American Midland Naturalist*, **110**, 433-439.

O'Dowd, D.J. & Catchpole, E.A. (1983). Ants and extrafloral nectaries: no evidence for plant protection in *Helichrysum* spp.-ant interactions. *Oecologia*, **59**, 191-200.

Parker, M.A. & Root, R.B. (1981). Insect herbivores limit habitat distribution of a native composite, *Machaeranthera canescens*. *Ecology*, **62**, 1390-1392.

Page, C.N. (1976). The taxonomy and phytogeography of bracken - a review. *Botanical Journal of the Linnean Society*, **73**, 1-34.

Page, C.N. (1982). Field observations on the nectaries of bracken, *Pteridium aquilinum*, in Britain. *Fern Gazette*, **12**, 233-240.

Paterson, S. (1982). Observations on ant associations with rainforest ferns in Borneo. *Fern Gazette*, **12**, 243-245.

Peterson, S.C., Johnson, N.D. & LeGuyader, J.L. (1987). Defensive regurgitation of allelochemicals derived from host cyanogenesis by eastern tent caterpillars. *Ecology*, **68**, 1268-1272.

Pickett, C.H. & Clark, W.D. (1979). The function of extrafloral nectaries in *Opuntia acanthocarpa* (Cactaceae). *American Journal of Botany*, **66**, 618-625.

Pierce, N.E. & Mead, P.S. (1981). Parasitoids as selective agents in the symbiosis between lycaenid butterfly larvae and ants. *Science*, **211**, 1185- 1187.

Pinhey, E.C.G. (1975). *Moths of Southern Africa.* Tafelberg, Cape Town.

Rausher, M.D. & Feeny, P. (1980). Herbivory, plant density and plant reproductive success: the effects of *Battus philenor* on *Aristolochis reticulata. Ecology*, **61**, 905-917.

Rhoades, D.F. (1979). Evolution of plant chemical defense against herbivores. *Herbivores. Their Interaction with Secondary Plant Metabolites* (Ed. by G.A. Rosenthal & D.H. Janzen), pp. 3-54. Academic Press, London.

Rigby, C. & Lawton, J.H. (1981). Species-area relationships of arthropods on host plants: herbivores on bracken. *Journal of Biogeography*, **8**, 125-133.

Rockwood, L.L. (1973). The effect of defoliation on seed production of six Costa Rican tree species. *Ecology*, **54**, 1363-1369.

Rymer, L. (1976). The history and ethnobotany of bracken. *Botanical Journal of the Linnean Society*, **73**, 151-176.

Schemske, D.W. (1980). The evolutionary significance of extra floral nectar production by *Costus woodsonii* (Zingiberaceae): an experimental analysis of ant protection. *Journal of Ecology*, **68**, 959-967.

Schemske, D.W. (1982). Ecological correlates of a neotropical mutualism: ant assemblages at *Costus* extrafloral nectaries. *Ecology*, **63**, 932-941.

Scholtz, C.H. & Holm, E. (1985). *Insects of Southern Africa.* Butterworths, Durban.

Simmonds, F.J. (1967). Possibilities of biological control of bracken *Pteridium aquilinum* (L.) Kuhn (Polypodiaceae). *Pest Articles and News Summaries* (C), **13**, 200-203.

Skaife, S.H. (1961). *The Study of Ants*. Longmans, London.

Smiley, J. (1986). Ant constancy at *Passiflora* extrafloral nectaries: effects on caterpillar survival. *Ecology*, **67**, 516-521.

Southwood, T.R.E., Moran, V.C. & Kennedy, C.E.T. (1982). The richness, abundance and biomass of the arthropod communities on trees. *Journal of Animal Ecology*, **51**, 635-649.

Stephenson, A.G. (1982). The role of the extrafloral nectaries of *Catalpa speciosa* in limiting herbivory and increasing fruit production. *Ecology*, **63**, 663-669.

Strong, D.R., Lawton, J.H. & Southwood, T.R.E. (1984). *Insects on Plants. Community Patterns and Mechanisms*. Blackwell, Oxford.

Sudd, J.H. & Sudd, M.E. (1985). Seasonal changes in the response of wood-ants (*Formica lugubris*) to sucrose baits. *Ecological Entomology*, **10**, 89-97.

Tempel, A.S. (1983). Bracken fern (*Pteridium aquilinum*) and nectar-feeding ants: a nonmutualistic interaction. *Ecology*, **64**, 1411-1422.

Thompson, J.N. (1982). Reversed animal-plant interactions: the evolution of insectivorous and ant-fed plants. *Biological Journal of the Linnean Society*, **16**, 147-155.

Tilman, D. (1978). Cherries, ants and tent caterpillars: timing of nectar production in relation to susceptibility of caterpillars to ant predation. *Ecology*, **59**, 686-692.

Tryon, R.M.T. (1941). A revision of the genus *Pteridium*. *Rhodora*, **43**, 1-31, 32-67.

Vansell, G.H. (1940). Nectar secretion in Poinsettia blossoms. *Journal of Economic Entomology*, **33**, 409-410.

Vari, L. & Kroon, D. (1986). *Southern African Lepidopteran. A series of cross-referenced indices.* Lepidopterists' Society of Southern Africa and the Transvaal Museum, Pretoria.

Waloff, N. & Richards, O,W. (1977). The effect of insect fauna on growth, mortality and natality of broom, *Sarothamnus scoparius. Journal of Applied Ecology*, **14**, 787-798.

Washburn, J.O. (1984). Mutualism between a cynipid gall wasp and ants. *Ecology*, **65**, 654-656.

Way, M.J. (1963). Mutualism between ants and honeydew-producing Homoptera. *Annual Review of Entomology*, **8**, 307-344.

Whalen, M.A. & Mackay, D.A. (1988). Patterns of ant and herbivore activity on five understory Euphorbiaceous saplings in submontane Papua New Guinea. *Biotropica*, **20**, 294-300.

Whitham, T.G. & Mopper, S. (1985). Chronic herbivory: impacts on architecture and sex expression of pinyon pine. *Science*, **228**, 1089-1091.

Whittaker, J.B. & Warrington, S. (1985). An experimental field study of different levels of insect herbivory induced by *Formica rufa* predation on sycamore (*Acer pseudoplatanus*) III. Effects on tree growth. *Journal of Applied Ecology*, **22**, 797-811.

Winterbourn, M.J. (1987). The arthropod fauna of bracken (*Pteridium aquilinum*) on the Port Hills, South Island, New Zealand. *New Zealand Entomologist*, **10**, 99-104.

Wolf, P.G., Haufler, C.H. & Sheffield, E. (1988). Electrophoretic variation and mating system of the clonal weed *Pteridium aquilinum* (L. Kuhn)(bracken). *Evolution*, **42**, 1350-1355.

Yokoyama, V.Y. (1978). Relation of seasonal changes in extrafloral nectar and foliar protein and arthropod populations in cotton. *Environmental Entomology*, **7**, 799-802.

APPENDIX 1. List of South African sample sites with quarter degree grid references and sampling dates.

LOCATION	GRID REFERENCE	SAMPLING DATE(S)
WESTERN CAPE PROVINCE		
Scarborough	3418AB	21.04.86
Kirstenbosch	3318CD	22.04.86; 17.09.86
Bainskloof Pass	3319CA	23.04.86
Paarl Mountain	3318DD	23.04.86; 19.09.86
Betty's Bay	3418BD	27.04.86; 16.09.86
Ceres	3319AD	15.09.86
Kleinmond	3419AC	16.09.86
Hermanus	3419AD	16.09.86
Cape Point	3418AB	17.09.86
Stellenbosch	3318DD	19.09.86
Citrusdal	3219CA	20.09.86
Clanwilliam	3119CC	20.09.86
SOUTHERN CAPE PROVINCE		
Bracken Hill	3423AA	29.10.85; 28.04.86; 14.09.86
Coldstreams	3323DC	06.02.86
Kransbos	3323CD	07.02.86
Sonskyn	3323CC	07.02.86
Phantom Pass	3422BB	07.02.86
Storms River	3323DD	09.02.86
Before Storms River	3424AB	13.09.86
Tsitsikamma Forest	3323DD	13.09.86
Wilderness	3322DC	14.09.86
Herbertsdale	3321DD	14.09.86
Langberg	3321DC	14.09.86
Tradoupas	3320DC	15.09.86
Marloth Nature Reserve	3320CD	15.09.86

EASTERN CAPE PROVINCE

Faraway	3326AD	12.09.85; 21.11.85; 26.07.86; 06.11.86
Hogsback 2	3226DB	28.09.85; 19.12.85; 14.04.86; 22.10.86
Howieson's Poort	3326AD	10.10.85; 05.01.86; 31.03.86; 23.06.86
Alexandria (open)	3326CB	21.10.85; 09.04.86; 31.08.86
Katberg 6	3226DA	05.11.85
Katberg 8	3226DA	05.11.85
Katberg 2	3226DA	08.11.85; 06.05.86
Katberg 3	3226DA	09.11.85
Katberg 7	3226DA	10.11.85; 29.05.86
Featherstone Kloof	3326BC	12.11.85; 28.11.85
Alexandria Forest	3326CB	09.12.85; 09.04.86; 31.08.86
Hogsback 4	3226DB	19.12.85
Hogsback 5	3226DB	08.01.85
Hogsback 7	3226DB	08.01.86
Mountain View	3326AA	16.01.86
Glenthorpe	3326BC	05.10.86

NATAL (INCLUDING TRANSKEI AND ZULULAND)

Elliot	3127DB	08.11.85
Heimville	2929DA	10.11.85
Sani Pass	2929CB	10.11.85
Spionkop	2929BD	11.11.85
Royal Natal 1	2828DB	12.11.85
Royal Natal 2	2828DB	12.11.85
Royal Natal 3	2828DB	13.11.85
Boston	2930CA	13.11.85
Weza Road	3029DA	14.11.85
Ingeli Forest	3029DA	14.11.85
Richmond	2930CD	07.06.86
Lorna Doone 1	3029DA	02.12.86
Lorna Doone 2	3029DA	02.12.86
Mapelane	2832AD	04.12.86
Sibaya 1	2732BC	10.12.86
Sibaya 2	2732BC	10.12.86
Bongwan	3030CA	13.12.86
Sugarbush	3029CC	14.12.86

TRANSVAAL

Badplaas	2530DD	19.01.87
Nelspruit	2530DB	19.01.87
White River 1	2531AC	20.01.87
White River 2	2531AC	20.01.87
Brondal	2530BD	20.01.87
Wonderkloof Pass	2530BC	20.01.87
Berlin Forest	2530DA	20.01.87
Henriksdal	2530BB	21.01.87
Long Tom Cannon	2530BA	21.01.87
Mac Mac	2430DD	21.01.87
Mount Sheba	2430DC	21.01.87
Blyde River Canyon	2430DB	22.01.87
Debengeni Falls	2330CC	25.01.87
Duiwelskloof	2330CA	26.01.87
Clouds End	2329BB	26.01.87
Ratombo	2330AA	26.01.87
Nzhelele	2330CC	26.01.87
Soutpansberg	2229DD	27.01.87
Magoebaskloof	2329DD	28.01.87
Rustenburg Nature Res.	2527CA	31.01.87

APPENDIX 2. Herbivorous arthropods recorded from bracken in South Africa. Lepidopteran species after Vari and Kroon (1986).

A) Species definitely feeding on the plant.

Acari

Eriophyidae

1) *Eriophyid* sp. near *helicantyx* (Keifer)

This mite (as yet undescribed, S. Neser, pers. comm.) is extremely widespread in South Africa and appears to be specific to bracken. It's presence can be detected by areas of tissue galling, which in heavily infested plants can lead to gross distortion of the fronds.

Hemiptera : Homoptera

Cicadellidae

2) *Eupteryx maigudoi* Dworakowska

This leafhopper has a widespread distribution on bracken, but was recorded at high densities at one site only ("Katberg", May 1986 and June 1988). It is probably bracken specific (Scholtz and Holm 1985; J.G. Theron, pers. comm.).

Coccoidae

3) *Coccid* sp.

A few individuals were found on bracken at "Glenthorpe" in the eastern Cape. They also appeared on potted bracken grown in a shade house. In both cases the scales were being tended by ants.

Pseudococcidae

4) *Pseudococcus* sp.

In the field, individuals were rare, but heavy outbreaks occured on bracken plants and other ferns maintained in shade houses.

Hemiptera : Heteroptera

Pentatomidae

5) *Erachtheus spinosus* (Signoret)

This shield bug was confined to sites in the Natal and Transvaal Provinces. Where it occured, eggs, larvae and adults were often very abundant. It has also been noted on bracken in Kenya (M. Cock, pers. comm.).

Thysanoptera

Thripidae

6) *Mycterothrips* sp. (?undescribed, R. Zur Strassen pers. comm.)

This species occured over a wide geographical range on bracken in South Africa. Nymphs and adults were found congregating in the curled pinnae tips of young fronds.

Coleoptera

Curculionidae

7) *Holcolaccus* sp.

Several adult specimens were collected from one site in Natal and were maintained on bracken fronds for several weeks in the laboratory.

Lepidoptera

Pyralidae

8) *Panotima* sp. (spp. ?) near *angularis*

Eggs, larvae or evidence of larval feeding were found at most sites sampled, indicating that this moth is very common and widespread. In the laboratory, feeding tests showed that it is probably bracken specific (Lawton et al. 1988).

Geometridae

9) *Idiodes saxaria* (Guenee) syn. *Nopia saxaria*

Only one larva was collected on bracken (in the eastern Cape), but this species was also found and reared on another fern, *Rumohra adiantiformis* (G. Forst.) Ching.

10) *Epigynopteryx maeviaria* (Guenee)

Three larvae were found at different sites in the southern and eastern Cape. One was successfully reared on bracken in the laboratory.

Lasiocampidae

11) *Pachypasa* sp.

One larva was collected from "Glenthorpe" in the eastern Cape and reared on bracken in the laboratory. Published records indicate that this genus feeds on a wide variety of host plants (Pinhey 1975).

Arctiidae

12) *Rhodogastria amasis* (Cramer) syn. *Dionychopus amasis*

Published records indicate that this species is polyphagous (Pinhey 1975). It was found on bracken on three occasions in the eastern Cape and Transvaal.

13) *Leucaloa eugraphica* (Walker) syn. *Spilosoma eugraphica*
syn. *Diacrisia eugraphica*

One larva of this polyphagous species (Pinhey 1975) was collected on bracken at an eastern Cape site.

Lymantriidae

14) *Knappetra fasciata* (Walker) syn. *Euproctis fasciata*

One larva was collected from bracken at "Glenthorpe" in the eastern Cape and two others were found in casual searches in Natal (T. Olkers, pers. comm.). All were reared successfully on bracken in the laboratory. This is a common and widespread species, occuring throughout South Africa and extending to the northern parts of the continent (Pinhey 1975). Host plant records include species of *Acacia*, *Cassia*, *Protea*, *Combretum* and *Solanum* (Pinhey 1975; P.E. Hulley, pers. comm.).

Noctuidae

15) *Appana cinisigna* (de Joannis) syn. *Conservula cinisigna*

This moth was the most widespread insect found on bracken in South Africa. Eggs and larvae were abundant at most sites, the larvae often causing extensive damage. Laboratory feeding tests suggested that it is likely to be bracken specific (Lawton et al. 1988).

16) *Appana minor* (Holland) syn. *Conservula minor*

Larvae were moderately abundant at two sites in the Cape, but they proved difficult to rear to adults on bracken. A few specimens were also collected at seven other sites in the Cape and Transvaal. This is generally considered to be a montane species in tropical or subtropical Africa (Pinhey 1975).

17) Hadeninae gen. et sp. indet.

Larvae of this lepidopteran were rare on bracken, only three individuals being found at three sites in the eastern Cape. One larva was also found and reared on the fern *Polystichum lucidum* (Burm.) Becherer.

(B) Species whose association with the plant is more uncertain.

Collembola

1) Sminthurid sp.

This unidentified sminthurid was found at four sites, all in the eastern Cape.

Hemiptera : Homoptera

Fulgoridae

2) Fulgorid sp.

Small numbers of nymphs were found at several sites in the western Cape and Transvaal. Two adults, possibly of the same species, were present at one of these sites, but feeding on bracken was not confirmed.

Cicadellidae

3) Cicadellid sp. (spp.?)

Unfortunately, specific identification of this cicadellid is not possible as nymphs, but no adults, were collected. However, it appeared to be fairly widespread, occuring at sites in the Natal and Transvaal provinces.

Aphidae

4-9) Miscellaneous Aphid species

The following species have been found on bracken:

Aphis citricola van der Groot?
Aphis craccivora Koch
Aphis gossypii Glover
Myzus persicae (Sulzer)
Hysteroneura setariae (Thomas)
Aulacorthum solani (Kaltenbach)

Hemiptera : Heteroptera

Anthocoridae

10) *Orius* sp.

This species has a widespread distribution on bracken, with abundance of nymphs and adults varying from rare to extremely common. However, there are no indications to suggest that this species is phytophagous; *Orius thripoborus* (Hesse) is reported as being predatory on cotton spider mites (Botha et al. 1986), and *O. tristicolor* (White) is noted to feed on cotton extrafloral nectar as well as on thrips and spider mites (Yokoyama 1978).

Miridae

11) *Taylorilygus ?pallidulus* (Blanchard)

A few adults and nymphs were found at sites (5 in all) in Natal and Transvaal. Two nymphs survived on bracken for over two weeks during which time one moulted, but feeding damage was not noted. It is a widespread species, occuring in Africa, Asia and the Pacific (M.R. Wilson, pers. comm.).

Thysanoptera

Thripidae

12) *Chirothrips pretorianus* Hood

Phlaeothripidae

13) *Haplothrips nigricornis* (Bagnell)

These thrips, both black in colour, were not distinguished during the faunal survey. Individuals were found in all provinces except Natal.