STUDIES ON SOME POTENTIALLY USEFUL INSECT ENEMIES OF NEEDLE-BUSHES (*HAKEA* SPP. - PROTEACEAE)

by

S. NESER

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S. Neser.

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FRONTISPIECE

Branch of Hakea gibbosa with two mature fruits, and husks of young fruits damaged by larvae of Erytenna sp. nr. consputa Pasc. Magnification: 1½ x .

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GENERAL

I INTRODUCTION

Four species of the Australian genus Hakea Schrader (Proteaceae) have become naturalized in several areas of the Cape Province of South Africa. Three of these, H. sericea[1] ('silky needle-bush'), H. gibbosa ('hairy needle-bush') and H. suaveolens ('sweet hakea' or 'sweet needle-bush') have become widely established in dense thickets, mainly on poorer soils, usually of low agricultural value in mountainous regions. These needle-bushes[2] have long been regarded as noxious weeds 'disfiguring' the mountains by replacing the sparse, unique natural flora, by the creation of a fire-hazard and by spreading steadily but uncontrollably.

Mechanical and chemical control measures were mostly impractical, uneconomical and on the whole unsuccessful, and biological control appeared to offer distinct possibilities. Upon suggestions by Dr. R.D. Hughes (Division of Entomology, CSIRO, Canberra), a preliminary study of the plants and their natural enemies in Australia was made by D.v.V. Webb (South African Department of Agricultural Technical Services) during 1962-64.

Practically no information was available on the potential usefulness of any of the insects found. Other workers have found

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[1] The authorities for the nomenclature of the needle-bushes and other plants referred to in all the following text are given in Appendix I.

[2] Although some other Hakea spp. are occasionally loosely referred to as 'needle-bushes' or 'needle-trees', the term will be used in this paper as referring only to the three common species known as 'needle-bushes' - incidentally those that have become weeds in South Africa.

that the overall effect of any individual insect species is hard to evaluate (Huffaker 1964; Wilson 1964; Harris and Zwölfer 1968). This is mainly because of possible interactions between different insects affecting the same part of the plant, and the possible collective influence of a large number of different species associated with the plant as a whole. Other more subtle environmental factors could also be important. Because of this, the present study of potential usefulness was undertaken, initially concentrating on two insect species that Webb and Hughes thought to show distinct promise. These insects were _Aphanasium_ _australe_ Boisd., attacking stems, and a complex of curculionids (_Cydmaea_ _major_ Blkb. and/or _Erytenna_ sp. nr. _consputa_ Pasc.) developing in young fruits.

Already during Webb's survey it was found that many of the insects attacking vegetative parts were not specific to one, or even a few _Hakea_ species, and some even attacked plants in different families. This immediately cast doubt on the host-specificity of any _Hakea_ insects, especially in view of the known diversity within the Proteaceae. Questions of host-specificity in its broadest sense (Harris and Zwölfer l.c.) are therefore paramount in this study.

To be able to estimate further the potential value of the insects, the factors governing their populations in the field were given some attention. Little was known about the host-plants and an ecological evaluation of the plants as hosts for insects was essential to determine the vulnerability of the phases in its cycle.

A main study area at Wilson's Promontory, Victoria, was selected because of the close resemblance of the climatic conditions there with those in the Cape Peninsula itself. However, the insects were also observed over a more extensive part of their geographical range from which they may be collected later. This would allow the inclusion of a maximum amount of genetic variability and the choice of forms possibly adapted to different climatic conditions.

Early in the work it became apparent that the life-cycle of the cerambycid was very long, and its possible mechanisms of host-specificity proved to be impractical to study during a short-term project. There were also indications that it might not be very effective and an alternative subject species was therefore sought. Throughout the study attention was given to other possibly useful insects - either of needle-bushes or of other Hakea spp. - that may prove necessary in addition to the selected insects.

A list of the insects found attacking the various parts of the plant is given in Appendix II. Many of these insects were encountered only in small numbers, or were known only from the adult stage. The damage caused by individual species was usually considered quite insignificant, especially from a biological control point of view. Notes are included on those regarded as causing more significant damage (Appendix III).

It was realized that insects capable of attacking the vast numbers of mature fruits that accumulate during the plant's life, would be desirable to complement the one chosen (which attacked young, developing fruits). A few such insects were briefly examined; the most interesting being the lepidopteran Carposina autologa Meyr. (Carposinidae), whose larvae develop in seeds inside mature fruits. Detailed studies were then restricted to the curculionid and carposinid.

II THE PLANTS AS HOSTS FOR INSECTS

2.1 THE FAMILY PROTEACEAE

There are 52 recognized genera and some 1,050 species in this diverse family of plants. Most occur in Australia (37 genera, 28 endemic) and South Africa (14 genera, 11 endemic). A few species occur in Madagascar, the Indo-Malaysian region, the western Pacific Islands and South America (Burbridge 1960; Phillips 1951).

There are two superfamilies: Proteoideae and Grevilloideae. Hakea, and the monotypic, endemic, South African genus Brabejum both belong to the latter superfamily whereas all the other African members belong to the Proteoideae (Johnson and Briggs 1963).

2.2 THE GENUS HAKEA

The genus Hakea is endemic to Australia. There are some 100 species, with the majority occurring in the South-Western Province (cf. Gardner 1944) of Western Australia. However, species occur in all the major phyto-geographic zones of Australia, including the tropics and the dry, central region.

The members of the genus are perennial, evergreen, woody plants. They usually develop into shrubs or small trees. The leaves may be heteromorphous, are usually rigid and leathery and may be terete, flat, entire, toothed or variously dissected. Juvenile leaf-forms occur in some species. The fruit-follicles are usually woody, quite large and solid, and persistent on the plants for many years. Two winged seeds are enclosed in a small cavity in the follicle. They are usually not released until after fires or after the death of the plant or branch on which they occur. The testa of the seeds is thin and soft.

The plants usually occur in exposed situations, and often form part of heath and taller sclerophyll vegetation. All the species encountered by the author, and probably at least all those outside the tropics, appeared to be particularly well adapted to survive periodic scrub- and bushfires. This is accomplished by releasing all the seeds simultaneously after fires, and/or by sprouting from underground lignotubers, depending on the species. Several of the species encountered apparently depended on periodic fires to assure regeneration and survival within a plant community.

2.3 NEEDLE-BUSHES

2.31 Natural distribution

Webb (unpublished reports: 1962-65) made a survey of the Australian distribution of those needle-bushes which have become weeds in South Africa. His findings (see also Figure 2) may be summarized as follows :

(a) H. gibbosa is restricted to the coastal regions and adjacent highlands of the central coast of N.S.W. (Wyong to Sutherland). The area experiences an annual rainfall of 40-60 inches, distributed fairly evenly throughout the year.

(b) H. sericea has the widest distribution of the three species. It has been reported from many coastal regions of N.S.W. and Victoria (Coff's Harbour to Jervis Bay, Eden to Geelong), from localities in detached highlands and coastal dividing ranges (Blue Mountains, Dandenong and Otway Ranges), from a few isolated inland localities (around Canberra[1] and the Grampians) and also from Flinders Island in Bass Strait. The annual rainfall within the distribution range of this species varied from as low as 15" at the south-western limit, to as high as 60" at the north-eastern limit. The maximum precipitation at the northern localities occurs during summer months, but the southern localities experience a mediterranean type climate.

(c) H. suaveolens occurs in isolated coastal communities in south-western Australia in the vicinity of Albany, Hopetoun, Esperance and Cape Arid, on Bald Island, and on six of the islands in the Recherche Archipelago. These localities experience a mediterranean climate, and the annual rainfall varies from 22" at the western, to 40" at the eastern localities.

2.32 General description

All three species may remain fairly small and slender or they may develop into low, compact shrubs, or slender, small trees (up to about 20' tall). Their shape and size depend on the habitat in which they occur. The plants may be long-lived, although they are normally in their prime from five to fifteen years after germination. The older stems are usually bare and smooth. The two eastern species generally have a main stem with only minor twigs persisting below the canopy level where it divides into a dense mass of leafy branches. On the other hand, the main stem of H. suaveolens growing normally

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[1] The isolated groups of plants on Black Mountain (Csnberra), Mt. Jerrabomberra (Queanbeyan, N.S.W.) and in the vicinity of Yass (N.S.W.) appeared to differ somewhat from typical H. sericea plants, and Burbridge (personal communication 1967) suspects that they may in fact be H. decurrens R. Br., presently regarded as a synomym of H. sericea Schrad.

in open situations usually divides at, or near ground-level, into a series of secondary stems, giving the shrub a more rounded appearance.

The mature leaves are cylindrical, about 1.0 - 1.5 mm in diameter and 2 - 8 cm in length. They are leathery and stiff, with a tough, fibrous centre, and have hard, needle-like tips. In *H. suaveolens* the leaves are often bi- or trifurcate, or otherwise variously divided, but each terminal segment is terete and pointed. The leaves are basically dark green, but a slight pubescence in young leaves of *sericea*, and on all leaves of *gibbosa*, may give them a silvery-grey appearance. The leaf-bases are densely packed around the twiglets. These twiglets are grey and pubescent in *gibbosa*, and may be similar (at least temporarily) in certain geographical forms of *sericea*. The leaves are long-lived and may remain on the twigs and branches for several years before they are dropped.

All three species germinate with rounded, fleshy cotyledons above ground-level. *H. suaveolens* is the only one that forms distinct juvenile leaves.[1] These leaves are broad and dentate (nevertheless leathery and prickly), and thus quite different from the final leaves. The seedling forms transitional shapes of leaves after about one year, and may produce the typical divided or needle-like leaves after two or three growing seasons.

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[1] The first few leaves of *H. sericea* from certain localities were also flattened, but not entirely distinct from older leaves.

The type of root system in mature H. suaveolens plants in their natural habitat was not examined, but was probably similar to that of H. sericea and H. gibbosa. These plants formed a tap-root in the seedling stage with several lateral roots going almost horizontally. The tap-root may be fairly well developed and may go down a few feet, or it may not develop much after the seedling stage. Alternately, it may decay as the lateral roots become well developed (Purnell 1960). Purnell recorded sub-surface lateral roots of up to 15' long for H. sericea growing on sandy, heathland soils. In the present author's experience, the development, length and persistence of the tap-root of H. sericea appeared to be closely linked with the type of soil, and probably importantly, to the type and structure of the subsoil.

The plants all form the peculiar 'proteoid roots' described by Purnell (1960). These are dense clusters of rootlets of limited growth, and presumably of limited functional life, occurring along the lateral roots. Purnell found suggestions that these structures may only be formed in the presence of certain biological stimuli, and that they may be involved particularly in the uptake of phosphorus and nitrogen.

With one notable exception (below), no suckering from lateral roots was observed in any of the needle-bushes, even after mechanical damage of their sub-surface roots. Also, none of them formed underground lignotubers or perennating buds from which sprouting may occur after death of or damage to the aerial parts. Furthermore, the faculty of regrowth from older leafless stems was found to be extremely limited, and often absent, so that older plants hacked off as high as three feet above ground-level failed to sprout, and died.

Figure 1

Twig of Hakea sericea with green, young fruit, showing 'additional' flower-bud on stem of fruit. Approximately six times life size.

In contrast to the other Hakea spp. in cultivation or in their natural habitat, the plants of Hakea sericea near Canberra propagated by vegetative means. Several of these were found to be interconnected by a series of sub-surface roots, or showed signs that they may have sprouted from such roots which had subsequently decayed. During the study period several instances of sprouting from roots were observed. Some sprouts even developed from roots of plants that had died for no obvious reasons.

The flowers occur in axillary racemes or clusters on terminal or sub-terminal twigs. The flower-buds are swollen, and remain dormant for several months prior to the flowering season. In H. sericea and H. gibbosa, 2 - 6 flowers usually develop from each bud, but in H. suaveolens each axillary raceme is composed of up to about 60 flowers. The small, creamy-white flowers are sweet-smelling, and very conspicuous on the plant at the peak of the flowering period. The flowers are protandrous and insect-pollinated.

As a rule, a small 'additional' flower bud is visible on the stem of each cluster of flowers after eruption of the original dormant bud (Figure 1). This additional bud usually increases in size during the flowering period, and remains quite soft. It may become dormant and persist to give rise to another cluster of flowers in a subsequent year, especially if no fruits matured in the original cluster.

The newly-set fruit soon turns green, and remains soft and juicy until it is nearly full-sized. The style is persistent, and occurs between two fleshy, apical horns (see Figure 1). The outer layers of cells are chlorenchymous and firm, while the seeds and surrounding tissue remain juicy until the seeds have reached full size. The epidermis of the fruit is soft, with a smooth, shiny surface. The fruits of *H. suaveolens* frequently occur in clusters of 4 - 7, whereas those of *H. sericea* and *H. gibbosa* occur mostly singly in the axils, but often very close to one or more other fruits of similar age on the same flowering twig.

As the fruits mature towards the end of the first summer after the flowering season, their surface assumes a purply-brown colour, and may develop a few cracks. The core becomes hard and woody, and later the epidermis thickens secondarily to give it the equivalent of a layer of bark. However, as long as the fruit is alive, there is a layer of juicy, chlorenchymous cells (several cells deep) underneath the bark. The fleshy, apical horns dry out, and persist on the fruit.

The mature fruits of *H. gibbosa* (Frontispiece) and *H. sericea* are relatively large and are very similar in general appearance. They are roughly globular with a distinct narrower apical beak on which the two apical horns occur. The fruits are typically about 2 - 4 cm in diameter along the axial plane, and 3 - 5 cm wide. The length, including the beak, may be 2.5 - 4.5 cm. The surface is rough and dull grey. (However, fruits in their first year are usually easily recognised by their smoother, purply-brown surface). The layer of chlorenchymous cells is relatively thin in the fruits of these species (1 - 2 mm thick, but up to 5 mm thick on the sides of the beak and around the base next to the thickened fruit-stem).

H. suaveolens fruits are generally smaller, more rounded and the beak is not very pronounced. The surface remains smooth and quite shiny, and has a pale, yellowish-brown colour, which fades to pale grey after some years on the plant. There are numerous irregular, black, rough pits, a few millimetres in diameter, all over the leathery layer of bark. There is a relatively thick layer of juicy chlorenchymous cells surrounding the woody core.

The two seeds occur together in a small seed cavity between the two halves of the fruit. The seed cavity is closer to the axial aspect[1], where there is a longitudinal suture, visible to the naked eye on mature fruits, due to the narrow crack developing on the surface as the fruit becomes woody. The suture is composed of a layer of closely interlocking, woody granules, about 0.4 - 0.8 mm thick. Looked at on an opened fruit, the granular layer is generally a few millimetres wide (see Figure 10, facing p. 143). It is at its widest next to the seed cavity, and narrower towards the apex of the fruit. However, the width varied considerably in different geographical forms of at least _H. sericea_ and _H. suaveolens_. These differences in fruit structure as well as those in other characteristics, e.g. shape and size, were apparently not entirely a result of local conditions, as they also occurred in cultured plants. Fruits that matured under adverse conditions were often considerably smaller than fruits formed in normal seasons, and although there were indications of secondary growth after maturation of the fruits, the amount of growth appeared to be too small to account for a considerable increase in size.

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[1] Morphologically the axial suture is formed between the lateral edges of the single carpel. However, due to twisting of the fruit-stem, there is no fixed orientation of the mature fruit in relation to the original floral axis or fruiting branch.

The seed has a thin, fibrous, black testa, which is produced to form a broad, membranous apical wing. The two seeds occur with their flat inner surfaces tightly together in the fruit, and the lateral, convex portions of the testae have several ridges and protuberances roughly conforming to the inner surface of the seed cavity in the follicle. The seeds contain no endosperm, and the cotyledons are relatively soft and juicy.

2.33 Habitat

The plants occur in typical sclerophyll heath, or occasionally as part of an understorey in open sclerophyll woodland or forest. They may survive in very exposed positions, e.g. on wind-swept coastal dunes and rocky outcrops. *H. suaveolens* may occur within a few yards of the high tide mark in Western Australia (Webb, personal communication 1964).

In their natural habitat the plants are restricted to well-drained, acid soils. These soils are typically podsols, residual podsols and sands on skeletal sandstone, and are consistently low in available nitrogen and phosphorus, and often lack the micro-elements copper, zinc and molybdenum (Specht and Rayson 1957). The amount of precipitation and its annual distribution, as well as other climatic factors do not appear to be a primary factor in the distribution of the needle-bushes.

2.34 General habits and adaptations to environment

Some plants growing in a suitable open habitat may live for 30 years or longer, and still remain vigorous. However, those occurring under a fairly closed canopy, and surrounded by tall trees, generally become scraggly and less vigorous and usually die off.

The young seedlings also favour open situations, and have little chance of survival in established plant communities, or under the parent plants. Seeds germinating in soils rich in organic matter were found to be very vulnerable to 'damping off', and this may be a further reason why regeneration in established communities was found to be practically non-existent.

There is a single annual flowering season, roughly between late autumn and late spring. However, its onset and duration are often very variable, and appear to be largely influenced by rainfall, and to some extent by the geographical form in H. sericea. The different species also have slightly different fruit-setting patterns. Thus H. gibbosa and H. suaveolens tend to set fruits during the early winter months, and usually early in their flowering season, whereas H. sericea seldom sets fruit until late winter or spring, even though it may commence flowering during autumn under favourable conditions. At Wilson's Promontory these plants usually flower from May onwards, with a peak during July, yet few fruits are set until August or September. H. sericea at drier, inland localities may not commence flowering until September or October and may continue to flower until November or even December. During some seasons a proportion of the plants may not flower at all, and very few, if any fruits, may be formed during unfavourable conditions.

A vast excess of flowers is produced by all three species, but the majority of flowers fail to set fruit. Many newly-set fruits are also aborted spontaneously.

The young fruits develop rapidly and mature within a few months. Those formed during late winter and spring are usually already quite hard and woody towards mid-summer, and they are full-grown and entirely woody before the end of the summer.

The mature fruits are retained on the plant for many years, and usually for the life of the plant. If undamaged, they remain alive and undehisced, and then only dehisce after the death of the plant or branch on which they occur, or particularly after fires affecting the plants.

One large plant may contain several hundreds, and sometimes several thousands of fruits, and even three-to four-year old plants may contain 50–100 fruits under favourable conditions.

The seeds remain viable for many years while they are still inside the healthy follicle. However, once released, they are not likely to survive very long in damp soil or leaf-litter without germination[1], as the testa is very thin and provides little protection against fungal attack, and the cotyledons are soft and fleshy.

The plants have no resistance to fires, even when the fires are mild and the leaves do not burn, and as affected plants have no mechanisms to facilitate regrowth, the entire plant dies. The fruits

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[1] It was found that released seeds stored dry in the laboratory may remain viable for several years, but that they may loose as much as 25% of their weight within 10 days under these conditions. Also, the germination period becomes considerably longer once the seeds have become desiccated. Thus fresh seeds of H. sericea germinated and the seedlings appeared within 20 – 24 days of planting, compared to approximately 50 – 57 days and 71 – 80 days under the same conditions for seeds stored for respectively one and two years prior to planting.

themselves do not burn easily, and even though their surface may be completely charred and the fruit-bearing twigs may burn under extreme conditions, the seeds are not likely to be released until after the follicles have become sufficiently dehydrated to cause dehiscing. Depending on conditions during and after fires, the seeds are normally released within a few hours or days.

Even the exposed seeds appeared to be tolerant of high temperatures. In a study of the resistance of various seeds to high temperatures, Beadle (1940) found that seeds of H. sericea were able to withstand exposure to 110°C in the dry condition for up to 4 hours without a great reduction in the percentage of germination.

As a result of the persistence of indehisced fruits on the plant, and the large numbers that may accumulate on plants, very large numbers of viable seeds may be released almost simultaneously from affected plants. It follows that numerous seedlings may appear very rapidly around burnt plants, as the proportion of germination may be very high, especially when the seeds are released into an ash-bed.

The seeds will germinate during any season of the year, but they require an initial good precipitation. The tap-root develops very rapidly even before the first true leaves are formed, and once established, the young seedling is quite resistant to drought. In the absence of vigorous competition by other species, initial growth may be very rapid. However, the first flowers and fruits are not likely to be produced until after the second, or more commonly, until after the third or fourth year. Cultivated plants of H. suaveolens apparently take several years longer to produce the first fruits, but it is possible that this may not be the case in their natural habitat.

2.35 *Hakea nodosa*

Very soon after commencing studies of the insects attacking the needle-bushes (*H. sericea* and *H. gibbosa*) of south-eastern Australia, it was noticed that another species of host-plant, *Hakea nodosa*, was more or less equally favoured. For one insect at least it provided a major source of field-collected material. Since this species differed from the other main hosts in many of the most interesting characteristics, it was often used in experimental studies. For these reasons the following brief description of the species is given to contrast with the 'true' needle-bushes.

The plants occur in Victoria, the south-eastern parts of South Australia, on some islands in the Bass Strait, and in Tasmania. They usually occur in a characteristic vegetation complex in moist, often swampy situations.

They frequently develop into tall, very slender shrubs (12 - 20' tall), but specimens in lower heath may remain smaller than 3' in height. They may have a single main stem, but more frequently they have several stems from the same root-crown. The slightly flattened leaves are more fleshy, and softer than those of needle-bushes and of a paler green colour. The leaf-tips are truncated, and are therefore not prickly.

The flowers are greenish and relatively small and inconspicuous, but they have a very characteristic musty odour. They occur in clusters in leaf-axils, and also against the older, bare stems.

The flower-buds are very small, and new ones may be formed during many successive years at the same position on the stems.

The young fruits do not have the typical 'horns' of needle-bushes, and taper apically to a blunt point where the style occurs. Mature fruits are approximately globular, and of the same general size as those of H. suaveolens, or, under optimal conditions, approaching the size of those of H. sericea. They typically have a series of nodules on the surface, except on the area along the suture, and in the groove along the adaxial aspect. The layer of chlorenchymous tissue under the bark is very thin, and the granular layer in the suture is very narrow (1 mm or less), with a wide space between it and the seeds. Fruits of various ages frequently occur together in clusters of 4 - 7 against the stems.

This species differs from needle-bushes in its faculty to sprout prolifically after fires from a lignotuber below ground-level. Sprouts also formed very readily on even the old, bare stems, e.g. when these were damaged or cut off. The new shoots of plants damaged by fires may flower and set fruit within two years, thus there may be a relatively short period during which fruits are not present on the plants.

At Wilson's Promontory flowering commenced during late summer, and fruit-setting occurred during late winter - generally a month or two earlier than in H. sericea at that locality.

2.4 PARTS OF THE PLANTS ATTACKED BY INSECTS

2.41 Vegetative parts

2.411 Foliage and young growth

These were attacked by a variety of lepidopterous leaf-feeders, mainly in the families Xyloryctidae and Geometridae. Some species of Nctodontidae, Tortricidae, Psychidae and Arctiidae were encountered. Nearly all these insects also fed on flowers and young fruits when these were available. Several of the same species were also reared from other proteaceous plants, and some had a very wide host-plant range in the field.

Curculionid and lepidopterous leaf-miners attacked young leaves, and some minute torymids (Hymenoptera) developed in leaves. A variety of hemipterous and homopterous sap-suckers attacked leaves and other soft tissue on the plants. The adults of a number of coleopterans, mainly in the family Curculionidae, but also chrysomelids, fed on foliage to a varying degree, and some of these were known enemies of unrelated plants.

2.412 Stems and twigs

Larvae of two cerambycids commonly attacked *H. gibbosa* and *H. sericea*. One (*Aphanasium australe*) usually occurred gregariously near the base of the main stem and sometimes going into the roots. The other, (*Uracanthus triangularis* Hope) occurred in thinner branches higher above ground-level. Both caused damage that may be regarded as of potential value in biological control of needle-bushes. Buprestid larvae tunnelled under the bark on thicker stems and branches of *H. suaveolens*, but the damage was apparently unimportant.

An incompletely investigated complex of gall-forming cecidomyids (Diptera) and possibly associated hymenopterans developed in thinner stems of the eastern species and caused deformation and die-back of shoots, and gregarious chalcidoids formed large galls, apparently of less significance in twigs of H. suaveolens. A variety of coccoids occurred on stems and twigs. They sometimes also occurred on leaves and fruits. The damage caused under field conditions was usually negligible.

2.413 Roots

Curculionid larvae were occasionally found feeding on vast amounts of scar tissue on roots just below ground-level, and may have been responsible for the local thickening and necrosis of affected roots.[1]

These larvae occasionally attacked stems covered by sand (e.g. on dunes). Growth and fruit production of affected plants appeared to be largely unimpeded.

Near Canberra larvae of the cerambycid A. australe (see above) tunnelled in the thicker sub-surface roots of the local form of H. sericea and caused the death of particularly the plants that had sprouted from these roots.

2.42 Reproductive parts

2.421 Dormant flower-buds

At least one torymid species (Hymenoptera) developed in bud-galls, and thus reduced the number of flowers produced. Occasional

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[1] Unidentified nematodes were found in some of these 'galls', as well as in deformed, and necrotic tap-roots of young plants at other localities, but their relationship with the plants was not determined.

branches, or even entire plants with practically no unattacked flower-buds were encountered despite heavy parasitism of these insects. They had been recorded from a number of *Hakea* spp. in eastern Australia (Riek 1966).

Eriococcids occurring in the leaf-axils apparently destroyed a few flower-buds of *H. sericea* and *H. gibbosa*.

The adults of several curulionids, notably of those whose larvae developed in leaves or young fruits of the host-plants (*Cydmaea* spp. and *Erytenna* sp.) fed extensively on the flower-buds during the non-flowering season, but the damage is probably insignificant under natural population densities.

2.422 Erupted flower-buds and flowers

Larvae of a small curculionid developed inside flowers of at least *H. sericea*. The flower is attacked just prior to opening; the ovary, pistil, stamens and inner surface of the perianth are consumed, and the larva apparently destroys several flowers during its development.

Adults of the *Cydmaea major*/*Erytenna* sp. complex (below), also damaged large numbers of flowers by eating mainly the ovaries, pistils and stamens in flowers of various ages. In addition they consumed, or caused abortion of newly-set fruits.

2.423 Young fruits

A large proportion of young fruits of *H. sericea* and *H. gibbosa* were destroyed by larvae of the *Cydmaea major*/*Erytenna* sp. complex, and there were some indications of similar damage to *H. suaveolens* by a closely related insect.

Larvae of *Parastranga macrogona* Meyr. (Tortricidae) developed in a small proportion of young fruits of *H. sericea*, and larvae of several leaf-feeding lepidopterans (mentioned above) also destroyed a small number of fruits. Lygaeids, mirids and psyllids apparently caused abortion of newly-set fruits by feeding on the sap.

2.424 Mature fruits

Larvae of the cerambycid *Aphanosperma occidentalis* Britt. tunnelled in fruits of *H. suaveolens* and destroyed the seeds of a large proportion of fruits. Similar larvae were occasionally found in fruits of *H. sericea*.

Larvae of an unidentified cryptorrhynchine curculionid tunnelled in the woody follicles of a small proportion of *H. sericea* fruits and consumed the seeds. Larvae of two other curculionids attacked the mature fruits without consuming the seeds. One of these, *Dixoncis pictus* Oke, developed mainly in the soft, chlorenchymous tissue under the bark, and caused dehiscing, and thus untimely release of a considerable proportion of seeds of *H. sericea* at Wilson's Promontory. This insect occasionally developed in stems of the host, causing die-back or snapping-off of thin twigs affected. Adults of a variety of curculionids and occasionally some leaf-feeding lepidopterans, fed on the surface of mature fruits, but apparently with no harmful effect on the plant.

2.425 Seeds

At some localities, larvae of *Eurytoma* sp. (Eurytomidae, Hymenoptera) developed in seeds of *H. sericea*, but the adults often failed to eat their way out of the fruits. A considerable proportion of seeds in mature fruits of all ages were destroyed by larvae of *Carposina autologa* Meyr. (Carposinidae, Lepidoptera), and attack appeared to be restricted to fruits of certain *Hakea* spp.

The adults of an acanthosomatid bug (Hemiptera) inserted their stylets into mature fruits, both through the woody follicle or through the suture, and fed on the seeds of *H. sericea* and some other *Hakea* spp. They appeared to transmit micro-organisms that caused rotting of affected seeds. At some localities the majority of seeds on plants were not viable as a result of attack.

III ERYTENNA/CYDMAEA COMPLEX

3.1 INTRODUCTION

3.11 Background

During 1963 Webb reported extensive insect damage to young fruits of *H. sericea* at Wilson's Promontory, Victoria. The fruits appeared to have been attacked when still quite small and the dried-out husks remained on the plants. During December of the same year, curculionid larvae were found in discoloured, young fruits exuding mucilage, and the adults were reared during the following weeks (Webb, *in litt.* 1964). Specimens were examined by A. Nebois of the National Museum of Victoria, who reported as follows:

> "In our collection under the name of *Cydmaea major* was a group of specimens which undoubtedly was a conglomeration of two species, one of which fitted yours reasonably well. As you probably would know *C. major* has been described from New South Wales. Following this discovery I sent both species represented in the group, as well as some of your specimens to Dr. Thompson of the British Museum. The reply came today confirming my suspicions of there being two species. The specimens from New South Wales, which differed from yours, agreed with the type of *C. major*, but the others are of the genus *Erytenna*. Dr. Thompson did not attach any specific names to this species. As far as Catalogus Coleopterorum goes, only two species are listed there, and both are represented by specimens in our collection. The nearest one to yours appears to be *E. consputa* Pascoe,[1] originally described from South Australia. Although your specimens agree reasonably well in general characters, they differ by being more reddish in colour and one or two minor characters."[2]

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[1] The second species referred to was *E. dispersa* Pascoe.

[2] The genus *Erytenna*, and *E. consputa* were described in 1870 by Pascoe. He also described the genus *Cydmaea* in 1872. *Cydmaea major* was described from N.S.W. by Blackburn (1893).

Also during 1963, K. M. Moore (Forestry Commission of N.S.W.) reported that larvae of *Cydmaea major* Blackburn attacked young fruits of *H. gibbosa* in the Hawkesbury and Gosford sandstone soils (between Sydney and Wyong, N.S.W.). The damage caused was similar to that seen in *H. sericea* at Wilson's Promontory (Webb, personal communication 1964). Moore (1964), in his list of the various insects he had encountered on six *Hakea* spp. on the central coast of N.S.W., included biological notes on *C. major* on *H. gibbosa*.

3.12 The aims of the study

Practically no information on the biological aspects of the insects was available at the onset of the study, and it was decided to study them especially in respect of their host-plant range, geographical distribution, life-history and phenology. It was hoped that the study would reveal definite mechanisms of host-specificity that would demonstrate the insects to be safe for introduction into any region where their host-plants have become noxious weeds.

3.13 The identity of the insects: *Erytenna* sp. versus *Cydmaea major*

Initially the insects appeared to be geographically isolated and restricted to their respective *Hakea* spp. Specimens reared from *H. sericea* at Wilson's Promontory were generally smaller and more reddish - brown than those collected from *H. gibbosa* at Gosford. However, as infestations were found at more localities, and larger series of specimens became available, overlaps in size and colour between the two groups became evident. In particular, a series of adults from H. sericea plants at Genoa near the N.S.W. - Victoria border appeared to be a mixture. While some of these specimens were grey-brown and resembled the typical C. major more closely, others were reddish, like typical specimens known from Wilson's Promontory. The majority however, could not be placed confidently in either group on appearance and size alone.

A series of specimens representing the range of sizes and colours within each of the two main groups (ex H. gibbosa, Gosford, and ex H. sericea, Wilson's Promontory), as well as those from Genoa, were submitted to Dr. E. B. Britton (Curator of Coleoptera, Division of Entomology, CSIRO, Canberra) for comparison. (One slightly larger adult, No. AcHa 156, taken from H. dactyloides near Eden, was included.) Dr. Britton (in litt. 1966) commented:

> "I believe these all belong to the same species, except possibly No. 156. This specimen agrees with a specimen in our collection labelled Cydmaea major Blkb. by Lea. On the other hand, the remainder of the specimens agree with Blackburn's description of major, as far as it goes. It is not impossible that No. 156 is also a variant, i.e. the box includes only one species - major."

He recommended that more specimens should be sent to R. T. Thompson for comparison with the type of C. major. The matter was again taken up with Thompson, but no finality was reached at the time of writing.

During the study it was not always possible to place specimens into one or the other group. No morphological differences warranting separation were known to the author. Congenerity and later conspecificity, were increasingly suspected on biological grounds. It was therefore decided to treat the insects from host-plants in

New South Wales and Victoria as a single biological entity for the purpose of the study, mainly on the strength of the following :-

1) *Similar biology and phenology*: The durations of the egg, larval and pupal stage in the laboratory were always comparable. Field-collected females from all localities were in similar 'reproductive diapause' during the same long period of the year;

2) *Similar habits*: Comparable behaviour of newly-hatched, feeding, and pupating larvae both in the field and in the laboratory. The sheltering, feeding and oviposition behaviour and preferences of the females were similar;

3) *Similar effect on the host plants*: Manifested in the damage to large numbers of immature fruits that remain visible on living plants for several years;

4) *'Interchangeability' of hosts*: Larvae from *H. sericea* in Victoria were reared on *H. gibbosa* from N.S.W., and *vice versa*;

5) *Apparent confusion in identity in collection records of museum specimens*: Specimens from Lucindale, S.A. are labelled '*C. major*' in the collection of the South Australian Museum, yet those in the National Museum of Victoria from the same locality are labelled '*Erytenna* sp.', grouped with specimens labelled '*Erytenna* sp. nr. *consputa*' from Wilson's Promontory, and are separated from 'C. *C. major*' and '*E. consputa*' in the latter collection. Under the *E. consputa* series in the South Australian Museum, there is a note in A. M. Lea's handwriting saying: "See if *Erytenna consputa* Pasc. from descr. - var. of *Cydmaea* Bl. and that either *Erytenna* or *consputa* a synonym" (G. F. Gross. *in litt*. 1968). Series of the two 'species'

TABLE I

The occurrence of copulation between males and females of the complex of *Erytenna* sp. nr. *consputa* Pasc./ *Cydmaea major* Blkb, from different host-plants from various localities within the distribution range of the insects.

No.	MALE		FEMALE		Copulation during first two hours
	Locality	Host*	Locality	Host*	
1	Wilson's Prom.	*sericea*	Gosford	*sericea*	Positive
2	Same male as in 1 above		Bargo	*sericea*	Positive
3	Same male as in 1 above		Mittagong	*sericea*	Positive
4	Same male as in 1 above		Wilson's Prom.	*sericea*	Positive; many attempts
5	Mittagong	*sericea*	Wilson's Prom.	*sericea*	Several attempts
6	Wilson's Prom.	*sericea*	Gosford	*gibbosa*	Two attempts
7	Gosford	*gibbosa*	Wilson's Prom.	*sericea*	No attempts
8	Mittagong	*sericea*	Same female as 7 above		No attempts
9	Wilson's Prom.	*sericea*	Same female as 7 above		No attempts
10	Wilson's Prom.	*sericea*	Wilson's Prom.	*nodosa*	Positive
11	Wilson's Prom.	*nodosa*	Wilson's Prom.	*sericea*	Positive

* From which collected as egg, larva or adult, or on which the previous generation female was found in case of adults reared from eggs laid in the laboratory.

are in both the above museum collections, and according to these, C. major had been collected in N.S.W., Vic. and S.A., and E. consputa in Vic., S.A. and W.A., often at corresponding localities in the two central states;

6) No apparent mechanisms for sexual isolation: Under experimental conditions, individuals from different geographical regions showed at least attempts at mating, and successful copulation also occurred readily. In Table 1 it is shown that males from Victoria (Wilson's Promontory) copulated with females from eastern N.S.W., and that several attempts were noticed between males from N.S.W. and females from Victoria. Furthermore, one particular male from Wilson's Promontory stock mated successively with females from three different localities in N.S.W. and then also with a female from Wilson's Promontory. No attempt was made to observe whether sperm transfer occurred as females reared in absence of males were not available at the time. Due to the long pre-oviposition period, and the failure of the majority of laboratory-reared females to produce any eggs within at least the first year, it is not known whether matings between the different groups were necessarily successful.

For the sake of convenience the insects of the complex of 'Erytenna sp. nr. consputa Pascoe' and 'Cydmaea major, or variants' will be referred to as 'Erytenna sp. nr. consputa Pasc.' (or 'Erytenna' for brevity), on the assumption that C. major Blkb. will be proved a synonym upon comparison of the types (Britton, personal communication 1968), and that the present complex may be distinct from E. consputa Pasc.

3.2 METHODS

3.21 Host-plant range in nature

While apparently only the young fruits of host-plants were attacked, initially all vegetative parts of these plants were examined for signs of insects developing in them. Examinations of potential hosts could be made at any time of the year because damage to the known hosts remained visible for several years, and the adult weevils were found to be present throughout the year.

The fruits of 17 species of Hakea encountered in eastern Australia (two of doubtful specific status, and two introduced to their localities), and of six species in western Australia, were examined for typical damage (i.e. dry, hollowed-out, young fruits on, or underneath the plants). When Erytenna attack was suspected, the damaged fruits were examined for exuviae and other indications of the insect responsible, and the plants searched for the presence of adult weevils and oviposition holes in the fruits, leaves or buds.

Other Hakea spp. in the vicinity of hosts were carefully examined for signs of damage and for sheltering adults. When the adults were known to be relatively active on the host-plants, beating onto a tray was used to determine their presence on plants in the vicinity.

At localities where the insects were known to be abundant, special attention was given to other proteaceous plants and to plants in other families, which had fleshy fruits of similar size to young Hakea fruits. Damage to other plants was examined microscopically when doubt existed.

3.22 Geographical distribution

The survey was not intended to cover the whole of Australia, or the distribution range of the numerous *Hakea* species. Fieldwork was restricted to mainly coastal regions of south-east Australia (between Brisbane on the east-coast and Mt. Gambier on the south-coast). Brief visits were made to south-western Australia and Tasmania. All the main regions where *H. sericea* and *H. gibbosa* were known to occur, were included in the survey.

When damage was encountered, adults were collected for identification or developmental stages were collected for rearing in the laboratory.

3.23 Phenology and general biology

Visits at various times of the year were made to different localities where the insects occurred. Observations were made on the stage of development of the host-plants and the relative abundance of the different stages of the insects. When present, samples of young fruits were collected for microscopic examination for the presence of eggs, larvae and the stages occurring in the pupal cells (mature larvae, prepupae, pupae, and newly-emerged adults). When it became evident that eggs were not necessarily all laid in the fruits, other parts of fruiting plants were examined *in situ* for eggs, and if necessary, removed for dissection. All stages encountered were collected for further observations in the laboratory, and adults were collected and dissected to determine the stage of development of the gonads.

Wilson's Promontory was selected as a suitable locality for repeated observations on the phenology of the insect (and for collection of laboratory material) and 17 visits to that area were made during the study period. Five visits at irregular intervals were made to the Sydney-Gosford area, and the observations made there, and those made during occasional visits to other localities, were compared with, and interpreted in the light of those made at Wilson's Promontory.

Prolonged observations in the laboratory were required for data on the maturation of the ovaries, fecundity and fertility, and longevity of the adults. Laboratory conditions never proved to be entirely satisfactory because of 1) the very long periods involved, 2) high premature mortality and low fertility, and 3) the relatively large numbers required for comparison under controlled conditions. It was therefore often necessary to rely heavily on the indirect, uncontrolled observations made on field-material.

3.231 Pre-oviposition period and maturation of eggs

For observations on the development of the gonads of females in relation to the food consumed, groups of weevils were placed in sleeve-cages on branches of plants in the field. The cages were cylindrical, about 18" long and 10" in diameter. Fibreglass-gauze was used after ordinary fly-wire was found unsatisfactory. The sleeves were shifted at two-month intervals. The plant material contained was examined both before enclosing the insects and afterwards for signs of feeding and oviposition. The adults placed in the sleeves

(21 per sleeve) and those used as control groups in Canberra, were all from the same population collected on Hakea nodosa during April. Each group was selected to contain the normal proportions of males and females, and of 'old' and 'young' individuals (see below). Three females were removed from each sleeve at two-month intervals for comparison of their general physiological state and development of the ovaries.

The adults were dissected in a saline solution, and for more critical examination, the ovaries were stained with aceto-carmine and mounted, following techniques outlined by Smith (1943).

3.232 Selection of oviposition sites

There were indications that the narrow, apical horns on the green fruits of the hosts known initially, may have been an important factor in the selection of egg-laying sites. Females were observed on model-fruits of painted balsa wood on which simulated horns of balsa wood, polyporus, plasticine or the fleshy, elongated leaf-tips of H. nodosa were **attached**. When it became known that eggs were also laid naturally in leaf-tips, females were observed in small containers with the elongated, fleshy leaves of known hosts and non-host plants. Females were also provided with leaves of H. nodosa, painted black, white or green; or covered with a layer of wax. The results of these experiments, and other observations indicated that laboratory conditions were unrealistic. The phenomenon of egg-site selection was subsequently only studied on plants in the field.

TABLE 2

The characteristics used to estimate the age of adults of *Erytenna* sp. nr. *consputa* Pasc. collected at Wilson's Promontory early in the non-reproductive season.

		IN FIRST SEASON 'Young adults'	IN SECOND SEASON 'Old adults'	IN THIRD OR LATER SEASON 'Very old'
GENERAL APPEARANCE	General appearance	Almost velvety, reddish brown with coppery sheen.	Paler reddish-brown to grey-brown.	Mainly smooth brown and black, often 'lacquered and dusty'.
	Scales on integument	Practically full complement. Orderly arranged and undamaged.	Brushed off or damaged, exposing bald integument at exposed situations.	Very few of larger scales left, or mostly damaged, exposing integument.
	Colour of scales on venter	Coppery	Silvery, with faint coppery sheen.	Dull white (very few present).
PHYSIOLOGICAL CONDITION	Fat-body, and urate cells (olive-green)	Absent, or at most a few pale yellow cells in slender strings. No urate cells early in season.	Yellow, normal size, in thick ribbons on gonads and tracheae. Some urate cells, mainly around caudal spiracles.	Yellow, normal size and shape. Many urate cells throughout tissue.
	Spermatozoa in spermatheca	None found early in season.	Present, active.	Present, active.
	Oviducts	Short, smooth.	At least one, usually all four stretched and shrivelled.	All stretched and shrivelled.
	Yellow-body at base of oviducts.	None	Small quantity in at least one oviduct. Pale, to deep yellow and clearly visible.	Clearly visible, sometimes orangey.

3.233 Estimating the age of field-collected adults

During the study it became evident that the adults probably lived two or more years in the field. Initially the specimens were divided into four arbitrary groups, using mainly the colour and state of the scales on the body. Later a method was developed to confirm their age on physiological evidence obtained by dissection. As a result, the arbitrary categories were regrouped and designated as 'young adults' (those in their first season), and 'old adults' (those in their second or later season). The occasional individuals showing considerably more wear than the average 'old' specimen, were estimated to be at least one year older again, and in later samples separated and designated as 'very old adults'. Table 2 gives the external characteristics on which the grouping was based, and compares these with the physiological evidence observed after dissection of many of the specimens.

When classifying adults into age groups according to the characteristics listed in the Table, allowance was made for the continuation of fading and wear of the scales as the season progressed. It was furthermore kept in mind that the fat supply of young adults gradually increased, eventually to equal that of older adults, and that urate cells appeared, or increased in number during the season.

Towards the middle of the non-breeding season, some specimens showed resemblances with both young and second year adults, but dissection usually removed any doubt. The presence of spermatozoa was not used as a determinative characteristic, because mating may occur during the first season.

In the older adults there was more variability, and it was not always possible to draw a definite line between the two groups. The occasional doubtful cases were then somewhat subjectively placed into either group, mainly on the quantity of the olive-green urate cells in the fat-body, and the size and colour of the yellow bodies in the ovaries.

3.234 Determination of the sex of adult weevils

There were no conspicuous external differences between the sexes. Initially live specimens were only to be sexed accurately after observing their copulation behaviour. It was known that the shape and size of the last abdominal tergyte differed, but as it is covered by the elytra, attempts to exposing it in live specimens were not very satisfactory due to the risk of wounding them.

Later during the study it was found possible to differentiate between the sexes by observing the general shape of the large first abdominal sternite (morphologically the third), which was slightly concave in males, and generally convex in females. Males were also found to have two short, colourless bristles between the scales on the last abdominal sternite, and these, when visible, were of use in doubtful cases.

3.24 Host-range of larvae under experimental conditions

The feeding tests made were not intended to include representatives of a series of plant families, or to cover the whole range of plants with which the insects may come into contact. The primary aim was to observe the reactions of the larvae and to expose any possible mechanisms of host-specificity.

The larvae were placed on fruits of host-plants, other related plants and on a variety of other fruits and plant material available. When spontaneous entry attempts were not made by the newly-hatched larvae within a few hours, they were placed with their heads into small holes punctured in the medium to induce entry and feeding. If necessary, they were replaced repeatedly. Occasionally larvae were forced to stay inside the medium by a barrier of wax. Some of the plant materials tested (e.g. flat or needle-like leaves) were not of sufficient size to contain larger feeding larvae. In these circumstances a more substantial medium was prepared by either rolling the leaves, or placing them in layers or bundles, held together with wax or parafilm.

The larvae were compared with those in natural hosts under laboratory conditions, especially regarding the degree of acceptance of the medium, the amount of tunnelling and feeding, and the growth rate if they survived for more than a few days. When any development occurred, but the larvae died prematurely, the experiment was repeated at least once.

The media tested included i) young fruits of 11 Australian proteaceous plants (of the genera *Hakea*, *Grevillea*, *Lambertia* and *Persoonia*); ii) young fruits of the South African proteaceous *Brabejum stellatifolium*, iii) young fruits of cultivated plants (e.g. *Pyrus* and *Prunus* spp. - Rosaceae), iv) leaves of *Hakea* spp., *Protea* spp., *B. stellatifolium* and *Sedum* sp. (Crassulaceae), v) the fleshy base of an inflorescence of *Protea* sp.; vi) pieces of carrot and potato, and vii) various artificial nutrient media (cf. Vanderzant and Davich 1958; Earle *et al* 1959) based on agar and mashed *Hakea* fruits.

3.25 Testing recognition of host-plants by adults

Observations were made in a 6' x 6' x 6' cage of fibreglass-gauze on a tubular frame, placed on a polythene groundsheet in a clearing in the field. From the centre of the roof a 10-spoked circular frame of wire was suspended in a way that free rotation on a central swivel was possible. Ten units of plant material were suspended by string to hang below the frame about 3' above ground-level, neither touching each other nor the sides of the cage, and weighted down to prevent excessive individual movement. The units were arranged in a way that each of five treatments occurred in an inner and on outer circle, and was adjacent to each of the other four treatments. The units of plant material were of similar size, and their stems were immersed in water (held in polythene bottles) to prevent dehydration of the freshly-picked branches. Nine adult weevils (4 females and 5 males) from the same non-breeding population were allowed to crawl onto each unit from pieces of tissue paper attached to the foliage. Each group of adults was marked differently, and the original position of each insect was thus known when their positions were recorded 5 days later.

3.26 Collecting and rearing techniques

3.261 Collecting of experimental material

Adult weevils were collected by shaking them from the host-plants or by collecting the dry, damaged fruits of previous years in which they sheltered. The first method was only satisfactory on the few occasions when the insects were found to be highly active (usually only under warm, sunny conditions). Though often slow and tedious, the collecting of dry fruit-husks was the most reliable method of obtaining adults under a variety of weather conditions at any time of the year. Using the general size, colour and degree of dehiscence of the fruits, it was later possible to recognize at a glance, and to collect only those more likely to contain adults.

The dead, partly dehisced fruits were collected directly into polythene bags (or, under wet conditions, temporarily into bags made of fibreglass-gauze). Half-full bags were then left upright in a warm situation, and the adults collected as they crawled upwards, usually within the first four hours. Approximately 80-90 p.c. appeared during the first 48 hours, but some of the individuals remained in the fruits for up to 35 days.

Eggs and young larvae. At localities where eggs were laid predominantly in the apical horns of fruits, large numbers of eggs could be collected during spring by selecting green, young fruits that showed the typical dried-out horns, These fruits were carefully picked and wrapped in soft, absorbent tissue, and held in a cool place in sealed polythene bags until examination in the laboratory. Any newly-hatched larvae and the horns containing unhatched eggs were removed from the fruits as soon as possible. [Those truncated fruits not already entered, could then be used for rearing larvae in the laboratory.] Collecting of large numbers of eggs from leaves and buds was not practicable as they were not easily detected on the plants.

Sexually mature females usually laid some eggs in the laboratory within the first few weeks of collecting, and thus a supply of eggs of known age was often available. Advanced larvae and pupae were obtained by collecting the dying fruits in which they occurred. These attacked fruits were darkened, often exuded mucilage and were usually quite conspicuous. For transport and temporary storage, the fruits were held between layers of absorbent paper in polythene bags.

Slightly later in the season, attacked fruits in the field were harder, dehydrated and often partly dehisced, and then usually contained advanced pupae, or young adults still inside the pupal cells.

Fruits containing mature larvae or pupae were also eventually a suitable source of newly-emerged adult weevils, when spread out in a humid, but well ventilated situation, and left there for a period of 4 - 8 weeks.

3.262 Rearing in the laboratory

Adults held in the laboratory or used for other observations were usually marked with small dots of enamel paint on the thorax and elytra to facilitate identification. A system in which various combinations of colours and positions of the dots were used, allowed ready reference to their sex, age, source, etc., and did not appear to have detrimental effects on the insects.

The adults were generally confined singly, in pairs, or in groups of up to 20 in polystyrene jars of various sizes. The lids were provided with holes over which gauze had been glued. Discs or squares of dampened filter paper were placed at the bottom and moistened or replaced when necessary. Jars with a thin layer of plaster of Paris at the bottom required less frequent moistening (and prevented rapid wilting of the plant material), but were not so easy to keep clean, and the insects were subjected to fungi growing on the integument. For general purposes, jars of 3" x 1½", with a hole of 3/4" diameter in the lid, covered by gauze of approximately 40 - 50 mesh, gave the best results, provided that the plant material was replaced at least three times a week. To prevent an accumulation of CO_2 in the containers, the amount of plant material supplied was kept as small as possible, and the tubes were exposed to natural, or suitable artificial light.

For special purposes, adults were confined in large cages of stainless steel and gauze, measuring 18" x 18" x 18", or in cylindrical gauze cages (6" x3½" diameter). These two types of cage were less convenient for general purposes because of rapid dehydration of the food and the difficulty of finding eggs.

The adults were supplied with young, terminal twigs of the host-plant unless otherwise stated. Supplies of twigs were collected during field trips and stored at 4 - 8°C. When the supplies ran out, or became unsuitable, twigs were collected at weekly intervals from the local <u>Hakea</u> plants on Black Mountain (Canberra). Whenever possible, twigs with flowers or swollen buds were collected, but during the summer months only small, dormant buds were present on the plants. Before it was suspected that the physiological state of the food may be critical in the development of the ovaries of the females, the source, state and age were not always recorded.

From one to three twigs, approximately 2½" in length, were routinely placed in each small container with adults and replaced up to six times per week, unless otherwise stated. Potted seedlings of H. sericea or cut branches with their stems immersed in water, (or in diluted commercial nutrient solution), were supplied to adult weevils in larger cages not required for specific or regular observations.

For incubation in the laboratory, the eggs were freed from the surrounding plant tissue when possible. They were placed on moistened filter paper in petri-dishes, sometimes additionally supplied with a layer of plaster of Paris on the bottom. Polystyrene jars with gauze lids also gave good results. The filter paper had to be kept reasonably moist during incubation. Eggs 'dropped' by females in the laboratory, and those successfully freed from plant material were less likely to go mouldy. (In an attempt to reduce contamination of larvae, some batches of eggs were rinsed in a mould inhibiting solution and placed on a layer of filter paper moistened with the same solution.) The eggs were allowed to develop at room temperatures, or preferably at a more controlled temperature of about 20°C.

Eggs survived cold storage (2 - 3°C) for up to 5 weeks, after which normal development continued. In this case those left undisturbed in the plant tissue in which they had been laid, generally survived better than loose eggs.

When attempting to rear larvae in sterilized media or processed fruits, the eggs were soaked in a 5 - 6 p.c. formalin solution for one hour, rinsed in an excess of sterilized water, and then immediately placed on the medium, observing general aseptic procedures. [A mercuric chloride egg sterilant (Vanderzant _et_ _al_. 1958) was also used.] Some eggs of various ages remained viable, but those about to hatch were the most satisfactory.

Various artificial media, reported in literature and adapted for the insects, were unsuccessfully tried, both for continuous observations and for mass-rearing of larvae. The main drawbacks of these media were their texture, consistency and vulnerability to attack by micro-organisms.

The most satisfactory technique for rearing larvae was to use the largest available, soft, green fruits from the field, and to transfer the larvae to new fruits as soon as the old ones became unsuitable. The fruits were held separately on damp filter paper in small polystyrene jars with gauze lids, similar to those described for the adult weevils. The fruits were routinely examined daily. The paper was moistened when necessary, and the larvae transferred to new fruits when they emerged prematurely. The fruits were regarded as unsuitable when they turned black, went mouldy on the surface, or became watery. As a rule, the replacement fruits were punctured with a sterile needle or surgical blade, and the larvae placed partly into the hole to encourage penetration. Freshly-picked fruits usually lasted for up to one week, but cold-stored, bruised or very young fruits had to be replaced rather more frequently.

For regular observation of larvae, the fruits were opened daily and the larvae placed into new fruits. This technique was not very satisfactory due to the time required to dissect the larvae from their tunnels, the high mortality as a result of accidental wounding and the excessive disturbance of the larvae. Furthermore the condition of the fruits supplied hardly approached that of the gradually dehydrating fruits in the field.

In an attempt to simulate this progressive change in the laboratory, twigs with the young fruits still attached were partly immersed in nutrient solution and held in a fairly dry atmosphere. Unfortunately the fruits wilted rapidly, and larvae abandoned them prematurely. Fruits without larvae intended for use when the original fruits became unsuitable, also wilted and dried out.

Larvae were successfully reared to the adult stage in steam-sterilized fruits of H. sericea held under uncontaminated conditions. The most satisfactory procedure was to place 2 fruits in a 4" x 1" glass tube with a large plug of absorbent cotton-wool at the bottom, and another of non-absorbent cotton-wool in the mouth of the tube. The fruits were autoclaved for 15 minutes at 12.5 lb/in^2, and when cooled, one or two surface-sterilized eggs were carefully placed on the fruits. Mortality was high, especially in newly-hatched and full-grown larvae, and inspection of the larvae was not possible due to the danger of contamination and the resulting decomposition of the fruits.

However, as sterilized fruits stored well, this technique allowed rearing of single larvae at times of the year when suitable fruits were not available in the field.

An only partly successful attempt was made to rear larvae in thawed deep-frozen fruits. These fruits had been frozen more than a year previously be immersing them in liquid nitrogen for a few seconds. The fruits cracked during the freezing process, and in consequence decomposed rapidly after thawing.

When the larvae being reared by any means, approached maturity, they were transferred to containers with a layer of moistened plaster of Paris into which they normally burrowed for pupation.

Pupae in undisturbed pupal cells, either in damp plaster of Paris, or inside fruits, did not dehydrate easily, and needed little attention. However, pupae whose cocoons had been opened for inspection, had to be protected against dehydration and attack by mites.

3.263 General problems associated with studying the insects in the laboratory

The long non-breeding season resulted in the immature stages being available only at a certain time each year. This adaptation to a host-plant which carried fruits suitable for larval development for only a short period each year, imposed a severe restriction on biological studies in the laboratory. The possible number of repetitions and modifications of experiments was further limited because these experiments often lasted longer than one year.

TABLE 3

The occurrence of Erytenna sp. nr. consputa Pasc. in Hakea species in different parts of south-eastern and south-western Australia.

		NSW						VIC.					TAS.			W.A.
		Newcastle	Gosford-Sydney	Picton-Goulburn-Braidwood	Blue Mountains	Canberra and district	Eden-Bombala	Genoa-Wilson's Promontory	Dandenongs	Grampians	Otway Ranges	Portland - Mt. Gambier	Lake St. Clair - Cradle Mt.	Mt. Freycinet	Mt. Wellington - Hobart	Albany district
HOSTS	H. gibbosa		●													
	H. nodosa							●	●							
	H. sericea	●	●	●	●	○?	●	●	●	●	●					
IN VICINITY OF ATTACKED HOSTS	H. dactyloides		○	◉	○		◉									
	H. ?dactyloides		○													
	H. propinqua		○		○											
	H. rostrata									○		○				
	H. salicifolia†								○							
	H. suaveolens†							○				○				
	H. teretifolia			○	○			○	○							
	H. ulicina							○	○	○	○					
WITHIN SUSPECTED DISTRIBUTION RANGE	H. epiglottis												○			
	H. eriantha						○									
	H. ?lissosperma												◉	○	○	
	H. microcarpa					⊖										
	H. rugosa											○				
OUTSIDE SUSPECTED DISTRIBUTION RANGE	H. cucullata															○
	H. elliptica															⊖
	H. glabella															○
	H. suaveolens															⊖
	H. undulata															○
	H. varia															○

● Present
○ No evidence of presence
◉ Identity not confirmed
⊖ Probably different species of Erytenna

? H. ?decurrens
† Cultivated plants

A major practical problem was the complete lack of potted host-plants in the fruiting stage during the first three years of experimenting. At the onset of the study potted seedlings were obtained, seeds were sown, and various attempts were made to transplant older shrubs from the field, but all these yielded at the most a few fruits during the study period.

The isolated and atypical plants occurring in the vicinity of Canberra, flowered irregularly and produced very few fruits. It was therefore necessary to obtain suitable host-plant material from at least one hundred miles from Canberra (and usually from localities considerably more distant).

The plants in Canberra were extensively used to provide food for the adult weevils, but it was only towards the end of the study that reasonable doubt was cast on their exact identity. It follows therefore that material from these plants may possibly have been an unsuitable substitute for that from natural host-plants.

3.3 RESULTS

3.31 Host-plant range in the field

The larvae developed only in green, young fruits during the short period before the fruits reached full size and became woody. Attack appeared to be restricted entirely to *Hakea sericea*, *H. gibbosa* and *H. nodosa* within the area covered by the study (Table 3).

There were two unconfirmed records from *H. dactyloides*: Single adults, presumed to be *Erytenna* sp. nr. *consputa*, were found sheltering in dry fruits in which they may have developed - one at

Mittagong amongst H. sericea plants; another at Eden, with no other attacked plants within sight[1]. Also, dry, young fruits of H. dactyloides near Goulburn appeared to have been attacked by curculionid larvae.

A few dry, young fruits of H. microcarpa at Pine Island (A.C.T.) showed signs of oviposition in their 'horns' and attack by curculionid larvae. The size of the exuviae and tunnels suggested that a weevil, considerably smaller than Erytenna, may have been responsible. No adult weevils were found.

Fruits of a species of Hakea (H. ?lissosperma) at Lake St. Clair, Tasmania, showed damage resembling that caused by Erytenna to hosts on the mainland. Young fruits containing larvae were found (early March 1967), but no adults were obtained or successfully reared from the larvae. (Several of the larvae were parasitized by a branconid, similar to the one attacking Erytenna.)

A few dry, young fruits of H. elliptica and H. suaveolens at Albany, W.A., showed damage and contained exuviae, apparently of curculionid larvae similar to those of Erytenna, and one H. suaveolens fruit had a typical oviposition hole in one of its horns. A single adult (?Erytenna sp. - det. E.B. Britton), closely resembling the insects from eastern Australia, was found sheltering between a cluster of fruits of H. elliptica. However, it had a very pale colour, and the elytra appeared slightly elongated, and did not have the typical pronounced tubercles near the caudo-lateral corners (see section 3.331).

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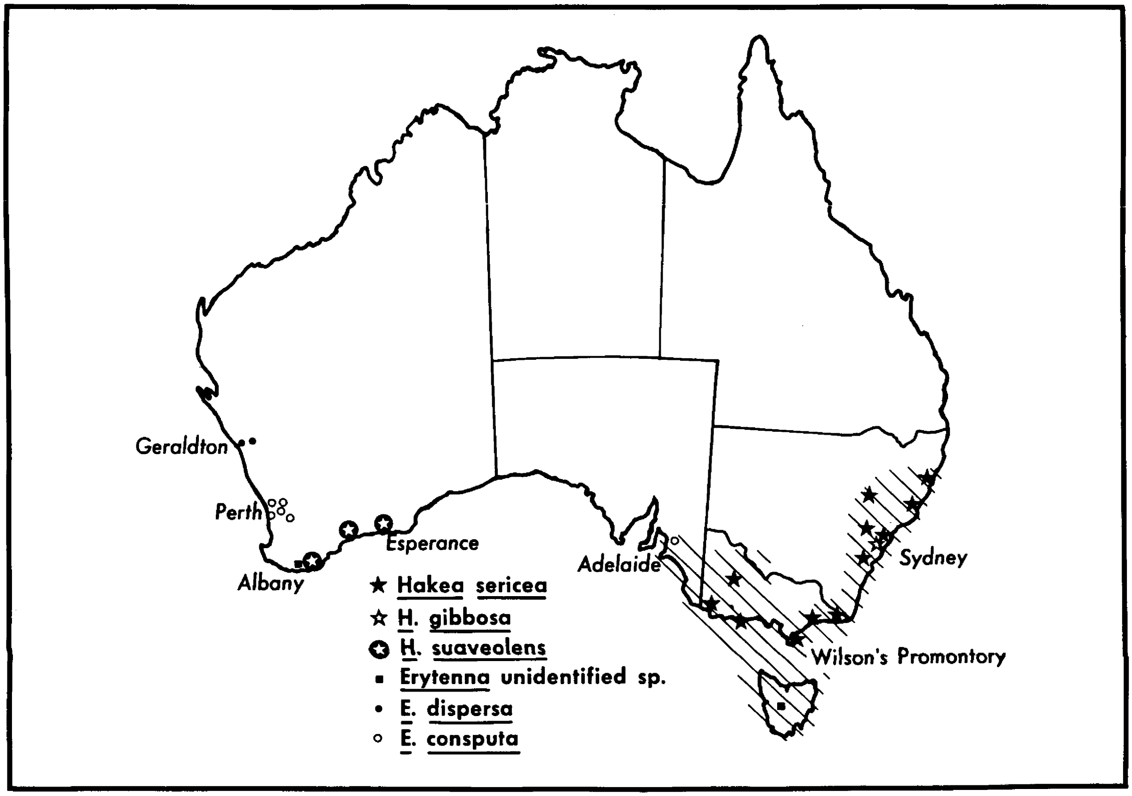
[1] Specimens in collection labelled AcHa 200 and 156 respectively.

Figure 2

Distribution of needle-bushes in Australia with the hypothetical distribution range (shaded) of Erytenna sp. nr. consputa Pasc. and localities where E. consputa and E. dispersa Pasc. had been collected



3.32 Geographical distribution

Typical damage caused by these insects was encountered in all the regions visited within the distribution range of *Hakea sericea*, *H. gibbosa* and *H. nodosa*. The insects were found to be present on *H. sericea* at various localities within the coastal regions Newcastle to Jervis Bay and Eden to Wilson's Promontory, and at the following slightly more inland localities around the coastal dividing ranges: in the Blue Mountains (Faulconbridge); at Goulburn; in the Dandenong and Otway ranges (upper Pakenham and Barwon) and also in the Grampians (Hall's Gap). *H. gibbosa* was attacked throughout its relatively restricted distribution range (central east coast of N.S.W. and adjacent highlands: Wyong - Sutherland). *H. nodosa* was attacked at all the localities where plants were encountered between the Dandenongs and Wilson's Promontory (south-eastern Victoria).

A hypothetical distribution, based on the occurrence of the known host-plants and collection records for *Erytenna* sp./*Cydmaea major* and *E. consputa*, is shown in Fig. 2. At many of the localities where the plants were known to have occurred (judging by old herbarium records), none was found, and it must be assumed that the hosts probably disappeared there as a result of European settlement.

The insects were notably absent from the three groups of *H.* ?*sericea* plants around Canberra (Black Mountain, Yass and Queanbeyan). Even within the general distribution range, occasional plants showing no signs of the presence of *Erytenna*, were found, e.g. near Mittagong, Harcourt, Pakenham, Leongatha and Foster. These plants were usually completely isolated, and were apparently remnants of former larger groups, or roadside shrubs, surrounded by cleared land.

3.33 Life-cycle

3.331 Descriptions of the different stages

The egg is ovoid to almost spherical in shape (measuring approximately 0.90 x 0.55 mm) and is yellow when newly-laid. The delicate, membranous chorion is minutely striated, but practically smooth and transparent. During incubation, a black pigment appears at the posterior, and later at the anterior pole. In eggs removed from the natural egg-chamber, the entire chorion may assume a shiny black colour. Larval parts, especially the head, mandibles, ocelli and Malpighian tubules are visible in the egg within the first half of the incubation period. Just prior to hatching, the larva may be seen moving within the chorion.

The newly-hatched larva is legless and some 1.5 mm in length. The body is relatively elongated, and tapers and flattens towards the caudal segments. The head-capsule is sclerotized and brown, with yellow lines along the sutures. The antennae are vestigial, and a pair of black ocelli occurs on either side of the head. The remainder of the body is yellow, with faint, smoky pigmentation on the dorsum of the prothorax. The integument has a number of inconspicuous, colourless hairs and is shiny and translucent. The reddish Malpighian tubules are clearly visible within the abdomen.

The older larvae, also eruciform and apodous, differ very little from the first instar larvae apart from size. The body becomes pearly white to yellowish, and progressively more curved (dorso-ventrally) and relatively broader as feeding continues. There were four larval instars under laboratory conditions. The mature larva is normally about 5 - 8 mm long. Prior to pupation the larva gets a shrivelled appearance, the thoracic segments become swollen and each develops a pair of small, ventral tubercles.

The pupa is of the exarate type with a pale, soft integument. There are fleshy, spine-bearing tubercles on the head, thorax and dorsum of the abdomen. The elytra have a series of concentric grooves. The eyes, and later mouthparts, claws and wing-tips become pigmented, but the remainder of the body is pearly white until shortly before moulting, when details of the imaginal integument become visible.

The newly-emerged adult is at first pale and soft. After inflation of the wings and elytra, the integument gradually hardens and assumes the final colours while it is still inside the pupal cell.

The adult weevil has a solid, rounded shape, and is typically about 2.3 - 2.7 mm over the widest part of the elytra, and 4.0 - 5.0 mm in length (excluding the length of the rostrum). Individuals of under 3.0 mm and of over 5.5 mm long were occasionally collected. The pronounced rostrum is slender and curved (approximately 1.3 - 1.5 mm long) and is normally held folded backwards underneath the body. The antennae are geniculate and club-shaped. The elytra each have an inconspicuous tubercle near the postero -lateral corner. The general

TABLE 4

The occurrence and relative abundance of the different stages of *Erytenna* sp. nr. *consputa* Pasc. at Wilson's Promontory, Victoria, with indications of the developmental stage of one of the host-plants, *Hakea sericea*, as found during various visits during the study period.

		1964						1965												1966												1967												1968							
		J	A	S	O	N	D	J	F	M	A	M	J	J	A*	S	O*	N	D*	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A
H. sericea	Flowering	+++		+			-		-			+	+	++	+		-		-					+			+++				-			-						+				-			-		++		+++
	Newly-set fruits	+		+			-		-			-	+	+	++		+	+	-					-			++				-			-						+++				-			-		-		+
	Green, young fruits	-		+++					-			-	-	-	++		+++	+	+					-			+				-			-						+				-			-		-		-
	Hardening young fruits	-		-			+		-			-	-	-	-		-	++	+					-			-				+			-						-				-			-		-		-
	Green, woody fruits	-		-			+		-			-	-	-	-		-	-	++					-			-				+++			-						-				-			-		-		-
	Newly-matured fruits	-		-			+		+			-	-	-	-		-	-						-			-				-			-						-				+++			-		-		-
Erytenna sp.	Full-sized eggs in ovaries	+		+			-		-			+		++				+						-			++				+			-						+++				-			-		-		++
	Eggs found	-		++			-		-									+						-			++				-			-						++				-			-		-		-
	Young larvae	-		++			+		-			-		-	-		-	+	+					-			-				++			-						+				-			-		-		-
	Older larvae	-		+			++		-			-		-	-		-	++	++					-			-				++			-						-				-			-		-		-
	Pupae	-		-			+++		+			-		-				+	+++					-			-				++			-						-				-			-		-		-
	Adults in pupal cells	-		-			+		++			-		-				-	-					-			-				-			-						-				+			-		-		-
	Newly-emerged young adults	-		-			+		+			-		-			-	-						-			-				-			-						-				+			-		-		-

-	None found
+	Some present
++	Common
+++	Predominant

*Samples of fruits received, or observations in field not made personally colour in young adults varies from grey-brown to coppery, with a paler underside. With the exception of the head, practically the entire body is covered in a dense layer of small scales of varying shapes, generally lying flat against the body. There is a series of shallow grooves, parallel to the sides, on each elytron, causing some of the scales to form slightly raised ridges in patches. The scales, forming vague colour patterns, are mainly of various shades of yellowish to reddish brown, but areas with silvery and black scales occur on the dorsum. The tubercles on the elytra generally have mainly pale-coloured scales. There are typically a few definite black lines on the dorsum of the prothorax, and its sides and postero-lateral corners are typically of the same uniform pale coppery-brown to grey-brown colour as the legs and underside of the body. With age (see Table 2) the scales fade slightly and become worn and broken, and many are rubbed off, thus exposing the black, pitted surface of the head, prothorax and underside. The elytra are basically honey-coloured to very deep brown. At certain localities older specimens were covered in a layer of dirt, giving them a uniform dark grey to dull black appearance. A few black, shiny individuals with practically no scales left, were collected.

3.34 Phenology in the field

The stages of the insects found, and their relative abundance during the visits to Wilson's Promontory are shown in Table 4. These observations indicated that eggs were laid over an extended period

TABLE 5

The sex-ratios and estimated ages of specimens of Erytenna sp. nr. consputa Pasc., in samples of the population collected at 2-month intervals during the non-breeding season from Hakea sericea and H. nodosa at Wilson's Promontory, Victoria. The figures (in brackets) indicate the numbers of 'very old adults' encountered in the samples (not noted for the February samples).

			YOUNG ADULTS			OLDER ADULTS			TOTALS		
			Males	Females	Total	Males	Females	Total	Males	Females	In sample
FEB 68	sericea Picnic Pt.	active	16	13	29	12	11	23	28	24	52
	nodosa Darby	active	19	14	33	11	9	20	30	23	53
APR 68	sericea Mt. Oberon & Tidal R.	sheltering	21	19	40	14	12	26	35	31	66 (6)
	nodosa Darby & Tidal R.	sheltering	75	54	129	28	27	55	103	81	184 (13)
JAN 68	sericea Darby	sheltering	24	20	44	14	11	25	38 (4)	31 (3)	69 (7)
	nodosa Darby	sheltering	26	19	45	11	8	19	37 (1)	27 (2)	64 (3)
TOTALS			181	139	320	90	78	168	271	217	488

TABLE 6

An analysis of the composition of the age-groups in the June and April samples in Table 5(with the numbers expected if the numbers in the three age-classes formed a geometric series, based on the observed mean ratio between the classes).

		Total no. in sample	I YOUNG		II OLD		III VERY OLD		Observed mean ratio I/II and II/III
			Observed	(Expected)	Observed	(Expected)	Observed	(Expected)	
H. sericea	April	66	40	(40.7)	20	(17.8)	6	(7.7)	1.620
	June	69	44	(44.1)	18	(17.8)	7	(7.1)	1.567
H. nodosa	April	184	129	(129.0)	42	(41.6)	13	(13.4)	1.426
	June	64	45	(45.4)	16	(14.1)	3	(4.4)	1.415

during spring and early summer; that the larvae all completed their development to the adult stage before the end of summer; and that the adults remained active and feeding on the plants for the six or more months until suitable fruits for larval development became available.

The estimated age of individuals in samples of the population present 5 - 9 months after the last breeding season (Table 5), suggested that many of the individuals of both sexes survive after their first laying season. Some may survive until a third or later season[1]. The individuals in the last two pairs of samples indicated in the table were separated into 'old' and 'very old' specimens (Table 6). The numbers in each age group are then seen to approximate to a geometric series. (In the table the calculated geometric series for the observed mean ratio between the three age classes is given in brackets.) The close fit of such data strongly suggests that a constant rate of mortality occurs throughout adult life.

There was a slight preponderance of males in all the age-groups in all the samples indicated in Table 5. This probably reflects the situation in the entire population, as the samples were taken both by shaking active individuals from plants, and by collecting sheltering specimens.

Using the observed incidence and relative abundance of the different stages of the insect at Wilson's Promontory, as well as data

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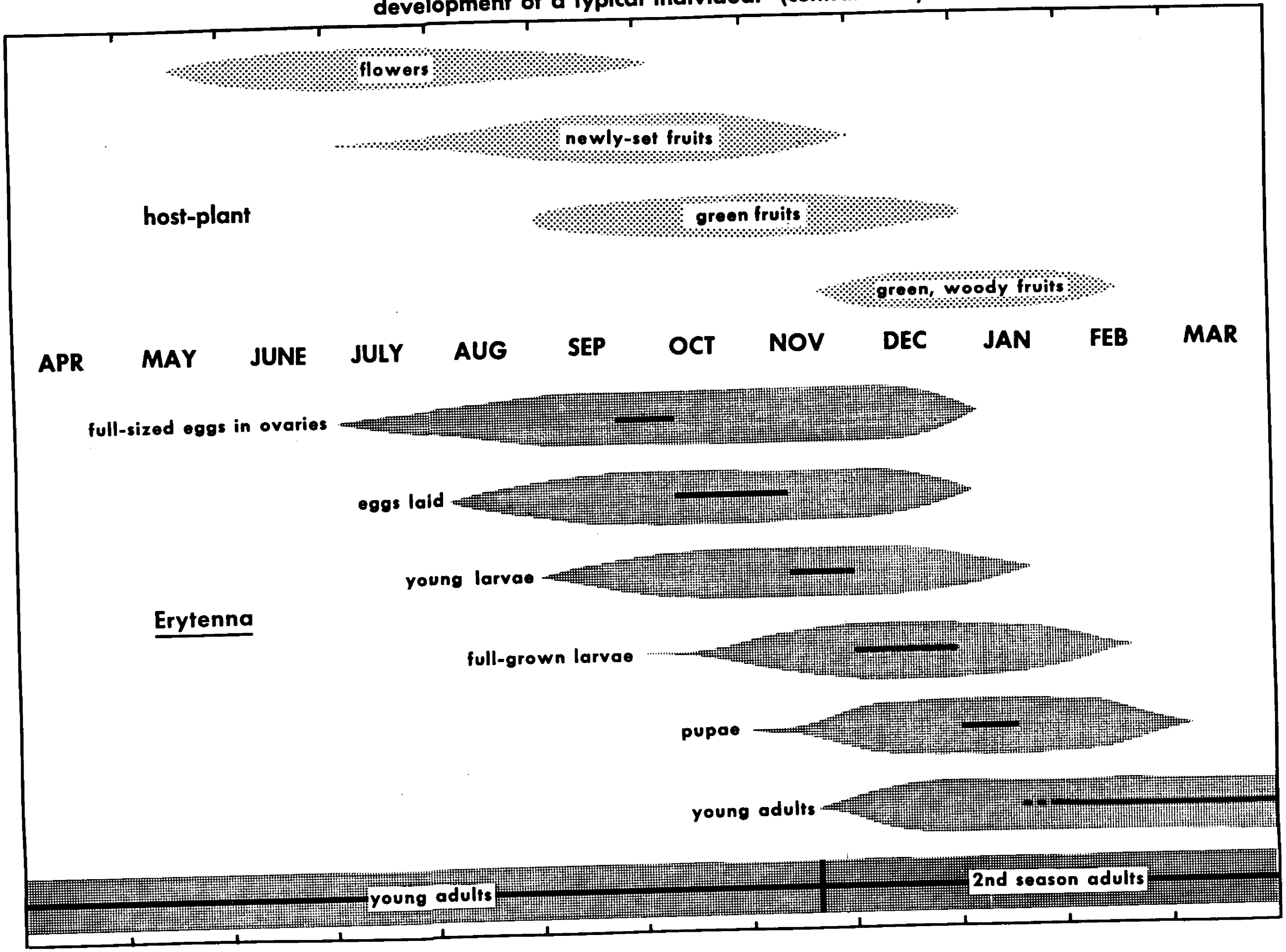
[1] Old to very old individuals were collected from at least some of the other localities in S.E. Australia and a subsequent study of pinned, dry specimens confirmed that survival until a second or later season may be a regular phenomenon throughout the distribution range.

Figure 3

Hypothetical phenology of *Erytenna* sp. nr. *conspuTa* Pasc. at Wilson's Promontory Vic. with indications of the phenology of a host-plant, *Hakea sericea* (shaded areas), and the estimated course of development of a typical individual (central lines)



on the duration of the developmental stages in the laboratory, a hypothetical phenology in relation to the host-plant at that locality was calculated (Figure 3). Seasonal fluctuations occurred in the phenology of the host-plants during the study, and therefore this model does not necessarily reflect the situation during any single year. However, the estimated course of development of a typical individual on *H. sericea* is indicated on the figure.

H. sericea commenced flowering during April at Wilson's Promontory and suitable fruits for larval development were present from approximately September to December. However, this species flowered and set fruit considerably later at inland localities. There it was not observed to flower before August, and fruits suitable for larvae of *Erytenna* only appeared during the summer months. The development of the gonads of the adult weevils occurring on these inland plants also appeared to be delayed by about three months, and females were mostly found to be sexually immature as late as September and October. (A single instance of an even greater delay was observed when an immature larva was found at Goulburn in autumn. However, survival of such 'late' larvae in the field on *H. sericea* is problematical, as the fruits become woody before the end of summer.)

The synchronization with the host-plant was even more strikingly illustrated on *H. gibbosa* in the Gosford - Sydney area, where this plant was reported to commence flowering as early as February (Moore 1964). A female containing apparently mature eggs in the ovaries was collected during May on a plant already containing small young fruits, and all the females appeared to be sexually mature during a visit in July. Mature larvae and some pupae were found as early as September. On the other hand, H. sericea in this area appeared to flower several months later than H. gibbosa (June-October according to Moore). Several plants had not yet flowered during June and July visits to the area, and during a visit in September the observed plants carried only a few newly-set fruits. However, the fruits of previous seasons showed severe attack, indicating that they do not escape oviposition by the curculionids.

The presence of mature larvae of possibly the same species in Tasmania (cf. section 3.31) may indicate an adaptation to breeding in a host-plant setting fruit during the summer months.

Pronounced fluctuations in the flowering time of host-plants were noticed, especially in the drier, inland areas. These variations were often quite local. Due to this variation, the few irregular visits made to localities other than Wilson's Promontory, and the small number of years over which these observations had been made, it was not possible to determine the typical phenology of the insects at any of these places.

In general, considering hosts at all the localities, it appeared that the females reached sexual maturity shortly after the plants commenced flowering. Eggs were available to be deposited when the young fruits appeared, and oviposition occurred over an extended period, apparently until after the fruits ceased to be favourable for larval development.

Moore (1964) stated that C. major had 3 generations each year on H. gibbosa at Gosford. However, despite the extended breeding season at Wilson's Promontory and the complete overlap of developmental stages present throughout much of this period, there was no definite evidence of even a second generation each season. The overlap appeared to be caused entirely by the long egg-laying period of the females.

Before there was evidence for a single annual generation and the variability in the breeding season was known, it was suspected that there was a facultative diapause in the females, possibly induced by climatic factors. However, further observations indicated that there was no true imaginal diapause, and that the pre-oviposition period of females appeared to be governed largely by the food available to be eaten. As this seems to provide a mechanism to co-ordinate egg-laying with the seasonal availability of fruits suitable for larval development, the subject will be dealt with here under phenology, before going on to the general biology and habits.

3.341 Factors governing the pre-oviposition period and maturation of eggs

Females collected at Wilson's Promontory during July and August usually laid eggs within a few days in the laboratory, despite the fact that oviposition in the field did normally not commence until September or October. Females in the field usually occurred singly and were more likely to come in contact with males during periods of general activity with the onset of warmer weather. To indicate

TABLE 7

The numbers of eggs laid, and the oviposition period in two groups of females of _Erytenna_ sp. nr. _consputa_ Pasc., held either in the presence, or in the absence of males from the time of collection (30.vii. 1965, Wilson's Promontory, Victoria.)

		No. of eggs laid Weeks					Total eggs	1st egg Day No.	Last egg Day No.	Longevity after collection (days)
		1st	2nd	3rd	4th	5-13th				
Females held singly	1	1	4	1	1	died	7	5	28	67
	2	0	0	0	0	0	0	-		91+
	3	0	0	0	0	died	0	-		31
	4	0	0	1	0	died	1	17	17	77
	5	3	0	0	died		3	6	7	27
	6	0	2	0	0	0	2	9	13	91+
	7	0	0	0	0	0	0	-		91+
Totals for group		4	6	2	1	0	13	(5-17)	(7-28)	31-91+
Females held with males	1	1	1	0	0	died	2	1-4	9	73
	2	0	0	0	died		0	-		24
	3	1	0	0	0	0	1	7	7	91+
	4	3	0	0	died		3	4	7	24
	5	2	0	0	0	0	2	1-4	4	91+
	6	2	1	0	0	died	3	6	13	73
	7	0	0	0	0	died	0	-		44
	8	1	0	0	0	0	1	6	6	91+
Totals for group		10	2	0	0	0	12	(1-7)	(4-13)	24-91+
Totals: All females		14	8	2	1	0	25			

whether the close contact with males under laboratory conditions may have triggered oviposition in females containing developed eggs, a number of such females were held separately from the time of collection, and compared with females from the same population confined with males. In Table 7 it is shown that there were no obvious differences in the egg-laying patterns of the two groups, except for an indication of a slight delay in the absence of males.

Sexually mature females brought into the laboratory usually ceased laying entirely within two weeks of collection, even when only one egg had been laid. This suggested that laboratory conditions, and probably the type or conditions of the food supplied to them, were not optimal for egg-laying. This suggestion was supported by the frequent failure of laboratory-reared females to lay any eggs during at least the first year. To indicate whether the type or quality of the food supplied may be important, a group of ten females were daily given freshly-picked flowers of the local Hakea, and the flowers were removed every evening to reduce feeding on flowers possibly slightly wilted, or otherwise biochemically changed. Two control groups of similar sexually mature females were supplied from a stock of flowering twigs from Wilson's Promontory and twigs without flowers respectively. The supply of food for these two groups was stored under refrigeration and replaced three times per week. A fourth group of the females, also held at 20°C, was supplied with flowering twigs of Grevillea rosmarinifolia. Although the numbers of females and eggs laid were

TABLE 8

The egg-laying pattern in groups of sexually mature females of *Erytenna* sp. nr. *consputa* Pasc. from the field supplied with different types of food in the laboratory.

FOOD SUPPLIED			No. of females	OVIPOSITION PERIOD		EGGS LAID	
Species and condition	Changes per week	Source		First egg	last egg	Total	Av.
Hakea ?sericea freshly-picked flowers	7	Canberra	10	7	15	4	0.4
H. sericea stored flowering twigs	3	Wilson's Prom.	10	2	34	15	1.5
H. sericea stored flowerless twigs	3	Wilson's Prom.	7	2	3	5	0.7
Grevillea rosmarinifolia stored and fresh flowering twigs	3	Canberra	5	106	106	1	0.2

too small to be able to draw valid conclusions in view of variation between individuals, the females feeding on stored flowers appeared to lay more eggs over a longer period (Table 8). These results suggested that flowers of the local Hakea may not provide a suitable diet for ovipositing females, and that the type of food may be involved in the maturation of eggs.

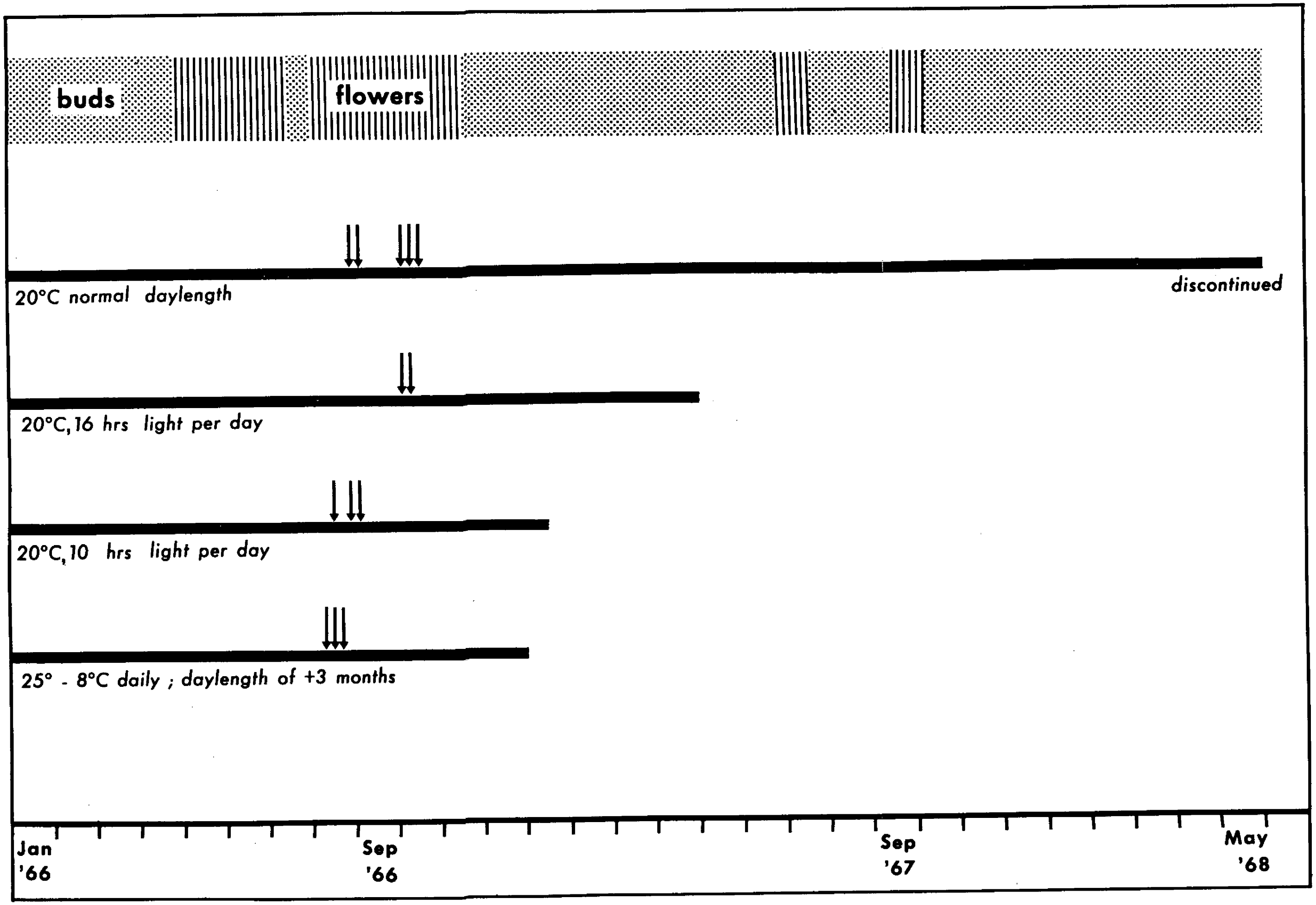
The females used in the above experiments were field-collected and mostly about to lay eggs. Attempts were therefore made to cast light on the factors - perhaps climatic conditions - causing the long pre-oviposition period. It was known that starvation was not primarily involved, as females in the field continued feeding throughout the non-breeding period, and newly-emerged females succumbed very readily in the absence of food.

To determine any possible influence of climatic conditions, a number of pilot experiments using field-collected females were made. The females were exposed to a number of different photoperiods ranging from continuous light to 10 hours light per day, and to different fluctuating and constant temperatures. No obvious differences in the general egg-laying patterns emerged, apart from (as would be expected) some delay in those females that experienced inactivating low temperatures during the observations.

When laboratory-reared adults became available, groups of females were exposed to the following physical environment treatments from the day of emergence (all the females had been reared at 20°C from

Figure 4

Influence of different daylengths on 4 groups of females of *Erytenna* sp. nr. *consputa* Pasc. with indications of the food given to them. The weeks during which eggs were laid are indicated by arrows



mature larvae collected in the field two months earlier, and were supplied with H. sericea twigs from available supplies):

1) 20°C - normal daylength
2) 20°C - 16 hrs light per day
3) 20°C - 10 hrs light per day
4) 25° - 8°C - normal daylength pattern of +3 months
daily fluctuation (regulated by means of a solar clock)

Eggs were laid by females in the first four groups after about 5 - 6 months during the first natural laying season (Figure 4), and there was only a few weeks difference between the deposition of the first eggs in the different groups. None of the females survived to go into a second laying season during the 2½ years before the entire experiment was discontinued. The variations in the length of the oviposition period, in the stage when the first eggs were laid, and in the number of eggs laid by each group, were regarded as representative of the variations expected in laboratory-reared adults. They apparently did not indicate any inherent differential effects of the treatments.

Upon subsequent analysis of the experiment in which laboratory-reared females had been used, it was evident that, apart from similar climatic conditions during the developmental stages of the individuals, the different treatments of the groups of females had in common only one obvious factor that might serve as an indicator of the season, or of the stage of the host-plant: the quality of the food they received. They had all been given exactly the same sequence of types of food throughout the experiment, as indicated on the figure.

TABLE 9

The physiological state and development of the ovaries of old (O) and young (Y) females of *Erytenna* sp. nr. *consputa* Pasc. based on dissections of groups of about 10 females collected on *Hakea sericea* and *H. nodosa* at Wilson's Promontory, Victoria at 2-monthly intervals. Data is given for the average female in each group, and where appropriate, the range in all the females is indicated.

	Relative size of fat-body		Relative amount of urate cells		Relative amount of food in gut		Colour of food in gut	Av. length of ovarioles (range in brackets) 50 units = 1.0 mm		Mean no. of oocytes in ovaries (range in brackets)		Spermatozoa in Spermatheca	
	O	Y	O	Y	O	Y		O	Y	O	Y	O	Y
February	+++	+	+++	0	+	+	greenish to creamy greenish	55 (40-70)	28 (17-40)	0	0	+	0
April	+++	+++	+++	0	0	+	whitish	52 (37-70)	40 (30-64)	8 (4-8)	0	+	+
June	+++	+++	+++	+	++	++	whitish to pale yellow	78 (58-120)	68 (55-105)	12 (8-14)	10 (4-10)	+	+
August	+++	++++	+++	+	+++	+++	greenish to pale green	160 (140-188)	164 (124-190)	26 (20-30)	26 (16-36)	+	+*

* Occasional young females with no spermatozoa found up to August

In the light of the possible significance of the type of food consumed, females were collected and dissected at 2-monthly intervals at Wilson's Promontory during the non-breeding season. Their general physiological state and developmental stage of the ovaries were compared with the phenology of the host-plant (see Figure 3) and the apparent nature of the food in the gut. In Table 9 it is indicated that there was a gradual development of the ovaries throughout the non-breeding season, especially noticeable in young females. The first oocytes were differentiated at about the time when the flower-buds became swollen prior to the appearance of flowers. The fat-body in young females appeared and rapidly increased in size prior to the flowering period. In all females there was a further increase in size of the fat-body at about the time when the newly-set fruits appeared. Due to the finely divided state of the food in the gut, it was not possible to determine the source, but the colour at different stages suggested that definite changes occurred in the feeding pattern. It is thought that the greenish colour early in the season might be due to dormant buds eaten, the white and yellow contents might be derived from floral parts, and the green colour towards the commencement of oviposition might be due to feeding on ovaries of older flowers and newly-set fruits. There was a rapid increase in the number of oocytes during the flowering period of the host-plants.

The possible sequence in the type of food taken by the adults is supported by the food-preferences observed in the laboratory. When given a choice and an excess of food, the preference appeared

TABLE 10

The development of the fat-body and ovarioles in females of *Erytenna* sp. nr. *consputa* Pasc. after two and four months in sleeve-cages on different plants at Wilson's Promontory, compared with females of the free-living population, and those reared on *H. ?sericea* in Canberra (either in a sleeve or in the laboratory). Indications of the food eaten is given. The conditions of the females at the onset of the experiment (April) was the same as that depicted for April in Table 9.

			JUNE		AUGUST					
			Oocytes per ovariole	Size of fat-body	General state of ovarioles	Follicles per ovariole	Yellow eggs per ovariole	Size of fat-body	Amount of food in gut (and colour)	PARTS OF PLANT EATEN
Canberra	In lab	*H. ?sericea*	0-1	++	approaching rudimentary, non-breeding state (germarium compact)	0-1	0	++	+++ yellow	buds, flowers
	In sleeves	*H. ?sericea*	0-1	++	normal, well-defined; germarium granular, distended	3-4	0	+++	++ creamy	buds
Wilson's Promontory		*Leptospermum laevigatum* foliage, flowers, fruits	sleeve set up in June		proximal oocytes pinkish, surrounded by white layer; other oocytes ± transparent; indistinct mass between oocytes and germarium; germarium small, not granular.	3-4	0	++	0	leaves?
		Banksia marginata foliage, buds, flowers	3-4	++	not clearly defined; proximal oocytes degenerated; germarium ill-defined ovarioles completely degenerated in one female	0-1?	0	+	0	pollen?
		H. teretifolia foliage, buds, fruits	0-1	+	proximal follicle contains diffuse mass; germarium compact	4-5	0	+++ (greyish)	+ brown	leaf-bases, fruit
		H. suaveolens flowers, later fruit also	2-3	++++	proximal follicle contains diffuse mass; germarium normal	4	0	++++	0	inflorescences, fruit
		H. nodosa foliage, vegetative buds	2-4	++++	normal, well-defined; germarium not distended	2-5	0	++++	+ green	non-dormant buds
		H. nodosa flowers, later fruiting	0-1	+++	normal, well-defined; germarium granular, distended	3-8	0-4	++++	+ creamy	buds, flowers fruits, leaf-tips
		H. sericea buds, later fruiting	0-1	++++	normal, well-defined; germarium granular, distended; 2 full-sized eggs per female	7-8*	2	++++	+++ green	flowers, buds, young fruits
	Free-living	*H. nodosa*	2-4	+++	normal, well-defined; germarium granular, distended	4-9	1-2	++++	++ green	?

*Ovary of one 'trapped' female still undeveloped to be roughly in this order: 1) newly-set fruits, and also the ovaries, pistils and stamens of open flowers; 2) the contents of not yet open flowers; 3) the contents of swollen flower-buds in the leaf-axils; and 4) vegetative buds, young growth and the surface of young stems around the leaf-bases. When fruits of a size suitable for oviposition were supplied, numerous pin-holes were eaten into the apical horns, and around the fruit stem, but this may have been related to oviposition behaviour (even though the females may not have been sexually mature).

To confirm the role of food in the development of ovaries, the general physiological state of females confined in sleeve-cages on a variety of plants in the field was observed. The plants included natural hosts, some other *Hakea* spp. and other non-hosts. Dissections were made at 2-monthly intervals during the pre-oviposition period. The results of these examinations are set out in Table 10. It can be seen that after four months in the sleeve-cages (August), only the females confined on flowering and fruit-setting branches of *H. sericea* and *H. nodosa* were in every way comparable to those of the free-living population on plants surrounding the sleeves. In these three groups the ovaries were normal and contained several developing oocytes and some nearly full-sized eggs. The only other group of females whose ovaries showed normal development during the June-August period were those confined in sleeves on *H. ?sericea* in Canberra, although the development and increase in size of the fat-body were somewhat delayed. It is interesting that the control group kept in the laboratory and supplied with food from the same host, showed practically no development despite higher temperatures. After two months (June) the females on the non-hosts H. suaveolens and Banksia marginata, and those on a non-flowering branch of H. nodosa, appeared to show development of the ovaries that exceeded that of females on the normal hosts, and also their fat-bodies usually showed considerable increase in size compared with the condition at the onset of the experiment. However, after another two months on these plants (August) their ovaries showed little further development, and possibly regression. There were definite indications that the ovaries were not normal, and showed signs of degeneration, or at least resorption of the proximal oocytes. The same phenomenon was evident in females on Leptospermum laevigatum after only two months. In this case, and on B. marginata, the fat-body was drastically reduced on size and it is possible that at most very little feeding occurred on these plants.

Some discrepancies on H. sericea with flowers and fruits are thought to have been caused by females being trapped for extended periods inside the dry fruit-husks placed in the sleeves for shelter.[1] Overcrowding and depletion of the food-supply on the flowering H. nodosa branch during the first two months may have been responsible for the initial delay in development on this plant.

The results of this experiment supported the previous suggestions that the maturation of the ovaries may be very closely linked with the

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[1] Suitable husks were selected from a supply in the laboratory, but in the moister conditions of the field, they closed up, thus trapping some sheltering adults.

quality and quantity of food eaten during the non-breeding season.

There appeared to be four distinct phases in the maturation of the gonads, each possibly dependent on the presence of different factors in the food eaten. The indicators of these phases were: 1) development of the fat-body to a certain minimal size; 2) development of the germarium; 3) differentiation of oocytes; and 4) maturation of the oocytes. The cycle appeared to be easily interrupted in the absence of the correct stimuli, and if the interruption continued for a prolonged period, resorption of oocytes occurred, and also a regression of the germarium towards the non-breeding condition. There were also indications that degeneration of the ovaries (as distinct from return to the non-breeding phase) may occur in the absence of the correct food. It appeared that development of the fat-body and initial differentiation of oocytes may occur after feeding on vegetative parts of the host (cf. H. nodosa with no flower-buds) and on different non-hosts (e.g. H. suaveolens and B. marginata), but that the continuation of oogenesis, prevention of resorption of oocytes, and maturation of eggs only occurred after some time of feeding on older flowers and newly-set fruits of suitable hosts.

By feeding on the different parts of the correct host, as they appear in the phenology of the plants, the females may be provided with a reliable mechanism to co-ordinate the maturation of eggs with the presence of suitable fruits for oviposition. This phenomenon can

TABLE 11

The typical egg-laying positions of *Erytenna* sp. nr. *consputa* Pasc. on different host-plants at four localities in eastern Australia

	H. sericea Wilson's Prom. early in season	*H. sericea* Wilson's Prom. later in season *	*H. sericea* Grampians Victoria	*H. sericea* Goulburn N.S.W.	*H. gibbosa* Gosford N.S.W.	*H. nodosa* Wilson's Prom. Victoria
In horns of fruit	++	++++	0	+	+++	N.a.
In 'additional' buds on fruit-stem	+++	0	++++	++	++	+
In leaf-tips near fruit	+	+	0	+++	++	++++

* Estimates only, due to extensive oviposition earlier in season

Ratings used:

N.a. = Not applicable
0 = None found
\+ = Some eggs (1-10%)
++ = Common situation (11-30%)
+++ = Generally favoured situation (31-70%)
++++ = Very common to exclusive (71-100%)

also be seen as an adaptation to hosts that may be very variable during different seasons and at different localities, and which may fail to provide breeding sites during adverse conditions or for a period after general fires.

3.35 General biology and habits

The eggs are laid singly in suitable young fruits, or in their immediate vicinity. The typical site appeared to be determined by characteristics of the host-plant, which may in turn be influenced by local climatic factors. In Table 11 it is shown that the large, naked 'additional' buds, frequently occurring on the fruit stems of *H. sericea* and *H. gibbosa* (see Figure 1), were favoured especially early in the season when the fruits were very small. Later in the season, when these buds were mostly destroyed, the fleshy horns on the fruits, or leaf-tips within a few inches from the fruit, were utilized for oviposition. At inland localities, the horns on fruits were usually dry, and thus not suitable for egg-laying. On *H. nodosa* eggs were laid mainly in the leaf-tips. On this plant the fruits lacked the typical twin-horns found in the other hosts, and the 'additional' buds on the fruit-stems were usually very small.

The mechanisms involved in selection of egg-laying sites, are considered below (section 3.352).

When ovipositing a fruit, the female eats a small hole into the horn and extends it inwards by inserting the rostrum into the hole. She then turns round, and explores the cavity with her ovipositor.

After this 'inspection' (and possibly further enlarging of the cavity with the mouthparts), the egg is deposited in the cavity, which is then re-examined with the extended ovipositor. A large number of typical oviposition holes in fruits had no eggs deposited in them. The reason for this was not clear. If an egg has been laid, the female then hurriedly plugs the small hole with a small amount of excreta which is carefully packed down and smoothed with the tip of the abdomen to leave little evidence of the presence of the egg. The hollowed-out horns of fruits usually dried out during incubation of the eggs.

Oviposition in leaves is very similar to that described for fruits. The cavity is eaten into the soft tissue just off the hard spike at the tip and extended towards the base of the leaf. The cells surrounding the wound may dry out and discolour, especially in young leaves.

Buds containing eggs or egg-shells dry out and are very easily dislodged, as the cavity is eaten from the base into the centre.

Upon hatching, the larva eats a small hole outwards, often through the plug inserted by the female. The legless larva moves around very actively by rapid, caterpillar-like looping of the body. In this way it may cover at least two centimetres per minute, until it finds a suitable penetration site on a healthy, young, green fruit. It eats a small hole through the skin, and gradually tunnels inwards, loosely stuffing the entrance hole with plant tissue. Fruits are usually entered somewhere on the bulging sides or on the axial aspect, but as a rule not near the base or apex.

Initially the young larva tunnels close to the surface in the relatively firm tissue of the fruit. It develops rapidly and moults in the tunnels, often damaging the cast head-capsule when feeding is resumed. The older larvae tunnel into the centre of the fruit, and consume the developing seeds and surrounding soft tissue.

Larvae were observed to complete their development in a single fruit on the plant but especially earlier in the season, when the fruits were still less than 2.5 cm in length, the majority needed two, or even more fruits for normal development. Under natural conditions, fruits attacked while very young, dry out or turn yellow prior to the completion of larval development, and are then promptly abandoned by the larvae. These older, immature larvae moving to a new fruit, enter in much the same way as newly-hatched larvae, but leave a more conspicuous entry hole. Fruits attacked in an older, green state become swollen at the entry site and exude mucilage at the wound and into the tunnels, but then gradually dry out and develop a purply-brown pigment in the epidermis. Fruits attacked after they have already become woody, usually crack, and exude masses of mucilage, and develop large, deep scars where the larvae attempted entry.

Occasionally more than one larva may enter a young fruit in the field. Larvae in fruits in the laboratory were very aggressive when disturbed, and apparently cannibalistic. When two were placed in a single fruit, one was usually found at least partly consumed within the first few days.

The fully-fed larva at the centre of the fruit eats a hole into one side, and works the sawdust back into the seed-cavity. It then constructs a regular, rounded cell, which is lined with a brownish exudation. The larva remains active in the cocoon for several days, and then pupates. During pupation the fruit continues to dry out, and becomes woody, with a leathery, brown surface.

The newly-emerged adult remains inside the intact pupal cell for several days while its integument hardens and assumes the final adult colouration. It then eats its way out, usually via the seed-cavity. At least at Wilson's Promontory the majority of fruits dehisced slightly prior to the emergence of the adult weevil. Occasionally adults remained trapped in the fruits until sufficient dehiscing occurred, or until they succeeded in eating a hole through the husk.

In the laboratory, adults leaving pupal cells commenced feeding as soon as possible. They were not able to survive starvation of 7-14 days at room temperatures. On the other hand, adults collected in the field later in the season survived starvation for up to 60 days but were then rather vulnerable to dehydration in the laboratory. They readily accepted droplets of water when starved.

Although feeding occurred throughout the season, the rate of ingestion in laboratory-kept adults appeared to increase markedly towards mid-winter, and remained high until about mid-summer.

The adult weevils spend most of their life sheltering in protected situations on the plant. The damaged fruits of previous seasons provide ideal shelter, especially those only slightly dehisced. The weevils are very well camouflaged, and appear to favour fruits that are somewhat woody and contain sawdust and other wood-litter in the seed-cavity. They come out to feed at irregular intervals throughout the year, apparently only under sunny, warm and still conditions. However, the factors governing general activity are not fully understood. On occasions the majority, or even all, were found sheltering under conditions that appeared ideal for activity. Observations in the laboratory failed to elucidate the phenomenon.

When active, the adults run up and down the needles of the host-plant, and may occasionally fly off from the tips of leaves. They are very easily disturbed, and drop from the plant, either feigning death, or flying off before reaching the ground. They appeared to be strong flyers, capable of accurately controlled flight.

Copulation was observed in field-collected adults throughout the year, but it appeared more frequent during the egg-laying season. Older females and all males contained active sperm throughout the non-breeding period. Laboratory-reared individuals were noted to copulate within the first two months of emergence, but not all young females in the field were fertilized during the non-breeding season.

3.351 Recognition of host-plants by the adults

That there were some mechanisms for recognizing host-plants, was shown by the following observations: 1) the complete absence on plants surrounding hosts in the field - even during periods of general activity, and when the non-hosts *H. ulicina* and *H. teretifolia* were in full flower, no adults were shaken from these plants at Wilson's Promontory; 2) cultivated plants of H. suaveolens near Wilson's Promontory were not attacked, although they were fruiting heavily, and occurred in close proximity to H. nodosa, on which damage occurred; 3) active females in the laboratory generally did not remain for long periods on non-host material (e.g. foliage of Protea susannae and Grevillea rosmarinifolia), although they sheltered on both these plants, and fed on flowers of the latter; and 4) adults confined in sleeve-cages on Leptospermum laevigatum, Banksia marginata and H. teretifolia in the field were sometimes found concentrated near the tops of the sleeves during periods of activity, while in sleeves on H. sericea and H. nodosa their distribution was more even throughout the containers.

In an attempt to confirm these tendencies when a choice was available, groups of marked individuals were observed in large cages containing two potted plants (H. sericea and P. susannae) of similar size. The adults were either released together in a central position and their positions noted after 24 hours, or equal numbers of distinguishable groups were placed on each plant, and their positions were recorded twice a week. The results were inconclusive, apparently as a result of the small size of the cages, and the important effect that the availability of shelter had on the number of insects present on any plant.

Observations were then made on adults offered a choice of host-plant material in a large cage in the field, using the methods outlined

TABLE 12

The positions after 5 days of individuals of *Erytenna* sp. nr. *consputa* Pasc. in groups of 18 placed on units of different plant material in a field-cage. Those not accounted for in the table were found on the walls, or sheltering in the corners of the cage.

	No. in shelter on original plant	No. active on foliage	Arrivals (and origin)	Total on plant	No. left without returning
A *Hakea sericea* with flowers	16	-	-	16	2
B *H. sericea* with buds	15	1	2 (C,E)	18	2
C *H. sericea* with flowers, without fruit-husks	8	5	-	13	5
D *H. sericea* with buds - dry	13	-	1 (E)	14	5
E *Leptospermum laevigatum*	9	-	-	9	9

in section 3.25. The choices offered to the insects were: 1) *H. sericea* foliage with flowers, 2) *H. sericea* foliage with swollen flower-buds, 3) *H. sericea* foliage with flower-buds, but previously killed and dried out in a current of hot air, and 4) foliage of *Leptospermum laevigatum*. To eliminate the effect of shelter, 5 similar fruit-husks were attached to the twigs of each unit of plant material, but a fifth treatment, similar to 1), but without fruit-husks for shelter, was included for comparison.

After five days the position of each individual was noted. In Table 12 it is shown that there had in fact not been much movement between the plants, and that the majority were still sheltering on the plants where they had been released. However, the number of departures showed a clear trend. Significantly more had left *Leptospermum laevigatum* than live *H. sericea* with shelters. The situations on *H. sericea* without suitable shelter and on dead *sericea* foliage, were intermediate. The lack of suitable shelter apparently caused increased activity, as there were several weevils moving around on the foliage of *H. sericea* where no shelter had been provided.

Overall observations on activity and host-plant selection suggested that there were basically two responses: 1) the selection of suitable shelter during periods when stimuli for feeding and activity are not predominant, and 2) activity directed at finding a suitable host. The latter may be influenced by availability of food and physical structure of the plant. (The habit of adults to run up and down the needles of host-plants may be related to the latter factor.) The responses may also be different depending on the physiological state of the females and additional responses directed at finding oviposition sites may come into action.

3.352 Selection of oviposition sites

Before it was known that eggs were laid in buds and leaf-tips, and that H. nodosa, whose fruits did not have the typical apical horns, was a host, it was thought that the shape of the fruits of H. sericea and H. gibbosa may provide a tactile stimulus to ovipositing females. The behaviour of females laying eggs in fruits, e.g. the way in which they ran up and down the fruits, and clung to a horn while excavating the egg-chamber, also supported this theory. Furthermore, females appeared to be attracted to the horned fruits of H. suaveolens in the laboratory, and laid eggs in the horns of green young fruits of this plant.

When simulated horns of plasticine, balsa, polyporus and leaf-tips of H. nodosa were attached to fruit models, eggs were laid only in the nodosa leaf-tips, and none of the others were excavated.

That the overall fruit-shape may not be important in the selection, was suggested by the fact that females in small containers laid eggs in the tips of all the elongated fleshy leaves offered to them (H. nodosa, H. suaveolens and Persoonia juniperina).

To determine the effect of colour and nature of the surface of the leaves, painted and wax-covered leaves of H. nodosa were supplied to females in small containers in the absence of other host-plant material. Although the weevils appeared to have ceased laying at that stage, cavities were eaten into the tips and elsewhere into leaves in all the treatments. The observations indicated that colour and surface may not be of significance during selection of egg-laying sites, as excavation was not inhibited as it had been on balsa, polyporus and dry young fruits.

The provisional indications were thus that the tip of any narrow, fleshy plant tissue may be suitable (provided that feeding was not inhibited).

When it became known that H. nodosa was a host, and that eggs were not laid in its fruits, the situation was reconsidered. As practically all the leaves of this plant were relatively fleshy and soft, and regarded as very suitable for oviposition, a vast loss in larvae was likely to result on this host if the egg-laying response were initiated primarily by the leaves. A search for egg-cavities in leaves, revealed, however, that the majority, and possibly all, occurred in the immediate vicinity of fruits.

An examination of egg-laying sites on H. sericea at Goulburn, where eggs are seldom laid in the usually dry horns of young fruits (see Table 11), again confirmed the suggestion that eggs were laid only in close proximity of suitable young fruits.

The experiments in the laboratory were then seen as unrealistic, as the females had apparently been under oviposition stress, and had been observed in the absence of suitable fruits. The observations made during the study, prompted the following hypothesis: The female recognizes a fruit of suitable size and condition for larval development (possibly by feeding and moving about on its surface) and an oviposition response is initiated. She then searches for an egg-laying site. To be suitable, it has to be on or near the fruit; should be of suitable size, shape and exposure to allow the female to cling firmly onto, and to eat into, it; and it should have the appropriate hardness and moisture content as sensed during excavation.

General feeding behaviour and feeding during excavation of an egg-site were usually indistinguishable, and it was therefore not known whether empty cavities that occurred in horns and buds (both in the field and in the laboratory) were a result of rejection of egg-sites. At least in the laboratory, partly excavated leaf-tips were abandoned (sometimes after the epidermal layer had been punctured from the inside) and as general feeding does not normally occur on leaf-tips, this appeared to indicate interruption of an egg-laying response. The cavities eaten into horns of fruits by females known to be non-breeding, may have been a result of an initial egg-laying response that resulted in general feeding.

3.353 Fecundity and fertility

The majority of laboratory-reared females failed to produce any eggs during their first year, and most died prior to the second laying season. Sexually mature females collected in the field seldom laid more than a few eggs each, and they usually ceased laying within a few weeks.

A maximum of 36 (and possibly 40) developing eggs were found in the ovaries of sexually mature females. At the most, four eggs

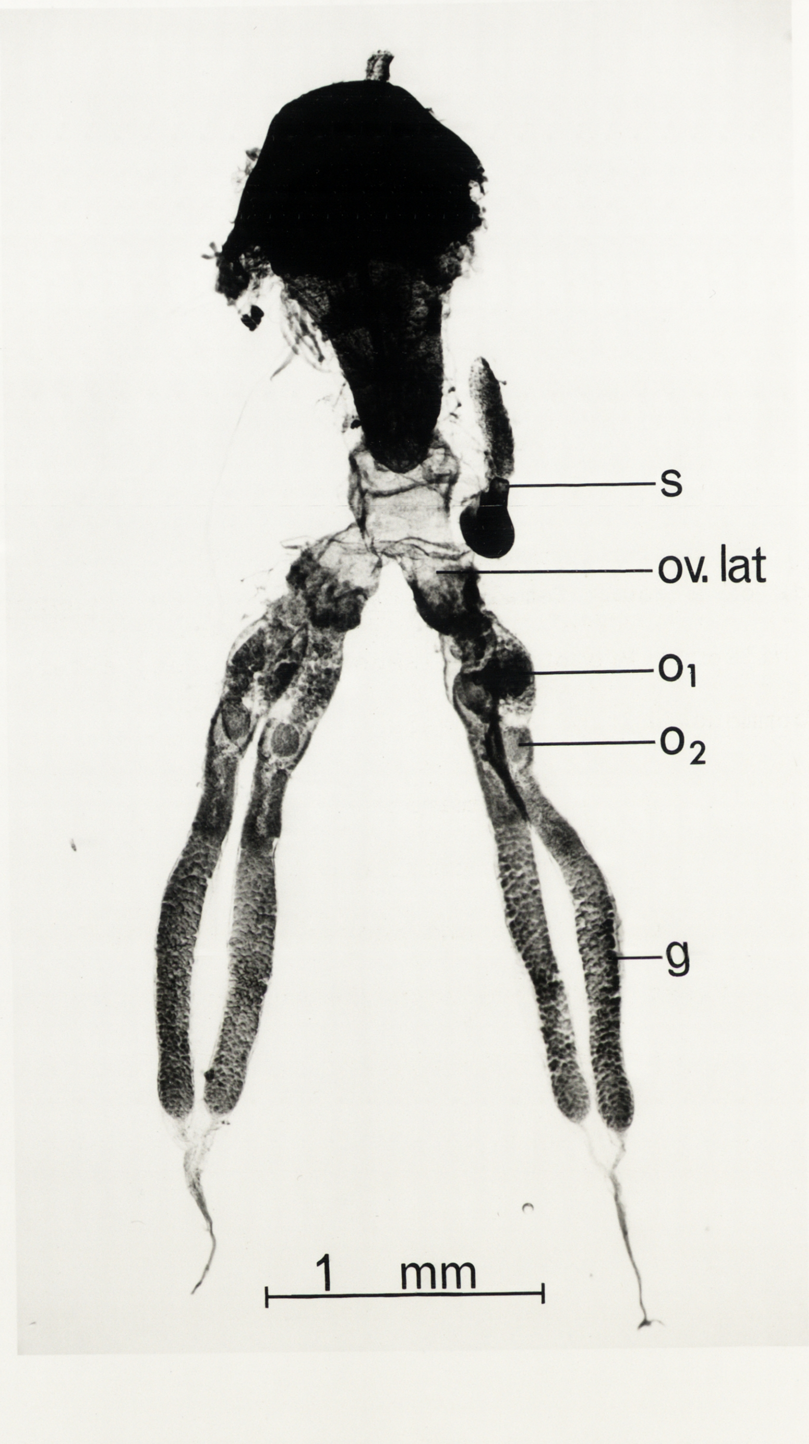
s
ov. lat
o1
o2
g
1 mm

Figure 5

Gonads of a young female of *Erytenna* sp. nr. *consputa* from Wilson's Promontory dissected (in June) after the commencement of oogenesis.

g = germarium

O_1 = proximal oocyte

O_2 = second oocyte in ovariole

ov.lat = oviductus lateralis

s = spermatheca

appeared to be mature at any stage. However, corpora lutea were present in some of the females dissected, indicating previous egg maturation. The four ovarioles are of the acrotrophic type (Figure 5). The range in sizes of the developing ova, and the gradual appearance of oocytes in follicles observed in dissected females at successive stages during the pre-oviposition period showed that oocytes were sequentially differentiated.

Laboratory-reared females produced from one to seven eggs each during a single season. Several females lived two years or longer. The only female noted to lay eggs in successive years, deposited a single egg during the first year in the laboratory, and another four over a period of 102 days during the second laying season. Females confined singly, laid eggs at a rate of less than one per two days, although two eggs were sometimes laid on the same, or on successive days.

One group of 15 field-collected females deposited 160 eggs over a period of 83 days, and then no more eggs were laid until they all died after a further 76 days (before the end of the first summer after collection). This unusually high average number of eggs laid per female (10.7) indicates that considerably more than the four full-sized eggs usually seen in any one dissection, may mature during a single season.

It appeared (section 3.341) that maturation of eggs, the number produced and the length of the oviposition period may be closely linked with the physiological condition of the females.

The fact that sexually mature females from the field 'dropped' their eggs soon after collecting, especially when suitable egg-laying sites were not provided, seemed to indicate that resorption of mature eggs did not occur. It was noticed that young oocytes were present in the ovarioles of these females for several weeks after oviposition was discontinued, suggesting that oogenesis is discontinued under unfavourable conditions. However, the fact that females surviving the first laying season did not show any signs of oocytes in follicles several months later during the non-breeding season, suggested that resorption of young oocytes occurred after the laying season.

On one occasion a female was observed in the laboratory while depositing an egg on the surface of a leaf. The egg adhered to the leaf, and the female rapidly turned round, 'examined' the egg, and then consumed it entirely. The frequency of this phenomenon is not known, but if it were at all a regular procedure, the data on fecundity of laboratory-reared females would be highly inaccurate. On the other hand, females showed no definite interest in several loose eggs often left on the bottom or elsewhere in the containers for several days.

More than half of the eggs 'dropped' in the laboratory were sterile, but those laid in leaves, etc. usually developed normally.

3.354 Rates of development

Incubation occupied from 10 - 20 days in the laboratory at room temperatures of approximately 18° - 22°C. At 20±1°C, the mean duration was 15 days for 132 eggs observed (range 13-19 days).

TABLE 13

The duration (in days) of the feeding, prepupal and pupal stages of individuals of *Erytenna* sp. nr. *consputa* Pasc. reared at 20° ± 1°C on picked, green fruits of *Hakea* species.

LARVA (a) NO.	FRUIT (HAKEA SP.)		FEEDING PERIOD (b)	LARVA OR PRE-PUPA IN CELL	PUPATION		HATCHING TO END OF PUPATION
1/65C	sericea		23				63
3/65C	"		27	11	•		•
4/65C	"		—(>14<21)—	—35—	18		53
22/65E	"		19				52
27/65E	"						45
31/65E	"		18	•	•		•
16/66C	"		26	22	19		67
20/66C	"		20	•	•		•
29/66C	"		—(>24<27)—	—40—	19		59
7/66E	"		22	•	•		•
25/66E	"		31	20	18		69
32/66E	"		42	•	•		•
37/66E	"		40	16	•		•
38/66E	"		32	18	18		68
43/66E	"		41	14	19		74
44/66E	"		45	9	19		73
72/66E	"		36	11-13	17-19		66
1/67E	"		(>19<26)				73
2/67E	"		(>14<26)				c. 71
3/67E	"		26	•	•		•
5/67E	"		22				(>69<87)
11/67E	"						c. 68
14/67E	"		22				67
17/67E	"						70
21/67E	"		22		18		70
22/67E	"		21	29			70
18/67E	"				18		70
20/67E	"		22	29	19		70
23/65E	suaveolens		18				67
24/65E	"		(>18<23)				61
26/65E	"		(>15<19)	•	•		•
26b/65E	"		19	•	•		•
27/65E	"		17				57
30/65E	"		19				68
40/65E	nodosa		(>21<28)	37			55
MEANS			—(22)—	—50—	18.5		68

(b) Up to stage when found making cell, or when it emerged from fruit to pupate

(a) E indicates '*Erytenna* sp' - from Wilson's Promontory (Vic.) material

C " '*Cydmaea* sp' - mainly from Sydney - Gosford (NSW) material

• indicates that larva or pupa died; blank space indicates exact duration of stage not observed

At 2°-3°C no appreciable development occurred, but at a somewhat higher temperature (8 - 11°C) larvae hatched from a number of field-collected eggs. (These larvae were very inactive and mostly did not emerge from the cavities in the horns of the fruits in which they occurred.)

The duration of the larval stage on picked fruits of Hakea spp. was very variable. This was probably a result of the condition of the fruits used, and the amount of disturbance during routine examinations. In Table 13 it is shown that the feeding period varied around a mean of 22 days for 30 larvae observed, but extended to more than 40 days in some cases.

The phase between cessation of feeding and pupation varied greatly in the laboratory (from 9 to 29 or more days). This variation was probably partly a result of the routine opening of the pupal cells for inspection. Furthermore, the exact time when feeding ceased and excavation of the cavity for the pupal cell was commenced, was not always clear.

Pupation occupied a regular 18 or 19 days in the laboratory in the 10 cases for which the exact moulting dates were known.

The period between hatching and the end of pupation, varied between 45 and 74 days (with a mean of 68 days for 26 observations).

The newly-emerged adult weevils remained in the pupal cells for 4 - 15 days under laboratory conditions. However, as the cocoons had been opened or damaged for inspection, this may not necessarily be the normal period. It is estimated that the adults in the field may

TABLE 14

The duration in days of larval and pupal development of Erytenna sp. nr. consputa Pasc. reared at 20 ± 1°C on fruits and media (other than picked, green Hakea fruits) on which the larvae developed beyond the third instar

Larva No.[(a)]	Reared on:	Feeding period[(b)]	Larva or prepupa in cell	Pupation	Hatching to end of pupation	Notes
76/66E	H. sericea fruit on plant	11				apparently mature, then lost after emergence from fruit
73/66E	H. gibbosa fruit on plant	19				
20/65E	H. suaveolens young leaves	>42				apparently full sized when it died
51/65E	H. teretifolia young leaves	>28				died during final instar
36/65E	Grevillea alpina young fruits	(>21<27)		19	55	
19/66C	" " " "	>14				died as 3rd instar larva
13/66C	H. sericea fruits deep-frozen	—(>28)— 58 —	—	20	78	
15/66C	H. sericea fruits deep-frozen and fresh	40	17	19/20	76/77	
38/65E	H. sericea fruits autoclaved	—(>14<18)— 38 —	—	17	55	
39/65E	" " " " "	—(>31<35)— 51 —	—	17	68	
28/67C	Sedum sp. fleshy leaf (Crassulaceae)	>70				4th instar, but only half-grown when discarded (leaf changed 16 times)
3/65E	Brabejum stellatifolium young fruits	70				apparently mature when it died, but not in cell
1/66E	" "	>34				died in 3rd instar after transfer to 2nd fruit
62/65E	" "				118	found as newly-emerged small male at 1st inspection
61/65E	" "	(>60<83)				died as mature larva in cell
63/65E	" "	48	>14			died as mature larva in cell
1/66C	" "	>37				died as third instar after transfer to 2nd fruit
2/66C	" "	>59				died as ≥ 3rd instar after transfer to 2 new fruit
4/66C	" "	>57				died prior to reaching full size
5/66C	" "	71	— 39 —	—(>22<24)—	110	small male
23/66C	" "	>50				died only half-grown

(a), (b): refer to previous table

TABLE 15

The development of larvae of Erytenna sp. nr. consputa Pasc. on various plants and media in the laboratory. Each observation was repeated at least once, and maximum development observed is given.

		Spontaneous entry by young larva	Tunnelling	Feeding (or growth rate)	Acceptance of medium	Max.no. of days survived when dead prematurely	Developmental stage reached (Larval instar) A = Adult stage	Notes
FRUITS (PROTEACEOUS) (Young)	Hakea suaveolens	?	+++	+++	+++	→	A	See Table 13
	H. elliptica	?	+	+	+	11	-	Escaped, did not re-enter
	H. ?crassifolia	0	+	+	0	3	-	Escaped, did not re-enter
	H. sericea (autoclaved)	++	+++	+++	+++	→	A	See Table 14
	Grevillea alpina	0	+++	+++	+++	13	4th	Apparently full-grown when lost
	G. rosmarinifolia	0	+++	+++	+++	→	A	See Table 14
	Lambertia formosa	0	+	+	+	8	-	Escaped, re-entered, died outside
	Persoonia sp.	0	+	0	0	<6	-	Died outside
	P. juniperina	0	+	0	0	8	-	Died outside
	Brabejum stellatifolium	0	+++	++	+++	→	A	See Table 14
VARIOUS FRUITS (Young)	Pyrus sp. (flowering apple)	0	0	0	0	8-10	-	Escaped soon, died outside
	Pyrus malus (apple)	+	+	0	0	<13	-	Re-entered several times, but died outside
	Prunus sp. (flowering plum)	+	++	+	++	10	-	"
	P. persica var. (flowering peach)	0	+++	++	++	7	-	Died during 1st moult
	Phaseolus vulgaris var. (bean pod)	?	+++	++	++	24	3rd	Appeared diseased
LEAVES	H. suaveolens	0	+++	+++	+++	42	4th	See Table 14
	H. teretifolia	0	+++	+++	+++	28	4th	See Table 14
	B. stellatifolium	0	0	0	0	5	-	Died while escaping
	Protea susannae	0	+	+	0	7-10	-	Apparently eating way out
	P. cynaroides	0	0	0	0	9	-	Escaped into parafilm
	Sedum sp.	0*	+++	++	+++	>70	4th	See Table 14
VARIOUS	Carrot pieces	0	+++	0	+	7	-	Re-entered, died in tunnel
	Potato tubers	0	+	0	0	7	-	Died outside
	Flower base, Protea subpulchella	+	+	0	0	?	-	Re-entered, then lost
Artificial nutrient media (based on agar and mashed fruits)		+	++	+	+	24	2nd	Majority died within 10 days with no signs of growth

Ratings used:
0 = Negative
+ = Some signs, but inconsistent or temporary
++ = Positive, but not to same extent as in normal host
+++ = Very readily - To same extent as in normal host
? = Not observed
- = No appreciable development

*Larva entered fresh leaves spontaneously on several occasions remain in the pupal cell for 7 -14 days before eating their way out.

The rate of development on autoclaved or deep-frozen *H. sericea* fruits (Table 14) was comparable to that on unsterilized green fruits. The feeding period of larvae placed in fruits of *Grevillea rosmarinifolia*, appeared to be similar to that on *Hakea* fruits. In fruits of *Brabejum stellatifolium*, larval development was almost twice as long as in *Hakea* fruits, and the mortality was very high.

There were indications that the feeding period may be considerably shorter when the larvae develop in living young fruits on potted plants. For instance, two such larvae in the laboratory appeared to be full-grown when they left the fruits within 11 and 19 days respectively. As no other developing fruits on potted plants were available at the time, it was not possible to repeat the experiment.

3.36 Host-plant range of the larvae in the laboratory

Table 15 shows the various fruits and other plant material into which larvae were placed for observations on the degree of acceptance, the amount of tunnelling and feeding that occurred, and the success of the larvae on these media. It is indicated that larvae developed to the adult stage on young fruits of *Hakea suaveolens*, *Grevillea rosmarinifolia*, *Brabejum stellatifolium*, and also on autoclaved fruits of *H. sericea*. Appreciable larval development occurred in a fruit of *Grevillea alpina*, in a French bean pod and in the leaves of *Sedum* sp., *H. suaveolens* and *H. teretifolia*. However, when compared with the rate of development in natural hosts (cf. Table 13), it appears that it was comparable only in the fruits of Grevillea spp. and some other Hakea spp. Development in Sedum leaves was very slow. Premature mortality was high in young leaves of Hakea spp. and in fruits of B. stellatifolium, in which several larvae died when apparently full-grown, but without signs of pupation.

3.37 Subtractive factors

3.371 Intraspecific competition

Super-oviposition occurred frequently. Even early in the egg-laying season, when there appeared to be an abundance of young fruits at Wilson's Promontory, two eggs occurred in 5 p.c. of the fruits selected for egg-laying. Later, when it became known that eggs were also laid in buds and leaves in the vicinity of suitable young fruits, it was found that at a comparable stage of the season, up to 12 p.c. of the fruits with eggs had another egg in their immediate vicinity. The degree of super-oviposition appeared to increase with the advance of the season. However, it was not possible to estimate the overall numbers of eggs laid per fruit during the season because it was difficult to distinguish between cavities that had contained none, one, or more eggs. Others may have contained eggs during previous seasons. Also the buds excavated by females tended to drop off after some time.

As only a single larva developed in a fruit because of cannibalism, and many larvae needed more than one fruit to complete their development, it follows that there may be some competition for food between the larvae. There were distinct indications that they seldom entered fruits already occupied by other larvae (e.g. the very small proportion of attacked fruits that showed more than one entry hole). Observations on young larvae in the laboratory (e.g. their failure to enter picked fruits spontaneously) suggested that they may be able to recognize fruits that are not perfectly healthy.

Fruits each containing two pupal cells, or with other signs that they had contained two larvae (e.g. a parasitoid cocoon and a healthy individual), were occasionally found. It was usually clear that these fruits had been entered by larvae about to pupate.

In the field under normal conditions and with the observed population densities, there were no definite indications of any adverse effect of competition between adult weevils for shelter or food. Also, an excess of flowers was produced, and the fruit-setting period of most plants was extended. There appeared to be no severe reduction of the numbers of young fruits produced as a result of feeding by the adult weevils on flower-buds, flowers and newly-set fruits. Favoured egg-laying sites may be rendered unsuitable after feeding by adults not depositing eggs. However, the faculty of ovipositing in leaves probably offsets this effect on the limitation of egg-laying sites under natural conditions.

3.372 Parasites

There were two main parasitoids.[1]

A mymarid egg parasitoid (*Patasson* sp.) accounted for the loss of a small proportion of eggs at Wilson's Promontory but a braconid (*Bracon* sp.), parasitizing the larvae, appeared to be the most important parasitoid.

A presumably haemolymph-sucking mite was found on between one and seven percent of adults in samples from Wilson's Promontory. Up to four of these mites were found attached to the soft, abdominal tergites under the elytra of a weevil. Occasionally they occurred on the inner surface of the elytra. Their influence on the hosts was not clear, but affected weevils often had a series of small, black wounds on their tergites, and it was noted that fungal growth occurred there under laboratory conditions, especially after the death of the hosts.

A small proportion of pupae in the field became mummified, and appeared to have succumbed to a fungal disease.

(a) *Patasson* sp. (det. D.P. Annecke). Solitary mymarids emerged from approximately 4 p.c. of *Erytenna* eggs found in the horns of *H. sericea* fruits at Wilson's Promontory. The parasitoids emerged within three weeks of collection of the eggs. The proportion of

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[1] Some other hymenopterans, suspected to be hyperparasitoids through the braconids in at least some of the cases, were reared from fruits in which *Erytenna* larvae had succumbed. Amongst these insects whose host relationships were not clear, were: 1) *Eupelmus catoxanthae* Ferr. (Eupelmidae); 2) a specimen in a genus near *Orgilus* (Blacinae, Braconidae - det. E.F. Riek); 3) specimens in a genus near *Astomaspis* (Cryptinae, Ichneumonidae - det. J.F. Perkins), and 4) an unidentified gregarious parasitoid.

parasitism in eggs occurring elsewhere on the plants was not determined but it is known that eggs in leaf-tips are also attacked by this parasitoid. No evidence of diapausing mymarids was found during the non-breeding season of Erytenna, and it is therefore likely that there are alternate hosts.

No egg-parasitoids were reared from small samples of eggs collected at localities other than Wilson's Promontory. Nevertheless, the occurrence of minute emergence holes from the chambers containing remains of Erytenna eggs at some other eastern localities, suggested that the same or a similar parasitoid, was present at these localities.

(b) Bracon sp. (det. R.D. Eady). This parasitoid caused the death of a considerable proportion of larvae. The same, or a similar species occurred at all the localities where the host was encountered. The incidence of parasitism in larvae leaving the fruits to pupate elsewhere, and the role of the parasitoid in the death of young larvae, are not known. However, between 12 and 22 p.c. of larvae that formed pupal cells in fruits of H. sericea and H. nodosa at Wilson's Promontory, succumbed to successful braconid larvae. (In occasional samples, apparently from localities where the population density of the host was low after repeated collections during the study period, up to 52 p.c. of the larvae about to pupate in the fruits, were parasitized.)

The host larvae are apparently attacked for oviposition while they are inside the green fruits, and are killed while still feeding, or shortly after construction of the pupal cell. The parasitoid larva emerges from the host and spins a white, irregular cocoon in the vicinity of the host. It remains in a fairly inactive state for several months until the following spring or early summer, when it pupates. The adult then emerges within a few weeks.

On several occasions larvae of the suspected hyper-parasitic *Eupelmus catoxanthae* were found in fruits with signs of the previous emergence of braconid larvae from the curculionid hosts. Once a pupa of *E. catoxanthae* was found in a pupal cell of *Erytenna* with the remains of the nearly-mature curculionid pupa, from which the eupelmid had evidently escaped.

3.373 Predators

There was some slight evidence of predators attacking the eggs of *Erytenna*. A peculiarly elongated mite with a soft, whitish body was found on two occasions inside apparently intact egg-chambers. One of these mites was inside a hollow egg-shell and the other was apparently feeding externally on a partly-collapsed egg.

A variety of predatory insects occurred on the host-plants at all the localities visited. These insects were commonly found associated with the fruits in which *Erytenna* larvae had developed. Larvae and exuviae of an unidentified clerid, and of another coleopteran, *Carphurus* sp. (Melyridae) were found in the pupal cells of *Erytenna* (with at the most remains of their prey) at Wilson's Promontory. It was not clear whether they entered pupal cells unaided, or whether they gained accidental access.

Adults of *Carphurus cyanopterus* Boh., of three other unidentified *Carphurus* spp., and of the clerids *Lemidia exilis* West., *L. militaris* Schenk, *L. subaena* Gorham and *Lemidia* sp. were found sheltering in fruit-husks of *H. sericea* at various localities in eastern Australia.

The adults of at least some of these beetles, as well as the larvae collected, readily attacked and consumed any exposed curulionid larvae or pupae in the laboratory, and it is thought that they may account for the death of a considerable proportion of larvae in the field.

Other predatory species were found on fruiting plants, but their host-relationships were not clear. These included: 1) *Cleobora mellyi* Muls. (Coccinellidae), whose adults were abundant on *H. sericea* at Wilson's Promontory during spring, when an average of 2-3 occurred on each plant; 2) occasional adults of the coccinellid *Leis conformis* Boisd. and of four other coccinellids; 3) of *Xanthopaea* sp. (Carabidae); 4) *Heteromastix mcdonaldi* Lea (Cantharidae); 5) *Geocoris hakeae* Eyles (Lygaeidae); and of 6) *Oechalia schellenbergii* Guer. (Pentatomidae). A large variety of spiders occurred in the dry fruit-husks on the plants, and there appeared to be some competition for shelter between spiders and the adult weevils. However, there was no evidence of healthy weevils being caught and consumed by these spiders. There is a possibility that the numerous 'jumping spiders' (Salticidae) may attack exposed larvae on the plants.

3.38 Physical factors

3.381 Weather

Plant tissue surrounds the eggs, feeding larvae and the pupae in their pupal cells so that these are not directly exposed to the normal daily extremes in temperature and humidity. While within the plant tissue, they were apparently never adversely affected by weather conditions. However, there were frequent indications of the disappearance of newly-hatched larvae, and of older larvae in search of another fruit, and in these, adverse weather conditions may have been a contributing factor. The adults, which are known to be resistant to dehydration and low temperatures, also sheltered deep inside dry fruit-husks. Being capable of surviving several months of starvation, these sheltering adults are not likely to be adversely affected by extended periods of unfavourable conditions during the winter. Severe drought was seen as a conditioning influence acting on the host-plants, rather than a direct subtractive factor, and will be considered later. Fire, to which the host-plants are normally exposed from time to time would probably cause death in all immature stages present. Nevertheless the periods of high fire danger are usually more likely to occur during late summer, when the curculionids are all in the adult stage. The adults are known to be greatly activated by intense heat, and may be able to survive fires by flying off. The general adaptations of the species to survive widespread fires will be discussed later.

3.39 Conditioning influences

3.391 Quality and availability of food

The important influence of the quality of the food taken by the adults has already been indicated. The influence of the sequence of types of food taken by females during the non-breeding period results directly in larvae being present only when there is a suitable food supply for them.

The first fruits formed by very young plants, and those developing during severe droughts are small and often become hard and woody when they have reached only about one quarter of the normal size. One larva may then require several fruits to be able to complete its development, and survival may be low. However, it is doubtful whether many eggs would be laid on the plants under these conditions. At localities exposed to long, dry cycles there may thus be a reduction in the population of *Erytenna*, also as a result of plants failing to set any fruits at all.

Dry conditions may also have a more subtle conditioning influence. It was indicated (see Table 11) that very few eggs were laid in the horns of fruits at Goulburn and in the Grampians. At these relatively dry localities the horns dried out at an early stage, rendering them unsuitable for oviposition. As the eggs were then laid in buds, or in leaf-tips, the chances of larvae finding the fruits would thus be expected to be reduced, also as a result of exposure to predators and adverse climatic conditions.

There were indications that under high population densities, there could be a similar limitation of the egg-laying sites on the fruits due to feeding on, and oviposition in, the horns of fruits and the 'additional' buds on the fruit stem. This was especially evident at Wilson's Promontory towards the end of the egg-laying season. More eggs were then laid in leaf-tips, and larvae hatching in these situations would be expected to have a smaller chance of survival.

Once the fruits became woody towards the end of the season, even older larvae were unable to reach the seed-cavities, and tunnelled in the relatively soft tissue near the surface. Mortality in these larvae was always very high, apparently as a result of large quantities of mucilage exuded at the wounds. Furthermore parasitism by *Bracon* sp. was then very common. This may have been a result of either a larger degree of exposure, or a possible increase in the population of adult parasitoids towards the end of the season.

3.392 Interspecific competition for food

There was little evidence of affective direct competition for food for either larvae or adult weevils.

The proportion of young fruits attacked by larvae of *Parastranga macrogona* (Tortricidae - see Appendix III) was very small where it was encountered at Wilson's Promontory on *H. sericea* and *H. nodosa*. Similarly, a very small proportion of fruits appeared to have been attacked by the unidentified geometrid larvae attacking young fruits (see Appendix III) in eastern N.S.W., and the amount of competition afforded appeared to be negligible.

There always appeared to be an abundance of food for adult weevils in the field, and thus the feeding of other insects on buds and flowers could probably be disregarded in relation to competition with Erytenna.

The overall effect of the entire complex of other insects not in direct competition with Erytenna, but attacking the various parts of the plant (Section 2.4) and thus eventually limiting the number of fruits formed, was hard to evaluate. As this will be discussed elsewhere, it will not be considered here.

3.4 DISCUSSION

Despite indications of non-specific food requirements of larvae in the laboratory, the host-plant range in the field appeared to be very narrow, and restricted to only three quite similar species of Hakea.

The insect's distribution range, on the other hand, was wide. They occurred under diverse climatic conditions ranging between those in relatively wet, summer rainfall regions in the sub-tropics, through constant rainfall regions, to variable conditions in winter rainfall regions. This in itself is interesting, but their adaptation to host-plants that have a different phenology under various conditions, was even more remarkable.

The most conspicuous adaptation was the co-ordination of the breeding cycle with the presence of fruits suitable for larval development. The Hakea fruits are only suitable during a relatively short period each year after they have reached a certain minimum size, but before they become woody. Therefore, as this period may be variable in its onset and duration as a result of local climatic fluctuations, accurate timing of the egg-laying period is essential for survival. The type of food eaten by females appeared to be a reliable indication of the general condition of the host, and gave them an early stimulus for oogenesis. Even when the flowering period was extended before fruit-setting, this mechanism still allowed maturation of the eggs only when newly-set fruits became available. Facultative interruption of egg-maturation and of oogenesis, or return of the ovaries to the non-breeding conditions, was also possible.

Variations in the breeding period (from as early as autumn on some hosts to as late as mid-summer on others), confirmed that the insects have a capacity to time their cycle independent of climatic conditions, except as manifested through the hosts.

It is considered quite possible that there may be a second annual generation in some individuals experiencing favourable conditions, such as when there is an extended flowering- and fruit-setting period, either in one host-species, or in two occurring in close proximity.

Another interesting factor emerged during observations of larvae in the laboratory. Their requirements appeared to change progressively to parallel the changes that normally occur in attacked fruits. Thus larvae seemed to prefer a drier medium as their development advanced, and they never pupated inside soft young fruits, or in fruits entered while these still were very young and soft (and therefore likely to dry out into thin, dry non-persistent husks). Pupation in the field only occurred in the larger, already somewhat woody fruits, and the larvae maturing in young fruits, or fruits still juicy at the completion of feeding, appeared to pupate in the soil, It is also interesting that young fruits containing pupae usually dried out sufficiently to dehisce slightly towards the end of, or soon after, the pupal period, thus allowing escape of the adult weevils.

The habit of newly-hatched larvae to emerge from the horns of the fruit and to re-enter the fruit at a different position was originally seen as a weak point in the adaptation to the host, as this was thought to increase exposure to predators and adverse weather conditions. However, when it became known that eggs were frequently laid a small distance from the fruit, this emergence from the oviposition site seemed to be necessary to allow finding of fruits, and rejection of unsuitable ones. There were frequent indications that larvae may be able to recognize a fruit not perfectly healthy (perhaps being aborted, or already attacked by another larva) while moving about on the fruit's surface. Although attempts to study this phenomenon under experimental conditions failed, it seems reasonable to believe that the surface of the cuticular layer of healthy fruits may differ from that of slightly wilted fruits (see Harris and Mohyuddin 1965), and that the larvae may be able to recognize this. If this is established, the habit of larvae to walk on the surface of fruits may be seen as of survival value.

Parasitoids and predators appeared to be the most important single subtractive factor in the cycle of the insects. Under normal population densities, intraspecific competition appeared to be relatively unimportant, and the number of insects developing on a plant was mainly influenced by the number of young fruits present. It was similarly observed that the number of adults sheltering on any plant, showed a close correlation with the amount of suitable shelter on the plant, and thus, as a rule, with the number of larvae that had developed on the plant during previous seasons. As this is in turn largely governed by the plant's physiological condition and size (the number of fruits produced annually), this could well be seen as a self-regulatory system in which the number of adults remaining on a plant may be closely related to the availability of food for themselves and their offspring.

Observations on the hosts, which usually became less vigorous and tended to be replaced by taller vegetation in the absence of frequent fires, suggested that periodic fires may indeed be beneficial for this insect by causing rejuvenation and multiplication of the hosts. This phenomenon may well explain the absence of the insects on the groups of struggling plants around Canberra (should they prove to be _H. sericea_). Under present conditions these plants fruited only occasionally and then very sparsely, and the fruits formed were unusually small - conditions that were likely to cause disappearance of the fruit-attacking weevils.

Adults were always present throughout the year, and those of the new generation appeared before the normal periods of high fire danger. Being activated by high temperatures many may be able to survive even wide-spread fires by flying off. Survival after fires may be facilitated by the long life of the adults; the faculty to starve for extended periods, or possibly to survive on non-hosts or the vegetative parts of young hosts; and the faculty to co-ordinate the maturation of eggs with the availability of fruits suitable for larval development.

The results of the experiments on recognition of host-plants suggested that there may be greater activity, and a tendency to dispersal flights in the absence of favoured sheltering situations, or on non-hosts. These alone would lead to recolonization of young plants after fires, either from outside or from occasional surviving plants.

3.41 Bases for host-specificity

The close adaptation to the characteristics of the plants of not only the adults, but also of the larvae, as revealed in the study, is seen as a sound base for host-specificity. It is unlikely that any one plant with even minor differences should be able to qualify for the combination of requirements of the insects, even if it is not rejected straight away. The restricted host-range in the field supported this theory. Particular points in the life of the insects that may each individually cause rejection of, or failure on, non-hosts are: 1) host-plant selection and recognition by the adults; 2) the specific food requirements of the females to be able to produce eggs[1]; 3) the oviposition behaviour of females; 4) penetration behaviour of, and recognition of suitable fruits by larvae and 5) the progressive changes in the food necessary during development of the larvae.

Although various other plants may all provide some form of shelter for adults, it is thought that even a minor aspect like the non-availability of suitable shelter may be sufficient to cause abandonment of the plant.

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[1] A similar phenomenon was reported for *Microlarinus* spp. (Curculionidae) by Andres and Angalet (1963).

IV *CARPOSINA AUTOLOGA* MEYR.

4.1 INTRODUCTION

4.11 Background

Mature fruits of *Hakea nodosa* with their seeds destroyed and with a characteristic small tunnel through the woody portion of the fruit leading to the seed-cavity were noticed in an isolated patch of plants at Wilson's Promontory in October 1964. Initially no more than occasional attention was given to the causative organism, as the insects attacking *H. nodosa* were not a primary object for study, and fruits of *H. sericea* showing this type of damage were not encountered. In November 1965, egg-shells with a series of characteristic spikes on the exposed part of the chorion were noticed on affected fruits of *H. nodosa*, and small lepidopterous larvae were found eating the seeds of fruits that appeared quite healthy from the outside. No entry holes were observed on these fruits, but some of the larvae had apparently commenced eating a narrow tunnel into the woody portion surrounding the seed-cavity.

Fruits of *H. sericea* with their seeds destroyed and a narrow tunnel through the woody follicle to the seed-cavity, similar to the damage seen on *H. nodosa*, were found in eastern N.S.W. in May 1966. During the same month spiky eggs, similar to those found on damaged *nodosa* fruits, were found on *sericea* fruits, from one locality at Wilson's Promontory, and lepidopterous larvae were dissected from these eggs. It was then decided to rear and identify the lepidopteran attacking the seeds of H. nodosa, and to undertake a survey of H. sericea at various localities to determine whether this plant is successfully attacked by this, or a similar species.

In the laboratory the first moth (tentatively identified as C. autologa by I.F.B. Common, Div. of Entomology, CSIRO, Canberra) emerged during November 1966.

The damage caused to fruits is very inconspicuous and easily overlooked, especially on H. sericea. Detection was difficult because of the very small diameter of the tunnel in the wood, the presence of natural rough areas and scars on the surface of the fruits and the frequent occurrence of fungi and spiders' webs in the mouth of the tunnel. Furthermore a large proportion of mature fruits of H. sericea was known to be attacked by larvae of the curculionid Dixoncis pictus Oke (below), and escaping adults and parasitoids of these insects leave a series of holes in the surface of the fruits, which were initially ascribed to the latter species or associated insects. The general presence of larvae of the lepidopteran in fruits of H. sericea at Wilson's Promontory remained obscure until late in 1966 mainly because the distribution was very patchy and the insect appeared to be entirely absent at certain localities.

4.12 General information on the Carposinidae

The Carposinidae (Tortricoidea) is a small family close to the Tineoidea and occurs mainly in Australasia and the Hawaiian Islands (Jeffreys 1940). The majority of species in the genus Carposina Herrich-Schäffer (1853) occur in Australia and Hawaii, but species have been described from most zoogeographical regions of the world. However, some doubt exists as to the status of the Australian members (Common, personal communication 1966, 1968). Host-plant records encountered in literature include the following: New Zealand: *C. adreptella* Wlk. on raspberry, blackberry and the native blackberry, *Rubus australia*, feeding on buds, shoots, fruit and leaves (Wilkenson 1938); Japan, China and Korea: *C. sasakii* Mats. attacking peaches, apples and pears (Yago and Ishikawa 1930) and also plums and quinces (Haeussler 1940); United States: *C. fernaldana* Busck. boring in apples and in fruit of a native species of *Crataegus* (Rosaceae) (Haseman 1930); Eritrea (North Africa): *C. chersodes* Meyr. on olives (Silvestri 1915) and in Germany: *C. schirrhosella* Her. - Schäf. and *C. berberidella* Her. - Schäf. attacking *Rosa* sp. and *Berberis* sp. (Berberidaceae) respectively (Swatschek 1958).

Characteristics of the family and a key to the known genera are given by Diakonoff (1954) and the general characteristics of the larvae are discussed by Swatschek (1958) and Peterson 1948). The larvae and other developmental stages of *C. adreptella* are described by Jeffreys, and the larvae of *C. gonosemana* (Meyr.) and *C. fernaldana* by Hudson (1951) and Forbes (1923) respectively.

C. autologa was described by Meyrick in 1909 from a female collected at Geraldton, W.A. ('November'), but no host-plant records or descriptions of any of the developmental stages of the Australian *Carposina* spp. were given.

Moths of _C_. _autologa_ in the National Insect Collection of the Division of Entomology, CSIRO, were all collected from the south-western districts of Western Australia in coastal regions south of Geraldton and west of Albany (see below). According to Common the specimens were mostly taken at light traps.

Although this species was not known to have been collected in eastern Australia (Common, personal communication 1966), the moths from Wilson's Promontory were tentatively identified as _C_. _autologa_, although the genitalia differed slightly. Moths and immature stages have been studied in both eastern and south-western Australia. Recently doubt has been cast on their conspecificity, mainly due to superficial wing colour variation. It is thus possible that a complex of closely allied forms were in fact involved in the study. Because of the similar ecological relationship to the host-plant, and the fact that viable eggs resulted from matings in the laboratory between individuals from western and eastern Australia, the moths were, for the purpose of general discussion, regarded as a single biological entity, and referred to as _C_. _autologa_.

4.13 The aims of the study

After the insect had been found attacking fruits of _H_. _sericea_, it was decided to study the insect especially in relation to its host-plant range, geographical distribution, phenology and life history. It was hoped that this study would reveal mechanisms of host-specificity and also account for the patchy distribution observed at Wilson's Promontory, and so ultimately indicate whether _H_. _sericea_

Figure 6

Plugged entry hole of young larva of *Carposina autologa* Meyr. on the suture of a fruit of *Hakea nodosa*. The shallow groove where the protective cover was formed, is visible.

Magnification: Approximately 15 x .

was likely to support a natural population of the insect in the absence of other, possibly more suitable, host-plant species.

4.2 METHODS

4.21 Geographical distribution

Fruits of different *Hakea* spp. were examined for the presence of developmental stages of, or typical damage caused by *C. autologa*. Straight, narrow escape tunnels from the seed-cavity through the woody follicle of mature fruits were the typical sign of damage and were taken as an indication of the presence of the insect. These escape tunnels were found to be more readily visible to the naked eye in the exposed seed cavities when the fruits had dehisced for some reason.

The general procedure was to examine, *in situ*, mature fruits of different ages from a number of plants growing in different situatioms (e.g. in exposed positions, or under trees or in gullies). Later it became evident that the presence of the insect was not always detectable by the naked eye, and that escaping adults of *Eurytoma* species (Hymenoptera, see Appendix III) occasionally made very similar tunnels through the follicle of certain *Hakea* spp., and microscopic examination of fruits proved to be necessary. When no depidopterous larval exuviae were found in the debris in the seed-cavity, and the inconspicuous, minute, but characteristic entry tunnel through the suture of the fruit (Figure 6) was absent, the damage was ascribed to *Eurytoma* sp., especially if a typical brownish meconial mass was present in the hollow seed. For the microscopic examinations samples of about

100 - 200 mature fruits were collected randomly from a series of localities. These collections were not made at any particular time of the year, because the damage was known to remain visible for many years on the persistent fruits of Hakea spp.

Studies were limited to parts of south-eastern and south-western Australia, but did not systematically cover these general areas, or necessarily involve all the species of Hakea occurring there. Visits were mainly made to areas where H. sericea was frequent, but whenever other species of Hakea were encountered, their fruits were examined for the presence of C. autologa.

H. sericea fruits from the following coastal localities in eastern Australia were examined: Sydney, Eden, Narrabarba, Timbillica, Genoa, Lake's Entrance, Foster, Wilson's Promontory and Leongatha. Inland localities sampled were Mittagong, Bargo, Goulburn, Springwood and Braidwood in N.S.W., and the Grampians in Victoria. Fruits of at least 12 other Hakea spp. from eastern Australia were examined. At least eight species were sampled in Western Australia, where H. sericea does not occur.

The identity of plants involved was checked with the help of staff at the Division of Plant Industry, CSIRO, Canberra, and at the National Herbarium of Victoria, Melbourne, but exact identifications for some specimens were not possible.

4.22 Host-plant preferences

All Hakea spp. encountered during the study were regarded as potential hosts of C. autologa and were examined as described above.

Besides this qualitative examination, the proportion of fruits infected was determined where conditions were favourable. Although there is considerable variation in the size and shape of the fruits of the different species, they are all woody and have a longitudinal suture where dehiscence occurs to release the two winged seeds. With a few possible exceptions, the seeds of all species encountered were considered to be large enough to permit normal development of *C. autologa* larvae.

Some proteaceous plants with dehiscent, woody fruits and seeds comparable in size to those of *Hakea* spp. (e.g. *Banksia* spp. and *Lambertia formosa*) were also considered potential host-plants and were examined at localities where *C. autologa* was found to be abundant.

After the early stages of the study, the fruits of other proteaceous plants encountered in the field were given little more than casual attention, mainly because the habits of *C. autologa* larvae suggested that these fruits were unlikely to be suitable for normal development. Included were species whose fruits are either 1) coriaceous and dehiscent upon maturation (e.g. *Grevillea* spp., *Telopea* sp., *Lomatia* sp.), or 2) too fleshy (*Persoonia* sp.) or 3) too small and in cone-like heads (*Isopogon* sp. and *Petrophile* sp.).

Experiments to study host-plant selection and oviposition preferences of females were made in the large field-cage in which the various types of plant material attached to the suspended frame were presented to the moths in an experimental design similar to that used for *Erytenna* adults (section 3.25). In this case the cage was erected in the field among tall Leptospermum laevigatum plants. Plants were left within the cage to simulate the natural conditions where the moths occurred, but pruning to 3' height was necessary to allow free movement of the sample frame. Plant material consisting of foliage plus a single fruit was attached at two points on each of the ten spokes of the frame. Each of the five types of material was represented twice in both the inner and outer circles, and adjacent to each of the other four types. The units were secured to the wire frame so as not to be in direct contact with each other, with the sides of the cage , or with the plants in the cage. The wire frame was weighted down to prevent excessive movement and rapid rotation under windy conditions. The entire frame with plant material was removed late each afternoon, and returned to the cage with the new units of material during, or soon after dusk. Honey and water were sprinkled on the plants in the cage each evening to prevent starvation of the moths.

Fifteen one-day old females and several males were placed in the cage, and the experiments were commenced on the third day. When egg-laying proved to be slow, a further ten field-collected females were added as they became available from a light trap. A series of different experiments were carried out on four successive nights, and were replicated in the same sequence on the next four. An attempt to replicate these experiments a third time was prevented when the rate of oviposition declined sharply during the next four nights.

4.23 Phenology and general biology

Visits were made to Wilson's Promontory at two- to four-monthly intervals over a period of about two years. Fruits were examined for the presence of eggs and larvae of different developmental stages. During the second year the presence and development of the different stages on a number of tagged fruits were noted at two-monthly intervals and a light trap (160W blended light bulb) was operated to determine the presence of moths. The activity of moths was also observed by examining plants in the field with a flashlight. In all cases when developmental stages were encountered, specimens were returned to the laboratory for further observations. As the habits of the insects were only gradually revealed, systematic and qualitative sampling for the different stages was not carried out over the whole period.

The different stages occurring on the small samples of fruits collected at other localities were noted and compared with phenological data for Wilson's Promontory,

Early observations rating the favourability of various situations for egg-laying sites, suggested that the age and condition of fruits affected oviposition on them. The distribution of naturally laid eggs was studied in March 1967 by the careful searching of two whole *H. nodosa* plants.

As no larvae were reared from the egg to the full-grown stage until very late in the study, and observations were mostly made on field-collected larvae, a method was needed to allocate field-collected larvae to a certain instar. The steps in the procedure were as follows:

1) The width of all head-capsules available were measured; also the length between the caudal end of the frons and an imaginary line between two distinct setae on this sclerite.

2) The relationship between these two measurements was determined in order that the width of broken or distorted capsules could be estimated.

3) A histogram of the sizes between 10 and 60 units (50 units = 1 mm) showed about 8 peaks with possibly minor peaks in-between.

4) The mean head-widths of all larvae known to be in the final instar was found to be 50 units (range 40 - 58); similarly, newly-hatched larvae (i.e. 1st instar) were found to average 13 units (10.5 - 14).

5) The eight main peaks in the histogram appeared to correspond to a geometric series, suggesting that the growth rate and number of instars in this species were normally constant. However, the minor peaks in the histogram, corresponded to geometrical series of six and seven units, which meant that the occurrence of six or seven instars for some larvae could not be ruled out.

6) The usual growth factor was estimated by taking the average ratio of increase in head-widths in 18 larvae in which 3 successive instars were observed and measured. The G.F. thus calculated was 1.22, giving theoretical instar sizes of approximately 13, 16, 19, 23, 29, 34, 41, and 50.

7) Using this estimate of instar sizes, consecutive head-width measurements were arranged in instar series, and from this table an estimate of the range in each instar was made.

8) The instar of field-collected individuals was then designated by comparing their head-widths with the estimated ranges, and the

designation was regarded as reliable when at least two capsules (successive, or with one presumably lost in-between) conformed to the pattern.

As oviposition seldom occurred in the laboratory, and the females appeared to die prematurely, estimates of their egg-laying capacity were based on the results of dissections of females of various ages, both before and after some eggs had been laid.

4.231 Studying penetration behaviour of newly-hatched larvae

As newly-hatched larvae exhibited a remarkable faculty to recognize the very small area along the suture of host-fruits where penetration was possible, observations were made to get some insight in the mechanisms that may be involved.

Individual newly-hatched larvae were closely observed on selected fruits of *H. nodosa*, and their movements and activity during the first hour were noted. General illumination alone, or with a second unilateral light source, was used. Larvae were also observed on various artefacts, non-host fruits and flat surfaces to evaluate the influence of certain physical factors. To confirm the validity of the trends exhibited, other larvae were placed on fruits of potential hosts, and fruits of hosts altered in different ways, and their positions and activity were noted at intervals.

4.24 Rearing techniques

Samples of fruits collected during field trips were held in polythene bags until they were examined in the laboratory. If considerable fluctuations in temperature were expected, or a delay of more than a week was expected before inspection would be possible, the fruits were loosely wrapped in paper which absorbed excessive condensation. Eggs remained viable and hatched under these conditions, and larvae in the fruits or in the process of penetrating did not appear to be unduly disturbed.

Fruits had to be held at high humidities to prevent drying and the resultant dehiscing, but it proved impracticable to keep them in the laboratory long enough to allow complete development of the insects. Newly-entered individuals could be reared to almost mature larvae by keeping the fruits in polythene bags or by waxing the surface of individual fruits, but mortality was high due to rotting of the seeds and/or the development of mite infestations. Further limitations were imposed if regular observations were to be made.

The eggs dehydrated easily in a heated laboratory when no provisions for additional humidity were made. It was possible to observe hatching of eggs either on the original fruits held in humid containers, or by removing exposed eggs and allowing them to hatch on a layer of moistened filter paper in a petri-dish.

Penetration of fruits by the newly-hatched larvae was seldom achieved in the laboratory, and it certainly was not possible to observe the normal progress, as any separation of the two halves of the fruit altered the conditions of penetration, and the larvae were often wounded or disturbed excessively. Furthermore, placing newly-hatched larvae directly into the seed-cavities of separated fruit halves was also unsatisfactory , as the larvae appeared to attempt to escape.

For more detailed studies of the feeding larva, the halves of a fruit could be carefully separated to expose the seeds and to record the contents of the seed-cavity. Individual larvae developed satisfactorily for a time on the original seeds when the halves of the fruits were carefully replaced in the original position and held tightly together by means of rubber bands. To prevent dehydration of the fruits, which caused cracking and distortion of the woody valves of the follicle, and the resulting dehydration of the seeds and larvae, the fruits were held in polystyrene jars. Air circulation was necessary to reduce the chances of the seeds rotting, and so the lids were each provided with a hole, 3/4" in diameter and covered with fine gauze. To maintain a high humidity, a layer of plaster of Paris at the bottom of the jars was saturated with water at least twice a week. This technique allowed regular inspection of the larvae, and it was possible to replace mouldy or rotting seeds with fresh seeds from fruits stored under refrigeration. Using this method it was possible to observe all the phases of the life-cycle within the fruit, but as most of the larvae were accidentally wounded in the process of replacing the halves of the fruits after inspections, only a composite picture of the development could be constructed.

Under the conditions of high humidity, moulds often developed on the surface of the fruits, and as a result the surfaces of the seeds where the larvae were feeding became contaminated very easily during regular inspections. This caused rotting of the seeds or the formation of large quantities of fungal spores in the seed-cavities of fruits, especially at stages when the larvae temporarily ceased feeding. Rearing at constant temperatures tended to prevent condensation inside the containers, and as a result the fruits did not become mouldy so easily,

A variety of mites occurred on the surface (and even inside the seed-cavity) of field-collected fruits, and survived in the laboratory. During the study it became evident that some of these mites, previously thought to be harmless scavengers, actually attacked and killed otherwise healthy larvae and pupae. Attempts were then made to control the mites by means of chlorbenzide dust, but very high doses were necessary to kill the adult stage, and the seed-cavity had to be dusted heavily to prevent fresh infestations from mites underneath the loose bark of the fruits, where large numbers often survived undetected. There were indications that at least the young _C_. _autologa_ larvae were detrimentally affected by the chlorbenzide dust.

To facilitate continuous observations, attempts were made to rear larvae singly in 2" x 1" glass vials on seeds removed from fruits. This method was not satisfactory. The larvae did not feed in exposed positions, and either formed a cover of silk, frass and pieces of seed, or fed in sheltered situations, e.g. under seeds attached to the substrate with silken threads, between seeds spun together and also under cover of the testae of the seeds. They had to be removed for inspection, and then often abandoned the seeds repeatedly. Another problem was that the seeds had to be held on dampened cotton-wool or plaster of Paris to prevent dehydration, but under these conditions the cotyledons rapidly absorbed water and developed chlorophyll. Even when the containers were held in virtual darkness, the seeds still germinated while being eaten by the larvae.

In order to more closely simulate the conditions of natural fruit and seed, and still allowing repeated observations, a method was developed which largely overcame the problems associated with using separated halves of the original fruits. One or two seeds were placed in a small, roughly circular hole made in a piece of 1/8" thick balsa wood, one inch square, and the larva was placed on the seeds. Coverslips of just under 1" diameter were placed on either side of the cavity to enclose the larva; two unperforated squares of balsa of similar dimensions to the central square held the coverslips in position and a rubber band was used to hold all the squares together. Advantages of this method were: 1) the larvae did not cover themselves with silk and debris and were often visible after removal of one of the covering balsa squares; 2) there was little risk of wounding larvae during routine inspections due to the transparency of the coverslip; 3) larvae were able to form 'natural' escape tunnels and were often then visible if these were formed against one of the coverslips; 4) the likelihood of undetected or inaccessible mite infestations was considerably reduced; and 5) seeds did not so readily get contaminated with fungi, bacteria and mites, and were easily replaced, especially since the cavities could be enlarged as required. The balsa containers were held in jars on a layer of dampened filter paper or plaster of Paris as described above.

Newly-hatched larvae placed in the balsa containers often escaped via the natural pores in the wood, or tunnelled into them and were frequently lost. It was later found that these larvae were more likely to settle on seeds in a container and to commence feeding if they had first been allowed to attempt entry on normal host-fruits for about one week.

Towards the end of the study, attention was given to the development of this method to allow rearing of large numbers of larvae. The hand-made balsa containers were replaced by small (0.75 ml) snap-cap polythene vials. Damp cotton-wool prevented dehydration of the seeds placed inside, and gauzed ventilation holes cut in the lids prevented excessive mould. The larvae fed readily, and made escape holes through the polythene to pupate in the jars in which the vials were held. The method was more satisfactory when the larvae were kept in darkness.

Full-grown larvae readily formed cocoons beneath the surface of damp sand, leaf debris or moistened vermiculite, placed in the containers, but also pupated in other sheltered positions therein. Pupae developed satisfactorily, provided that measures were taken to prevent dehydration and mite infestations, especially when the cocoons had to be opened for inspection of the pupae.

TABLE 16

The occurrence of Carposina autologa Meyr. in fruits of different species of Hakea at localities in south-eastern and south-western Australia

		sericea	?ambigua	cucullata	dactyloides	?dactyloides	?decurrens	elliptica	eriantha	gibbosa	glabella	?leucoptera	?lissosperma	microcarpa	nodosa	propinqua	rostrata	rugosa	suaveolens	teretifolia	?trifurcata	ulicina	undulata	?undulata	varia	?varia	victoriae
WA	Albany		●	●				●			?								●		○		?	T	?	●	
	Cape le Grande																										●
NSW	Heathcote	●			○																						
	Terrey Hills	?								?						○				○							
	Eden	○			?																						
	Narrabarba	○																									
	Timbillica	○																									
	Mittagong	●																									
	Bargo	●																									
	Springwood	○			○																						
	Blackheath															○											
	Goulburn	●			E																						
	Nerriga																										
	Yass						○																				
	Hay																										
	Canberra						○							○													
VIC	Genoa	?																									
	Cann River	●																									
	Bombala								○																		
	Bell Bird	○																									
	Foster	○													●				E*								
	Dandenongs	?													●												
	W. Prom.- Darby	●													●							○					
	W. Prom.- Oberon	○																				○					
	Grampians	○															○					○					
	Harwood	○																									
	Portland																●	○									
TAS	Freycinet												?														
	Lake St. Clair												?														
	Mt. Wellington												○														

● Evidence of full life-cycle
○ No evidence of presence
E Eggs only
T Escape tunnels, but not necessarily of C. autologa
? Not found, but examinations insufficient
* Cultivated plants amongst heath

Moths readily fed on honey diluted with water, but optimal conditions for inducing mating and oviposition in the laboratory were not determined owing to the small numbers of moths that were available for breeding and behavioural studies.

4.3 RESULTS

4.31 Geographical distribution

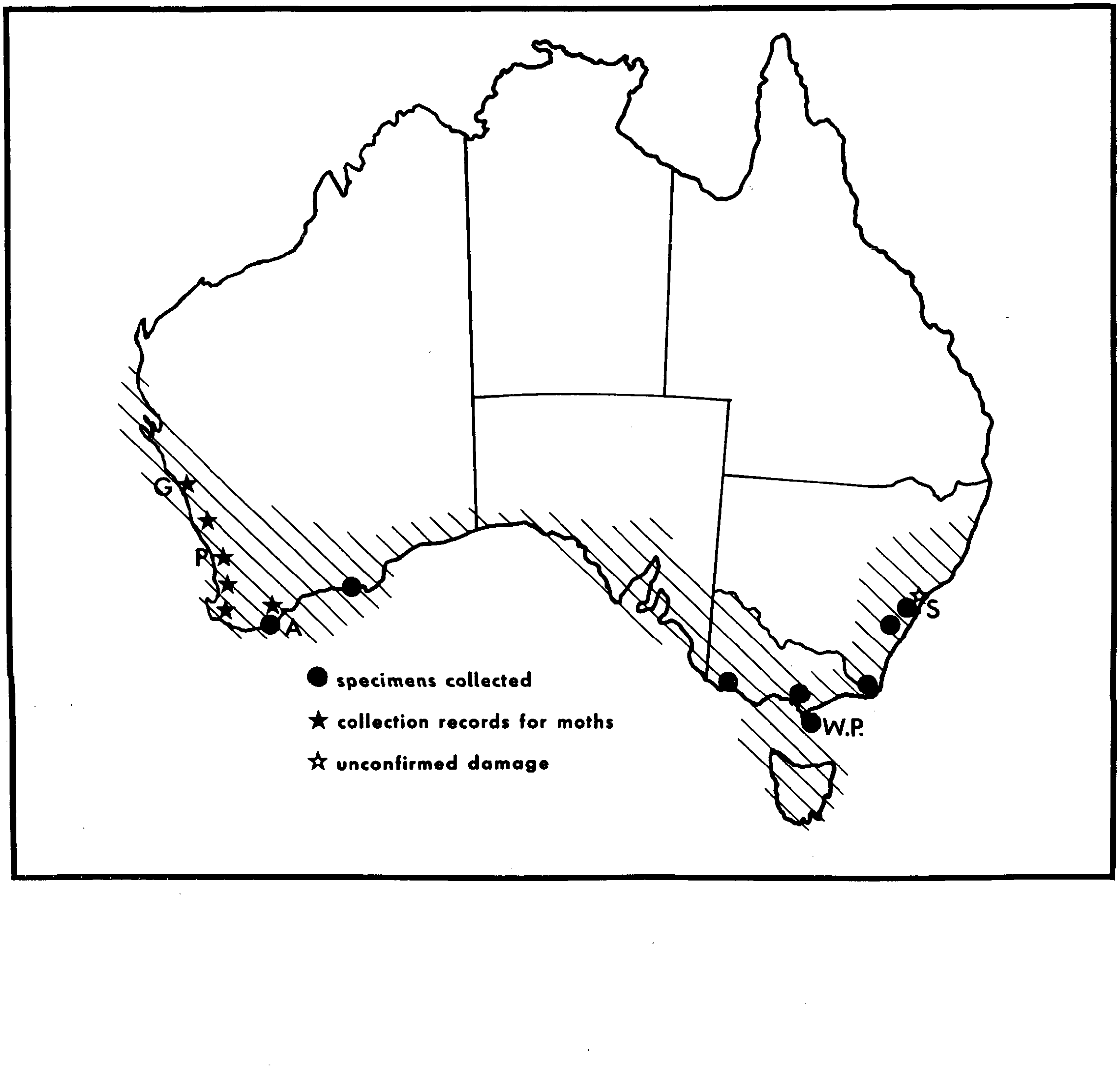
A synopsis of the observed occurrence of *C. autologa* at various localities in south-eastern and south-western Australia during the study period, based on the presence of typical damage and/or of developmental stages in the fruits of 19 species of *Hakea* examined (and 7 others for which exact identifications were not possible) is shown in Table 16.

C. autologa moths in the National Insect Collection (Division of Entomology, CSIRO, Canberra) had been collected at the following localities (all in W.A.) in the months indicated:

Nannup (Nov.)
Denmark (March)
Bunbury (Oct.)
Kalamunda (Nov.)
Tallanalla (Nov.)
Badgingarra (Nov.)
Kelmscott near Perth (Sept.)
Geraldton (30 miles south of) (Nov.)
Perth (20 miles S.E.) (Sept.)
Stirling Ranges (Oct., Nov.)
Blackwood River (Nov.)

Figure 7

Hypothetical distribution range (shaded) of Carposina autologa Meyr. in Australia



Of the specimens of *Hakea* nodosa in the National Herbarium of Victoria, those collected at Dandenong Creek and Arthur's Seat (Vic.) showed typical *Carposina* damage.[1]

From these records and the occurrence of the major host-plants a hypothetical overall distribution has been constructed (Figure 7).

4.32 *Host-plant preferences*

Attack appeared to be restricted to mature fruits of a number of species of *Hakea*. At three localities where *C. autologa* was known to be present in relatively large numbers, fruits of other (mainly proteaceous) plants, regarded as possible hosts, were examined. *Banksia spinulosa*, *Petrophile pedunculata* and *Lambertia formosa* at a locality next to the Bargo River near Bargo, N.S.W., and *Banksia* sp. at Albany, W.A., showed neither eggs of *C. autologa* nor typical entry tunnels.

At Wilson's Promontory a survey was made of the range of plants attacked by the insect at a situation where the four local *Hakea* spp., three *Banksia* spp. and *Casuarina pusilla* occurred together. Fruits of all these plants were examined for eggs and typical damage. Attack

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[1] Of the fruits present on herbarium specimens of other *Hakea* spp. in the Div. of Plant Industry, CSIRO, Canberra, some of those of the following species showed attempted or completed escape holes from the seed cavities:

H. arborescens	(Munbulloo, Katherine, N.T.)
H. cunninghamii	(24 miles south of Dorisvale Station, N.T.)
H. bipinnatifida	(south of Canning Dam, W.A.)
H. intermedia	(4 miles south east of Allan Homestead, Alice Springs distict, N.T.)

However, no egg-shells or any other evidence confirming that the damage may have been caused by a species of *Carposina* was found.

TABLE 17

The incidence of attack by *Carposina autologa* Meyr. on fruits of 7 proteaceous plants and *Casuarina* sp. occurring near a swampy area at Wilson's Promontory, Victoria, together with characteristics (and ratings*) of fruits

	Egg-shells per fruit	% entered	Habitat	Size of plants	Leaves	Flowering season	Conspicuousness of fruits from a distance	Size of fruits length x width x depth (cm) $\sqrt[3]{\text{dimensions}}$	Size of cones length x diameter (cm) $\sqrt[2]{\text{dimensions}}$	Shape of individual fruits	Groove associated with suture	Min. width of barrier in suture (mm)	Size of seeds weight in mg
Hakea nodosa	4.9	79	dense swamp vegetation	8' to 14'	sparse subulate pale green	autumn to winter	very conspicuous	large 3.0 x 2.5 x 2.7 2.70		globular blunt beak	broad conspicuous	narrow 0.7	large 20.4
Hakea sericea	2.5	26	heath next to swamp	4' to 8'	dense acicular deep green	winter to spring	very conspicuous	large 3.3 x 4.2 x 3.0 3.44		globular flattened, horned beak	broad conspicuous	very wide 4.0	very large 29.4
Hakea ulicina	0	0	heath next to swamp	3' to 5'	dense narrow-linear yellowish	spring	detectable	small 1.6 x 1.3 x 0.9 1.23		ellipsoid flattened, pointed beak	narrow inconspicuous	narrow 0.5	small 9.8
Hakea teretifolia	0	0	heath and in swamp	4' to 12'	dense acicular deep green	summer	inconspicuous	small 2.0 x 0.8 x 0.8 1.62		narrow, spiked elongated; acicular apex	inconspicuous	narrow 0.5	medium 10.4
Banksia serrata	0	0	edge of swamp	20' to 40'	dense broad, serrated pale green	summer	very conspicuous†	large 4.0 x 3.1 x 2.0 2.74	10 x 10 10.0	smoothly‡ rounded; velvety	invisible	very wide 3.0	medium
Banksia integrifolia	0	0	heath next to swamp	3' to 4'	sparse cuneate silvery-green	spring?	very conspicuous†	medium 1.9 x 1.5 x 1.2 1.51	10 x 5 7.1	flat,‡ smooth	shallow inconspicuous	medium 1.0	small
Banksia spinulosa	0	0	edge of swamp	2' to 4'	sparse narrow-linear silvery-green	summer?	conspicuous†	small 1.4 x 1.2 x 0.4 0.88	8 x 3 4.9	flat,‡ smooth	on ridge; inconspicuous	medium 1.0	small
Casuarina pusilla	0	0	heath and swamp-edge	2' to 6'	sparse** filiform deep green	summer	conspicuous†	very small 0.7 x 0.4 x 0.4 0.48	2.5 x 1.7 2.2	smoothly‡ rounded	small inconspicuous	wide 2.0	very small

*See explanations of ratings at foot of Table 18

†Applies to cones - individual fruits very inconspicuous

‡Applies to exposed part of wedge-shaped fruits forming cones

**Leaf-like branches

TABLE 18

The observed incidence of damage of *Carposina autologa* Meyr. on different *Hakea* spp. at various localities (see Table 16), with some characteristics of the plants. When these characteristics are not comparable to those of the three most favoured hosts, they are underlined.

	nodosa Wilson's Prom.	*cucullata* Albany	*elliptica* Albany	?*ambigua* Albany	*sericea* Bargo	*suaveolens* Albany	?*undulata* Albany	*victoriae* Cape le Grande	?*varia* Albany	*rostrata* Portland	*dactyloides* Goulburn	*eriantha* Bombala	*gibbosa* Terrey Hills	?*leucoptera* Hay	*lissosperma* Hobart	*microcarpa* Canberra	*propinqua* Blackheath	*rugosa* Portland	?*sericea* Canberra	*teretifolia* Wilson's Prom.	*ulicina* Wilson's Prom.	*undulata* Albany	*varia* Albany
Estimated incidence of damage (No. of plus-signs a linear rating)	+++	+++	+++	++	++	++	++	++	+	+	0	0	0	0	0	0	0	0	0	0	0	0	0
Size of fruits	l	m	m	m?	l	m	m	m	m	l	m	m	l	m	m	s	l	s	m	s	s	m	s
Size of seeds	l	l	l	l	l	m	m	l	m	l	m	m	vl	m	m	s	vl	m	l	m	s	s	s
Approximate shape of fruit (l = elongated g = globular, e = elliptical, f = flattened)	g	gf	gf	gf	gf	g	gf	gf	g	ef	g	ef	gf	g	g	e	g	e	e	l	gf	g	e
Shape of beak on fruit (x = absent, p = prominent, a = acuminate, r = recurved)	a	a	a	p	a	a	a	a	a	r	x	a	p	p	a	a	x	r	p	p	a	a	a
Surface of fruit (s = smooth, n = nodular or spiky, r = rough)	n	s	s	s	r	s	s	s	n	s	s	s	r	s	n	s	n	r	n	n	s	s	n
Width of suture	n	m	n	n	m	vw	n	n	n	w	n	vw	n	w	vw	n	vw	m	w	n	n	m	n
Leaves (n = needly or narrow, b = broad)	n	b	b	n	n	n	b	b	n	n	b	b	n	n	n	n	n	n	n	n	n	b	n
Exposure of fruits (e = exposed, i = inconspicuous, h = hidden, c = clustered	e	h	e	e	e	e	e	h	e	e	e	e	e	e	e	e	e	ih	e	i	e	e	e
Flowering season (Sp = spring, Su = summer, A = autumn, W = winter	A	A	Sp	?	Sp	A	Sp?	Sp?	A	Sp	?	Sp	A	?	Su?	Su	W	Sp	W	Su	Sp	Sp?	A

Ratings used in Tables 17, 18 and 19

Fruit-size: $\sqrt[3]{\text{length x width x depth}}$

0.0 - 0.49 = very small (vs)
0.5 - 1.49 = small (s)
1.5 - 2.49 = medium (m)
2.5 - 3.49 = large (l)

Width of suture (mm next to seed cavity)

0.4 - 0.99 = narrow (n)
1.0 - 1.99 = medium (m)
2.0 - 2.99 = wide (w)
3.0 - 3.99 = very wide (vw)

Size of seeds (mean dry weight in mg)

under 10 = small (s)
10 - 19 = medium (m)
20 - 29 = large (l)
30 - 39 = very large (vl)

was found to be restricted to the two Hakea spp. with larger fruits and seeds. The incidence of eggs and successfully attacked fruits, together with some characteristics of the plants considered to have possible relevance in the selection or suitability of the fruits, are shown in Table 17.

Apart from the size of the fruit and seed, the results suggested that the conspicuousness, and general shape and appearance of the fruits may have some influence on their selection. Furthermore, the flowering period and type of leaves appeared to have possible importance in the recognition of the plant.

The apparently higher proportion of larvae reaching the seeds of H. nodosa suggested that the narrower barrier presented by this fruit to the entering larvae may be a factor in its favourability.

In order to determine whether these characteristics may have an influence on the host suitability or preference, the observed incidence of C. autologa was compared with the characteristics of the several Hakea spp. encountered at various localities (Table 18). There were again suggestions that conspicuousness, size and shape of the fruit, and flowering period may be conditioning in selection, and that the size of seed (at least 15 mg when dry) and a relatively narrow barrier in the suture may determine the favourability.

As the incidence on H. sericea (see Table 16) was very patchy, even within an area as confined as Wilson's Promontory, it was suspected that other, more local, factors may have an additional

TABLE 19

The observed occurrence of damage by *Carposina autologa* Meyr. on *Hakea sericea*, with some features of their fruits (with a rating[*] of their size) and of the environment at the different localities

	% fruits with escapes	WIDTH OF BARRIER in suture (mm)	SIZE OF FRUIT	HABITAT	*HAKEA* SPP. IN VICINITY (underlined if attacked by *C. autologa*)
Squeaky Beach W. Prom.	21.5	4.0	large	swampy heath	*nodosa*
Darby River W. Prom.	17.2	4.0	large	heath	*nodosa*, ulicina, teretifolia
Bargo River N.S.W.	6.8	1.1	small	bushland	dactyloides
Cann River Vic.	6.5	1.1	large	open forest	-
Heathcote N.S.W.	c.4	0.9	medium	clearing in scrub	dactyloides, teretifolia
Goulburn N.S.W.	2.7[†]	1.2	medium	roadside scrub	*dactyloides*?
Mt. Oberon W. Prom.	0	4.2	very large	heath	ulicina teretifolia
Foster Vic.	0	2.9	large	roadside	ulicina
Bell Bird Vic.	0	1.3	small	open forest	-
Zumstein Vic.	0	1.7	medium	open bushland	ulicina
Genoa Vic.	0	1.5	medium	tall scrub	-
Canberra and vicinity[+]	0	1.4	very small	undergrowth	-
Castlemaine Vic.	0	1.0	small	clearing	-
Nerriga NSW	0	0.9	small	clearing in scrub	-

[*] Ratings on similar basis as those for Table 18

[†] Damaged fruits more plentiful on burnt plants 1 mile further east (Narrambulla Creek)

[+] *H.* ?*decurrens*

influence on the incidence of C. autologa on a given plant. In Table 19 the incidence on H. sericea at various localities is shown, together with some of the possibly relevant characteristics in which the plants were found to differ, and a comparison of the habitat in which the plants occurred is made.

Although the insect appeared to attack H. sericea in the absence of other, or more suitable host-plants, the forms with a relatively wide barrier in the suture (more than c. 1.2 mm) appeared to be successfully attacked only when alternate hosts occurred in the vicinity.

4.33 Life-cycle

4.331 Descriptions of the different stages

The egg is thin-walled, typically spherical to ovoid in shape (approximately 0.6 x 0.7 mm), with a series of slender, barbed spikes occurring in concentric polygons in a typically hexagonal pattern on a reticulated region around the micropylar area on the anterior pole. The surface of the remainder of the chorion is raised in numerous circular areas, and is white and translucent, so that the reddish contents are visible, and later the dark head and prothorax of the developing larva. A reddish pigment was sometimes deposited on the inner surface of the chorion towards the end of the incubation period. In practice the shape of the egg is determined by the shape of the space into which it had been inserted, and normally only the spiky anterior pole, or a portion of it, is exposed. In the ovarian egg the spine-bearing area is recessed so that the spikes do not protrude.

The newly-hatched larva is roughly cylindrical, 1.5 mm long and the body tapers slightly towards the last abdominal segment. The colour varies from pale reddish-yellow to reddish, with the caudal segments slightly deeper in colour than the anterior segments, and the legs and under-side pale yellow and translucent. The head-capsule, first thoracic tergite and suranal plate are sclerotized and dark brown, and long, slender hairs occur on the head and all thoracic and abdominal segments. The abdominal legs occur on segments 3-6 and 10.

The second to final instar larvae are roughly of the same shape and appearance as the first instar larvae, but the head-capsules are of a pale golden-brown colour, and the first thoracic tergite and suranal plates are similarly paler in colour. The setae on the body are less conspicuous, and the general colour varies from pale yellowish to almost bright red, with the pigment mainly along the dorsal aspect. Larvae collected in Western Australia and reared on their natural host-plants were of paler colour than their eastern counterparts. The integument is partly translucent and the contents of the gut are visible. The body of the full-grown final instar larva is typically shiny and the segments are bulging out. The length varied between approximately 7 and 13 mm and the weight between 9 and 32 mg with a mean of about 23 mg. The crotchets on the abdominal legs are uniordinal and uniserial.

The pupa is creamy white with the integument shiny and transparent during the first 24 hours after pupating. The eyes gradually turn deep red, and later virtually black, and the colour of the body gradually darkens. During the last part of the pupal stage, black areas on the imaginal integument are virtually continuous. The pupal integument is delicate, not sclerotized and creamy in colour. A brownish, roughly triangular, slightly raised stridulatory area on the mid-ventral aspect of the sixth abdominal segment is usually covered by the distal ends of the appendages. The cremaster is reduced to a pair of small conical spikes.

<u>The moths</u> are small, delicate, and very inconspicuous due to their dull and cryptic colouration. They are about 10 - 13 mm long from the tip of the labial palpi to the wing-tips when resting, and have a wing-span of about 18 - 22 mm. In the resting position, the narrow front wings are folded over the abdomen, with their straight outer edges at a slight angle with the body-axis, and with their fringed rear edges in a V-shape. The club-shaped labial palpi are densely covered in long, slender scales, and are held parallel in front of the head. They are very conspicuous, especially in females, in which they are about twice the length of the head, and twice as long as those of males. Two crests of elongated scales occur on the head between the eyes. The antennae are filiform, and folded against the body. The proximal two-thirds of the forewings are of a buff to coppery-grey colour[1], with a series of tufts of raised scales of a darker colour than the background. The distal one-third of the wing is often a paler colour.

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[1] Specimens from Albany, W.A. were usually of a paler colour, but both dark and pale forms were reared from larvae collected at Wilson's Promontory.

TABLE 20

The different stages of *Carposina autologa* Meyr. found at different months during visits to Wilson's Promontory, Victoria, over a period of about three years. Estimates are given of the relative abundance of the stages found. Pupae were not found.

	JAN	FEB	MAR	APR	MAY	JUNE	JULY	AUG	SEPT	OCT	NOV	DEC
Eggs		0	0	+++	+++	+++	0	(+)	0		0	0
Penetrating larvae		0	0	(+)	0	+	++	(+)	0		0	0
1st instar larvae in fruits		0	0	0	0	(+)	+++	+++	++		0	0
2nd - 4th instar larvae		0	0	0	0	0	(+)	(+)	+++		(+)	0
Older larvae in fruits		+++	0	0	0	0	0	0	0		+++	+++
Larvae newly-escaped		+	0	0	0	0	0	0	0		0	(+)
Moths		0	-?	+++	-	0	-	0	0		-	-

Ratings:		
	+++	very abundant or predominant
	++	common
	+	occasional individuals
	(+)	very rare
	0	none found
	-	not sampled
	-?	none found, but suspected to be present

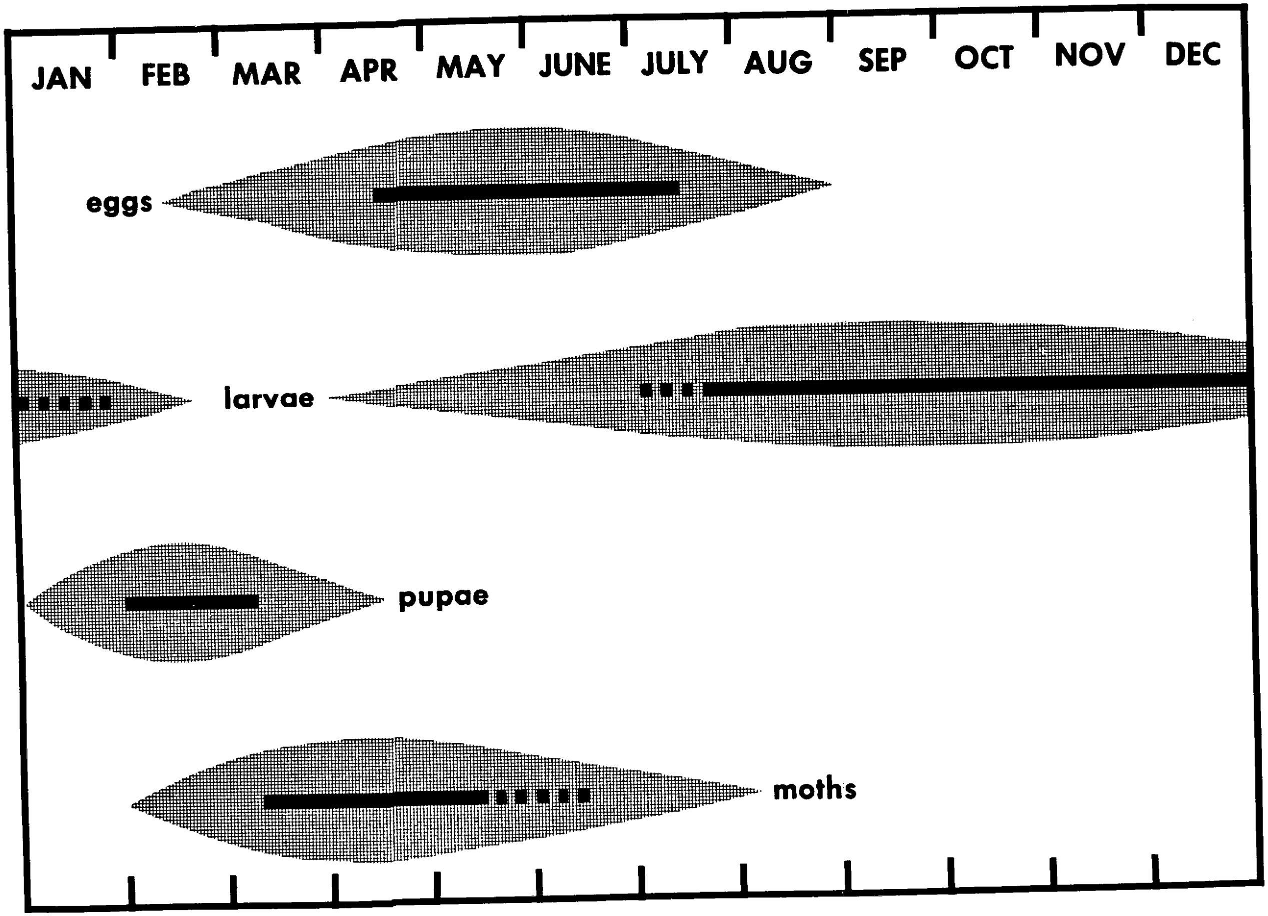
TABLE 21

The occurrence of the different developmental stages of <u>Carposina autologa</u> Meyr. found in odd samples of fruits of all host-plants collected at various localities during different months of the year

	FEB	MAR	APR	MAY	JUNE	JULY	AUG	SEPT
Heathcote NSW					newly-hatched			
Bargo - Yanderra NSW				eggs		young larvae (1st inst.)		young larvae
Goulburn NSW			eggs					
Cann River VIC		eggs	eggs (some hatched)					eggs young larvae (1st-3rd inst.)
Pakenham VIC					eggs entering larvae			
Albany Many Peaks WA	full-grown larvae					eggs young larvae (1st-2nd inst.)	some eggs young larvae (1st-3rd inst.)	

Figure 8

Hypothetical phenology of *Carposina autologa* Meyr. at Wilson's Promontory Vic. The presence of individuals is indicated by the shaded areas; that of a hypothetical individual by a horizontal, central line



The concealed hindwings are pale grey to whitish, and have a fringe of slender scales. Males have erectile tufts of pale slender, hair-like scales near the base of the sub-costal vein of the hindwings.

4.34 Phenology in the field

Table 20 shows the occurrence and abundance of *C. autologa* at Wilson's Promontory at different times of the year. The observations showed that eggs were laid in autumn, that the larvae hatched during late winter, but that larval development was not completed until the summer months.

Using the information shown in the table above, combined with trends exhibited by field-collected material and rates of development in the laboratory, the construction of a hypothetical phenology was attempted (Figure 8). It is suggested that eggs are present during the winter months, but that a few larvae may hatch before winter. The estimated rate of development of a typical individual is indicated on the figure.

The occurrences of the different stages in small samples of fruits of host-plants from a number of localities in south-eastern and south-western Australia at various times during the study period is shown in Table 21. The phenology all over south-eastern Australia appeared to correspond closely with that observed at Wilson's Promontory. The general pattern appears to be similar at least at Albany in south-western Australia, or for at least some of the individual insects. However, the fact that moths had been collected during September to

TABLE 22

The favourability of different types of egg-laying situations for Carposina autologa Meyr. (on, or in the vicinity of fruits) on Hakea host-species at Wilson's Promontory, with comparable ratings for smaller samples of host-fruits from other localities

		nodosa Wilson's Prom. 804 eggs		sericea Wilson's Prom. 599 eggs		sericea Heathcote	suaveolens Albany	elliptica Albany	cucullata Many Peaks
		% of eggs	rating	% of eggs	rating				
POSITIONS ON OR NEAR FRUITS	Natural irregularities on surface	70	++++	<1	-	+++	0	0	0
	Folds next to beak	N.a.	0	63	+++	+	0	0	0
	Wounds or rough areas	1	+	6	+	+	+	+	+
	Base of suture	1	+	2	+	+	+	0	0
	In crack along suture	<1	-	2	+	-	+	0	0
	Between fruit and another fruit or stem	2	+	9	+	+	++++	+++	-
	Folds in fruit-stem	1	+	17	++	++	+	-	++
	Adaxial groove	25	++	1	+	0	0	0	0
	Pubescence of fruit-stem	N.a.	0	N.a.	0	0	0	0	++++
	Egg-shells of Dixoncis pictus	<1	-	1	+	0	0	0	0

N.a. = not applicable

TABLE 23

The distribution of 32 newly-laid eggs of *Carposina autologa* Meyr. on two plants of *Hakea nodosa* at Wilson's Promontory, Victoria early in the egg-laying season (March 1967). Eggs were found only on fruits

23 (a) EXTERNAL APPEARANCE OF FRUITS

	No. of fruits	No. of fruits with		No. of eggs	No. of eggs as % of no. of fruits
		1 egg	2 eggs		
A Newly-matured fruits	23	7	2	11	48[*]
B Older undehisced fruits	140	15	3	21	15[*]
C Dehisced fruits	67[†]	0	0	0	0

[†] Including 22 dehisced after attack by *Erytenna* larvae
[*] Differences significant at $P < 0.001$

23 (b) ANALYSIS OF OLDER, UNDEHISCED FRUITS (B ABOVE)

With unattacked seeds	35	5	1	7	20
With attacked seeds	45[‡]	3	0	3	7
With completed escape (seedless)	60	7	2	11	18

[‡] Includes 6 fruits with rotten seeds, attacked by acanthosomatid bug (see Appendix III)

November in W.A. (see section 4.31) suggests that the phenology there may be different. The possibility of a second generation by at least some of the individuals will be discussed later.

4.35 General biology and habits

Ovipositing females run around on twigs and fruits with their wings raised and vibrating, and 'examine' the surface of the substrate with their extended, slender and flexible ovipositors. Observations of the situations in which eggs were laid on *H. nodosa* and several other *Hakea* spp., showed that they were laid singly, usually with only the spiked anterior area exposed, in small crevices or other protected situations, on, or in the immediate vicinity of mature fruits (Table 22). When comparing the shape and other characteristics of the different hosts with the egg-laying situations on them, it was evident that the eggs were laid in the most sheltered positions occuring on the fruits, or in their vicinity in the case of very smooth fruits (e.g. *H. suaveolens* and *H. cucullata*).

That there is a clear selection of fruit type in the field is shown by the results in Table 23. Mature fruits in their first year (therefore the youngest fruits available at the time of oviposition) were the most favoured. Older, but undehisced mature fruits were less than half as favourable. Dehisced fruits were not used for oviposition. A closer analysis of the older, undehisced fruits, (Table 23b) classified as to whether they 1) were unattacked, 2) had been entered, but in which the larvae or their parasites succumbed prior to completing the escape tunnels or 3) were in a stage after successful attack (also by parasites of the larvae) failed to substantiate suggestions that moths may be able to detect fruits not previously attacked.

The hatching larva eats a small hole through an exposed part of the chorion, and walks actively over the fruit. When it encounters the more or less straight, but often quite inconspicuous, suture along the axial surface, it often walks along its length and finally settles somewhere on, or directly next to it. The possible mechanisms of locating the suture are discussed below (section 4.352).

Construction of a narrow protective cover on the surface of the fruit then follows (the position in relation to the suture being influenced by the type or species of fruit). This cover is made of small pieces of wood nibbled from the surface and incorporated into a sleeve of silken threads, eventually camouflaging the entire body of the larva.

While below the cover, a minute tunnel is eaten into the fruit, either through the granular tissue in the suture, or through the surrounding dry tissue. The tunnel is extended until it reaches either the seed-cavity, or the space (if present) near the wings from which access to the seeds is possible. The entry tunnel is lined with silk, and a densely woven silken disc is formed in the mouth. There were indications that the protective cover is at least partly demolished prior to closing of the tunnel.

The young larva feeds on the surface of the seeds and some debris is gradually worked into the entry tunnel. A small circular hole is eaten into one of the seeds, and the larva, moving about actively on the surface of the seed, feeds alternately on the exposed cotyledon and the surface of the testa.

If another larva enters the fruit, it is soon attacked and usually killed. However, the original larva, or even both, may die as a result of the fighting.

Moulting occurs in the vicinity of the general feeding site, or sometimes elsewhere in the seed-cavity. During each subsequent instar the small hole in the testa is enlarged to facilitate feeding on, and into the cotyledons. The accessible parts of the seed-wings are usually consumed or chewed up. The second seed is only attacked towards the end of the feeding period after the first has been consumed. The volume of faeces present in the seed-cavity is remarkably small at any stage during the development of the larva.

As a rule the larva commences tunnelling outwards into the woody part of the fruit during the fourth or fifth instar, and the straight tunnel is gradually enlarged and deepened until it reaches the surface of the fruit, leaving only a thin layer of bark covering the exit. The gnawed-up wood is worked into spaces around the seeds and tightly compacted. Tunnelling through the wood may be completed long before the larva is full-grown (even during the fifth or sixth instar). When the larva is fully grown during the final instar it eats through the remaining layer of bark over the escape tunnel and leaves the fruit.

In the field the escaping larva falls to the ground and crawls about actively until presumably, it finds some protected situation. Larvae in the laboratory pupated in, or under a layer of leaf mould placed on damp sand, usually without tunnelling into the sand, even when the layer of leaf mould was relatively thin. When forced to pupate in compacted sand, the larvae tunnelled into the sand, but only deep enough to allow embedding of the entire cocoon.

When making the cocoon, the larva attaches pieces of the surrounding material to the silken sleeve formed. If the latter is formed against some solid object, e.g. dead wood or part of a plant, pieces are gnawed off and attached to the exposed surfaces thus camouflaging the cocoon which is then usually also slightly embedded in the substrate. The main body of the cocoon is ellipsoidal. A narrower vestibule of varying length, leading to the outside (if the cocoon is embedded), is formed at one end. The exposed end of the vestibule is only loosely closed with a few silken threads, but a dense, circular disc (operculum) with a line of weakness around the periphery is constructed in the open end of the main part of the cocoon while the latter is lined with a thin layer of silk. Before pupating, the larva turns to face the operculum.

In the process of casting the pupal skin, the moth dislodges the operculum and the exuviae are held back by the restriction in the throat of the cocoon. Emergence occupies only a few seconds. The moth is initially very active, but soon settles on some near vertical surface, where the wings are spread and dried within 15 -20 minutes.

Afterwards it selects a sheltered situation, usually with a dark background, where it rests with the wings folded in the normal resting position until the next period of activity.

Observations suggested that the moths were mainly crepuscular, but specimens were taken at light traps at all hours of the night.

The pre-oviposition period may be very short (1 - 3 days). Females did not readily lay eggs in cages, and some of these became so distended with eggs that they were not capable of normal flight.

The moths appeared to be short-lived, and it appeared that they may not survive longer than several weeks in the field.

4.351 Host-plant selection by females

As there was no evidence of egg-laying on fruits of non-host species of *Hakea* in the field, even when these plants occurred in virtual contact with hosts, attempts were made to determine the possible influence of leaf- and fruit-types on the host-plant selection of females. The oviposition of females was studied, using the multiple choice methods described in section 4.32. To determine the possible influence of the shape of the leaves, single newly-matured fruits of *H. nodosa* were attached to branches or foliage of *H. nodosa*, *Casuarina pusilla* (whose green branches approximate the leaves of needle-bushes), the fern *Gleichenia* sp. (finely divided leaves), *Eucalyptus capitellata*, and to bare, dead twigs of *Leptospermum juniperinum*. Although relatively few eggs were laid during both repetitions of the experiment (Table 24A), considerably

TABLE 24

Oviposition by females of *Carposina autologa* Meyr. in a field-cage when given choices between different types of foliage and different types of fruits.

		TYPE OF FOLIAGE (various, no flowers)	NO. OF EGGS LAID			NO. OF FRUITS SELECTED (of 8 per treatment)		
			I	II	Total	I	II	Total
A	Young *nodosa* fruits	*H. nodosa*	10	2	12	4	2	6
		Casuarina	1	1	2	1	1	2
		Gleichenia	2	1	3	2	1	3
		Eucalyptus	4	0	4	2	0	2
		Dead *Leptospermum* twigs	0	0	0	0	0	0
		TOTALS	17	4	21	9	4	13

		TYPE OF FOLIAGE (*HAKEA* SPP.)						
B	Young *nodosa* fruits	*nodosa* with flowers	14	2	16	3	2	5
		nodosa without flowers	6	4	10	2	2	4
		nodosa dead foliage	2	0	2	1	0	1
		teretifolia	19	1	20	2	1	3
		sericea	17	5	22	2	3	5
		TOTALS	58	12	70	10	8	18

		TYPE OF FRUIT (*HAKEA* SPP.)						
C	Flowering *nodosa* branches	*nodosa*	5	23	28	2	4	6
		sericea	6	12	18	2	3	5
		suaveolens	0	6	6	0	4	4
		ulicina	0	0	0	0	0	0
		teretifolia	2	1	3	2	1	3
		TOTALS	13	42	55	6	12	18

		TYPE OF FRUIT (various structures)						
D	Flowering *nodosa* branches	*H. nodosa* (nobbly)	14	11	25	2	4	6
		H. nodosa (smooth)	5	6	11	3	3	6
		Dehisced *Casuarina* cones	0	0	0	0	0	0
		Fresh *Casuarina* cones	8	0	8	1	0	1
		Brabejum stellatifolium	6	1	7	3	1	4
		TOTALS	33	19	52	9	8	17

more eggs were laid on the fruits in *H. nodosa* foliage than on those in the other types of foliage and none were laid on fruits in the dry ti-tree twigs.

Egg-laying on *H. nodosa* fruits set up in foliage of the non-host *H. teretifolia*, was compared with that on fruits set up in *H. sericea* and *H. nodosa* (the latter either normal with flowers, or without flowers to be comparable to the other *Hakea* branches) and on fruits in dry foliage of the same plant (Table 24B). There appeared to be no significant differences in the numbers of eggs laid on the fruits in live foliage of *sericea*, *teretifolia* and *nodosa*, but only two eggs were laid in dead *nodosa* foliage.

These two experiments showed that there was a definite response to the type of foliage.

To determine the influence of the type of fruit, egg-laying on newly-matured fruits of the hosts *H. sericea* and *H. nodosa* was compared with that on *H. suaveolens* (of similar size as those of *H. nodosa*) and the smaller fruits of the non-hosts *H. ulicina* and *H. teretifolia*. To eliminate differential effects of foliage, all were placed in flowering branches of *H. nodosa*. In Table 24C it is shown that more eggs were laid on fruits of *H. nodosa* and *H. sericea* than on the other fruits.

In planning these experiments, it was realized that fruits of *nodosa* and *sericea* offered more potential oviposition sites on their surfaces than those of the other species. The role of surface-structure was examined in another experiment (Table 24D) using fruits of similar size of some very different plants. Nobbly and smooth fruits of H. nodosa were presented together with fresh and dehisced cones of Casuarina pusilla and the velvety fruits of Brabejum stellatifolium in flowering H. nodosa foliage. The last two types of fruit offered innumerable egg-laying sites on them compared to the fresh Casuarina cones and either of the H. nodosa types. More eggs were laid on the nobbly type of H. nodosa fruits. Of the non-host fruit types, only Brabejum was given significant attention.

The results of these four experiments therefore showed that there was a positive response both to the foliage and to the fruits of the hosts used. The size and superficial structure of the fruits were probably of secondary importance.

4.352 Penetration behaviour of newly-hatched larvae

Six individual larvae[1] were closely observed in the laboratory on separate, newly-matured fruits of H. nodosa. Continuous observations during which their movements and activity were carefully noted, were made for one hour, or until the larvae commenced construction of a protective cover or appeared to settle somewhere on the fruit. They were then confined on the fruits and inspected at intervals to observe their positions and activity.

Two other larvae from the same batch were similarly observed on a smooth fruit-shape carved out of balsa wood. These observations

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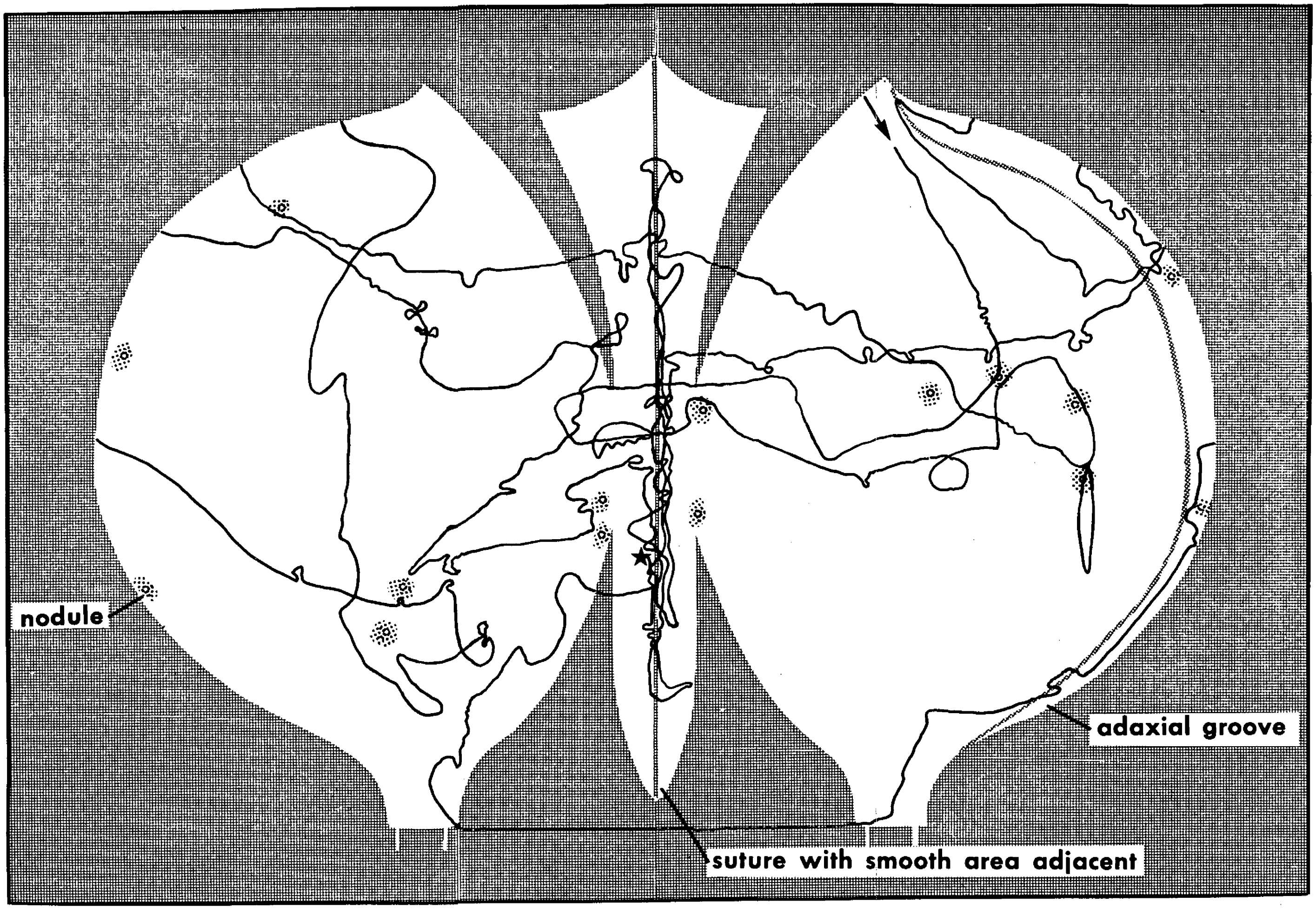
[1] The larvae were removed as they appeared on the surface of field-collected fruits held in the laboratory, and were presumed to be newly-hatched.

Figure 9

Movements of a typical newly-hatched larva of *Carposina autologa* Meyr. on a fruit of *Hakea nodosa* in the laboratory. Point of release is indicated by an arrow ; position where it settled (after 45 minutes) on the suture by ★



were repeated on a cylindrical, smooth piece of balsa with a straight groove cut along its side, simulating the suture on host-fruits. Another larva was observed on the intact, dry husk of a walnut, which had a groove along its side, not unlike the suture on host-fruits.

Of the larvae on the host-fruits, one encountered the suture within 11 minutes, and temporarily settled at a small natural pit on the suture within 16 minutes, where a protective cover was eventually formed after abandoning a second attempt elsewhere on the suture. One larva was sluggish, and moved into a crevice within 20 minutes, and remained there under a loose cover of silken threads. The other four larvae moved around on the fruit in an apparently random fashion, each crossing the suture a number of times with no visible response, each walking along the suture a number of times, and each walking off it a number of times. Two of them finally settled on the suture and commenced with the construction of protective covers after 28 and 45 minutes respectively. The movements of the latter larva are shown in Figure 9. The other two larvae were still moving around on the fruits after two hours. On the following day, one of these was constructing a cover on the suture after it had abandoned a partly constructed cover in the adaxial groove, and the other larva had left its fruit.

The larvae on balsa wood also moved around fairly randomly, but generally along a more even course and with less frequent distinct changes in direction. They showed no response at all to the simulated sutures, and moved off the wood a number of times during the first two hours. After 18 hours, both showed tendencies to move into sheltered positions, such as the grooves, or pores in the wood. The larva on a walnut behaved similarly, and covered itself with a loose silken cover and pieces of dirt in a shallow groove on the side of the fruit.

Detailed observations of the active larvae on host-fruits showed that at times they moved evenly without marked changes in direction, while at other times they stopped briefly at frequent, irregular intervals, when they raised and waved the stretched front half of the body in the air. Distinct changes in course often occurred at these 'stretching' points. They inserted their heads for various lengths of time into small irregularities encountered in the surface, as if examining them with their mouthparts. They also briefly entered crevices between nodules. They left a minute silken thread along their path, apparently attached wherever the mouthparts touched the surface. During some of the 'stretching' actions the silken thread was attached to the substrate on one or both sides of the body, resulting in a criss-cross effect along the path followed. While moving along the suture, more frequent 'stretching' usually occurred, and more frequent changes in direction, either resulting in direct return to the suture, or in wandering off. This also occurred when the apex of the fruit was reached.

The larvae on artefacts and on the walnut also 'stretched' and waved the front parts of their bodies, but their silken thread was apparently not laid down in a zig-zag fashion so often, and marked changes in direction at the 'stretching' points occurred less frequently. During the first hour of observation, they usually paid no attention to irregularities, such as the grooves, or pores in the wood.

The behaviour of these larvae on host-fruits and artefacts suggested that the following factors may have been of significance in the finding and recognition of a suitable penetration site: 1) the generally even course (less frequent marked changes in direction) and failure to respond to the simulated suture on artefacts and non-host material; 2) the obvious response to the suture (possibly to the straight line) on suitable fruits; 3) the nibbling at small irregularities in the surface of host-fruits; and 4) abandonment of unsuitable sites.

To investigate some of these factors, further observations were made on other artefacts and host-fruits altered in different ways.

Larvae placed on plastic artefacts, either flat surfaces or simulated fruit-shapes, behaved in a similar way as those on balsa wood, and failed to show any response to either a straight, dark line, or a straight groove on the surface. They showed positive signs of rejection, either by walking off repeatedly or descending on silken threads. They also for the first time showed signs of orientation in relation to the source of light or intensity of illumination by moving more frequently on the aspect of the artefact receiving the brightest illumination. As these artefacts were dry, observations were also made on live fruits of Brabejum stellatifolium. Larvae had difficulty in moving on the velvety surface, and made no entry attempts even when the hairs were shaved off and a straight, longitudinal groove was made along one side. One larva covered itself under a loose network of silk and plant tissue while in the groove, but this was seen as sheltering behaviour, which will be considered later.

To investigate the reaction to the straight line on suitable host-fruits, larvae were observed on fruits of H. nodosa and H. sericea whose sutures had been covered with a thin layer of melted wax. On H. sericea the straight line of the suture still remained visible on the surface of the wax. These larvae showed no response to the sutures. However, when a straight, shallow cut was made diagonally across the side on a smooth part of one such fruit, a larva constructed a typical protective cover across this cut, but abandoned it frequently and failed to tunnel visibly into the underlying layer of softer tissue.

To determine the influence of minute holes and irregularities in the surface on the penetration behaviour, small pin-pricks were inserted on the surface of H. nodosa fruits, both on the sides and in the adaxial groove. Although all four larvae observed inserted their mouthparts into punctures they encountered, only one showed the initial phases of entry behaviour while away from the suture, and that in the adaxial groove. When similar pin-pricks were inserted along the suture, the larvae infallibly selected these sites for penetration.

The fourth aspect of possible significance in the finding of a suitable penetration site, viz. the frequent abandoning of entry attempts, either during the initial stages, or after completion of the protective cover, was not experimentally examined. It seems reasonable that larvae may respond to the quality of the material into which they are tunnelling. Thus on encountering unusually hard tissue, or soft, juicy tissue, as would be expected once the bark has been punctured on any aspect of the fruit apart from on, or near the suture, the larva may abandon the attempt.

Under unfavourable conditions, such as when larvae become slightly dehyrdated in a dry atmosphere, their activity may be inhibited, and they may become thigmoitactic. This phenomenon may explain the changed reactions of larvae after some time.

Although several unexplained aspects in the finding and recognition of a suitable penetration site still remain, the present observations allow the following hypothesis:

1) there is an initial recognition of a suitable host-fruit (possibly based on the quality of the surface, sensed when the mouthparts contact the substrate);

2) in the presence of this, there are more frequent changes in direction, and 'examination' of minute irregularities in the surface;

3) there may be a tactile response to the straight line of the suture or the symmetry of the fruit on either side of the suture, and this may give rise to more frequent swaying of the head, more frequent adjustments to the course, and thus more frequent returns

TABLE 25

Indications of the potential egg-laying capacity of females of *Carposina autologa* Meyr., based on dissections of females of various ages. Some of the females were dissected after they died 'naturally' in the laboratory, and the numbers of undeveloped eggs could not be determined. Some were field-collected, and the numbers of eggs already deposited were then not known

FEMALE	Age (days)	Eggs laid	IN OVARIES			TOTAL NO. OF CHORIONATED EGGS	ESTIMATED[‡] POTENTIAL TOTAL
			Full-sized eggs	Coloured but small	Young oocytes		
59/67	0	0	12	28	48	40	88
newly-emerged	0	0	12	24	c.80	36	116
84/67	1	0	24	15	56	39	95
80/67	3	0	23	15	c.80	38	118
ex field-cage	6[†]	?	30	8	c.80	≥38	≥118
61/67	8[†]	0	23	?	?		
67/67	8	0	23	17	57	40	97
42/67	12[†]	0	24	19	69	43	112
47/67	12[†]	26	6	6	?	38	
field-collected	?	?	14	11	51	≥25	≥76
field-collected	?	?	14	8	27	≥32	≥49

[†] Dissected some time after death
[‡] Not allowing for possible progressive oogenesis

to favoured positions along the suture;

4) the presence of numerous cross-threads at a site, or of a minute pit in the surface, may intensify the response to construct a protective cover; and

5) during construction of the cover there may be a response to physical or chemical properties of the substrate (thus determining the course of the tunnel and acceptance of the site).

4.353 Fecundity and fertility

The majority of females held in the laboratory failed to lay any eggs, although they contained fully-developed eggs and their abdomens were often distended with apparently ripe eggs at the time of death.

The number of eggs laid by one female, and the numbers of full-sized and developing eggs present in the gonads of dissected females of different ages (whether they died 'naturally' or were killed for dissection), are shown in Table 25. The results suggest that i) a proportion of the eggs is fully developed at emergence of the moth, ii) the normal pre-oviposition period may therefore be less than 1 day, and iii) that immature ova probably develop gradually as the ripe eggs are deposited. Oocytes in various stages of development were present in the ovarioles of healthy females dissected, but it is not known whether additional oocytes are differentiated during the life of the moth. However, if all those observed in the ovarioles mature, the number of eggs produced by a single female may be in excess of 100 (possibly 12 - 14 per each of the 8 ovarioles).

TABLE 26

The durations of the different instars (and pupation) at $20^{\circ} \pm 2^{\circ}C$ of field-collected larvae of *Carposina autologa* Meyr.

HOST *Hakea* sp.		LARVA NO.	ESTIMATED INSTAR WHEN FOUND	DURATIONS OF INSTARS IN DAYS								Inside fruit after 3rd moult	PUPATION (days)	SEX
				2nd	3rd	4th	5th	6th	7th	Final instar Feeding	Final instar Outside			
WILSON'S PROMONTORY	*nodosa*	4	2	12+	24	17	22	14	-	18	7	71	28	
		12	2		20	27	25	8	-	15	7	75	29	
		18	3		7+	18	24	9	-	10	11[†]	61	32	female
		19	3		20+	19	15	16	-	16	7	66	29	
		20	3		13+	28	22	23	-	30	8	93	27	
		21	3		9+	19	47[†]	10	-	22	7	98[†]	28	
		23	2	16+	18	23	17	10	-	13	7	63	28	male
ALBANY W.A.	*elliptica*	42	4			16+	21	33	-	26	7	96+	27	female
		43	2	6+	14	22	18	16	16	13	7	75	28	male
		46	2	5+	20	12	13	12						
		47	1	20	21	14	15	14	-	23	6	62	27	female
		48	1	12	15	11								
	cucullata	55	2(3rd?)	4+	10	12	16	19+19[●]	19	25	7	120	31	male
		56	4				11	18	-	21	7		27+	female
MEANS					19	19	18	14		19.5	7	69	28	
No. of observations for calculations of means					7	11	12	12		12	11	9	11	

[†] Atypical as a result of starvation, or being interfered with excessively

[●] Additional instar after '6th' - but probably had a total of 10 instars

The eggs (5) laid in the laboratory by one experimental female (from eastern Australia) were all sterile but 11 of the 26 laid by the second (from western Australia cf. female 67/67, Table 25) hatched. Initial embryonic development was evident in 23 of the latter eggs, but some of the larvae failed to hatch despite the fact that they were apparently fully differentiated at the time of death. Both females had been confined with males from eastern Australia.

4.354 Rates of development

Eggs laid in the laboratory and incubated at about 20°C, hatched in 31–54 days, with a mean of 41 days for 26 eggs observed. Of 69 field-collected eggs, all hatched within 3 - 54 days in the laboratory, with those collected later in the season (e.g. September) always hatching in fewer days than those collected early in the season (e.g. April).

In as many cases as possible the durations of successive instars of field-collected larvae (reared on seeds of the original hosts) were noted. As the exact developmental stage of these larvae was not known at the time of collection, their head-widths (as well as those of any cast capsules found in the fruits) were measured. They were then designated to an instar according to the observed ranges in the theoretical 8-instar plan to which the majority of larvae in the field appeared to conform. In Table 26 it is shown that nearly all these individuals pupated after what appeared to be the 7th instar. The variations in the duration of each instar in these larvae were quite large, especially in the last two instars. In contrast, the duration

TABLE 27

The durations of the larval instars of *Carposina autologa* Meyr. reared at 20° ± 1°C on seeds of *Hakea nodosa*.

P indicates reared in small polythene vials; B indicates balsa squares.

LARVA NO.		DURATIONS OF INSTARS IN DAYS							LARVAL STAGE	SEX
		1st	2nd	3rd	4th	5th	6th	7th	Final		
9	B	14	25	26	16	15	-	-	17	113	female
11	B	18	35	31	16	11	-	-	30	141	female
15	P	21	29	17	19	12	-	-	35	133	male
18g	P	53		12	14	11	-	-	28	118	female
19a	P	54		13	20	19	-	-	24	130	male
19b	P	54		14	15	20	-	-	26	129	female
19k	P	24	28	13	12	19	-	-	39	135	male
20	P	63		21	22	17	-	-	26	149	female
		52									
MEANS		19 52	27	18	19	16	-	-	28	131	
16	P	17	30	12	30	12	16	-	30	147	male
17	B	59		20	22	16	13	-	22	152	male
18f	P	71		16	19	16	14	-	(10+)	(146+)	(died)
19i	P	56		15	12	11	21	-	22	137	female
MEANS		58		16	21	14	16	-	25	145	
18b	P	21	29	16	21	16	12	16	23	154	male

of the spinning and pre-pupal period was very constant. The longer durations of the instars for many of the larvae appeared to be related to the relatively large amounts of tunnelling and other non-feeding activity that occurred. It was thought that variation was caused by the frequent disturbance of the larvae during observations using the early techniques of rearing (see above). They always covered themselves, or stuffed open cracks with debris and silken threads, or commenced new escapes when the fruit-halves were changed.

When more satisfactory rearing techniques, with which less disturbance was necessary, became available, the observations were repeated on newly-hatched larvae (Table 27). Of 13 larvae reared in balsa squares and in small polythene vials, 8 had 6 instars, 4 had 7, and one had 8 instars. Larval stages (from the commencement of feeding to pupation) occupied 129 - 152 days. There were indications that it may be generally longer in those larvae going through more instars. The numbers of instars or rates of development did not appear to be related to the sex of the individuals.

The duration of the pre-feeding phase (i.e. the penetration period) was very variable, depending on the barrier to be eaten through to reach the seed-cavity. In an attempt to determine the approximate duration of this phase, 34 larvae were placed on picked fruits of _H. cucullata_, _H. nodosa_, _H. sericea_ and _H. suaveolens_. All of the 29 that attempted entry at the sutures, were found to have commenced with protective covers within 3 days, and at least 23 commenced within the first two days. Some located the suture within the first hour (see section 4.352).

While most of these larvae lived for more than two weeks, all died within 34 days without reaching the seed-cavities, apparently as a result of adverse conditions on picked fruits in the laboratory. Casual observations on field-collected material and less accurately observed larvae suggested that the 'normal' penetration period in the laboratory could be less than 6 - 8 days on an easily-entered fruit, e.g. of H. cucullata or H. nodosa.

Pupation occupied between 24 and 33 days at $20^{\circ} \pm 2^{\circ}C$ (see also Table 26), with a mean of 29 days for 39 individuals.

In the laboratory individuals from eggs and young larvae collected in early winter reached the adult stage as early as October and November. However, in the field (at least at Albany and Wilson's Promontory) development was much slower : the larvae were still feeding during mid-summer, and the moths did not appear until about autumn. When observing eggs and larvae on tagged fruits at Wilson's Promontory, it was found that incubation occupied more than 2 months, that penetration may take more than 2 - 3 weeks, and that the 1st instar (penetration and feeding) may occupy more than two months during winter.

The measurements of head-capsules found in field-collected fruits strongly suggested that the occurrence of 8 instars may be predominant. It is therefore possible that the predominance of 6 instars in laboratory-reared larvae (or of 7 in larvae collected during the estimated second or third instar) may have been a result

TABLE 28

The development of *Carposina autologa* Meyr. on seeds of various nuts on which they were confined. All the larvae were placed in small polythene vials on pieces of seeds, but when this proved unsatisfactory, they were transferred to balsa squares, and were later confined on whole seeds in polythene vials. (Larvae reared at 20° ± 1°C)

SEEDS SUPPLIED	NO. OBSERVED	NO. REACHING 2nd INSTAR	LARVA NO.	DURATIONS OF INSTARS IN DAYS							TOTAL DAYS IN FIRST 5 INSTARS
				1st	2nd	3rd	4th	5th	6th	7th	
Corylus avellana (Hazelnut)	4	4	25a	59	25	21	26	26	10+		157
			25b	39	23	23	16	17	15	32+	118
			30a	37	28	32	13	51	1+		161
			30b	36	11	16	24	25+			112+
			MEANS	43	22	23	20	30+			137+
Prunus amygdalus (Almond)	4	2	26b	35	7	then died					
			31a	36	33	29	14	23	19	6+	135
Macadamia sp.	3	1	35c	37	12	21	18	19	15+		117
Brabejum stellatifolium	6	2	36a	27	13	10	then died				
			36b	29	12	9	13	20	27*		83
Juglans regia (Walnut)	8	0		very little feeding observed							
Bertholletia excelsa (Brazil-nut)	4	0		no feeding observed in any larva							

*Moulted to abnormal pupa, in which some parts of the body had larval characteristics.

+ After no. of days indicates larva still alive (October 1968) of higher (± constant) temperatures in the laboratory, and/or of the surplus of fresh food available to them with the rearing techniques used.

4.355 Development on seeds of non-hosts

The larvae were not completely specific in their food requirements. This was first suggested when larvae were observed developing apparently normally on parts of germinating seeds (e.g. the hypocotyl or green cotyledons) during initial attempts to rear them on loose seeds.

In Table 28 it is shown that larvae developed fairly normally when confined on seeds of hazelnut (Corylus avellana - Corylaceae), almond (Prunus amygdalus - Rosaceae), and Macadamia sp. (Proteaceae). The larvae did not readily take to feeding and mortality was greater during the first instar on the latter two types of seeds. The duration of the first instar on these nuts was exceptionally long in comparison to larvae reared on Hakea seeds under similar conditions (5 - 8½ weeks in comparison to 2 - 3½ on host-seeds). Similarly, the total duration of the first five instars was longer than in larvae on host-seeds (cf. Table 27).

On young seeds of the Cape wild almond (Brabejum stellatifolium - Proteaceae) mortality in young larvae was similarly high, and the first instar was longer than normal. After this initial delay, the surviving larvae appeared to develop even more rapidly than on host-seeds but one larva soon died, and the other gave rise to an abnormal 'pupa' that failed to survive.

Seeds of walnut (Juglans regia - Juglandaceae) and brazil-nut (Bertholletia excelsa - Myrtaceae) appeared to be completely unsuitable for larval development, and at most very little feeding occurred.

4.36 Subtractive factors

4.361 Intraspecific competition (between larvae)

On no occasion were two or more larvae found developing in the same fruit. However, dehydrated, mouldy bodies, or head-capsules of first instar larvae were often found near the penetration sites in fruits containing developing larvae, or in which one larva had completed at least a substantial part of its development.

Multiple egg-laying was prevalent on fruits of favoured host-plants at localities where C. autologa was abundant (e.g. as shown by data in Tables 17 and 31). Up to 25 eggs were found laid during one season on a single fruit on an experimental plant of H. nodosa at Wilson's Promontory, and up to four successful (plugged) entry tunnels were found on one fruit. Several larvae may also successively enter a fruit through the tunnel made by an earlier larva. Thus, on this same plant, eight larvae were found to have entered a fruit with only two completed entry tunnels.

No sign of aggressiveness was noticed amongst newly-hatched larvae confined together or walking on the surface of a fruit. Even larvae in the process of entering fruits did not appear to be distinctly aggressive towards other larvae disturbing them.

Newly-entered larvae, however, were generally aggressive. They often appeared in the entry tunnel within seconds of the silken disc in the entrance being removed, and readily attacked bristles of a small brush. Rival larvae were seen to be attacked as they entered the seed-cavity, and the then open entry tunnel is sealed by the surviving larva. On one occasion the decapitated body of a larva was found still under the protective cover on the surface of the fruit. Its head was found inside the fruit, which contained a developing larva. The observed habit of young larvae to move about in the seed-cavity probably enables them to attack entering larvae immediately.

As has been stated above, there were indications that both larvae may succumb as a result of fighting. Fruits containing apparently suitable seeds, but with the remains of two or more young larvae, were found. Such fruits often had a conspicuous, unsealed entry tunnel.

On two occasions a young larva was placed in a fruit already occupied, and fighting was observed when the fruits were re-opened after a few minutes. These larvae, although normally easily disturbed by light when fruits are opened, continued fighting. They faced each other and moved backwards and forwards, each apparently trying to bite into the body of the opponent without being bitten itself. The sides of the thoracic segments appeared to be the most vulnerable parts during fighting, as many of the killed larvae inside fruits were found to have wounds, or moulds growing on these segments.

The larva already inside a fruit probably has an advantage in being able to attack other larvae while they are still entering. The reactions of older larvae towards intruding larvae were not observed.

However, fruits containing two sets of second, or even third instar head-capsules were found, probably indicating that an older larva had been killed by a young, newly-entered one. Larvae in the process of moulting are thought to be vulnerable to attack by young ones.

4.362 Parasitoids

Two types of hymenopterous parasitoids caused considerable mortality in larvae and eggs of *C. autologa*. A braconid attacked and killed older larvae while they were still inside the fruits, and a trichogrammatid developed in the eggs of the host. A single ichneumonid[1] emerged from a pre-pupa, about two months after the host had been collected as a larva at Albany, W.A. Adults of an unidentified eupelmid emerged from fruits in which remains of *C. autologa* larvae were found, but it is suspected that this insect may be hyperparasitic through the braconid. Remains of two other hymenopterans, one a eurytomid, the other an unidentified black, cocoon-forming species distinct from the braconid, were found in fruits in which they had succumbed prior to completing escape tunnels. The fruits had also been entered by *C. autologa* larvae, but not necessarily prior to oviposition by the hymenopterans. The eurytomid is probably phytophagous, normally developing in seeds of smaller-fruited *Hakea* spp. (see Appendix III).

During January 1967 a single nematode (Mermithidae, det. W.L. Nicholas) was found in the seed-cavity of a fruit of *H. nodosa*

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[1] *Diadegma* sp. (det. Josephine C. Cardale)

TABLE 29

Estimated mortality in larvae of *Carposina autologa* Meyr. while inside host-fruits. Estimates based on a sample of 140 fruits of *Hakea nodosa* from Wilson's Promontory, Victoria.

					%
Carposina	successful	39	(≤52)[†]		
	died young	16		55 (≤68)	49.5 (≤61.3)
Braconids	successful	21	(≥8)		
	in 'diapause'	8			
	unsuccessful	24		53 (≥40)	47.8 (≥36.0)
Other parasitoids, etc.				3	2.7
TOTAL ATTACKED FRUITS				111	

[†] 13 fruits appeared to have been left by adult parasitoids, but no confirmation of parasitism was found

at Wilson's Promontory. The nematode had apparently emerged from a final instar larva of C. autologa, whose partly collapsed body was also found in the fruit.

a) Braconid (Unidentified, specimens numbered AcHa 214 sent to B.M.) This insect was abundant at Wilson's Promontory, especially in fruits of H. nodosa , and on two plants accounted for the death of an estimated 36-48 p.c. of C. autologa larvae that had entered all the fruits (Table 29).

The adult female of this parasitoid has a long, slender ovipositor, the sheath of which is 8 - 10 mm long. Due to the fact that the adult wasps emerged only during summer, when the host larvae were fairly advanced, and that young host larvae from the field did not yield parasitoids, it is likely that the female oviposits in the host by inserting the ovipositor into the seed-cavity through the suture of the fruit, or very likely through the blocked entry tunnel.

The host larva is normally killed towards the end of its feeding period, i.e. when it approaches full size and the escape tunnel is almost completed. (The sizes of head-capsules of parasitized larvae ranged between 37 and 55 units (cf. section 4.23), suggesting that predominantly final instar host larvae succumb.) The braconid larva then spins a white, irregular cocoon in the available space in the seed-cavity and escape tunnel, and remains there as a full-grown larva for 8 - 9 months until the following spring and summer, when it pupates. None of the field-collected larvae pupated before

September to October in the laboratory, and the adults then appeared within three weeks. The wasp completes the escape tunnel and emerges from the fruit. However, in all the samples of fruit examined, a large proportion of the adults failed to complete the escape tunnels and died inside the fruit (see Table 29). It is not known whether some of the parasitized larvae may succumb only after they have left the fruits.

The same, or a very similar parasitoid occurred at the other eastern localities where relatively large numbers of fruits attacked by C. autologa were examined (Bargo and Cann River). No certain signs of attack by a similar parasitoid were found in the small fruit samples from Albany. There was one doubtful case where the parasitoid whose cocoon was found in a seed-cavity of H. suaveolens, may conceivably have developed in a larva of Aphanosperma occidentalis Brit. (Cerambycidae), a species abundant in certain Hakea fruits at that locality (discussed in section 5.1).

b) ?Trichogramma sp. (AcHa 208). C. autologa eggs with blackish areas on the chorion, or that were entirely black inside, were collected in eastern and western Australia. These eggs failed to hatch, but minute parasitoids (provisionally identified as Trichogramma sp.) emerged from some of them within 26 days of collecting. Egg shells from which these had emerged, showed a typical black deposit on the inside and usually a single small hole.

A survey was made of the occurrence of this type of damage in samples of eggs from four localities in eastern and western Australia

TABLE 30

Mortality in the egg stage of *Carposina autologa* Meyr. on different hosts. Estimates based on examinations of eggs and egg-shells found on fruits of various ages

	Total eggs or egg-shells examined	UNAFFECTED EGGS		UNSUCCESSFUL EGGS				% parasitized by *Trichogramma*	% [(a)] unsuccessful eggs
		Apparently hatched	Not yet hatched	Parasitized by *Trichogramma*	Collapsed or contents mouldy	Larval remains in punctured chorion	TOTAL		
H. nodosa Wilson's Prom.	82[(b)]	70	2	0	7	3	10	0	12.2
H. sericea Wilson's Prom.	172	149	-	7	9	7	23	4.1	13.4
H. sericea Cann River	140	117	1	0	22		22	0	15.7
H. elliptica Albany W.A.	21	6	1	14	0	0	14	66.7	66.7
H. cucullata Betty's Beach W.A.	135	97	1	36	1	0	37	27.4	27.4
TOTALS	550	444		57	49		106	10.4	19.3

(a) No allowance was made for entire eggs disappearing prior to hatching, or for egg-shells that may have been lost prior to the examination

(b) Examined *in situ* on tagged newly-matured fruits at intervals during the first season. Of the 99 eggs laid, 17 disappeared during the observations; 2 apparently after hatching. Therefore actual overall mortality would be 25.3%.

(Table 30), and the numbers of eggs that had apparently failed to hatch for other reasons were also noted. Typical ?*Trichogramma* damage appeared to be more common in the samples from the Albany area, and absent or very rare in eggs from eastern Australia.

One to three parasitoids emerged from a single host egg (typically two females and one male), but individuals from one egg were sometimes of the same sex. They fed on a solution of honey in water in the laboratory and the females mated and were ready to oviposit within hours of emergence. They were short-lived, and neither sex survived more than 2 - 3 days in the laboratory.

As no *Carposina* eggs were available, the parasitoids were tentatively given eggs of the potato tuber moth (*Gnorimoschema operculella* (Zeller)). It was then possible to rear them for more than one generation. Each generation lasted 20 days at a temperature of 20 ± 2°C.

It seems unlikely that these insects are obligatory parasitoids of *C. autologa*, and their abundance on a given host-plant is probably dependent on the availability of alternate hosts in the periods when *C. autologa* eggs are absent in the field.

4.363 Predators

In eastern Australia dehydrated *C. autologa* eggs with their contents mouldy were commonly encountered (e.g. as shown in Table 30). Some of these eggs had a small hole in the chorion similar to that made by the hatching larva, but larval parts, usually only the head, were found inside. It was thought that these were likely signs of attack by predators.

A variety of predatory mites occurred on fruits of all host-plants examined, and sometimes in the seed-cavities of fruits. An unidentified mite (AcHa 216) was found with its mouthparts inserted in an otherwise apparently healthy *C. autologa* egg on *Hakea cucullata* (Many Peaks, W.A.).

?*Pediculoides* sp. (AcHa 217), is abundant on and inside fruits of various *Hakea* spp., especially in eastern Australia. It will readily attack all immature stages of *C. autologa*, the larvae being particularly vulnerable when they were moulting, or in a weakened condition during an extended penetration period. Adults and nymphs were found feeding on dead, young larvae that succumbed while entering the fruits, and mite eggs were found attached to the protective covers and in the entry tunnels of field-collected larvae. Although these mites appear primarily to be scavengers, they may cause some mortality in *C. autologa* in the field if they succeed in reaching the seed-cavity of fruits, e.g. via an entry tunnel.

Larvae of unidentified melyrids, clerids and neuropterans were encountered on, or sheltering in fruits of *Hakea* spp. These insects attacked and killed young *C. autologa* larvae offered to them, but they also fed on other insects, such as curculionid and tortricid larvae, in the laboratory. At least the clerid larvae found their way naturally into the seed-cavities of some fruits containing *C. autologa* larvae. In one Wilson's Promontory sample of 61 *H. nodosa*

TABLE 31

Estimated mortality in larvae of *Carposina autologa* Meyr. prior to the commencement of feeding at two localities in eastern Australia. The figures in brackets were derived from part of the sample only.

Host-plant Locality No. of fruits in sample[(a)]	*H. nodosa* Wilson's Prom. 630		*H. sericea* Wilson's Prom. 226		*H. sericea* Cann River 234	TOTALS 1090
Ave. no. of eggs per fruit	4.97		2.47		0.72	3.53
Hatched larvae[(b)]	100		100		100	100
Observed entry attempts	(29)		43		42	29
Successful entries	(20)	*	13	**	20	19
		**				
Successful entries (maximum of one per fruit)	19		12		20	18

[(a)] All the indehisced, mature fruits from a selected plant. In the Cann River sample, 95 randomly selected fruits were included.

[(b)] Calculated from the estimated mortality in eggs on these hosts (as in Table 30), expressed as unit of 100.

* Difference significant $P<0.05$ on raw data

** Difference significant $P<0.001$

fruits entered by C. autologa larvae but which did not have escape tunnels, 4 (6.5 p.c.) were noted to contain remains of clerid larvae in the seed cavities. Three of these larvae had apparently entered the seed-cavities through tunnels of a wood-boring curculionid in the follicle (see section 4.385 below). It appeared that this predator was not specific in its attack on C. autologa as it was commonly found in situations where the latter would not be present, e.g. in fruits dehisced or attacked by various curculionids.

4.364 Mortality in larvae prior to the commencement of feeding

On fruits of all the host-plants examined, only a small proportion of the eggs laid during the several years of the life of the fruit, yielded larvae that succeeded in reaching the seed-cavities. Mortality during the egg stage (see Table 30) appeared to account for a relatively small reduction in the number of larvae. In order to get information on the stages at which young larvae succumb after hatching, samples of mature fruits of H. nodosa and H. sericea from Wilson's Promontory, and of the latter species from Cann River were carefully examined for egg-shells, signs of unsuccessful entry attempts and the number of successful entries from all previous years (Table 31). The numbers of larvae that had hatched on these fruits were estimated from the numbers of egg-shells found and the observed mortality of eggs on the hosts involved. It is thought that the figures in the table may reflect the real situation on H. sericea in which possible over-estimates caused by larvae attempting more than one entry (as some did in the laboratory) would probably be cancelled by under-estimates as a result of several larvae attempting to enter at the same position. However, on _H. nodosa_, where the larval density was very high, several may enter a fruit through a single tunnel. The figures for the numbers of successful entries under these conditions were therefore probably under-estimates.

If it is assumed that the number of attempted entries observed was an indication of the actual number of larvae involved, the figures suggest that more than half of the larvae did not make a visible attempt at entry (therefore no protective cover) in the vicinity of the suture of the fruits. The proportion of larvae that succumbed while attempting to enter was smallest in _H. nodosa_ and highest on the form of _H. sericea_ occurring at Wilson's Promontory, where only 13 p.c. of the estimated number of hatched larvae reached the seed-cavity.

To determine whether the trends exhibited in fruit samples analysed above were real, a number of fruits were examined at intervals during a later season for the period while eggs and young larvae were present. It was hoped that the main causes of mortality in the young larvae would be revealed.

Fifty-two newly-matured fruits of _H. nodosa_, occurring on 15 plants at 4 different localities at Wilson's Promontory, were tagged prior to the egg-laying season. The fruits were selected to represent the different situations on the plant, e.g. towards the centre or on the periphery; at various aspects of the plants; and at various heights from ground-level. The sample included the main types

TABLE 32

The occurrence and apparent causes of mortality in eggs and young larvae of Carposina autologa Meyr. on 52 tagged fruits of Hakea nodosa at Wilson's Promontory, Victoria

AGE INTERVAL	NO. FOUND	% MORTALITY	INDICATIONS OF MORTALITY	NO. OF CASES	SUSPECTED CAUSE OF MORTALITY
Newly-laid eggs	99				
		≥29	i) Collapsed, dehydrated prior to development	4	Infertility
			ii) Disappearance	17	Predation Dislodging
			iii) Larvae dead in unpunctured egg-shells	5	Predation (Mites?)
			iv) Larvae partly consumed in punctured egg-shells	3	Predation
Hatched larvae (≡ chorions punctured as if by hatching larva)	≤70				
		67	v) Disappeared without trace	47	Migration Failure to find suture Predation Physical factors
Larvae attempting entry (≡ signs of entry attempts)	23				
		9	vi) Larval remains under protective cover	1	Predation (?) Physical factors (?)
			vii) Attempted entry in adaxial groove	1	Failure to find suture
Successfully entered larvae (≡ plugged entry holes)	21				
		5	viii) Second successful entry on single fruit	1	Competition (fighting)
			ix) Fruit abandoned via entry tunnel	1	Rotten seed(s)
Feeding 1st instar larvae	≤19				

of fruits (from relatively small to large, and from relatively smooth to quite rough and nodular). The tagged fruits were subsequently examined four times at 6 - 8 week intervals, and the exact position, condition and apparent fate of each egg and entry attempt were noted. Several of the fruits were removed for microscopic examination during the last inspection, when practically all the surviving larvae were inside the fruits.

The observations (Table 32) showed that approximately 17 p.c. of the eggs disappeared, apparently prior to hatching; that 9 p.c. failed to hatch, and that most (67 p.c.) of the larvae that appeared to have hatched, disappeared without leaving any visible attempt at entry. An estimated 17 p.c. of the larvae that had hatched from observed eggs, successfully entered the fruits. This is very similar to the estimated 19 p.c. in the previous sample of H. nodosa fruits from the same locality (see Table 31).

It was not practicable to include in these observations fruits occurring in clusters; against a thick stem; or against another fruit, as careful overall examination by handlens, without disturbance, was necessary. Observations at the end of the egg-laying season showed that the egg-density on the selected single fruits was considerably lower (1.58 egg-shells per fruit at the last inspection) than on fruits in clusters, for which averages of up to 9 eggs per newly-matured fruit were recorded.

From the data of Table 31 in which egg-densities averaged 4.97 eggs per fruit , it is possible to extract a set of data for the

TABLE 33

A comparison of pre-feeding mortality of *Carposina autologa* Meyr. on 52 newly-matured fruits of *Hakea nodosa* of the sample in Table 31, and the 52 tagged fruits from the same locality.

	Random	Tagged	Chi-square test on differences between fractions lost
Av. no. eggs per fruit	6.71	1.58	
Egg-shells found	349	82	
Fraction lost	$\frac{295}{349}$	$\frac{48}{82}$	$P < 0.001$
Entry attempts	54	34	
Fraction lost	$\frac{21}{54}$	$\frac{9}{25}$	Not significant
Successful entries	33	25	
Fraction lost	$\frac{2}{33}$	$\frac{2}{25}$	Not significant
Fruits entered	31	23	

younger fruits in the sample - closely comparable to those tagged. The losses occurring between the egg stage, larvae attempting entry and successful larvae, could then be compared statistically (Table 33). The only significant difference in the losses was between the egg number and the number of larvae attempting entry - a greater proportion of the larvae under higher egg-densities disappearing. Mortality during penetration may not be greatly influenced by population density.

These observations failed to show the cause of the high mortality in newly-hatched larvae. However, it was evident that the larvae had disappeared after hatching, but prior to construction of protective covers. This supported the suggestion that predators may have been involved.

4.37 Physical factors

4.371 Weather

Due to the habits of the insect and the situations where it occurs, none of its stages normally experience prolonged exposure to unfavourable weather conditions.

The eggs, laid in sheltered situations, in, or near the fruits, are normally not in direct sunlight. They are unlikely to be subjected to unfavourably low humidities during the winter months when they are present, and furthermore they usually occur on, or are surrounded by transpiring tissue. High humidities were not observed to have adverse effects on development of eggs in the laboratory.

Fungal growth occurred on the surface of the chorion especially when eggs were held in a saturated atmosphere, or in contact with free water, but this phenomenon was not observed on healthy eggs in the field.

Prior to construction of the protective cover, the newly-hatched larva is vulnerable to dehydration. This is probably of little significance in nature, however, since they need only a few hours to cover themselves, and may do this during the cooler, moister periods of the day. It was observed on several occasions in the laboratory that hatching larvae discontinued enlarging the hole in the chorion under adverse conditions, and that they remained in the egg-shells for several hours, sometimes spinning silken threads across the aperture.

Developing larvae inside healthy fruits are not exposed to extremes in weather conditions. The thick, woody follicle surrounding the seed-cavity provides good insulation. Furthermore the layer of juicy, chlorenchymous cells under the bark of the fruit would be expected to have an additional stabilizing effect - cooling the fruit under hot, dry conditions. The humidity inside the seed-cavity is maintained at a high level while the fruit is healthy and alive, regardless of external conditions.

Mature larvae about to escape from fruits in the laboratory were observed to remain in their escape tunnells when the atmosphere was warm and dry, or when conditions were otherwise adverse. Once fallen from the fruits, larvae were found to be vulnerable to dehydration when forced to form their cocoons in dry sand rather than in leaf-litter. The observed phenomenon of delaying emergence from the fruits may be linked to this potential hazard.

The stages inside the cocoon are protected against extremes in temperature and humidity due to the fact that the cocoon is normally made under a thick layer of vegetation and leaf-litter, or at least embedded in the substrate in a shady situation. In the laboratory the cocoons withstood partial flooding with water for several days, leaving the pupae dry and unaffected. This faculty may be of significance in the case of larvae developing on *H. nodosa*, since this host often occur~~r~~s in swampy areas exposed to temporary flooding.

Unusually severe droughts may cause the death of a proportion of the host-plants, and of the weaker and more sickly branches on others, resulting in dehiscing of a proportion of the available fruits, and thus in the destruction of suitable habitat for developing larvae. Mortality caused by severe drought is not likely to be general.

Fire. Scrub- or bushfires are likely to occur mainly during the summer months in the distribution range of *C. autologa*, when older larvae or pupae are expected to be present.

Larvae already inside fruits are not likely to be killed directly during fires. Even mild fires will however, cause the fruits to dehisce within a few days, and unless the larvae are mature, their chances of survival are very limited. As all the fruits on a certain branch or plant are usually affected to the same extent, the chances of a larva migrating to another healthy fruit are remote. An added subtractive factor would then be the relatively prolonged exposure to predators.

The situation of the cocoons is likely to safeguard pupae against excessive heat and desiccation during fires, even if the layer of dry litter itself burns. Observations made after burning had occurred, suggested that the deeper layers of debris, where the cocoons would be expected, were normally not inflammable (cf. Beadle 1940).

It seems likely that the species manages to survive general fires by recolonizing the new generation of host-plants from individual surviving plants, or from isolated patches of vegetation that escaped the fire. A severe, general fire occurred at Wilson's Promontory during 1939, and another, less severe, during 1953. By counting the numbers of whorls of branches on <u>Banksia</u> spp., the period since the last fire in a particular patch of vegetation may often be estimated. Observations in the study area suggest that a number of plants survived at least the 1953 fire. <u>C. autologa</u> probably maintained itself on such surviving plants until the new generation of <u>H. sericea</u> plants, or sprouts from surviving crowns of <u>H. nodosa</u>, reached the fruiting stage.

4.38 Conditioning influences

4.381 Penetrability of the fruit

Upon examination of the typical positions where the different types of <u>Hakea</u> fruits are penetrated, and comparison of the lengths









Figure 10

Dehisced halves of fruits of Hakea spp. to indicate the differences in typical size and shape, and the structure and width of the sutures (to the left of the seed-cavities). All natural size.

From left to right:-

Top:	H. sericea (Wilson's Promontory; H. sericea (eastern N.S.W.) and H. gibbosa (Gosford).
Centre:	H. nodosa (Wilson's Promontory); H. suaveolens (Albany) and H. propinqua (N.S.W.).
Bottom:	H. elliptica (Albany); H. ulicina (Wilson's Promontory) and H. rostrata (Portland).

of the tunnels that the entering larvae have to form through relatively hard tissue, it is immediately obvious that certain fruits are more easily entered than others. The granular layer in the suture between the two halves of the fruit through which most of the larvae enter, provides the most significant, single barrier. The width of this layer varies from very narrow to very wide between different _Hakea_ spp. (Figure 10) or in forms within one species (e.g. between 0.4 mm and 8.5 mm as indicated in Tables 17, 18 and 19.)

Penetration under field conditions is a slow process, often occupying two or more weeks (see section 4.354). It follows that this period will be extended further if a wider, or harder, barrier has to be eaten through, thus exposing the larvae to predators for a longer period. Figures in Table 31 suggested that on the three forms of _Hakea_ compared, mortality during penetration was lowest on _H. nodosa_ (with the narrowest granular layer), and highest on the form of _H. sericea_ from the same locality, which had the widest barrier. The remains of larvae in the tunnels suggested that predators were often the cause of death during penetration. If the penetration period is extended beyond the normal estimated 2 - 3 weeks, mortality due to dehydration, and presumably starvation also, comes into effect.

Apart from width of the barrier in the suture, the penetration period may be lengthened by the following two morphological characteristics of the fruit:

(a) _The absence of free space between the seed-wings and the granular layer_. This applies especially when the fruits are entered

Figure 11

Cross-sections through mature fruits of *Hakea sericea* to show the structure of the sutures next to the seed-cavities. (Fruits already minutely dehisced.)

Magnification: Approximately $2\frac{1}{2}$ x .

Top: Typical fruit from Wilson's Promontory, Vic.

Bottom: Fruit from Stellenbosch, South Africa.

along the apical half of the suture, or at the apex, and the larva has to find its way to the seed-cavity. In, for example, *H. cucullata* and *H. nodosa*, larvae have no obstruction between them and the seeds once the granular layer is penetrated, whereas in e,g. *H. suaveolens* and most forms of *H. sericea*, a tunnel has to be eaten through the wings and surrounding follicular tissue. This may involve up to 25 mm of tunnelling, which is rarely accomplished. (In some hosts it is possible for larvae to move directly to the seeds through the space between the wings.)

(b) *The hardness of the granular layer or tissue surrounding the suture*. In the fruits of certain *Hakea* spp. the equivalent of the granular layer comprises densely-packed, small, hardened cells, which apparently prevent the larvae from entering via the suture. Thus while on *H. nodosa* and *H. sericea* approximately 80 p.c. of successful entries were commenced from positions on, or touching the suture, on *H. cucullata*, *H. elliptica* and *H.* ?*ambigua* practically all entry tunnels were situated at least 0.3 mm on either side of the suture.

Sections through fruits of various hosts and non-hosts clearly showed the thickness and nature of the tissue to be eaten through, and it varied considerably even within different forms of the same species (Figure 11). Furthermore, there appeared to be a progressive hardening of the cells around the suture with age, and penetration of such old fruits was found to be extremely slow - less than 1 mm tunnelled in about two weeks by some of the larvae in the laboratory.

4.382 Shape and structure of the fruit

Apart from providing the ovipositing females with a means of recognizing a suitable host (discussed in section 4.351), certain shapes of fruits and surface types may be conditioning in two main ways: limiting the number of egg-laying sites; and reducing the chances of young larvae in finding suitable penetration sites.

(a) Limiting the number of suitable egg-laying sites. In the field more eggs were laid on the very rough, nodular fruits of *H. nodosa* offering an abundance of sheltered positions, than on relatively smooth fruits on the same plants. In the oviposition experiment in a field cage (referred to above), more than twice as many eggs were laid on the rougher *nodosa* fruits than on their smoother controls under the same conditions. In a series of observations in which tagged fruits in the field were examined periodically (section 4.364), it was possible to predict the favourability of fruits for oviposition by observing the number of suitably sheltered positions likely to be selected. The entirely smooth fruits received very few eggs during the observations.

On an interspecific basis, fruits of certain species may be less favoured for oviposition because of their smooth surface, especially when this is coupled with the absence of other suitable egg-laying sites in the immediate vicinity of the fruits. A comparison of the typical situations where eggs were laid on some representative host-plants (see Table 22) clearly illustrated that other situations, usually characteristic of the plants, had to be exploited for oviposition in the case of the smooth-fruited _H. cucullata_, _H. elliptica_ and _H. suaveolens_.

(b) _Reducing the chances of finding a suitable penetration site_. Recognition of the suture on the axial aspect of the fruit is a prerequisite for successful entry by the newly-hatched larva, as the sides and adaxial aspect (apart from a small region near the apex in some species) present too great a thickness of tissue to be eaten through (see Figure 11). In certain _Hakea_ species, or geographical forms, the shape and external appearance of the fruit may be such that it is difficult to differentiate between the axial and adaxial aspects:

1) there may be similar, deep, narrow, longitudinal folds on both aspects of the fruit. Additionally, a crack may occur in the surface along the adaxial aspect, closely simulating the true suture (e.g. occasional fruits of _H. sericea_ and _H. nodosa_, and apparently all fruits of _H. salicifolia_). The latter species has granules in the 'exaggerated' adaxial crack, giving the fruit the appearance of having the suture on the adaxial side;

2) the suture may not be situated in a groove, and may even be along a slightly raised area, while the adaxial aspect may be grooved, or similar to the axial aspect (e.g. _H. cucullata_);

3) the suture may be very inconspicuous (e.g. _H. elliptica_, _H. cucullata_), or the longitudinal line may be entirely concealed by a series of deep cracks criss-crossing an area of several millimetres on either side (_H. sericea_ at some localities, e.g. Bargo, N.S.W.);or

4) the fruit may have the apical beak produced, flattened and recurved to be flush against the suture, thus leaving little of the latter exposed (e.g. *H. rostrata* - see Figure 10).

On the known hosts, a small proportion of larvae were found to attempt entering at unsuitable positions on the fruits, e.g. on the recurved apex of fruits of *H. rostrata*; too far off the suture to be able to reach the seed-cavity on *H. sericea* at Bargo; and in the adaxial groove on *H. nodosa* and *H. sericea* at Wilson Promontory - 2.6 p.c. of the detected unsuccessful attempts referred to in Table 31.

4.383 Quality of the food

As indicated earlier (e.g. Table 28, section 4.355), the larvae were not very specific in their food requirements. Under experimental conditions they were able to develop for at least some time on a variety of foods, such as the hypocotyl and green cotyledons of germinated *Hakea* seeds, seeds of different *Hakea* spp., and under special circumstances, on seeds of the macadamia nut (*Macadamia* species), Cape wild almond, *Brabejum stellatifolium*, almond (*Prunus amygdalus*), and of hazelnut (*Corylus avellana*). However, under similar conditions, no development occurred on seeds of walnut (*Juglans regia*) and brazil-nut (*Bertholletia excelsa*).

In the laboratory a variety of moulds flourished on seeds attacked by the larvae, especially at stages when the larvae temporarily ceased feeding. Similar moulds were occasionally found on attacked seeds in the field. It appears that the mould spores may be accidentally introduced into the fruits, and that they normally have no detrimental effect on the development of the larvae, even when the seed is affected to a degree to cause discolouration.

On the other hand, a possibly secondary form of bacterial rot, which liquefied the seed contents, occurred in the laboratory and caused the death of larvae. Affected seeds usually appeared healthy, if somewhat inflated, from the outside, but when the testa was punctured, a drop of dark brown fluid often exuded. This type of damage to seeds has subsequently been found in the field, where affected fruits sometimes contained dead larvae, or were found to have been abandoned by newly-entered larvae.

4.384 Interspecific competition for food

There was remarkably little direct competition for food at any particular locality. Very few organisms appeared to have conquered the hard, woody follicle protecting the seeds while they are still on the plants.

Parrots, notably yellow-tailed cockatoos (*Calyptorhynchus funereus*) opened a varying proportion of the mature fruits (see Table 35 below) and consumed the seeds at many different localities in eastern Australia, thus competing with *C. autologa* for food, and possibly consuming some of the larvae.

Three quite different insects were found to feed on seeds of host-plants of the lepidopteran.

a) *Acanthosomatid bug* (see Appendix III). Seeds attacked by this insect typically have at least a small portion of their seeds discoloured or mouldy, and quite often entire cotyledons are decayed.

TABLE 34

The incidence of rotten seeds in a sample of fruits of *Hakea nodosa* (all the indehisced, mature fruits on a selected plant) from Wilson's Promontory, Victoria, and the influence on the favourability for larvae of *Carposina autologa* Meyr. Expected numbers if no differences existed are indicated [in square brackets]

34a All the fruits	Both seeds healthy	One or both seeds rotten	TOTALS
A Not entered by larvae	69 [92]	42 [19]	111
B With larvae that developed 'normally'*	451 [384]	13 [80]	464
C With larvae dead or missing	2 [46]	53 [9]	55
TOTALS	522	108	630

*Composed of fruits with completed escapes (373); with larvae killed by unsuccessful, trapped parasitoids and predators (12); and with live, developing, young larvae (66)

34b Analysis of fruits with dead or missing larvae (C above)

		Both seeds healthy	One or both seeds rotten	TOTALS
Young larvae	Missing	2	10	12
	Dead	-	13	13
Old larvae	Missing	-	12[⊖]	12
	Dead	-	18[⊖]	18
TOTALS		2	53	55

[⊖] Not always clear that rotting occurred prior to feeding by larvae

It appears that secondary micro-organisms are introduced into the seed during feeding by the bugs, and that the seed gradually discolours, starting at the feeding site. Liquefaction (as described above), and later desiccation of the seed, usually result.

Fruits of various *Hakea* spp. from many localities in southern Australia showed this type of damage. Although it was often found on plants attacked by *C. autologa*, the general incidence on any plant appeared to be inversely proportional to the incidence of the latter.

The amount of sap taken from seeds during feeding by the bugs appeared to be too small to be detrimental to *C. autologa* larvae. Those in affected fruits were often found feeding on a remaining healthy seeds, or the still healthy portion of a seed. However, several larvae were found to have died in similar fruits, or to have abandoned them soon after entering, or after eating into discoloured tissue. In order to evaluate the effect of rotten seeds on the suitability of fruits for *C. autologa* larvae, a large sample of fruits from a locality where both insects were present, was examined. The results (Table 34) indicated that fruits containing rotten seeds were clearly less favourable for *C. autologa*. The numbers that had died in, or abandoned these fruits were significantly higher than in fruits with both seeds healthy (Table 34b).

b) *Eurytoma* sp. (see Appendix III). This insect was found to destroy one, or both seeds in about 5 p.c. of fruits of *H. sericea* at some eastern localities (Goulburn, Bargo, Heathcote) where *C. autologa* occurred. Evidence of attack on *H. nodosa* and *H. sericea* at

Wilson's Promontory was very rare, possibly because its main host there, H. teretifolia, fruits at a different season.

As the larvae develop in seeds of some potential hosts of C. autologa, and presumably attack the seed in a much earlier stage of development, this insect may successfully compete at a low level for food with C. autologa larvae at certain localities.

c) Aphanosperma occidentalis (Cerambycidae - see section 5.1). The larvae feed mainly on the follicular tissue of the fruit, but enter the seed-cavity in the process and generally consume both seeds.

At Albany, W.A., damage by this insect was found in fruits of H. cucullata and H. suaveolens. Up to an estimated 45 p.c. of all fruits on plants of the latter species on Mt. Clarence were attacked, although certain groups of plants were only lightly affected.
C. autologa also occurred on these plants, but H. suaveolens was one of the less-favoured hosts at that locality (see Table 18).

There was some indication that Carposina larvae succumbed after they had entered fruits containing A. occidentalis larvae, or fruits whose seeds had already been consumed by the cerambycid larvae.

4.385 Other insects indirectly affecting the food supply of C. autologa

These can be categorized as 1) the numerous insects attacking vegetative parts of the plants and presumably indirectly reducing the numbers of fruits produced,

2) the variety of insects attacking flower-buds, flowers and young fruits, therefore directly reducing the numbers of fruits available

TABLE 35

The incidence of dehisced fruits on *Hakea sericea* and *H. nodosa*, with indications of the causes of dehiscence

HAKEA	LOCALITY	NO. OF FRUITS IN SAMPLE	DEHISCED, SEEDLESS FRUITS ON, OR UNDERNEATH PLANTS					
			D. pictus	Curculionid[(b)]	Minor insects, or cause not known	Parrot[(a)] damage	TOTAL	%
nodosa	Darby, W. Prom.	202	Cause not determined 39			None on plant	39	19
nodosa	Darby W. Prom.	706	1	22	53	None on plant	76	11
sericea	Squeaky Bay W. Prom.	200	27	?	3	None on plant	30	15
sericea	Picnic Point W. Prom.	145	9	?	5	19	33	23
sericea (young plant)	Bellbird Creek, Vic.	133	-	-	-	18	18	14
sericea	Cann River Vic.	139	-	?	4	6	10	7
sericea	Genoa Vic.	206	-	-	9(c)	not collected	9	4

(a) Damage does not remain visible for long, as damaged fruits are dropped

(b) Originally the larvae of *D. pictus* and this cryptorrhynchine curculionid were not recognized as belonging to different species. However, it was subsequently shown that *D. pictus* was predominant in fruits of *H. sericea*

(c) 7 of these had large scars caused by 'late' attack of *Erytenna* larvae to *C. autologa* larvae, and 3) the few insects affecting the suitability of fruits, mainly by causing untimely dehiscing of mature fruits, or by exposing the larvae to attack by predators. Only this third category will be considered here in relation to *C. autologa*.

a) *Dixoncis pictus* (*Curculionidae* - see section 5.1). The larvae tunnel under the bark of mature fruits, or in the thickened fruit stems, and eventually cause dehiscence as a result of dehydration of the tissue or girdling of the stems. There were indications that dehiscence may be slow, especially under humid conditions (in contrast to rapid dehiscing after fires, or when parts of the plant suddenly die). The conditioning effect on *C. autologa* was only seen in *H. sericea* at Wilson's Promontory. There, up to 20 p.c. of mature fruits were found dehisced as a result of attack by larvae of this curculionid. In one sample of 200 fruits from Squeaky Bay (Table 35) 14 p.c. showed severe *D. pictus* damage and were dehisced, while a further 28 p.c. showed early damage, but were intact. Some of the dehisced fruits showed *C. autologa* entry tunnels and signs that the larvae had died prematurely, but with the slow dehiscence some larvae may complete their development.

D. pictus larvae also occurred on *H. nodosa* at Wilson's Promontory, although they seldom appeared to have caused dehiscing of the fruits. Eggs and young larvae were common on the mature fruits, but successful attack was almost entirely restricted to stems. Although many mature fruits of this species were dehisced (as shown in Table 35), the causes were not always clear, and *D. pictus* appeared to play an insignificant role.

b) *Unidentified curculionid* (Cryptorrhynchinae, det. E.B. Britton). The larvae tunnel in the woody portion of mature fruits of *H. nodosa*, and to a lesser extent in fruits of *H. sericea*. The insects were quite common at Wilson's Promontory. Older fruits, especially those with scars caused by the larvae of *Erytenna* and *D. pictus*, were more likely to be attacked.

Heavily attacked fruits characteristically have a maze of tunnels in the woody follicle and around the seed-cavity. The tunnels usually contain densely-compacted, powdery sawdust. More than one larva may develop simultaneously or successively in the same fruit. As a rule the seeds are not consumed, although the tunnels may enter the seed-cavity, or puncture its lining.

These insects appeared to be one of the main causes of untimely dehiscing of *H. nodosa* fruits at Wilson's Promontory. However, several fruits with old damage were still intact. One group of 76 dehisced *nodosa* fruits (see Table 35) were carefully examined to determine the cause of dehiscence, and the apparent effect on *C. autologa* larvae. Less than one half of these fruits had been entered by *C. autologa* larvae (i.e. prior to dehiscence) and only about 24 p.c. had completed excapes (compared to 72 p.c. entered and 60 p.c. with completed escapes in the 130 intact fruits from the same plant).

The figures suggest that the main effect of dehiscing on *C. autologa* may be the reduction of the numbers of suitable fruits. The curculionid was apparently responsible for dehiscing of only 22 of the 76 fruits. However, the tunnelling of this curculionid also appeared to have a quite different effect - enabling other insects to gain access to the seed-cavity. Predatory beetles, their larvae or exuviae were occassionally found with remains of _C. autologa_ larvae in the seed-cavities of such fruits. Unidentified clerid larvae, and _Carphurus_ sp. (Melyridae) were responsible for the death of 6 _C. autologa_ larvae in a sample of 78 fruits that contained unsuccessful larvae. One more _C. autologa_ larva had apparently succumbed as a result of competition by chloropid (Diptera) larvae[1] that had developed in such exposed seeds.

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[1] ?_Lioscinella_ sp. (cf. genus near _Botanobia_). Apparently an undescribed species according to D.H. Colless (personal communication 1967). Eggs, larvae, pupae and empty puparia were frequently found in seed-cavities of _Hakea_ fruits, sometimes after these fruits had been successfully attacked by _C. autologa_, or by the rot-inducing acanthosomatid bugs. These gregarious dipterans are probably basically scavengers. A second species, with habits similar to those of the first, were collected in W.A. (specimens numbered AcHa 134 and 173.)

4.4 DISCUSSION

The factors governing the host-plant range in the field were not entirely clear. The different *Hakea* species attacked by this insect had a large variety of leaf-shapes, and the external appearance of their fruits was diverse. However, they usually had in common a medium-sized to large, approximately globular fruit, relatively large seeds, and a narrow barrier in the suture.

Upon comparison of favoured hosts (e.g. *H. nodosa* and *H. cucullata*) with other hosts and non-hosts, there were suggestions that a flowering time coinciding with the egg-laying period may affect their favourability. Also, during the experiments on host-plant selection in a field-cage (section 4.351) fewer eggs were laid during the second and sixth nights (Table 24A) when no flowers were present in the cage. However, flowering may at most be a contributory factor in host-plant selection, as many other hosts in the field were selected when they were not flowering.

During the oviposition experiments the females showed a positive response to the foliage of the non-host *H. teretifolia*, but a negative response to dead foliage of a favoured host, and to foliage of the other plants used. The preference shown for live *Hakea* foliage was thus more likely an olfactory response to factors probably present in different *Hakea* spp. The unfavourability of dry host-fruits in the field, and of other fruits (of similar size as those of hosts) tested in the field-cage, suggested that a similar mechanism may be involved in the recognition of fruits of *Hakea* spp.

On the whole it therefore appeared that there was an olfactory response to the foliage and fruits of Hakea spp., but that smaller fruits were not favoured. The presence of oviposition sites was a conditioning factor.

The form of H. sericea occurring at Wilson's Promontory was regarded as only marginally suitable, because of the very wide barrier presented to entering larvae (see Figure 10). It was observed that the proportion of successful attacks on these fruits was usually higher in the vicinity of the swampy areas where H. nodosa occurred. An overflow from the latter plant was probably partly responsible for the patchy distribution on H. sericea at that locality. However, the subsequent discovery of a group of infested H. sericea plants at Wilson's Promontory (near Windy Saddle) where no alternate hosts occurred in the vicinity, showed that even 'unsuitable' forms may be able to support a population of the insects.

That other, more suitable forms of H. sericea were able to support natural populations of C. autologa in the absence of alternate hosts, was shown by its presence at several localities where these plants occurred isolated, or in the vicinity of only non-hosts.

It was only late in the study that the possible significance of competition by the acanthosomatid bug was realized, and it is thought that heavy attack by this insect could have caused the absence of C. autologa at certain localities.

The phenology of this insect is unusual for the fact that, at least at the southern localities, the eggs hatch during the winter months. This phenomenon may afford the following advantages to the species: larvae are unlikely to be exposed to unfavourably hot and dry conditions during the search for a penetration site and during the relatively long penetration period; oviposition on favoured hosts occurs soon after maturation of fruits each year (before they had been exposed to competitors for an extended period); and the larvae and pupae are in the soil during late summer, when fires are more likely to occur.

At eastern localities, and at Albany in W.A., there was only a single generation each year. No definite evidence for a mechanism to regulate the egg-laying season was found, apart from a possible delay in the onset of active feeding and development once the larvae had reached the seed-cavity during winter months. Hence larvae entering fruits as late as spring, may commence active development at about the same time as those that entered during winter. The fact that moths had been collected in Western Australia mainly during the spring months (see data for museum specimens, section 4.31) is somewhat puzzling, since the phenology on hosts at Albany was found to be similar to that in eastern Australia, with no evidence of a second generation each year. According to Common (personal communication 1968) the apparent preponderance of spring-collected moths in the CSIRO collection may largely be an artefact, as traps were seldom operated during autumn and winter. It is feasible that moths may appear as early as November at warmer localities (e.g. Geraldton in W.A.), and that a second generation may complete their development before winter, but this is not likely at the colder, more southern localities listed.

The larvae exhibited some very specialized adaptations to the characteristics of the host-fruits. Most remarkable were the location of a penetration site, the commencement of the escape tunnel as early as the fourth instar when they are less than one third of the full-grown size, and the completion of development in the confined space of the seed-cavity which they themselves practically fill bodily towards the end of the feeding period. At that stage the relatively large amount of wood excavated from the escape tunnel also has to be accommodated, and movements (e.g. alternate feeding and excavating) appears to be possible only as a result of the very small volume of faeces, the compacting of wood material and seed remains into small crevices, and the constant shifting of debris into and out of the uncompleted escape tunnel.

One fruit allows development of only a single larva, and the larva as a rule consumes both seeds completely before it is full-grown. The occurrence of fighting in newly-entered larvae and the effective way of attacking rivals as soon as they enter, provides a mechanism to prevent starvation, as only a single larva is then likely to feed on each pair of seeds.

A further phenomenon of survival value is the faculty of young larvae (at least until late in the first instar) to emerge from unsuitable fruits (e.g. when they encounter rotten tissue) and to re-enter a second fruit in the same way as newly-hatched larvae.

The fact that newly-hatched larvae experimentally put directly into seed-cavities or onto a seed,seldom commenced feeding, and usually attempted to escape, indicated that normal penetration behaviour may be a necessary preliminary to feeding.

Mortality in newly-hatched larvae was very high, and even on relatively easily-entered hosts, it was still in excess of an estimated 50 p.c. This appeared to be the most important single cause of mortality. However, as the egg-laying capacity of the moths is high, and the egg-density on fruits usually compensated for this loss (one fruit allowing the development of only a single larva), this did not appear to be of significance under natural conditions.

The preference that larvae in search of a penetration site showed for small pits on the suture, and especially for the attempted entry tunnels of earlier larvae, may be of considerable significance on the less readily entered fruits. If a few larvae attempt entering successively at one site, the chances of successful entry increase progressively. If predators were in fact responsible for the very high mortality in newly-hatched larvae, the species may be more successful on relatively unfavourable hosts in the absence of these predators, as more larvae may survive to successively attempt entry.

4.41 Bases for host-specificity

Despite the fact that the larvae were not specific in their food requirements and developed fairly normally in the dry seeds of various nuts into which they were placed, the host-range in the field was remarkably narrow.

The moths appeared to be rather selective during oviposition, and did not readily lay eggs under unnatural conditions (indicated by their usual failure to oviposit in cages in the laboratory). Furthermore they showed distinct signs of reacting to some chemical token of the host.

The striking adaptation of the larvae to their host-fruits, which are quite unique, even within the family Proteaceae, suggests that there may have been a very long association between insect and plant. The highly specialized penetration behaviour of the larvae (e.g. the initiation of the response on host-fruits, location of the suture, and early rejection of unfavourable positions on the fruit) provides a sound basis for specificity.

Harris and Zwölfer (1968) place a high degree of reliability on the host-specificity of a systematic group (species, genus, family, etc.) which is restricted to a small group of closely-related plants, especially if it is evident that the insect group has speciated on the plants concerned. The apparent diverse host-plant range and wide distribution of Carposina spp. would therefore discount C. autologa on this basis. However, the specialized adaptation of this insect to fruits of Hakea spp., and the fact that there is doubt on the congenerity of the Australian Carposina spp. with their American and European counterparts (Common, personal communication 1966, 1968), may cancel this argument against host-specificity in C. autologa.

The fact that the feeding response was only initiated after normal penetration behaviour, indicates further that feeding is not likely to result on even an exposed food source. It is very unlikely that the moths will lay their eggs on non-host plants, and even if this happens, the selective and specific behaviour of the larvae should preclude feeding on such plants.

A comparison of the structure of the fruits of different *Hakea* spp. (e.g. the width of the granular layers in the sutures; the absence of free space at the outer edges of the seeds and between the seed wings; the inconspicuousness of the sutures, and even the presence of a deep groove or 'false suture' on the adaxial aspect; or recurving of the beak to cover the suture in a few species) makes it tempting to suggest that they may have evolved to their present expression under strong evolutionary pressure by insects capable of recognizing the suture and attacking the seeds. The very high proportion of seeds destroyed on favoured hosts immediately suggests that there would be strong selection against forms of host-fruits relatively easily entered by *C. autologa*.

Theoretically, there may have been a similar strong selection against those individuals of *C. autologa* that laid their eggs on fruits heavily attacked by competitors (e.g. on *H. teretifolia* whose seeds are largely destroyed at an early stage by *Eurytoma* sp.), or on fruits in which the larvae may be very exposed to attack by their parasitoids (e.g. *H. ulicina*, whose seed-cavities occur close to the narrow suture). The present host-range amongst *Hakea* spp. may therefore be a result of a long history of selection, and the recognition of these plants may provide a sure and 'permanent' basis for host-plant restriction.

V FRUIT- AND STEMBORERS

Preliminary observations were made on three other insects that appeared to cause significant damage. These were 1) the cerambycid *Aphanasium australe* Boisd. whose larvae tunnel in the bases of thicker stems and sometimes in roots; 2) a closely related species, *Aphanosperma occidentalis*[1] whose larvae tunnel in mature fruits and fruit-stems; and 3) *Dixoncis pictus* Oke (Curculionidae) whose larvae cause dehiscing of mature fruits either by tunnelling in the chlorenchymous layer under the bark of fruits and fruit-stems, or by boring out the centres of twigs.

Small numbers of these insects were usually easily obtained by collecting infected host-material and keeping it in polythene bags until the adults appeared, usually within the first 6 - 9 months, after which the material became unsuitable and was discarded, even if younger larvae were still present. For more regular observations, larvae were reared on stems, twigs and fruits which were replaced every two or three weeks, but this was generally unsatisfactory due to the slow development of the insects and the tedious process of finding the larvae in their tunnels, without wounding them accidentally.

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[1] Proposed new genus and species - E.B. Britton in press 1968.

5.1 GEOGRAPHICAL DISTRIBUTION AND NATURAL HOST-PLANT RANGE

Aphanasium had the widest distribution. It occurred in patches of plants of *H. sericea* and *H. gibbosa* along the central east-coast of N.S.W., and also at a few inland localities, e.g. near Canberra (on *H. ?sericea*) and in the Grampians, Vic.

Aphanosperma occidentalis appeared to have a similar patchy distribution, and was encountered in fairly large numbers from certain groups of *H. suaveolens* plants at Albany, W.A., and in small numbers from *H. cucullata* near Betty's Beach (W.A.). Webb (unpublished report, 1965) collected similar larvae from *H. suaveolens* fruits at Esperance in W.A. Due to the unfamiliarity with *Hakea* spp. in that state, the host-plant range is not known. [Adults of a very similar species, *Aphanosperma orientalis* (Proposed name - Britton, in press 1968) had been collected in N.S.W. at localities where *H. sericea* is known to occur, and it seems likely that they may develop in fruits of this plant. Occasional cerambycid larvae were found in mature fruits of *H. sericea* and *H. nodosa* at Wilson's Promontory, but these were not successfully reared to allow identification.]

D. pictus appeared to have a very restricted distribution and host-plant range. It was quite common on *H. sericea* at certain localities at Wilson's Promontory, where it also occurred in small numbers on *H. nodosa*. Damage was not encountered on *H. sericea* anywhere else, and the only other records encountered were from

H. nodosa in the vicinity of Melbourne and from possibly the same plant at Cradle Mountain (Tasmania).

5.2 PHENOLOGY AND LIFE-CYCLE

None of these three insects exhibited a distinct seasonal phenology, and eggs and larvae in all developmental stages were encountered at various times of the year. Adults of D. pictus were shaken from plants during most of the visits to Wilson's Promontory, although they appeared to be more plentiful during early summer. Similarly, there is a possibility that there may be a peak emergence period during autumn and early winter in Aphanosperma at Albany. The life-cycle of all these occupied more than a year in the laboratory, and there is thus a distinct possibility that it may be considerably longer in the field. The only adult of Aphanasium reared from the egg-stage appeared after 2½ years at 20°C, and although feeding conditions (on frequently replaced 'dead' stems in the laboratory) may not have been optimal, this figure appears normal for field conditions. There was no evidence of diapause or timing of emergence in any of the insects.

5.3 GENERAL BIOLOGY AND HABITS

The adults of Aphanasium are pale- to blackish-brown in colour (sometimes with a pale longitudinal area along the inner edges of the elytra) and vary in length from about 11 - 27 mm (the usual size being about 20 mm). Those of Aphanosperma are generally smaller (10 - 18 mm in length) and of a paler colour (straw-coloured to orangey) with black eyes. The eggs of both are pale yellow and ellipsoidal, and are attached to the substrate. The egg-shells are minutely sculptured. The eggs of Aphanasium are slightly larger (2.0 - 2.2 mm in length), and are usually deposited in groups of 10-20. Their larvae and pupae are typical of those of the family, and were indistinguishable, apart from general size (the larvae of Aphanasium sometimes reaching a length of almost 50 mm). The adults of D. pictus are basically orangey to brown with yellow markings on the elytra. They are relatively smooth and elongated, and about 5 - 7 mm in length. The soft, white eggs are attached singly to the substrate, and are covered with a layer of excrement. The yellowish larvae do not differ from typical curculionid larvae, and the pupae are whitish and also of typical shape and appearance.

The hatching larvae of all three species enter the substrate directly from inside the eggs, and do not appear on the surface. Sawdust is worked into the egg-shells, and stuffed into the tunnels behind them. Mucilage is usually exuded by the plant tissue at the entry points. The young larvae of all three species tunnel in the softer tissue beneath the surface.

The larvae of D. pictus tunnel extensively in the softer tissue all over the surface of the fruit, and apparently favour the positions around the beaks and fleshy stems of the fruits, where the soft layer is thicker. One to four may occur in a single fruit, and they may tunnel into twigs. Those in twigs tunnel inside the wood, but may reach fruit-stems and fruits. When mature, they eat a cavity into the nearest woody tissue, where they pupate. The adults then eat their way out to the surface.

Aphanosperma larvae later tunnel into the woody tissue of the fruit, and the seeds are generally consumed when the larvae are about half-grown. The larvae usually occur singly. They may move into the fleshy fruit-stem and thence into another fruit in a cluster. Pupation occurs in a cavity in woody tissue, and escaping adults leave conspicuous holes.

The larvae of the stem-cerambycid Aphanasium frequently occur gregariously in groups of 6-20, usually close together just below the surface of the soil. Affected stems become riddled with tunnels, form some scar tissue, becoming thickened locally, and exude masses of mucilage under moist conditions. Around Canberra the larvae usually occurred singly, and tunnelled into the sub-surface roots of the smaller plants. The pupae of this species similarly occur in cavities in the wood.

The egg and pupal stage were of similar durations in all three species (4 - 7 weeks in the laboratory), but, as indicated above, sufficient observations on larvae were not possible. However, even on potted plants in Canberra, larvae of D. pictus took in excess of one year to complete their development, and similar durations were recorded for larvae reared in picked fruits and twigs.

The females of the cerambycids each deposited about 20 - 40 eggs within a few days of emergence, did not feed on host-plant material offered to them, and died within a few days or weeks. Those of *D. pictus* fed extensively on leaves, flowers and the surface of twigs and mature fruits, and had a pre-oviposition period of about 3 weeks. They deposited their eggs gradually and over a period of several months, and some totals in excess of 90 were recorded.

In the field the eggs were laid in protected positions at the feeding sites of the larvae. However, in captivity the females of the cerambycids (in particular those of *Aphanasium*) deposited their eggs indiscriminately on various materials and on stems of a variety of plants offered to them. The hatching larvae then entered the substrate, and tunnelled in it whether development was possible or not. Captive females of *D. pictus* appeared to be more discriminating and selected fruits and stems of host-plants for egg-laying, usually after some feeding at the site. However, they also attached eggs to the sides of the containers and stems of some non-hosts.

The eggs of *A. australe* were parasitized by two *Ooencyrtus* spp. (Encyrtidae - det. D. P. Annecke and D.S. Hill), and the larvae by wasps in a genus near *Belonia* (det. Dackus) and by others in an unknown genus of Aulacidae (det. T. Huddleston). Eggs and larvae of *D. pictus* were parasitized by unidentified eulophids and braconids (genus nr. *Rhamnura*, det. R.D. Eady) respectively, both causing considerable mortality. Eggs and larvae of *Aphanosperma* were also parasitized, but these hymenopterans were not successfully reared to allow identification.

5.4 GENERAL REMARKS

Aphanasium was very common in old plants at some localities. Although the tunnelling at the base of the stems was very conspicuous, there was little evidence of older plants being killed under normal conditions. These plants appeared to be able to recover from extensive attack, and on a short-term basis, growth and fruit-production appeared unimpeded. Froggat (1895) reported dying back of branches of H. sericea as a result of larval attack, but it is **thought** that he may have confused the damage with that of Uracanthus triangularis. Due to the weakening of the junction between stems and roots, heavily attacked plants were easily pushed over, and in fairly open vegetation some were apparently blown over by wind.
Webb (personal communication 1964) regarded this phenomenon as of particular value in a biological control program. Where larvae tunnelled into sub-surface roots (e.g. around Canberra) they caused the death of some root-suckers.

Aphanosperma and D. pictus damage was very conspicuous on some plants, but severe attack was very localized. Both these insects were regarded to be in some way detrimental to C. autologa larvae, and their role in this respect was discussed in sections 4.384 and 4.385.

5.41 Bases for host-specificity

The narrow known host-plant range in the field, even at localities where other Hakea spp. occurred, suggests that some form of host-restriction always occurred. If this is a positive restriction (and not merely survival on plants suitable for larvae) the females must have some mechanisms for selecting suitable hosts. However, there was no evidence for this in captive females - apart from perhaps the feeding habits of *D. pictus* females. In the apparent absence of host-specific behaviour, feeding tests for larvae appeared to be necessary. Under laboratory conditions, the requirements of *D. pictus* larvae were not specific. They developed for several months in stem-pieces of a variety of proteaceous plants into which they had been placed, and even in the soft, fleshy stems of *Sedum* sp. (Crassulaceae). The rates of development were comparable to those on host-plant material, and sometimes more rapid.

The very long life-cycle of the cerambycids in the laboratory, and the ability of the larvae to survive several months of starvation, made feeding tests impracticable, especially since satisfactory rearing techniques for comparison on host-plants were not available. It was furthermore found that when reared in compacted sawdust of host-material, field-collected larvae of *Aphanasium* may appear to tunnel and moult normally, but that they may in fact gradually lose weight.

Feeding tests were finally abandoned when it became known that larvae of another native stem-boring cerambycid attacking *H. gibbosa* and *H. sericea*, also attacked stems of some plants of economic importance, including citrus in N.S.W.

VI GENERAL DISCUSSION

The inherent characteristics most relevant to biological control of the three species of needle-bush may be summarized as follows: 1) they are long-lived, and when mature, produce annually a vast number of flowers, of which only a small proportion give rise to fruits developing beyond the newly-set stage; 2) even so, very large numbers of fruits accumulate on the plants, and their seeds remain viable inside the indehisced fruits for the life of the plants; 3) vegetative reproduction is normally non-existent; 4) there is no regeneration in established plant communities; 5) survival and multiplication are normally dependent on massive, rapid regeneration from seeds released immediately after fires; and 6) the seeds do not survive long once released from the fruits, and germinate after the first heavy precipitation. The resulting generation of plants are thus generally of the same age, and do not produce seeds until after a few seasons. Furthermore both the seedlings and the older plants are vulnerable to competition by taller plants, and neither will survive as an understorey in surrounding vegetation.

On a theoretical basis it may be deduced that the plants may be most vulnerable to the following three modes of attack during their cycle: a) a drastic reduction of the number of seedlings reaching the reproductive stage; b) a gradual killing-off of mature plants whose seeds will have no opportunity of surviving in the surrounding vegetation; and c) a drastic reduction of the numbers of viable seeds present on the plant to prevent massive regeneration after the death of the plants in a community, whether as a result of fire or of other means. The third mode of attack may be achieved jointly or separately by prevention of seed formation, by destruction of mature seeds on the plant, and/or by causing the untimely release of seeds.

The effects of attack on these vulnerable phases are seen to be interrelated, and dependent on the degree of recovery and compensation that may occur elsewhere in the cycle. Competition by other plant species at critical phases, particularly during regeneration, may be a very important factor in the overall effect of insect-attack.

The levels of vulnerability of the different stages of the plants would be qualified by local growth-conditions,e.g. whether they occur in dense thickets, as isolated specimens in a diverse, established community, or as individuals in a habitat where a vacant niche for them exists.

Some indications of the effect of insects on the plants in their natural environment were found when isolated plants on which they did not occur, were compared with attacked plants growing under similar conditions. [Although other factors may be involved, it will also be possible to compare the plants in their natural environment with those under 'insect-free' conditions (e.g. where they occur in pest-proportions under similar climatic conditions in South Africa) to get some indications of the parts and stages of the plants where different types of insects may exert some harmful influence.]

The most striking effect of insects on the plants was apparently the large reduction in the numbers of fruits formed, and thus in the numbers of seeds present on a mature plant at any stage of its life. Even within their natural distribution range, the plants at the few localities where the curculionids attacking green fruits (Erytenna sp.) were absent, usually had an exceptionally leavy load of mature fruits[1]. A second significant, although often inconspicuous, effect of insects appeared to be the reduction in the number of viable seeds present on the plants, either as a result of direct insect damage, or because of untimely dehiscence of fruits.

Plants in their natural environment were often somewhat stunted or not quite as healthy and vigorous as some isolated or cultivated plants. This is, however, not surprising in view of the large number of different minor insects that may attack their vegetative parts, and the competition from other plants in the heath or woodland where these plants naturally occur. Although noticeable, these latter manifestations of insect attack were usually regarded as relatively unimportant, especially on the level of damage caused by each species.

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[1] For instance, in a group of c.15-year old H. sericea plants at Foster, Victoria, several had in excess of an estimated 2,000 mature fruits on them, whereas plants of similar age and size at Wilson's Promontory, some 20 miles distant, usually contained between 250 and 700 fruits each. The plants at Foster were within a few miles of the nearest other H. sericea, and although several of the insects normally attacking H. sericea in that area were present on them, Erytenna was somewhat inexplicably, entirely absent.

Very large proportions of fruits were attacked and of seeds were destroyed over much of the natural distribution range of the plants. Yet there was no marked detrimental influence on the survival of the species despite obviously severe competition by other plants. This gave rise to the theory that these plants may be adapted to survive in the presence of severe attack by seed-attacking insects, and that the inherent capacity to produce very large numbers of flowers and fruits, may be a mechanism to offset the effect of the insects.

It follows that a vast excess of seeds will be produced in the absence of such insects, and that the re-introduction of the insects may reduce the aggressiveness of the plants to a more normal level where other plants may be successful in competing with them.

In the extensive literature on the selection of useful insects (reviewed by Wilson 1964, and Huffaker 1964), the majority of workers expressed in some way or another the following ideas:
The insects likely to be useful in biological control of weeds are those severely damaging a vital part of the plant taking into account its longevity and its mode of reproduction. Especially important are those insects capable of destroying existing stands of the plants. The destruction of even a large proportion of seeds in perennial plants was usually thought to have little potential value. In the selection of potentially useful insects, the 'noxious' nature of the plants should be kept in mind, i.e. whether its general presence,

its presence in dense thickets, or its seeds, foliage, etc., is undesirable.

In the case of needle-bushes in South Africa, it is mainly their occurrence in dense thickets, and their rapid multiplication after fires from individual, isolated plants, that are most objectionable.

The arguments against the potential effectiveness of seed-attacking insects are not seen as strictly applying to needle-bushes in view of the obvious importance of large numbers of seeds to the noxious nature of the plants. With its combination of persistence of the fruits, the absence of regeneration in established vegetation and the non-persistence of seeds in the soil and leaf-litter, the plant may even be regarded as analogous to typical annual or biennial weeds, with the only difference in the periods between regeneration. Thus in the case of needle-bushes, the destruction of a large proportion of seeds may have an equally useful effect as in annual and biennial weeds, as is currently expected for Tribulus terrestris L. in the U.S. (Holloway 1964), or as was obtained on Cordia macrostachya (Jacquin) in Mauritius in conjunction with a leaf-feeder (Simpson 1958), and on Ulex europaeus L. in New Zealand (Hoy 1963).

The features of the plant, and especially of its fruits, offer some interesting bases for specificity of its insects. The very specialized nature of the mature fruits suggests that insects that conquered the woody barrier to reach the seeds, must themselves be very specialized, probably after a very long association with the group of plants, and probably even from its more primitive phases, before the fruits became woody and persistent on the plant (cf. Johnson and Briggs 1963).

Both Erytenna and Carposina revealed some striking adaptations to the plants and their phenology. These were discussed in the sections on those insects. In both cases the insect - Hakea relationship was very well defined, also in their restricted host-range within the genus. Harris and Zwölfer (1968, p.302) stated:

"The host range of a stenophagous insect is presumably integrated with many features of its biology as the result of a long history of selection. A change in any major aspect of its biology will destroy the harmony of the whole and decrease fitness for survival."

The host-plant selection, oviposition behaviour and habits of the larvae in both species all indicated such a relationship with the plants, and can therefore be regarded as excellent bases for host-specificity.

Due to their adaptations to survive fires affecting the host-plants and to recolonize the new generation of plants, these insects are not likely to be detrimentally affected by fire, even if they occur in isolated patches of plants. This adaptation to fires also indicates that concurrent attempts at chemical and mechanical control of the plants are not likely to hamper establishment and survival of the insects. These other control measures, and controlled burning, may in fact ideally augment the action of the insects, and would also be more effective, since regeneration remains an important problem after conventional control measures.

It was shown that parasitoids and predators appeared to be very important factors in the mortality of both *Erytenna* and *C. autologa*, and also competition by the acanthosomatid bug in the latter case. Both species should therefore be much more effective in the absence of these. *Hakea* spp. in South Africa were repeatedly reported to be free of an associated natural fauna, and it is thus unlikely that a range of general predators would be present. The two main parasitoids of the insects in Australia (both braconids) each attacked the host-larvae when these were inside the fruits. They also revealed some other specialized adaptations to the hosts (e.g. regulation of phenology in the case of *Erytenna*, and oviposition through the suture of mature fruits, and escaping from the fruits through the partly formed escape tunnel of the host-larva). Even though parasitoids of related insects present on related plants might possibly attack a potential host present in large numbers, it is very unlikely that they would have the necessary searching mechanisms, as the fruits of *Hakea* spp. do not have equivalents in the natural flora.

Under relatively high population densities in Australia, the effect of intraspecific competition did not have a detrimental effect on the numbers of seeds destroyed on each plant, even though survival of the excessive individuals was necessarily low. This was mainly as a result of the apparent recognition of already-attacked fruits by *Erytenna* larvae, and the survival of only one young larva of *C. autologa* in each fruit. In the field there were often high egg densities in the case of *C. autologa* and this offset the effects of the very high pre-penetration mortality. Should this mortality be lower, competition may be more severe. It may be argued that excessive competition in the latter case may frequently lead to the death of both larvae in a single fruit, but later larvae will probably succeed in fruits in which no larvae survived.

H. sericea has the widest distribution of the three needle-bushes in Cape Province. The other two species occur only at a few isolated localities. H. sericea and H. gibbosa are the normally favoured hosts of Erytenna, and H. suaveolens may also be attacked, despite indications to the contrary in Australia. Sections through mature fruits of H. sericea and H. gibbosa received from South Africa showed that they have a relatively narrow barrier in the suture, so that C. autologa may be very successful on them. As H. suaveolens appeared to be only a marginally suitable host for this insect at Albany, W.A., additional seed-attacking insects against this plant may be necessary. The fruit-boring cerambycid Aphanosperma occidentalis showed distinct possibilities, and further studies may reveal the mechanisms for the specificity apparently operating in the field.

The introduction of a complex of seed- and fruit-attacking insects may on their own account reduce the aggressiveness of the plants, prevent the formation of dense thickets suppressing the native flora, and prevent further spreading, or vast multiplication around isolated plants after fires.

The plants may still be vigorous on an overall basis due to the absence of the entire complex of insects attacking the various vegetative parts in their natural habitat, and the seed-attacking insects offer no means of destroying existing stands. The action of these insects may initially appear to have no appreciable effect on the plant as a weed in view of the potentially long life-cycle of the plants. However, on the whole this may be an advantage of these insects (as opposed to those possibly capable of destroying the plants rapidly), as this would allow gradual recolonization and successful competition by the native flora. The absence of very large numbers of seeds of the weeds may tip the balance in favour of the native flora, which must be assumed to be equally well, or better adapted to the environment in which they had developed (cf. Wilson 1950).

The relatively slow action of fruit- and seed-destroying insects may also be desirable under present conditions, where a significant number of other alien plants (mostly also of Australian origin) have become established, often in pest proportions, in the same general area where the needle-bushes occur. These plants include <u>Acacia cyanophylla</u> ('Port Jackson'), <u>A</u>. <u>cyclopis</u> ('Rooikrans'), <u>A</u>. <u>longifolia</u> and <u>Leptospermum</u> <u>laevigatum</u> (Taylor 1968) all of which may successfully exploit a habitat left vacant by dense stands of needle-bushes.

APPENDIX I

PLANTS REFERRED TO IN THE TEXT WITH AUTHORITIES FOR NOMENCLATURE

1. NEEDLE-BUSHES

Hakea gibbosa (Sm.) Cav.
H. suaveolens R.Br.
H. sericea Schrad. Sert. Hannov. 27 (Vol. I, fasc.3) 1797
Syn.: *Banksia tenuifolia* Salisb. 1796
Conchium aciculare Smith ex Vent. 1805
Hakea acicularis R.Br. 1810
Hakea decurrens R.Br. 1830

[Some botanists use the name *H. tenuifolia* (Salisb.) J. Britten for *H. sericea*. However, the latter name is not adopted by Australian authorities (personal communication L.A.S. Johnson 1964; Nancy T. Burbridge 1968), on the grounds that there is no type of *Banksia tenuifolia* Salisb., and the description is not sufficiently diagnostic to prove that it applied to *H. sericea* (K.Mair, Director, National Herbarium of N.S.W., *in litt.* 1964).]

2. OTHER *HAKEA* SPP.

H. ambigua Meisn.
H. arborescens R.Br.
H. bipinnatifida R.Br.
H. crassifolia Meisn.
H. cucullata R.Br.
H. cunninghamii R.Br.
H. dactyloides (Gaertn.) Cav.
H. decurrens R.Br.
H. elliptica R. Br.
H. epiglottis Labill.

H. eriantha R.Br.
H. glabella R.Br. (= *H. prostrata* R.Br.)
H. intermedia Hook.
H. leucoptera R.Br.
H. lissosperma R.Br.
H. microcarpa R.Br.
H. nodosa R.Br.
H. propinqua A. Cunn.
H. rostrata F. Muell. ex Meisn.
H. rugosa R.Br.
H. salicifolia (Vent.) B.L. Burtt
H. teretifolia (Salisb.) J.Britt.
H. trifurcata (Sm.) R.Br.
H. ulicina R.Br.
H. undulata R.Br.
H. varia R.Br.
H. victoriae Meisn.

3. OTHER PROTEACEOUS PLANTS

Banksia integrifolia L.f.
B. marginata Cav.
B. serrata L.f.
B. spinulosa Sm.
Brabejum stellatifolium L.
Grevillea alpina Lindl.
G. rosmarinifolia A. Cunn.
Lambertia formosa Sm.
Macadamia integrifolia Maiden & Betche
M. ternifolia F. Muell.
Persoonia juniperina Labill.
Petrophile pedunculata R.Br.
Protea cynaroides L.

P. subpulchella Stapf.
P. susannae Phillips

4. VARIOUS

Acacia cyanophylla Lindl.
A. cyclopis A. Cunn.
A. longifolia Willd.
Bertholletia excelsa Humb. & Bonpl.
Casuarina pusilla Mackl.
Corylus avellana L.
Eucalyptus capitellata Smith
Juglans regia L.
L. juniperinum F. Muell.
Leptospermum laevigatum (Sol. ex Gaertn.) F. Muell.
Phaseolus vulgaris L. var.
Prunus amygdalus Batsch.
P. persica Z. & S. var.
Pyrus malus L.
Rubus australis G. Forst.
Sedum L. (*Sempervivum* L.?)

TABLE 36

Insects found attacking needle-bushes (*Hakea* spp.) with the main parts of the plants affected and indications of the host-plant range. When final identifications were not possible, and specimens were preserved, the accession number (Code AcHa) is given.

		Parts of Host Attacked									Known				Hosts		
		Foliage	Buds	Flowers	Stems	Roots	Young fruits	Mature fruits	Seeds		*H. sericea*	*H. gibbosa*	*H. suaveolens*		Other *Hakea* spp.	Other Proteaceae	Various
A COLEOPTERA																	
1 Buprestidae	(Unidentified larvae 241)				+								+				
2 Cerambycidae	*Aphanasium australe* Boisd.				+	+					+	+			+		
	Aphanosperma occidentalis Brit.							+	+				+		+		
	Uracanthus triangularis Hope				+						+	+					+
	(Unidentified larvae)							+	+		+						
3 Curculionidae	*Cydmaea* sp. (109)			+							+	+					
	Cydmaea sp.nr.*diversa* Blkb.(116)	+									+						
	C. binotata Lea	+	+								+	+					
	C. luctuosa Pasc.	+	+								+	+			+		
	C. major Blkb.(114)]		+	+			+				+	+			?		
	Erytenna sp.nr.*consputa* (18)]		+	+			+				+				+		
	Dixoncis pictus Oke				+			+			+				+		
	Rhinaria pulicosa Lea					+					+				+		
	(Cryptorrhynchinae 235)							+	+		+						
	(" 202)							+			+				+		
B DIPTERA																	
1 Cecidomyiidae	(Unidentified 147)				+						+	+					
C HEMIPTERA																	
1 Acanthosomatidae	cf. *Sangarius* Stål (209)	?			?		?	?	+		+				+		
2 Coccidae	*Coccus* sp.(4)	+									+						
3 Delphacidae	(Unidentified 238)	+											+				
4 Diaspididae	?*Phaulaspis* sp.	+	+		+		+	+			+	+			+	?	
	(Unidentified 8)	+	+		+		+				+				+		
	(" 210)				+						+				+		
5 Eriococcidae	?*Rhizococcus* sp. (25)		+		+						+						
6 Lygaeidae	*Crompus oculatus* Stål	+					?				+						
7 Margarodidae	*Callipappus australe* Mask.	+			+						+						+
8 Membracidae	*Sertorius australis* Fairm.	+			+						+	+				+	
9 Pseudococcidae	?*Paracoccus* sp. (12)				+			+			+	+			+		
	(Unidentified 242)							+					+				
10 Psyllidae	(Unidentified 151)	+	+								+	+	+		+		
D HYMENOPTERA																	
1 Eurytomidae	*Eurytoma* sp.nr.*circumstriatus* Gir.								+		+				+		
2 Torymidae	*Xenostigmus mirostigmus* Riek		+								+	?			+		
E LEPIDOPTERA																	
1 Arctiidae	(Unidentified larvae 168b)	+											+				
2 Carposinidae	*Carposina autologa* Meyr.								+		+		+		+		
3 Geometridae	*Amelora* sp. (182)	+									+						
	Chlenias seminigra Rosenst.	+									+						
	?*Chloroclystis* sp. (237)	+									+						
	Oenochroma vinaria Guen.	+									+	+					
	(Enominae 182)	+									+						
4 Notodontidae	*Danima banksiae* Lewin.	+									+				+	+	
5 Tortricidae	*Acroplitis rudisana* Wlk.	+									+						
	Epiphyas postvittana (Wlk.)	+									+				+	+	+
	Parastranga macrogona Meyr.						+				+				+		
6 Xyloryctidae	*Neodrepta luteotactella* (Wlk.)	+			+						+	+	?		+	+	
	Xylorycta leucophanes Lower	+									+				+		
7 Yponomeutidae	?*Nematobola* sp. (181)	+									+						

APPENDIX II

INSECTS ATTACKING NEEDLE-BUSHES[1]

The insects found attacking the three needle-bushes are listed in Table 36, together with indications of the parts of the plant normally attacked, or where the damage caused was most conspicuous.

A large variety of other insects, suspected of being phytophagous, were also found associated with the plants. These insects (listed below) include those encountered in very small numbers and those whose host relationships were not known (e.g. when only the adults were found feeding on the plants, or when larvae or pupae were found (possibly secondarily) associated with damage caused by other insects). Identifications were not sought in some cases, or not available at the time of writing, and then an accession number under which they had been entered in the collection is given. Insects thought to be predatory were omitted from the list as far as possible.

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[1] Several of the species had been referred to by D.v.V. Webb (South African Department of Agricultural Technical Services, unpublished reports 1962-1964), and by Moore (1964). They also listed some additional species not encountered by, or not identified for the present author.

COLEOPTERA

ANTHRIBIDAE

(unidentified) (10) - adults emerged from dying stem (*sericea*)

(unidentified) (85, 202a, 207) - adults emerged from mature fruits (*sericea*)

ATTELABIDAE

Euops falcata Guer. - adults found on foliage (*sericea*)

BELIDAE

Belus rubicundus Lea - adults shaken from foliage (*sericea*)

Pachyura australis Hope - " " " " "

CERAMBYCIDAE

Ceresium scutellaris Hope - adults from foliage (*sericea*)

Strongylurus maculaticollis Blanch. - adults from foliage (?*sericea*)

CHRYSOMELIDAE

Calomela punctipes Germar - shelter (and pupate?) in dry fruits (*sericea*)

Ditropidus sp. nr. *elegantulus* (245) - shaken from foliage (*sericea*)

Ellopia pedestris Erichson - adults shaken from foliage, may pupate in fruit husks (*sericea*)

Geloptera porosa Lea - adults shelter in fruit husks, feed on foliage and fruits (*sericea*,*gibbosa*)

Geloptera sp. (75) - adults shelter in fruit husks, feed on foliage and fruits (*sericea*)

Paropsis reticulata Marshham - adult shaken from foliage (*sericea*)

Paropsis sp. (76) - adults emerged from split, young fruits (*sericea*)

Rhyparida sp. (246) - adult shaken from foliage (*sericea*)

CURCULIONIDAE

(a) *Adults feeding on plant*

Orthorrhinus cylindrirostris Fabr. - surface of mature fruits (*sericea*)

Perperus lateralis Boisd. - foliage in lab., (shaken from *sericea*)

Poropterus waterhousei Pasc. var. - surface of mature fruits (*sericea*)

Prypnus squamosus Blkb.- foliage (*gibbosa*)

Rhinoplethes foveatus Pasc. - foliage and twigs (*suaveolens*)

Syarbis alcyone Lea - foliage and flowers (*sericea*)

(b) *Adults found sheltering on plants*

? *Erytenna* sp. (220) - larvae may develop in young fruits of *suaveolens*

Melanterius unidentatus Lea - from husks of dry, young fruits (*sericea*)

Misophrice sp. (189) - between fruits (*suaveolens*, *elliptica*)

(unidentified)(196) - possibly sheltering (from sample of mature fruits) (*sericea*)

(c) *Adults shaken from H. sericea*

Aoplecnemis tasmanicus Blkb.

Aonychus hopei Boh. var.

(Cryptorrhynchinae) (252)

(?Curculionidae, ?Centorrhynchinae) (101)

Cydmaea bimaculata Pasc.

Cydmaea diversa Blkb.

Gonipterus crassipes Lea

Gonipterus scutellatus Gyll.

Imaliodes sp. (188)

Merimnetes sp (247)

(Otiorrhynchinae) (255)

Perperus insularis Boh.

Perperus sp. (120)

(unidentified) (253)

(d) Possibly secondary attack

(Cryptorrhynchinae) (204) - emerged from stem with cerambycid damage (*sericea*)

ELATERIDAE

Crepidomenus fulgidus Erichson - adult shaken from foliage (*sericea*)

LAGRIIDAE

Ecnolagria tomentosa Fabr. - adults shaken from foliage (*sericea*)

LATHRIDIIDAE

Corticaria adelaidae Blkb. - adult emerged from mature fruit (*sericea*)

SCARABAEIDAE (MELOLONTHINAE)

Diphucephala colaspidoides - adults shaken from foliage (*sericea*)

TENEBRIONIDAE

Lepispilus sulcicollis Boisd. - adults shaken from foliage (*sericea*)

DIPTERA

CHLOROPIDAE

?*Lioscinella* sp. A.(134) (cf. genus nr. *Botanobia* - larvae develop in seed-cavities of *Hakea* spp. (sometimes as scavengers).

?*Lioscinella* sp. B. (173) - as for previous species

HEMIPTERA

ACANTHOSOMATIDAE

Stauralia sp. (259) - adults found on plant (*sericea*)

Eupolemus sp. nr. *insularis* Dist.(104) - " " " " "

Eupolemus sp. nr. *wagneri* Jens. Haar.(112)- " " " " "

FLATIDAE

Siphanta acutipennis Kirk. - adults shaken from foliage (*sericea*, *gibbosa*)

Siphanta subgranulosa Kirk.- " " "

MIRIDAE

Pseudopantilius sp. probably *australis* (Wlk.)(113) - adults found on plant (*sericea*)

PENTATOMIDAE

Cuspicona thoracia (Wests.) - adults found on plants (*sericea*)

Diaphyta fulvescens (Dallas) - adults feeding on young growth (*sericea*)

Ocirrhoe sp. probably *lutescens* Dist. (103) - adults found on plant (*sericea*)

Omyta centrolineata Westw. - adults found on young shoots (*sericea*)

Pecilometis sp. probably *strigatus* (260) - " " " " "

L E P I D O P T E R A

ARCTIIDAE

Philenora ?elegans Butler (177a) - larvae tunnel in fruits attacked by cerambycid (*suaveolens*)

Xanthodule semiochrea Butler - cocoons found on fruits (*sericea*)

Xanthodule sp. (168) - female found ovipositing on foliage (*suaveolens*)

OECOPHORIDAE

Barea confusella Wlk. - larvae occur in stems attacked by cerambycid (*sericea*)

PSYCHIDAE

(unidentified) - larvae feeding on foliage (*sericea*)

TINAEIDAE

(unidentified) (177b) - larvae tunnel in fruits attacked by cerambycid (*suaveolens*)

APPENDIX III

OTHER PROMISING INSECTS ENCOUNTERED

These insects were not studied in the laboratory, or initial attempts to rear them failed. As some of them may prove to be useful, general notes and observations on them are included.

1. *Eurytoma* sp. nr. *circumstriatus* Girault (Eurytomidae) -
det. E. F. Riek.

About 5 p.c. of mature fruits of *H. sericea* at Bargo in N.S.W. had one or both seeds destroyed by larvae of this hymenopteran. The escape tunnels formed by the adults were originally confused with those made by *C. autologa* larvae. The larvae develop singly inside the testa of seeds, and each consumes only one seed. Before pupation in the hollow seed, a characteristic brown meconial mass is voided, and no cocoon is formed. The adult eats a narrow escape tunnel through the woody side of the fruit, and the antennal sheaths are cast only after completion of the escape. The majority of adults failed to complete the escape tunnels in *H. sericea* fruits and succumbed in the fruits. Similarly, near Heathcote, (N.S.W.) - where this insect also attacked *H. sericea* - about 30 p.c. of the mature fruits of *H. dactyloides* had one or both seeds destroyed, yet only a very small proportion of these had successful escapes. Occasional signs of eurytomid attack were also found on *H. nodosa* at Wilson's Promontory.

Recent observations showed that the insects may have flowed over to the larger-fruited 'hosts' from H. teretifolia whose small fruits often had the majority of seeds (up to 85 p.c.) destroyed by probably the same eurytomid at nearly all the localities where this plant was encountered. It appeared that oviposition occurred through the sides of the follicles at a stage when the fruits were almost full-sized, but not yet woody. The larvae were usually found fully-fed and inactive towards the end of winter (when the fruits were already woody) and they pupated during spring. Pupation in the laboratory occupied only 18-22 days, but the adults probably do not appear in the field until mid-summer.

A subsequent examination of herbarium specimens on whose fruits escape holes were found (see footnote p. 106) suggested that at least some of these fruits may have been attacked by a similar eurytomid, and a search may reveal species or forms adapted to hosts with larger fruits.

2. Genus nr. Sangarius Stål (Acanthosomatidae, Hemiptera - det. G. F. Gross)

The adults of this large[1], unusual brachypterous bug feed on the sap of seeds in mature fruits of a number of Hakea spp., including the forms of H. sericea with very large fruits and with a broad granular layer in the suture. The stylets are inserted into the seed-cavity through, or next to, the suture, or through the woody follicle, either at the side, or more commonly from a position

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[1] The females are about 11 - 14 mm in length; the males somewhat smaller.

on the adaxial aspect of the fruit. Insertion may occupy more than an hour, and if the seeds are not reached, the stylets may be partly withdrawn several times and inserted in a slightly different direction. A minute feeding tubule (0.03 - 0.05 mm in diameter) is secreted around the stylets, and is visible as a white, waxy, but brittle, fungus-like thread where the stylets pass through an open space (e.g. in the suture, between the walls of the seed-cavity and the testa, and between two seeds when the stylets are inserted through one seed into the second). During feeding on a seed the stylets may be slightly withdrawn several times and re-inserted into the seed at a small distance away, so that the tubules often have a multi-branched appearance where they are attached to the testa. The amount of sap taken from a seed appeared to be small, but the cotyledons discolour at the puncture sites, and the entire seed gradually discolours, apparently initially as a result of some form of bacterial rot or autolysis of the cells. The bugs appeared to transmit bacteria and fungal spores from one fruit to the other. Affected seeds do not germinate, despite the fact that they may appear healthy and firm from the outside.

Rotten seeds were noticed from time to time during the study, but the role of the bugs was established only at a late stage. Since the discovery, it was found that the incidence of damage was much higher than had originally been realized, since the damage and tubules were usually overlooked, especially when the latter did not pass through the suture.

About 17 - 24 p.c. of all older fruits of *H. nodosa* in large samples from Wilson's Promontory were found to have one or both seeds affected. Early in the season (autumn) newly-matured fruits were unaffected, but towards spring several of them had already been attacked.

Figures for larger samples of *H. sericea* fruits from that locality were not available, but in smaller samples of about forty fruits each, the proportion of attacked fruits varied between about 7 and 40 p.c. Fruits of *H. ulicina* were also attacked extensively. In a sample of 176 fruits, 59.7 p.c. had tubules or at least one rotten seed, and 44.3p.c. of the potential number of viable seeds were rotten. *H. teretifolia* at this locality was also attacked, but estimates of the proportion of attacked seeds were hard to make due to the high incidence of damage by *Eurytoma* sp.

At Bellbird Creek, near Cann River (Vic.), 85 p.c. of the 115 fruits on one young plant were attacked, and 71 p.c. of the seeds were affected.

Although samples from the majority of localities and from many of the *Hakea* spp. encountered were not closely examined for damage, the insects are thought to have a wide distribution in eastern Australia at least. Typical damage was seen in small samples of *H. sericea* and *H. dactyloides* fruits from Heathcote near Sydney, and an examination of herbarium specimens collected in W.A. (Albany) revealed that at least *H. undulata* showed typical feeding tubules.

Adults were encountered in the field at various times of the year (April, June, September, December), and laid groups of 11 - 14 eggs in the laboratory. The nymphs hatched in about 2 weeks by means of a decidual egg cutter on the head, fed readily on young growth offered to them, and moulted within two weeks. However, they all failed to develop beyond the second instar on potted plants of *H. nodosa* and *H. suaveolens*, although they lived for over two months, and were seen to insert their mouthparts into stems, leaves and young growth. Only a single nymph was shaken from a plant in the field (half-grown in December), and eggs were not found. The feeding habits of the immature stages are thus not understood, but it appeared that feeding on vegetative parts was not sufficient for normal development.

3. *Xenostigmus mirostigmus* Riek (Torymidae)

Further study of these hymenopterans developing in buds may reveal whether the reduction in flower-buds may be significant, and whether they are host-specific. They were heavily parasitized in their natural habitat, and may escape parasitism elsewhere. If attack on flower-buds is very general, this species may be useful in reducing the numbers of fruits formed, but they would then be limiting on *Erytenna* sp.

4. *Cydmaea binotata* (Curculionidae).

Moore (1964) reported extensive damage to buds of *H. gibbosa* by larvae and adults, and considered them of great potential value in a biological control programme. This species, and a complex of very similar *Cydmaea* spp. were common on *H. sericea* at Wilson's Promontory, and while it is known that the larvae of at least some tunnelled in young leaves, their habits, and effect on fruit-production are not known.

5. *Cecidomyids* occurring in stems (cf. Moore 1964).

Die-back of affected thin branches was common in N.S.W., and these insects, especially when escaping parasitism, may be of value in causing dehiscing of fruits, and possibly in attacking young plants.

6. *Parastranga macrogona* (Tortrididae). Due to competition with larvae of *Erytenna* sp., this species may at most be considered as an alternative for the weevils. It may possibly attack young fruits of *H. suaveolens*. Further investigations on its feeding habits and host-plant range are necessary.

7. *Unidentified geometrid attacking young fruits*.

These larvae attack green, young fruits and consume the seeds and surrounding tissue, leaving characteristic dry fruit-husks on the plants. Typical damage by this presumed geometrid (cf. Moore 1964) was found on both *H. sericea* and *H. gibbosa* in eastern N.S.W., but larvae were not obtained for observations and identification. The larvae may be basically leaf-feeding. Attacking fruits of a size suitable for larvae of *Erytenna*, the same qualifications as for the previous species apply.

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