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The biology and host plants of the Australian weevil *Rhinotia haemoptera* (Kirby)

(Insecta, Coleoptera, Belidae)

By Trevor J. Hawkeswood, James R. Turner and Matthew LeBreton

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The biology and host plants of the Australian belid weevil, *Rhinotia haemoptera* (Kirby) are reviewed from both the literature and previously unpublished observations. The species, although widespread, is uncommon to rare throughout its range where it occurs in dry sclerophyll forests and associated woodlands. The known larval host plants are *Acacia decurrens* (Wendl.) Willd., *A. elongata* Sieb. ex DC., *A. obtusifolia* A. Cunn., *A. pubescens* (Vent.) R. Br., *A. suaveolens* (Sm.) Willd. and *A. terminalis* (Salisb.) MacBride (Mimosaceae). All of these larval host plants have been recorded from New South Wales. The adults feed on the foliage or branchlets of various *Acacia* species, but have also been purported to visit nectar-bearing flowers of *Bursaria* (Pittosporaceae), *Angophora* and *Melaleuca* (Myrtaceae) and *Hakea* (Proteaceae); these latter observations need confirmation. Various ecological characteristics of the beetle, such as the ability to occupy highly seasonal regions, general spatial patchiness of resident populations within a region, dispersal ability of adults, habitat selection, colonizing ability, abundance of food plants, predation/parasitism, escape mechanisms, Batesian mimicry are all reviewed and discussed.

Trevor J. Hawkeswood, C/- North Star Caravan Resort, Coast Road, Hastings Point, 2489, New South Wales, Australia.

James R. Turner, 117 Derby Street, Penrith, 2750, New South Wales, Australia.

Matthew LeBreton, 68 Hilda Street, Blaxland, 2774, New South Wales, Australia.

Introduction

The Australian weevil, *Rhinotia haemoptera* (Kirby) (Coleoptera, Belidae) (Fig. 1) is one of the most distinctive of all Australian belid weevils. It occurs mostly in dry sclerophyll forests and woodlands of eastern Australia from north-eastern New South Wales to Victoria (Hawkeswood 1987a: 125, 1990a: 444) and occasionally into south-eastern Queensland (Hawkeswood 1990a) and to South Australia (Tepper 1887: 34) and Tasmania (Lea 1906: 20). The main body colour is black with reddish-brown; the head is black with some reddish-brown near the eyes; the pronotum is black with broad, reddish-brown margins and the elytra are reddish-brown with a thin, black, sutural line (Hawkeswood 1987a, 1990a). A review of the biology and host plants of *R. haemoptera* was provided by Hawkeswood (1990a) but since then, new data have been gathered and further references located that were previously overlooked, and these are all reviewed and discussed here in a revised account.



Fig. 1. Adult of *Rhinotia haemoptera* (Kirby) on the foliage of *Acacia longifolia* (Andr.) Willd. (Mimosaceae) at Batemans Bay, New South Wales, Australia. (Scale line = 10 mm). Photo: D. G. Knowles, from Hawkeswood, 1987a, 1990a.

Previously published data

In a reference which has been overlooked by all early workers and later reviewers, Tepper (1887: 349) briefly noted that the adults of *R. haemoptera* (incorrectly cited as *Rhinotia haematoptera* Kirby) frequented the flowers of *Bursaria*, *Hakea* and *Melaleuca* and flew briskly; these observations have not been confirmed and are thus questionable. Froggatt (1893: 37) noted that the main food plant of larval *R. haemoptera* was the wattle bush, *Acacia suaveolens* (Sm.) Willd. (Mimosaceae) but that he had also occasionally bred the beetle from *A. pubescens* (Vent.) R. Br. and *A. terminalis* (Salisb.) MacBride (cited by Froggatt as the old synonym of *A. discolor* (Andr.) Willd.). Froggatt (1893: 37) also noted that the eggs are laid by the female on the underside of a branch of the host plant, where a small patch of bark had been gnawed off by the beetle. According to Froggatt (1893), the larva hatches and a small hole is produced in the branch where the larva enters the wood; as the larva grows, it hollows out the whole of the stem and later pupates in the uppermost end. At Rose Bay (Sydney, New South Wales) during May 1892, Froggatt (1893) also noted that every branch of *Acacia suaveolens* contained one or more of the adult beetles or their larvae and that adults were common during early November in the Sydney district, New South Wales, feeding on the foliage of *A. terminalis* (cited as *A. discolor*). Froggatt (1902: 707) provided further details on the biology and hosts of *R. haemoptera* and noted that the beetle lays each egg into a scar on the bark of a branch which measures almost 15-20 mm in diameter and the tiny larva, when hatched, bores into the centre, burrowing down through the middle for about 5-10 cm and causing the bright green bark to change to a yellow colour. Froggatt (1902: 707) further noted that he had cut beetles out of *Acacia decurrens* (Wendl.) Willd. (Mimosaceae) in the Sydney district, New South Wales, but that in this area of the country, the primary (preferred) host was *A. suaveolens*, from which he had extracted larvae and adults from the stems during May and concluded that the fully developed beetle must remain in the pupal cell for a considerable amount of time before emergence in October (i.e. at least 5 months). Froggatt (1902) also recorded adults feeding on the foliage of *A. decurrens* in the

Sydney district. In a minor reference overlooked by all subsequent authors, Walker (1906) briefly noted that *R. haemoptera*, along with other weevils, frequented the wattles but did not specify any names for the record. Froggatt (1907: 187) briefly described the adult and noted that the large-headed larvae fed in the stems of *Acacia suaveolens*. Gurney (1911: 57) noted that *R. haemoptera* (incorrectly cited as *R. hoemoptera*) was a common feeder upon the wattles (*Acacia* spp.) but, like Walker (1906), did not list the host species. Gallard (1916: 113) confirmed Froggatt's (1902) larval host record of *A. decurrens*, noting that the larvae bore into the dead wood, but provided no other details. Froggatt (1923: 109) repeated the data from his 1902 paper without providing any new information. Tillyard (1926: 243) noted that the beetle was a mimic of the genus *Metriorrhynchus* (Coleoptera, Lycidae) but did not provide further biological details. McKeown (1942) in his excellent book on Australian beetles and insects in general, surprisingly did not even mention this distinctive beetle. Hawkeswood (1987a: 125) noted that the colour pattern of the adults mimics that of the noxious *Metriorrhynchus* beetles (Lycidae) which these supposedly harmless belids mimic in order to gain protection or avoidance from potential predators such as birds. Froggatt (1914: 19) noted that an unidentified *Rhinotia* sp. (incorrectly cited as *Rhinotea* sp., but probably *R. haemoptera*) was associated with *Angophora hispida* (Sm.) Blaxell (cited as *A. cordifolia* Cav.) (Myrtaceae) in the Sydney district, New South Wales, but this is most probably an incidental occurrence which indicates no true close association. Hawkeswood (1990a: 444-448) recorded a number of plant associations and collection records for *R. haemoptera*, which are summarized in Table 2, this paper. Hawkeswood (1990a: 447) noted that both adults and larvae of *R. haemoptera* appeared to be very closely associated with *Acacia* spp. (Mimosaceae) growing in dry sclerophyll forests and woodlands in eastern Australia, but that adults occasionally strayed onto other plants such as *Angophora* (Froggatt, 1914) and *Phyllota* (Hawkeswood, 1990a). Froggatt (1893) inferred that *R. haemoptera* was relatively common in the Sydney area at the turn of the century but in the Brisbane area and the Blue Mountains, Hawkeswood (1990a) noted that the beetle was rare and usually uncommon, e.g. during more than six years of intensive insect collecting at one site on the Griffith University campus, Brisbane, Queensland, only one specimen (15 Jan. 1987) had been collected (Hawkeswood 1990a). Hawkeswood (1990a) finally suggested that it was probable that (a) the beetle was particularly sensitive to habitat changes such as clearing of native land for residential development which had led to its decline and uncommon status, or (b) that populations of the beetle in these areas were naturally small. Faithfull & Carwardine (1991: 50) provided a recent adult host record.

New observations

On 11 May and 28 June 1993, stem pieces (billets) were cut from living plants of *Acacia obtusifolia* A. Cunn. (Mimosaceae), a shrub growing in dry sclerophyll forest/woodland near Constance Gorge, near Newnes, New South Wales (33°12' S, 150°17' E) by J. R. Turner. These billets were sent to the senior author soon after collection for examination. Most possessed slight swellings that indicated some kind of invertebrate infestation. Adult *R. haemoptera* emerged over several days during warm weather (average temperatures 22-24 °C) during early July and then the wood material which had dried out, was dissected fully and the results of examination presented in Table 3.

On 31 July 1993, a piece of living branch of *Acacia elongata* Sieb. ex DC. (diameter 7-10 mm, widest at the swelling), was collected by J. R. Turner from Agnes Banks Nature Reserve, north of Penrith, New

Table 1. Summary of the larval host plants (all Mimosaceae) and references for *Rhinotia haemoptera* (Kirby) (Belidae)

Host plant	Reference
<i>Acacia decurrens</i> (Wendl.) Willd.	Froggatt (1902, 1901), Gallard (1916)
<i>Acacia elongata</i> Sieb. ex DC.	This paper
<i>Acacia obtusifolia</i> A. Cunn.	This paper
<i>Acacia pubescens</i> (Vent.) R. Br.	Froggatt (1893, 1923)
<i>Acacia suaveolens</i> (Sm.) Willd.	Froggatt (1893, 1902, 1907, 1923)
<i>Acacia terminalis</i> (Salisb.) Mac Bride	Froggatt (1893)
<i>Acacia</i> sp.	Gurney (1911), Hawkeswood (1987a)

Table 2. Summary of plant association records of adults of *Rhinotia haemoptera* (Kirby). (? = doubtful record which needs confirmation)

Food plant	Plant family	Locality	Date	Comments	Reference
<i>Acacia decurrens</i> (Wendl.) Willd.	Mimosaceae	Sydney, NSW	-	-	Froggatt (1902)
<i>Acacia elongata</i> Sieb. ex DC	Mimosaceae	Castlereagh, NSW	16 Sept. 1992	Adult on flowering plant in open forest	M. LeBreton (unpub. data)
<i>Acacia falcata</i> Willd.	Mimosaceae	Kemps Creek, NSW	31 Oct. 1992	Adult alighted on flowering host plant in open forest	M. LeBreton (unpub. data)
<i>Acacia floribunda</i> (Vent.) Willd.	Mimosaceae	Blaxland, NSW	24 Dec. 1975	Adult on foliage of small plant, non-flowering, 0.5 m high, in dry sclerophyll forest	Hawkeswood (1990a)
<i>Acacia floribunda</i> (Vent.) Willd.	Mimosaceae	Mt Coot-tha, Brisbane, Qld	11 Jan. 1982	Adult feeding on green mesoderm tissue of a branch of a non-flowering plant in dry sclerophyll forest	Hawkeswood (1990a)
<i>Acacia linifolia</i> (Vent.) Willd.	Mimosaceae	Glenbrook, NSW	29 Jan. & 2, 10 Feb. 1976	Three adults on foliage of non-flowering plants (1.0-2.0 m high) in dry sclerophyll forest	Hawkeswood (1990a)
<i>Acacia longifolia</i> (Andr.) Willd.	Mimosaceae	Glenbrook, NSW	17 Jan. 1977	Two weevils mating, female feeding on foliage of non-flowering plant in dry sclerophyll forest	Hawkeswood (1990a)
<i>Acacia penninervis</i> Sieb. ex DC var. <i>longiracemosa</i>	Mimosaceae	Batemans Bay, NSW	-	-	Hawkeswood (1987a, 1990a)
<i>Acacia rotundifolia</i> Hook.	Mimosaceae	Costerfield, Vict.	11 Nov. 1990	-	Faithfull & Carwardine (1991)
<i>Acacia terminalis</i> (Salisb.) MacBride	Mimosaceae	Rose Bay, Sydney, NSW	Nov. each year	Adults common	Froggatt (1893)
<i>Angophora hispida</i> (Sm.) Blaxell	Myrtaceae	Colo, NSW	Dec. 1914	-	Froggatt (1914)
<i>Bursaria</i> sp. (?)	Pittosporaceae	South Australia	-	-	Tepper (1887)
<i>Hakea</i> sp. (?)	Proteaceae	South Australia	-	-	Tepper (1887)
<i>Melaleuca</i> sp. (?)	Myrtaceae	South Australia	-	-	Tepper (1887)
<i>Phyllota phyllocoides</i> (Sieb. ex DC.) Benth. (?)	Fabaceae	Glenbrook, NSW	25 Nov. 1976	One adult resting on foliage (not feeding) of a non-flowering plant 0.8 m high in dry sclerophyll forest	Hawkeswood (1990a)

Table 3. Summary of data obtained from examination of infested wood billets of *Acacia obtusifolia* A. Cunn. (Mimosaceae), collected on 11 May and 28 June 1993 from near Constance Gorge, near Newnes, New South Wales, by J. R. Turner

Stem piece (billet) no.	Diameter (mm)	Diameter (max.) at swelling (mm)	Comments on swellings and their contents
1	14.0-14.5	22	Incomplete chamber, exit hole on side measuring 1.8 mm in diameter probably that of a parasite as is too small for <i>R. haemoptera</i>
2	13.5-16.0	28	One ± straight pupal chamber measuring c. 35 mm long with an exit hole 1.6 mm in diameter, containing a colony of black ants; second chamber almost straight, situated adjacent to the other chamber, empty, apart from presence of a large dead black ant - the exit hole was too small for <i>R. haemoptera</i> so it is probable that the ants had devoured the <i>Rhinotia</i> larva in this chamber before the beetle had an opportunity of developing further - ants had apparently enlarged both chambers but were colonizing only one chamber at the time
3	13.0-15.0	20	One adult in slightly curved pupal chamber c. 32 mm long, head end upwards, emerged 7 Aug. 1993; exit hole 5.2 mm diameter (Fig. 2a)
4	13.0-15.0	22	One adult and one larva in separate chambers (curved and straight); adult chamber 33 × 5 × 5 mm; adult emerged 5 Aug. 1993; other chamber incomplete (Fig. 2b)
5	14.0-15.0	28	Two adults in chambers; chambers curved and slightly sinuous, 28 × 4 × 4 mm and 30 × 5 × 5 mm respectively; adults emerged 7 Aug. 1993; exit holes 4.0 and 5.0 mm respectively - one exit hole above branch node (Fig. 2c)

South Wales (33°37' S, 150°41' E). A dead adult of *R. haemoptera* was situated at one end of a chamber measuring about 36 mm long and mostly 4-6 mm wide, with a pupa of a parasitic wasp positioned above it in the same chamber. Most of the beetle's abdomen was missing, having probably been devoured by the developing wasp larva. The adult wasp emerged on 17 August 1993 through an oval-shaped exit hole measuring 2-2.5 mm in diameter and was later identified by J.R. Turner as a *Xanthocryptus* sp. (Hymenoptera, Ichneumonidae).

From the information that is presently known about the biology, behaviour, distribution and host plants of *R. haemoptera*, a summary of the major ecological characteristics of the weevil are presented in Table 4. A summary of larval host plants is provided in Table 1.

Discussion

From the previously published data on *R. haemoptera* and the new observations presented here, the following summary of its life-cycle and host plant relationships can be provided: a. The female weevil lays an egg into a natural fissure in the thin but tough, fibrous bark of the *Acacia* host plants, or chews a small opening in the bark with its mandibles and places an egg into this gap; b. the eggs may be laid on an underside or sheltered position on the branches or stems of living host plants, but this is not always the case; egg laying into the wood material collected from Newnes appears to have been random, judging by the position of the pupal chambers; c. the eggs soon hatch and the small first instar larvae bore deeper into the sapwood where they chew out chambers measuring 3-5 cm in length; at the completion of these chambers, the larvae are fully grown or almost so; Froggatt (1902) stated that the larvae hollowed out the centre of the stems for distances up to 5-10 cm but in the wood material from Newnes, this was not the case; the pupal chambers and their morphology are illustrated in Fig. 2a-c (this paper); d. the belid appears to pupate at the lower end of the pupal chamber which is the area gouged out by the earlier instar larvae, but Froggatt (1893) stated that pupation occurred in the upper end (near the exit hole ?); e. infestation by larvae induces a swelling in the stems of the host plant (at least in *Acacia obtusifolia*) as shown in Fig. 2a-c, this paper; these swellings however, are not gall-like;

Table 4. Summary of the major ecological characteristics^a of *Rhinotia haemoptera* (Kirby) (Belidae)

Phenotypic and other characters responding to selection	Determined and/or predicted ^b character states
1. Geographical range	Widespread
2. Local endemism and restriction of gene flow	Low*
3. Distribution across marked elevational gradients	Low to moderate
4. Ability to occupy highly seasonal regions	Good
5. General spatial patchiness of resident populations over approx. 1.000 metre sections of a region	High
6. Dispersability of adults	Low to moderate*
7. Intrapopulation variation	Low
8. Interpopulation variation	Low
9. Habitat selection	Specialized (high)
10. Main habitat	Dry sclerophyll forests and surrounding woodlands
11. Colonizing ability	Low
12. Local population density	Low
13. Regional breadth of larval food plants	Moderate
14. Relative abundance of larval food plants per unit area of suitable habitat	High
15. Oviposition strategy	Restricted
16. Oviposition proneness in captivity	Unknown
17. Predation/parasitism on immature stages	Low to moderate*
18. Overall fecundity (average per female)	Unknown
19. Egg to adult development time	1-2 years*
20. Activity of adults	Diurnal
21. Escape mechanisms	Poorly developed
22. Cryptic coloration	Batesian mimicry
23. Sex ratio of adults in random collections	Unknown
24. Diurnal rhythmicity of adult feeding	Probably not present

a Adapted and modified from Young (1982) for butterflies;

b Character states marked with an asterisk are predictions

f. the chambers may exhibit various degrees of curvature and sinuosity but are usually more or less straight (Fig. 2a-c, this paper); one chamber showed evidence of the larva constructing an unfinished side chamber before returning to the main chamber (Fig. 2b); these swellings on the host stems/branches have not been observed or commented upon by any previous authors; g. the adult emerges during warm weather in early or late spring (August–October) through a circular exit hole typical of other Australian weevils (e.g. Froggatt 1923, 1927) and Curculionidae in general; h. the life-cycle is probably one year in duration, although up to 2 years may be possible; the beetles appear to spend several months (up to five) in their pupal cells as fully developed and sclerotized adults (i.e. not teneral) before emerging in the warm months; i. adults emerge to feed on the foliage (phyllodes) or branchlets of various *Acacia* species, but have been reported in the literature (albeit vaguely) to visit the flowers of nectar-bearing plants such as *Hakea* (Proteaceae), *Angophora* and *Melaleuca* (Myrtaceae) and *Bursaria* (Pittosporaceae); these observations are of some interest but they appear to be no modern observations on this purported phenomenon and our own personal observations have shown that adults were usually associated with *Acacia* species, usually non-flowering plants.

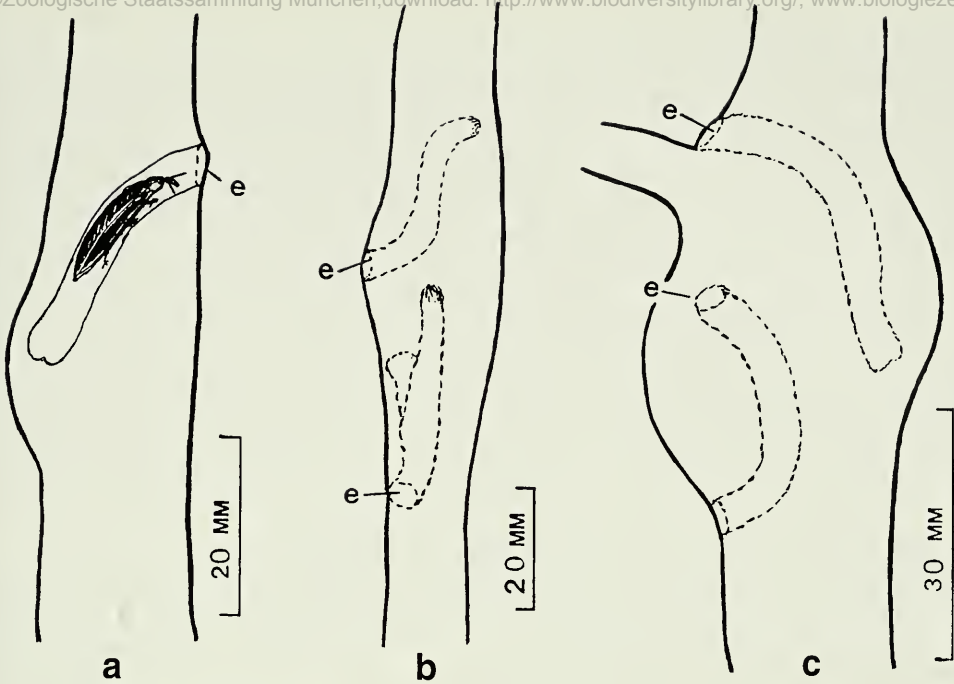


Fig. 2. Pupal (developmental) chambers of *Rhinotia haemoptera* (Kirby) in the branches/stems of *Acacia obtusifolia* A. Cunn. (Mimosaceae) (e = exit hole); drawn by T. J. Hawkeswood.

A summary of the major ecological characteristics concerning *R. haemoptera* is provided in Table 4. An explanation and discussion of these characteristics are provided here. The distribution of *R. haemoptera* is listed as widespread; for Australian insects, a widespread species has been defined by Hawkeswood (1992) as one which occurs over a distance of 1.000 km or more. The known distribution of *R. haemoptera* encompasses south-eastern Queensland, New South Wales, Victoria and South Australia (a distance of at least 2.000 km), but most of the published biological information on the weevil have been recorded from New South Wales. Because of its widespread distribution, *R. haemoptera* is clearly not a local endemic and because of this, there is probably a low natural resistance of gene flow between populations. The effect of clearing and residential development upon gene flow between populations is unknown at the present time, but has probably been restricted in recent times and in the future will probably be very restrictive due to widespread destruction of habitat for human habitation, resulting in widespread extinctions of localized populations. The species presently displays a low to moderate propensity to be distributed over marked elevational gradients, i.e. in New South Wales it has been recorded from low altitude areas (c. 50 m above sea level) to montane areas such as the Blue Mountains west of Sydney at an altitude of 200-500 m. The ability of this weevil to colonize highly seasonal regimes is good, e.g. in the Blue Mountains during summer, average daily temperatures range from 28 to 35 °C and often above, while average daily temperatures during winter range from -5 to 15 °C. The temperature regimes are more equitable in the subtropical area of south-eastern Queensland (in the northern part of the beetle's range) but winter temperatures in this area can still drop to 0 °C or a few degrees below during the winter months of June to August. From our observations on *R. haemoptera* in the Blue Mountains and in the Brisbane area, it was revealed that populations of *Rhinotia* were confined to certain *Acacia* plants or small groups of the host plant while intervening plants of the same species appeared not to have been utilized by *R. haemoptera*, either for food or resting/mating sites. The dispersal ability of adults is not known for certain at the present time but it is probably low or moderate at most. Tepper (1887) noted that the adults fly "briskly" which indicates that the beetles could disperse over considerable distance (e.g. a few km) during their life-spans but our observations indicate that

R. haemoptera is usually sedentary amongst foliage of the wattle plants. Clearly, more observations are needed on this aspect of its behaviour.

There appear to be little or no inter- and intra-population variation in the species, at least in terms of colour pattern. The habitats occupied by *R. haemoptera* are mostly dry sclerophyll forests and woodlands in both lowland and montane areas, which indicate some specialization. *R. haemoptera* has not been recorded from rainforests nor heathlands to date, although *Acacia* species are common in the latter habitat. The colonizing ability of this weevil appears to be low and it has not been found by us in any highly disturbed environments in or around human habitation. At all sites in which we have observed this weevil, the local population densities compared to those of other sympatric Coleoptera have been low (usually only single specimens) despite the abundance of suitable larval host plants. The oviposition strategy appears to be very restricted, i.e. the females appear to lay only a few eggs on the one food plant or on a small group of plants in the one area during the reproductive season. The oviposition proneness of the beetle is not known since the species has not yet been bred successfully in captivity.

The incidence of predation/parasitism on immature stages is probably low to moderate; however, the only data presently available on this aspect are those presented above. It is interesting to note that the same unidentified species of *Xanthocryptus* (Hymenoptera, Ichneumonidae) has also been found to be a parasite of larvae of the longicorn beetle *Ceresium seminigrum* Aurivillius (Cerambycidae) by Hawkeswood (1993) in Queensland. This wasp may be important in regulating populations of *R. haemoptera* but appears not to be host-specific. Wood-boring arboreal ants may also prey upon larvae and pupae in their chambers adding to the incidence of predation.

The egg to adult developmental time for *R. haemoptera* is probably one year but two years are possible; further observations are required. The observations on *R. haemoptera* by all previous and present authors have all been undertaken during the day so that the nocturnal habits of the weevil remain unknown. However, it is probable that adults rest amongst foliage during the night remaining inactive, resuming activity in the morning. The escape mechanisms of *R. haemoptera* are poorly developed; beetles tend to remain on the host plants, clinging to the foliage or branchlets if disturbed or may attempt flight; thanatosis (death-feigning) has not yet been observed. Tillyard (1926), Nicolson (1927), CSIRO (1970) and Hawkeswood (1987a) noted that the weevil is a Batesian mimic, with a colour pattern (i.e. brick-red elytra and black head, thorax and abdomen) matching that of the noxious (at least to vertebrates) *Metriorrhynchus* beetles (Lycidae), in particular, the best known species, *M. rhipidius* Macleay. It is interesting to note that Moore & Brown (1989) found that *R. haemoptera* produced negative results in tests for the presence of defensive chemicals in the weevil body, so that the weevil is apparently unprotected chemically and can be thus regarded as a true Batesian mimic. Escape mechanisms are not well developed, probably because the beetle relies more on protection through its Batesian mimicry of *Metriorrhynchus*. Adults of *Metriorrhynchus* species are usually found during summer on flowers of nectar-bearing plants such as *Leptospermum* (e.g. Hawkeswood 1987b, Webb 1986a), *Kunzea* (Webb 1986b) and *Bursaria* (Hawkeswood 1990b), but in all of these surveys, *R. haemoptera* has not been captured or observed on these flowers. If *R. haemoptera* is really a nectar/pollen feeder as inferred by Tepper (1887) and Froggatt (1914), it would be expected that this Batesian mimic inhabits the same niche(s) as the model *Metriorrhynchus*, in order to gain full protection. However, the mimetic colour pattern adopted by *R. haemoptera* may also enable it to be cryptically protected when resting amongst the *Acacia* foliage and branchlets/stems; the black and red coloration may enable the beetle to merge in with shadows and reddish areas on the *Acacia* stems. Further observations are needed to shed more light on the functioning of this mimicry phenomenon.

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Note added in proof

In a reference previously overlooked, Bernhardt (1989) collected three adults of *R. haemoptera* from flowers of *Acacia paradoxa* DC. in Victoria, but regarded the beetle as a foliage feeder and not important in pollination; this agrees with our comments concerning its phylophagy.

Reference: Bernhardt, P. (1989). The floral ecology of Australian *Acacia*. In: Stirton, C. H. & J. L. Zarucchi (Eds.) Advances in Legume Biology. - Monogr. Syst. Bot. Missouri Bot. Gard. 29: 263-281