

Notes on the biology of *Carcina quercana* (Fabricius) (Lepidoptera: Peleopodidae) and its parasitoids (Hymenoptera) in Germany and the Netherlands

BY MARK R. SHAW

Honorary Research Associate, National Museums of Scotland, Chambers Street, Edinburgh EH1 1JF, U.K.; email: markshaw1945@gmail.com

Article history: Received: 6 August 2025; Accepted: 4 September 2025; Published: 30 January 2026

ABSTRACT

Some puzzles concerning the life-history of *Carcina quercana* and its specialised parasitoid *Venanides carcinae* that were raised during a previous study (2018; 2019) in the Veluwe (Netherlands) (Shaw 2020) are resolved through a further study in the Harztor region of Thuringia (Germany) in 2024. Larvae are displaced from high positions in their host trees by storms, and re-establish on low sapling, seedling and epicormic growth. Factors allowing the host population to survive in the face of successive generations of *V. carcinae* attacking the single host generation include a proportion of the host generation reaching the safety of pupation before the first generation of adult *V. carcinae* has emerged, and probably extremely high levels of parasitism of (and associated host-feeding on) *V. carcinae* cocoons. Vespid or bird predation of parasitoid cocoons at the end of the season may also be significant. It is concluded that *C. quercana* larvae present in mid-September in the Hogue Veluwe in July 2019 were most likely a result of exceptional drought conditions earlier in that year, and not indicative of a second generation, for which no evidence could be found in the Harztor population in 2024. The parasitoids reared are enumerated and their biology briefly described.

Keywords: life history, voltinism, weather, Braconidae, Ichneumonidae, Eulophidae

INTRODUCTION

Fieldwork done in 2018 and 2019 in the Veluwe area of the Netherlands allowed the detection of a microgastrine braconid genus new to Europe and description of a new species, *Venanides carcinae* Shaw, a specialist solitary parasitoid of larvae of the peleopodid moth *Carcina quercana* (Fabricius) feeding on various smooth-leaved deciduous trees (Shaw 2020). However, several behavioural and phenological questions had remained unanswered, and a camping-van holiday in a well-wooded area (Harztor) in Thuringia, Germany over the period 7–23.vi.2024, with a subsequent overnight stop at the Hoge Veluwe National Park (Gelderland, Netherlands) on 25.vi.2024, provided an opportunity to try to find answers. The questions were: (i) wondering why I had previously missed the high density of hosts on low growth in collections before my final day of collecting in the Hoge Veluwe in 2019 when I found them (albeit already parasitized and the parasitoid cocoons heavily predated) so abundantly in that position on 3.viii.2019; (ii) wondering how populations of the reputedly univoltine host could endure the onslaught of its specialised and clearly plurivoltine parasitoid *V. carcinae*, which appears able to parasitize the host over all its larval instars; and (iii) wondering whether the presence of the host larvae from early summer to late September seen in 2018 in the Veluwe area signified plurivoltinism. Although *C. quercana* larvae are very slow growing and undoubtedly expend much

resource on constructing new webs, perhaps many times, it nevertheless seemed intuitively suspicious that such a population would be univoltine, as is widely held – e.g., Emmet (1988), who gives adult flight in July–September. On the other hand, the occasional occurrence of adult moths between May and early December in Britain has suggested to some authors (Sterling, Parsons & Lewington 2012), repeated without the word ‘early’ by Langmaid, Palmer & Young (2018) that there may sometimes be a second brood. The present study attempts to resolve the issue of voltinism.

MATERIALS AND METHODS

The host (see also Shaw 2020)

To understand the research carried out, it is necessary to know in outline the normal developmental biology of *Carcina quercana*. Larvae hatch from eggs laid in late summer and window-feed on the underside of leaves of deciduous trees and bushes at first from a small dense web spun alongside a major vein, later from small frail webs similar to those of post-hibernation larvae. Relatively smooth-leaved trees are preferred: *Quercus* L., *Carpinus* L. and *Fagus* L. being particularly frequent choices. The larvae seek hibernation sites as autumn arrives, by which time they are usually about 7 to 8mm long. In spring, they can be found from early May onwards, now beneath a thin web spun using many transverse strands across the underside of part of a leaf causing a weak concavity to form, in which the larva rests (holding onto the leaf surface, so largely upside-down) and makes feeding sorties to the leaf edge, now consuming the full depth of the leaf. The retreat is open at both ends and faeces are ejected well away from the occupied leaf. Growth is slow, with long periods of resting within the web. The larvae change leaves, constructing new webs, probably necessarily at least one or two times during their growth, but are easily disturbed into abandoning their web (either forwards or backwards) and the leaf it is on, so in practice a variable and perhaps sometimes large number of webs may be constructed progressively. Feeding may occur chiefly at night and the first preoccupation of an exposed larva is always to construct a new web. The full-sized retreats, about 1 to 2cm across and 3cm long, are usually constructed partly alongside the midrib or a main side vein. Pupation (from the end of June onwards) takes place on a leaf undersurface in a less elongate and more densely spun, posteriorly closed web. At adult emergence, usually within two to three weeks, the pupa does not protrude anteriorly. In July mating and oviposition follow with little delay, and larvae of the next generation first appear in August and can easily be found, still small, in late September. Intriguingly, in 2018 I had found half-grown larvae at the end of July in the Veluwe and final instar larvae were still present in the wild in the middle of September (Shaw 2020).

Field collection and rearing, 2024

During the period 7–20.vi.2024 at Harztor larvae of *C. quercana* were sought on *Quercus petraea* (Matt.) Liebl. (by far the dominant oak), *Fagus sylvatica* L. and *Carpinus betulus* L. After preliminary cursory and largely unsuccessful searches on sapling and low epicormic growth of *Quercus*, at first effort was directed to around head-high *Carpinus* because the overall leaf damage on that plant was relatively light, making the larvae more evident, but later in the period more effort was made to collect larvae from *Quercus* where they were in fact at higher density. Low and seedling growth of *Quercus* proved to be especially productive towards the end of the period. Leaf damage on *Fagus* was also light, but *C. quercana* larvae were markedly

scarcer there than on *Quercus* and *Carpinus* and, once that became evident, searching on *Fagus* was much reduced. Larvae from the different trees were pooled for rearing unless parasitism was evident at the time of collection. The moderate number of vacated webs encountered were not scored.

Leaves bearing larvae were collected carefully, trying not to cause the larva to vacate its retreat, and placed in 14×8×6cm closed clear plastic boxes lined with absorbent tissue in counted batches of up to 12, but without exact collection dates. Boxes were inspected daily and fresh clean *Quercus* leaves (the most durable of the foodplants concerned) were added as necessary and vacated and stale unoccupied leaves were removed; any prepupal cocoons or parasitized individuals were cut around and transferred singly to 7.5×2.5cm corked glass tubes with the date. The outcome date (emergence of moth or parasitoid) for each was scored. The overall collecting arena was divided into three sectors, separated by a few hundred meters, in order to assess whether any unusual parasitoid rearings were clumped. Otherwise no obvious differences were detected between sub-samples (either location or foodplant) and rearing results were pooled. A small collection of *C. quercana* was made in the Hoge Veluwe (Netherlands) on 25.vi.2024 from *Quercus robur* L. (the dominant native oak locally); the parasitoids resulting from this are noted, but this collection is excluded from the quantitative results.

In order to assess pseudohyperparasitism (defined below), all cocoons of Ichneumonoidea of a comparable size to those of *V. carcinae* that were encountered on the leaves of the three main trees being searched were collected and roughly identified, their status (primary parasitoid already emerged; hyperparasitoid already emerged; apparently intact) noted, and transferred singly to 7.5×2.5cm corked glass tubes with the date of collection. Any subsequent emergence was dated, and the insect concerned was identified.

Terminology

The term 'pseudohyperparasite' (now more appropriately 'pseudohyperparasitoid') was introduced and explained by Shaw & Askew (1976). It refers to the perpetrator in the common situation in which a primary parasitoid is itself parasitized after the primary parasitoid has completed its feeding on the original host. One very regular occurrence is attack on cocoons of ichneumonoids by phygadeuontine Ichneumonidae (as here), but various other parasitoid groups can behave in the same way towards similar or other primary parasitoids. In one sense pseudohyperparasitoids could be regarded as nothing but primary parasitoids of ichneumonoid cocoons (*etc.*) but, in another sense more pertinent to the population ecology of the original host, they function in the same way as 'true hyperparasitoids' (which develop in or on the primary parasitoid while it is still feeding on the original host) by reducing the population size of the primary parasitoid. For this reason, the term was chosen to include and convey the sense of hyperparasitism.

'Host-feeding' describes the situation in which an adult parasitoid wounds (often kills) a potential host for the sake of imbibing its haemolymph or other tissues. Like most pseudohyperparasitoids, the ones involved in this study are synovigenic (that is, their eggs are developed successively through the adult's life) and, having a high requirement for proteins in order to mature eggs, are likely to host-feed very regularly.

Most pseudohyperparasitoids, including the ones of this study, are idiobiont ectoparasitoids – that is, the host is killed or permanently immobilized at the time it is parasitized, and the resulting larva develops externally to (though within the cocoon

of) the primary parasitoid larva or pupa. Idiobiosis is in contrast with koinobiosis, in which the host is able to continue to feed and protect itself after being parasitized.

Parasitoid material and nomenclature

The ichneumonoid parasitoids reared in this study are deposited in the National Museums of Scotland (NMS) and the Eulophidae in the personal collection of R.R. Askew. I recognize *Oncophanes laevigatus* (Ratzeburg, 1852) as a species distinct from *Oncophanes minutus* (Wesmael, 1838) (Braconidae: Rhyssalinae), as had been the usual practice prior to the synonymy proposed by Belokobylskij (1998).

The next generation

Many of the adult *C. quercana* that emerged (by then in Edinburgh) were transferred to 18 × 12 × 6cm closed clear plastic boxes, several of each sex together, and offered (*ad libitum*) dilute honey soaked onto cotton wool in 2cm diameter dishes. Initially fresh *Quercus robur* leaves were added. Other moths were confined in pairs in 7.5 × 2.5cm corked glass tubes, without leaves, both before and after being offered dilute honey. Unfortunately, no record of adult longevity was kept, but some moths lived for at least 3 weeks (probably under sub-optimal conditions). After being laid, both on the *Q. robur* leaves and copiously around the lid closure of the plastic box, samples of eggs and ensuing larvae were assigned to two cohorts kept separately, one in an outdoor shaded shed, the other indoors at a higher overall temperature. The larvae were fed on *Quercus robur* leaves and, both singly in tubes and communally in plastic boxes, monitored until they attempted to hibernate.

RESULTS

General observations and spatial distribution

Larvae of *Carcina quercana* were not especially abundant at Harztor in 2024, around 30 hours of searching in the period 7–20.vi.2024 producing only 88 individuals (including those already predated or with parasitoids already present in their webs), almost entirely in their final two instars or three as prepupae and one as a pupa.

Up until 17 June most larvae were found on foliage at chest height to as high as could be reached or bent down, and the impression was that the vast majority were well out of reach. On 18 June there was a violent thunderstorm, with heavy rain and some wind lasting for about 2 hours. On the next two days much larger numbers of larvae were found, generally in clearly newly constructed webs, on the fairly plentiful seedling and establishing young sapling growth beneath or close to large *Q. petraea* trees, both isolated in road verges and along woodland edges. Similar vegetation had been surveyed prior to the storm without many larvae seen. Although not precisely quantified, the change in distribution was striking.

The larval period was over by the end of July. Pupation had started before the last sampling date (20.vi.2024), but only to a minor extent, although the first prepupa seen (in the field) was on 7.vi.2024. The last unparasitized larvae became prepupal around 15.vii.2024; larvae still feeding at that date all either produced endoparasitoids (erupting from the host by the end of July) or in a few cases wasted until dying (the last died in that way on 3.viii.2024) – conceivably some not having fed since being collected (late in the collection period) and probably at that time already ‘living cadavers’ following the prior egress of a *V. carcinae* larva (see later), though not scored specifically as that. Adult moths emerged from the very end of June, through July, and just into early August.

TABLE 1. OUTCOMES FROM THE 88 EARLY STAGES OF *CARCINA QUERCANA* COLLECTED AT HARZTOR, 7–20.VI.2024

Category	N	Notes
Host already predated before collection	3	Probably by predatory Hemiptera.
Unexplained mortality in captivity	15	Many were probably 'living cadavers' following egress by <i>V. carcinae</i> .
Pupated successfully (unparasitized)	40	(all but 3 in captivity)
<i>Dolichogenidea candidata</i> (Haliday)	12	Braconidae: Microgastrinae
<i>Venanides carcinae</i> Shaw	6	Braconidae: Microgastrinae (Fig. 2)
<i>Macrocentrus thoracicus</i> (Nees)	3	Braconidae: Macrocentrinae (Fig. 3)
<i>Oncophanes minutus</i> (Wesmael)	1	Braconidae: Rhyssalinae. Usually gregarious.
<i>Diadegma</i> sp. A.	3	Ichneumonidae: Campopleginae
<i>Gelis agilis</i> (Fabricius)	1	Ichneumonidae: Phygadeuontinae (Fig. 4)
<i>Elachertus artaeus</i> (Walker) ¹	3	Eulophidae: Eulophinae. Gregarious (Fig. 5)
<i>Hyssopus nigritulus</i> (Zetterstedt)–? agg.	1	Eulophidae: Eulophinae

¹ Scored as host mortalities.

Parasitoid load

The outcomes from the 88 hosts collected in the period 7–20.vi.2024 are detailed in Table 1. The level of parasitism should be understood as a mere snapshot, undoubtedly lower than the generational load would be if the larvae (and subsequent pupae) had been left exposed in the field. Even then, 30 out of the 70 individuals whose development could be fully traced is a high proportion (43%) and, with more parasitism (certainly by *V. carcinae*, but also possibly by pupal parasitoids) expected before the generation ended, parasitism was clearly a major mortality factor.

Additional parasitoid species reared from the small collection made on the later date of 25.vi.2024 at the Hoge Veluwe National Park were one brood (Fig. 1) of the rhyssaline braconid *Oncophanes laevigatus* (Ratzeburg), 9♀♀ 1♂♂ emerging on 11.vii.2024, and one brood (4♀♀) of the tetrastichine eulophid *Minotetrastichus frontalis* (Nees) emerging on 14.vii.2024.

Characteristics of the parasitoids

Venanides carcinae (solitary koinobiont endoparasitoid) parasitizes early instar larvae in late summer and autumn, overwinters inside the young host, and erupts as a first generation from well- but not fully-grown hosts. It is a haemolymph-feeder and makes its white cocoon in the host web alongside the still living host (Fig. 2). In the study cohort, cocoons arose in the short period 12–14.vi.2024, with adult emergence in the period 22–24.vi.2024 when plenty of host larvae in their last two instars were still available to support the subsequent (second) generation of the parasitoid. Because the sampling period ended on 20.vi.2024 (when we left the area), that generation of *V. carcinae* was not sampled: however, one later cocoon, forming on 28.vi.2024 from a host collected on 20.vi.2024 with adult (male) emergence on 12.vii.2024 was almost certainly a forerunner of the subsequent (second) generation (seen clearly and better sampled in previous years in the Veluwe; Shaw 2020). The host larva, following the egress of the *V. carcinae* larva, remains quiescent in its web, but is potentially highly active and easily leaves it if disturbed. In that case, sometimes it will find a vacated web to occupy, or it may construct a fresh web, but it appears not to resume feeding. The 'living cadaver' can live for several weeks, eventually dying in a dehydrated state; the exit wound left at the eruption of the *V. carcinae* larva is sometimes, but often not, visible.



Figs 1–6. — Parasitoids of *Carcina quercana* developing in situ: 1–5: 1, Cocoons of *Oncophanes laevigatus*; 2, Cocoon of *Venanides carcinae* with ‘living cadaver’ of *C. quercana*; 3, Ectophagous phase of *Macrocentrus thoracicus* larva (host silk removed); 4, *Gelis agilis* larva in host cocoon; 5, Fresh pupae of *Elachertus artaeus*, before darkening and overwintering. 6, Fertile eggs of *C. quercana* laid in cracks in cork, becoming pink.

In contrast to *V. carcinae*, *Dolichogenidea candidata* (solitary koinobiont endoparasitoid) consumes practically the entire host, probably with a final brief external feeding phase (on the basis of the witnessed behaviour of several congeners (MRS unpublished), although not observed in this study), before usually expelling the host skin from the web and constructing its white cocoon in a similar position to that of *V. carcinae*. Although the cocoon of *D. candidata* is on average slightly larger the difference is not consistent and cocoons of the two microgastrines are difficult to tell apart if there is no host present. Again unlike *V. carcinae*, the host was in its final instar (often prepupal) when killed, and in this study most *D. candidata* cocoons formed in the second half of July, more than a month after those of first generation *V. carcinae*, with adult emergence at the end of July or in early August. By this time unparasitized healthy host larvae (of that generation) were no longer available. No evidence of an earlier generation of *D. candidata* on the same host generation was found (emerged cocoons in webs would have been seen), and it seems that this parasitoid simply delays killing the host until its final instar. Unlike the highly specialised *V. carcinae*, it has a wide host spectrum of medium-sized arboreal microlepidoptera including Tortricidae and Choreutidae and, with emergence peaks in June and August and considering the hosts' phenology, it is clearly at least partly plurivoltine using different hosts in its separate generations (NMS collection, unpublished). However, with respect to the slow-developing *C. quercana* it could be univoltine, ovipositing into young pre-hibernation larvae during August.

Macrocentrus thoracicus (solitary koinobiont endoparasitoid) is known from various arboreal Tortricidae (NMS collection, unpublished). It erupts from the prepupal host and has a final external feeding phase (Fig. 3) before making its brownish cocoon within that of the host. In the current work it was found in two locations, with cocoon formation at the end of July and adult emergence in mid-August, and *C. quercana* seems likely to be a frequent host.

Both *Oncophanes* species (idiobiont ectoparasitoids) are usually gregarious and parasitize a range of semi-concealed microlepidoptera larvae, most often in field-layer vegetation (NMS collection, unpublished). The adults emerged in the first half of July. Only one parasitoid cocoon resulted from the single *C. quercana* larva parasitized by *O. minutus*, probably reflecting the failure of siblings to develop. It is unlikely that *C. quercana* is an important host for them.

Diadegma sp. A (solitary koinobiont endoparasitoid). Unfortunately, all three individuals reared were male and could not be determined, although they appear to belong to a single species. They arose at two locations and emerged as adults in the second half of July, from their cocoon formed in the host's cocoon. The species appears to be a regular part of the parasitoid complex of *C. quercana*, but obviously nothing can be said about its host repertoire until it is identified. One individual has been submitted to Seraina Klopstein (Basel) for DNA sequencing.

The apterous and thelytokous *Gelis agilis* (solitary idiobiont ectoparasitoid) parasitizes a broad range of cocoons or cocoon-like hosts in low vegetation (Schwarz & Shaw 1999). The present example (Fig. 4) was from a cocooned prepupal host collected from seedling *Quercus* on 20.vi.2024, and emerged on 8.vii.2024. Its presence in the parasitoid complex of *C. quercana* is casual, and it would only parasitize the host on low vegetation.

Elachertus artaeus (gregarious ectoparasitoid) was found in only one of the three subsites. Gregarious pupae were formed in the host feeding web (Fig. 5). Adults of one brood of six had already emerged by the collection date (20.vi.2024) but the other

two broods overwintered as pupae and emerged (2♀♀ 2♂♂ and 4♀♀ 2♂♂) around 1.v.2025.

Hyssopus nigrutilus (?agg.; R.R. Askew, pers. comm.) (solitary ectoparasitoid) was already present as a single pupa in a larval web collected on 20.vi.2024 on low *Quercus*. The female emerged on 8.vii.2024.

Pseudohyperparasitism

The outcomes from the 38 concurrently collected small ichneumonoid cocoons are given in Table 2. These were hypothesised to experience similar mortality from their own parasitoids as would *V. carcinae* cocoons. Taken together, parasitism and the effects of (almost certain) host-feeding by these secondary parasitoids accounted for 58% of the cocoons collected. All three species of secondary parasitoids reared are solitary Phygadeuontinae and known niche generalists, previously reared from similar situations (Schwarz & Shaw 1999, 2000). Being idiobiont ectoparasitoids (inside the cocoon) they are probably able to parasitize ichneumonoid cocoons from the time of formation almost to adult eclosion. Therefore, the mean time after collection of the cocoons of primary parasitoids to when they emerged successfully (*i.e.*, without being found by pseudohyperparasitoids), which was eight days, becomes significant. If unparasitized, adults from these cocoons would be expected to emerge within around 10 days after cocoon formation. This indicates that they had only endured about 20% of the vulnerable period before being collected, and therefore that a substantial proportion of those that emerged successfully might have fallen to attack by their own parasitoids (pseudohyperparasitoids) had they been left in the field. Thus 58% mortality of the cocoons put down to pseudohyperparasitoid activity is almost certainly a considerable underestimate.

TABLE 2. OUTCOMES FROM 38 SOLITARY ICHNEUMONOID COCOONS SIMILARLY-SIZED TO *V. CARCINAE* COLLECTED CONCURRENTLY

	Campopleginae	Microgastrinae	<i>Aleiodes</i>
Total number	4	19	15
Already successfully emerged	0	1	2
Successfully emerged in captivity ¹	0	5	1
Unidentified secondary parasitoid already emerged	0	7	0
<i>Gelis areator</i> (Panzer)	1	2	5
<i>Acrolyta marginata</i> (Bridgman)	1	1	0
<i>Acrolyta rufocincta</i> (Gravenhorst)	0	1	1
No emergence ²	2	2	6

¹ Emerged on average 8 days after collection.

² Almost certainly dead at the time of collection and mostly or entirely due to predation ('host-feeding') by pseudohyperparasitoid adults.

Subsequent host generation

Adults of *C. quercana* started to emerge on 1.vii.2024, continuing until the end of that month. Five (out of 40) pupae died with the pharate adult incompletely developed, but inspection in August 2024 confirmed that they were already dead and not attempting to overwinter. Although both sexes of adult *C. quercana* have a proboscis, no feeding was observed on the dilute honey provided, and it was judged that none had taken place from the continually scale-free surface of the steeped cotton wool. Copulation was not observed either (possibly occurring at night-time, or

perhaps only briefly) but clearly had occurred in many tubes in which a single pair had been constrained, as fertile eggs (initially pale greenish, becoming orange-pink, Fig. 6) were laid, in cracks of the cork in the absence of another substrate. A few such tubes received only infertile eggs (remaining pale green before collapsing). Comparable numbers of fertile eggs (typically just over 100) were laid in tubes containing moths that had not been given a chance to feed and tubes in which moths were confined after some time with access to food. The first larvae hatched on 30.vii.2024, about 21 days following oviposition, and left the eggshell unconsumed. Although it proved difficult to get first instar larvae to establish, many did so on *Q. robur* and were followed until they died or ceased feeding and sought hibernation sites, at a length of about 7.5–8mm, in late September and October. Feeding was almost completely restricted to lower-surface windowing (and Lammas growth was eschewed). There was no indication of either rapid feeding or development other than to hibernation at a small size, so it seems certain that a second generation could be ruled out at least for the Harztor population in 2024.

DISCUSSION

The first question posed, concerning the abundance of *C. quercana* larvae that had been feeding on low growth seen on 3.viii.2019 (after having produced parasitoids) during previous collecting in the Hoge Veluwe (Shaw 2020), was easily answered by the heavy thunderstorm on 18 June 2024 at Harztor, after which the larvae were far more abundant on low growth than hitherto. Thus it seems safe to infer that many larvae of *C. quercana*, being highly sensitive to disturbance, must have been dislodged from canopy positions, presumably by stormy weather, well before the date (3.viii.2019) on which they, or rather the remains of their webs and parasitoids, were found so abundantly in the Hoge Veluwe on low growth where they had re-settled. A similar phenomenon has been noted in some species of *Cryptocephalus* pot-beetles (Coleoptera: Chrysomelidae) with canopy-feeding larvae that, through disturbance, progressively end up concentrated on foliage close to the ground (Sprick & Floren 2007; cf. Piper 2025). In fact, it must be commonplace for anything in the canopy that is both flightless and greets danger or disturbance with thanatosis or energetic displacement, and no doubt additional cases will have been documented.

The second question concerning survival of the ostensibly univoltine and slow-developing host population in the face of onslaught by the specialised plurivoltine *Venanides carcinae* was informed, if not answered, by two things. First, an appreciable (though unquantified) proportion of the host population at Harztor in 2024 had reached a developmental stage too advanced to be susceptible to parasitism by *V. carcinae* by the time the first cohort of the adult parasitoids emerged, many *C. quercana* having prepared their pupation cocoons by then. Thus, a proportion of the larvae that escaped parasitism pre-hibernation avoided subsequent attack from the adult *V. carcinae* emerging from the same cohort. Second, the level of pseudohyperparasitism (and other probably associated mortality), estimated from all primary parasitoid cocoons broadly similar in size and accessibility to those of *V. carcinae* collected simultaneously from the same vegetation, was high which suggested that *V. carcinae* would be facing similar parasitoid mortality in its cocoon; and experience in the Veluwe in 2019 suggested that predation by birds or more likely vespids might also be severe, at least in later *V. carcinae* generations on low growth (Shaw 2020). All of this

makes the survival of the univoltine *C. quercana* population, despite the attentions of the plurivoltine and specialist *V. carcinae*, seem less remarkable.

Although no clear answer was found for the third question, namely how come there were several late-feeding larvae of *C. quercana* in the Veluwe in 2018, enough evidence for a reasonably firm conclusion was obtained. The larval season for the host in Harztor in 2024 seemed to end in July, with adult moths arising throughout July, and subsequently in culture absolutely no tendency for a second generation was found. The Veluwe area and Harztor have very different conditions of soil, hydrology and climate (and even a different dominant species of *Quercus*, respectively *Q. robur* and *Q. petraea*) and it is not in principle inconceivable that the Veluwe population might, at times if not regularly, produce a second generation. However, a few half-grown larvae found there (by casual, untargeted, collecting) on 29.vii.2018, with adult emergence late in August but in one case pupation in September and adult emergence not until 3.x.2018, were clearly part of the same phenomenon as the presence of larvae in late September 2018, and it seems unrealistic to ascribe them to a second generation. The first adult moths from the Harztor population sampled in 2024 did not hatch until early July, and my quite intensive collecting on *Quercus* during May 2023 at Harztor (beating *Quercus*, for other Lepidoptera larvae) had revealed only very young (clearly overwintered) larvae of *C. quercana*, compatible with the timing and size found in the June 2024 cohort. While the Harztor population in 2024 is probably not a good model from which to draw conclusions about the Veluwe one of 2018, it seems clear that adult moths would be unlikely to have appeared early enough for their progeny to achieve half-growth by late July in 2018 in the Veluwe.

The clear inference from all the foregoing is that *C. quercana* is not plurivoltine, but rather that a partially very slow developing and therefore prolonged univoltine population was present in the Veluwe at least in that particular year. It may be particularly significant that there had been an abnormally hot and dry spring and early summer in the Veluwe area in 2018 (the hottest May in 300 years: Warmste mei in ruim 300 jaar!; a very hot and extremely dry June: <https://www.weeronline.nl/nieuws/weeroverzichten-2018-juni>; and minimal rainfall in an exceptionally hot July: <https://www.weeronline.nl/nieuws/weeroverzichten-2018-juli> (see also KNMI – Archief maand/seizoen/jaaroverzichten)). This clearly had the adverse effects on vegetation (including substantial leaf loss from various tree species) clearly seen on 7.vii.2018 when my wife and I passed through the Veluwe, and it seems likely that feeding activity by *C. quercana* larvae had been badly disrupted by the drought conditions. Therefore, I suggest that the occasional British sightings of adult moths into December (Sterling, Parsons & Lewington 2012; Langmaid, Palmer & Young 2018) are more likely a result of disrupted feeding than a second generation; in addition to delay caused by adverse conditions such as drought, dislodgement from feeding sites might also seriously delay growth. Larval resilience to periods of starvation would be an interesting topic for further research on *C. quercana*.

A final comment on the numerous predated Microgastrinae cocoons found in the remains of *C. quercana* webs on 3.viii.2019 in the Veluwe and illustrated by Shaw (2020) is warranted. Although *V. carcinae* appears to be the commoner microgastrine parasitoid of *C. quercana* in the Veluwe, the presumption that all of those cocoons were *V. carcinae* should not have been made, as some or perhaps many could have been *D. candidata*.

ACKNOWLEDGEMENTS

I am grateful to Dick Askew for determining the Eulophidae reared, to Jeroen Voogd for references to the abnormally hot and dry summer experienced in the Veluwe in 2018, and to Gavin Broad for his helpful review.

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