Adult behaviour in two species of cerioidine flies, *Primocerioides petri* (Hervé-Bazin) and *Ceriana japonica* (Shiraki) (Diptera Syrphidae)

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[Abstract, captions of figs all in English]

Introduction

Most adult Diptera belonging to the Syrphidae are known to be diurnal pollinators which fly to the flowers of various seed plants and feed on nectar and pollen (1, 2, 3) Many different species have black-and-yellow or black-and-orange stripes and are thought to be simulating female adult Apoidea, which are the most important pollinators and have poisonous stings and similar body stripes (4, 5, 6). A tribe of the Syrphidae, Cerioidini, which we study in this paper, has body stripes similar to none of the Apoidea, but instead simulate Eumenidae or Polistinae, both belonging to the Vespoidea, which are generally called hunter wasps. The Cerioidini includes five genera (*Ceriana* Rafinesque 1815, *Monoceromyia* Shannon 1925, *Polybiomyia* Shannon 1925, *Sphiximorpha* Rondani 1850 and *Primocerioides* Shannon 1927) and 197 recorded species worldwide, but for only 19 of which are the life-style and development times known (7).

In Japan three species of the Cerioidini are known: recent records of the capture of adult insects show that they occur in Honshū, Shikoku and Kyūshū. Observations of adult *Monoceromyia pleuralis* (Coquillett) are relatively frequent so it became clear that they visit *Quercus acutissima* and *Ulmus*, which exude tree-sap from May to September (8, 9, 10, 11). The lifestyle and life history of the other two species, *Primocerioides petri* (Hervè-Bazin) and *Ceriana japonica* (Shiraki), are not known, and so accidental encounters remain the only possibility. Until the first half of the 1990s there had been hardly any records for decades, and we only knew about them through reports of the capture of adults (11, 12, 13, 14, 15, 16, 17). However, recently there have been some fragmentary reports about their life style. The adults of *Ceriana japonica* visit the flowers of *Ligustrum obtusifolius* and *Deutzia crenata*, and one was found by Ōhara visiting the flowers of *Pyracantha coccinea* and *Elaeagnus umbellata* (Ōhara, unpublished). The adults of *Primocerioides petri* appear from March to April (18), mate, and visit *Brassica rapa* L. var. *nippo-oleifera*, *Eurya japonica* and Eupteleaceae (19).

While we were researching all the insects that feed on the tree-sap of *Quercus acutissima* and other deciduous *Quercus* spp, we discovered and confirmed that:

- (1) adult Syrphidae such as *Volucella suzukii* Matsumura and *Monoceromyia pleuralis* (Coquillett) which have been thought to be rare species and so far unknown as flower-visiting insects, were feeding on the tree-sap of these trees.
- (2) Zelkova serrata, growing naturally or planted close to Quercus acutissima, occasionally produces tree-sap from its trunk.
- (3) the two cerioidine species *Primocerioides petri* (Hervè-Bazin) and *Ceriana japonica* (Shiraki), so far thought to be rare, were flying around the sap exuding from the trees. Although fragmentarily, we researched these two species along with the study of the sap of *Quercus acutissima*.
- (4) While we were pursuing general preliminary research on flower- visiting insects, we also paid attention to whether adult Cerioidini flew to flowers because they had rarely been captured while settling on flowers.
- (5) We also researched the male flowers of *Rhus sylvestris* as part of our study.

In this paper we report the results of our research on the behaviour of adult *Primocerioides petri* and *Ceriana japonica*, with observations on the factors which influence their time of emergence, the plants on which they oviposit and their flower-visiting activities.

Study sites & Methods

Research in 1999

First we conducted preliminary research between 16:00 and 17:00 on *Quercus acutissima*, which produces tree-sap, at places near to where *Rhus sylvestris* was growing. Then we studied *Rhus sylvestris* (a male tree, circa 3 m high) growing naturally by a mountain stream (situated at 34° 13' N, 134° 12' E, 219 m above sea level) in the Asan Mountain range in Sanuki City, Kagawa Prefecture (Shikoku). The tree was already in blossom on 27 May, the date of the observations. We captured the insects using an insect net after confirming that they settled on the flowers. The weather was fine.

Research in 2005

There are eight *Zelkova serrata* trees planted close to the study site in the forest park in Ueda-chō Takamatsu City, Kagawa Prefecture, where we have been studying the activities of overwintering *Vespa* queens. Among these eight trees, the trunk of one was divided into three sub-trunks (dbh 22, 23 & 27 cm): sap was exuding significantly at a 2m-high spot on the trunk during the first ten days of April. The observation period was six fine days between 7 April and 2 May (7, 8, 15, 17, 22 April and 2 May), from 10:08

to 16:15 each day.

We observed the surface of the tree trunk up to 2.5 m high visually, recording the place where adult syrphids were settling, observing their activities and making every effort to take photographs in order to identify species and gender even if they escaped before capture. We also used photographs to record our study in 2007 and 2008. If we were unable to find any insects flying there at the beginning of the observation, we did not continue observations during that time-span. We also removed the bark which was half coming off where the sap was exuding in order to study the underneath (7 April).

Research in 2007

We studied the same spot as in 2005, but this time all eight *Zelkova serrata* (dbh 11-33 m), numbering them from 1 to 8, east to west. The tree we observed in 2005 was No. 3. The method was as in 2005, checking for adult syrphids on the surface of the trees up to 2.5 m high. The observation period was 9 days (23, 28 March; 5, 12, 19 April; 3, 14, 18, 27 May) when the weather was fine (except 18 May, cloudy), from 12:45 to 15:35. We also recorded the places where sap was exuding and the features of these spots on each tree on every observation day except 14 May.

Research in 2008

We chose a single tree (dbh 35 cm) among five *Zelkova serrata* planted by a forestry road in Nishiueda-chō, Takamatsu City, Kagawa Prefecture (34° 13' N, 134° 05' E, 158 m above sea level). On the day we started on 22 April, we found that tree-sap was exuding from two parts of the tree (14 cm downward flow from a point 2.15 m high, and 72 cm downward flow from a point 2.3 m height above ground). We observed the surface of the tree from the ground up to 2.5 m high visually, paying special attention to whether there were adult syrphids present. Observations lasted 4 days (22 April, 3, 17 and 21 May, when the days were fine), from 12:45 to 15:50.

Results

1999

When observing insects on female flowers of *Rhus sylvestris* from about 16:00 on 27 May, at 16:10 a female adult *Ceriana japonica* landed on a flower; and after that at 16:25 a male adult of the same species came and immediately landed on the flower. At 16:30 a female *Eumenes rubronotatus* Pérez flew there and landed. After that we continued observing until 17:00 but did not see any more insects. We captured these three insects when they were settling just after landing, so we knew neither the detail of their activities on the flowers nor their length of stay. Both male and female *Ceriana*

japonica resemble *Eumenes mikado* when flying or settling on flowers, and we could not distinguish them from the female *Eumenes rubronotatus* which was captured last. Apart from these adults visiting flowers, there were no more records of *Ceriana japonica* until 2008.

Fig. 1 shows the three pinned specimens captured in the above-mentioned research, left to right in order of time of capture. The female Ceriana japonica has distinctive yellow stripes while alive, but the colour became darker when dried after death so the similarity with the colour of Eumenes rubronotatus is not so clear in the dried specimens. However, both species resemble each other in having two yellow stripes on a black base from narrow long chest to abdomen, although Ceriana japonica has one more stripe at the end of its abdomen, not very clear in Fig 1. Likewise the body shapes of these two species are both narrow and long, but there is one big difference, namely the second petiole of Eumenes rubronotatus is extremely narrow like other hunting bees while that of Ceriana japonica is not narrowed. So we can hardly say that in the photo of the dorsal view of the adults the bodies look similar, but as we mentioned above they only look similar while flying. The abdomen of Ceriana japonica, which has a bow-shaped curve to its back, resembling that of a female Eumenes rubronotatus. It also looks as though there is a narrow waist at the base of the abdomen. That is why they resemble each other while flying. This is clear if you examine the photos in Fig. 2 ([a] male Ceriana japonica and [b] female Eumenes rubronotatus) taken obliquely from behind.

2005

On 7 April when we started we found one male and one female *Primocerioides petri*. The male was found at 15:20, settling on the surface of the tree within 5 cm of a sapexuding bark hole in the surface of *Zelkova serrata* (Fig. 3). At 15:44 we found a female *Primocerioides petri* walking and bending the tip of its abdomen ventrally, and then stopping occasionally to touch the tip of its abdomen onto the surface of the treebark, ovipositing. While we were observing it, it stayed near exuding tree-sap, but did not oviposit on the flowing sap.

After this, we went to see another part of the tree where sap was also exuding; we removed the bark and half came off; we found several holes full of frass probably belonging to cerambycid larvae. Right under small holes exuding sap there was a large hole exuding sap. The small holes were full of frass, but the large one connected to the place where sap was exuding had hardly any frass. The tree-sap was very fluid, flowing down like water, and clearly different from the resin or gum which solidified after flowing.

We found two male Primocerioides petri at 14:40 on 8 April and at 13:33 on

15 April. Both insects were settling on the surface of the bark around the spot where the tree-sap was exuding. We observed one on 8 April for 10 minutes, but it was stationary, neither walking nor flying. There was also a female of the same species ovipositing on the bark within 5 cm but in a different place, where the tree-sap was exuding, at 13:33 on 15 April (Fig 4); and another at 15:12 on 17 April. The ovipositing activities of both female adults were the same as that found on 7 April. We did not confirm any more insects coming to the tree trunk, although tree-sap was exuding at 10:08 and 14:35 on 22 April, and at 14:10 and 15:40 on 2 May.

2007

Although we increased the number of Zelkova serrata observed to eight, and studied them intermittently from late March to late May, we only found one male Primocerioides petri. This male was on tree #8, settling on the surface of the trunk within 10 cm of one of four places where tree-sap was exuding, at 15:33 on 12 April (Fig. 5). It flew away at 15:35, stopped on the trunk at a height of more than 4 m and settled, but at 15:50 it had disappeared. We found one female Ceriana japonica on both 14 and 18 May on tree #3 tree where both male and female Primocerioides petri had been seen for the first time in 2005. Both flew away while we were observing so we could not capture them, but from photos and also from the specimen collected in 1999, we identified them as Ceriana japonica. The female found at 12:53 on 14 May was ovipositing on the surface of the bark within 5 cm of a place where sap had been exuding (confirmed on 3 May) but dry at the time. Likewise the female found at 12:57 on 18 May was also ovipositing on the tree bark, within 10 cm of a place where tree-sap had been exuding (confirmed on 3 May) but dry at the time (Fig 6). All these females were walking, bending their abdomen forward, stopping occasionally to oviposit. Their behaviour resembled that of the female *Primocerioides petri*.

Among the eight *Zelkova serrata* trees studied from 23 March to 27 May, we confirmed that tree-sap was exuding from the trunks of four (nos. 3, 6, 7 and 8), half of those studied. Sap was exuding (from two parts) from only one (#3) on 23 March, but on 28 March all four trees were producing sap from a total of 11 spots. (3 on #3, 2 on #6, 2 on #7 and 4 on #8). After that the sap was exuding continuously. On 3 May one more spot was added those of #6. On 14 May four spots (2 on #3, 1 on #6 and 1 on #7) and then on 27 May three spots (1 on #3 and 2 on #8) stopped exuding sap. Thus the total number of places from which tree-sap was exuding was five on 17 May.

We confirmed a common feature of the 12 spots where tree-sap was exuding, i.e. sap exuded from a small round hole which penetrated the bark (Fig. 7). The size of the holes of 11 spots (except one on #8, where the bark was torn and deformed) was a maximum of 3.1 ± 0.9 mm (mean \pm sd, n = 11) vertically and 2.7 ± 0.6 mm

horizontally. On #7 (found on 28 March) we could not see any small holes at the time of confirmation, but saw a pile of frass on the bark at first which when removed revealed the small round hole where sap was exuding as on the other trees.

2008

We could not see any insects when we started at 15:04 on 22 April. Then one came and stopped on the trunk surface within 10 cm of tree-sap (flowing from a 230-cm high point) at 15:09. It looked as if it belonged to a genus of hunting wasps. However, from the photo we took at the time and from the specimen caught in 2005, we identified this adult as a female *Primocerioides petri*. After stopping on the tree, she started walking, bending her abdomen forward, occasionally touching the tip of the abdomen onto the surface of the tree bark and ovipositing (Fig. 8). It crossed over the flowing tree-sap but did not oviposit in it, but after crossing over, started ovipositing again on the dry surface of the bark around the flowing tree-sap. After repeating these oviposition activities, it flew away at 15: 35. We saw no other insects and finished observation at 15:50.

We renewed observation for 15 minutes at 15:15 on 3 May, 15:15 on 17 May and 14:45 on 21 May, but only found an adult *Agriosphodrus dohrni* (Signoret) [Reduviidae] moving on the surface of the tree trunk.

Discussion

The cerioidines Ceriana japonica and Primocerioides petri are both very rare species. There were few records of the capture of the adult insects and their life history was almost unknown. By 1997 Ceriana japonica was known from Honshū, Shikoku and Kyūshū in Japan. Primocerioides petri was recorded as a new species in 1914, and after that there were only three records from Honshū (8). The related European species Ceriana vespiformis is widespread around the Mediterranean coast but its life-style is almost unknown, and there is a report of its larva found accidentally during comprehensive field research. As a result of our fieldwork it became clear for the first time that females of both Ceriana japonica and Primocerioides petri show oviposition behaviour on the bark of trees where sap exudes. If we consider that so far cerioidine larvae elsewhere have been found occasionally in treeholes or in tree-sap (18, 21, 22, 23), we can presume that after eclosing from eggs laid on the surface of the tree, the unknown larvae of these two species enter the sapping holes and develop in the tree-sap under the bark. In addition, our fieldwork showed that females of another Japanese cerioidine, Monoceromyia pleuralis (Coquillett), also oviposit on the surface of trees around where sap exudes, and hence their larvae live in sapping holes and also where rainwater gathers (Ichikawa et al, unpublished). From the fact that each Japanese

species belongs to a different genus, and that foreign cerioidine larvae were collected from holes in trees, we can presume that the life-history of Cerioidini is greatly dependent on tree-sap.

At the places where tree-sap exudes we recognised small 3-mm holes; on removing the bark around the holes in 2005, we found narrow paths leading to other small holes that we presumed were made by the larvae of Cerambycidae. Moreover, in 2007 we observed that, although only in one single hole, minute powdery frass was accumulated. This frass was produced by cermabycid larvae which perforate the tree and occasionally live there. According to Kojima & Nakamura (24), there are 47 species in four sub-families of Cerambycidae in Japan which penetrate Zelkova serrata and damage them from their feeding. It is also known that among these, 41 live in Shikoku (25). From this circumstantial evidence and the bibliographical record, it is highly possible that the tree-sap exuding from Zelkova serrata is from vessels and sieve tubes damaged by cerambycid larvae chewing under the bark. However, we found the abovementioned frass in only one single small hole among the 12 holes from which we confirmed exuding sap. Moreover, the colour of the frass was greyish, so it is unlikely that it was just discharged and fresh. The time when unidentified species of borers penetrated the bark and made the small holes was not winter, since these insects are inactive and hide until late March, the time when we started our research. It is highly likely that the hole was made during the previous year when they were active. The reason why we could not find the frass in the other eleven holes was probably that it was dispersed by the weather during the inactive period when there was no supply of new frass. As Zelkova serrata is deciduous, it is probably inactive from late autumn when it becomes dormant until early spring in the following year, and during that period even if the vessels and sieve tubes are damaged there is no possibility of repairing them. In late March 2007 the leaves of Zelkova serrata were developing. The places where sap exuded increased rapidly between 23 to 28 March, perhaps because water absorbed by the root and carried upwards escaped from the damaged as-yet-unrepaired vessels. It is plausible that the period when the unidentified borers make the holes is after the autumn when Zelkova serrata becomes dormant and its vessels cannot be mended. We need more research in order to clarify this.

Generally speaking it is difficult for animals to enter inside healthy trees because of the tough bark on the surfaces of the trunk and branches. In the case of trees which produce resin or gum from damaged bark that gradually solidifies, even if the bark is damaged it is difficult especially for small insects to enter the tree unless they use some strong countermeasures. In contrast, the small holes in *Zelkova serrata* producing highly fluid sap are perfect entrances for small larvae of *Primocerioides petri* and *Ceriana japonica* which have just hatched and cannot withstand dry conditions.

Thus the unidentified borers are essential for the survival and development larvae of *Primocerioides petri* and *Ceriana japonica*. The fact that the small sapping holes were all the same size means that it is highly possible that they belong to a single species. In order to be more specific we need to do further research.

Maier & Waldbauer (26, 27) studied male waiting behaviour, closely related to male mating behaviour in two syrphids, *Mallota posticata* and *Somula decora*. The males of these two species were settling for many hours around the tree hollows where the conspecific females oviposit. In addition to waiting to mate with visiting females, the waiting behaviour implies the maintenance of a territory against invasion by rival males of the same and other species. There were some cases when these males took other conspecific males for females and flew up to try to mate; in the case of male *M. posticata* there were incidents of chasing leaves blown by the wind, taking them for females. This means their eyesight is poor. It seems that their low ability of visual recognition expanded their territorial competition to competition among species. Maier & Waldbauer also studied the activities of 23 other species of Syrphidae, amongst which were male *Ceriana abbreviata* congeneric with *Ceriana japonica*. These males chased away flying males belonging to different as well as the same species.

In our research we clarified that *Ceriana japonica* and *Primocerioides petri* use the same spot, around sap-exuding parts of *Zelkova serrata*, for ovipositing, and we observed several times that males of the latter species were settling around the oviposition places. We cannot be completely sure as we did not observe individuals flying nearby, but it is possible that they were waiting for mating and keeping territory, as Maier & Waldbauer observed in the males of several syrphid species including Cerioidini.

From previous insect collections, records and this study, it became clear that the time of adult emergence of *Primocerioides petri* and *Ceriana japonica* rarely overlap. That is to say, according to past records the time when adult *Primocerioides petri* have been observed and captured is from early March to early May (10, 12, 13, 14, 16, 17, 18 19), while that of *Ceriana japonica* is mid- to late-May (10,15). Our data on the oviposition activities of both species on the same tree agrees with this, that is to say adult emergence of *Primocerioides petri* throughout April, and of *Ceriana japonica* in mid- to late-May. The primary cause of the difference in emergence times before and after mid-May between two different species can be attributed to several causes, such as abiotic environmental factors like weather, and biological factors such as food resources, natural enemies and the existence of competing species; thus we cannot specify at the moment. However, the fact that these two species living in the same place use the space close to exuding sap of *Zelkova serrata* for oviposition, and males of many syrphids including cerioidines show territorial activities defending oviposition

sites for hours against not only conspecific but also allospecific males, gives us relevant clues. If we assume the males of both *Primocerioides petri* and *Ceriana japonica* defend their territories as in other syrphids, inferior competitor species cannot oviposit in the same place at the same time as a superior competitor species. According to Darwin's widely accepted principle of competitive exclusion (28, 29), the ovipositing time of inferior species could have changed in the past because of severe competition between two species.

These two species indigenous to Japan, which live in the same place as the unidentified boring insects which make the small holes in *Zelkova serrata*, and so create desirable places for oviposition for both species, do not seem to have been introduced recently to Japan, so if there were such competition, we presume that it was not what we see at present, but a long time ago back in the geological era.

We think that both Primocerioides petri and Ceriana japonica can also use Quercus acutissima, which grows in the same places as Zelkova serrata and also produces sap. We looked at this tree this time as the ovipositing place of both insects, but there were no records that the adults came to sapping Quercus acutissima, nor was there any extensive study in the past. We have never found either species on Quercus acutissima in our research. From May to October the cerioidines observed on Quercus acutissima were all Monoceromyia pleuralis (Ichikawa et al, unpublished); males of which stayed for long hours during the day on the bark surface, the oviposition sites for females being around sapping spots. If approached by conspecific males they attacked the intruders and chased them away. This species is the largest of the three cerioidines, and considering its aggressiveness we presume that Ceriana japonica and Primocerioides petri are unable to use sapping Quercus acutissima because they lose the battle over sites for oviposition and nourishment. It is well known that many insects, including Trypoxilus dichotomus [Japanese Rhinoceros Beetle], Lucanidae [Stag Beetles] and Sasakia charonda [Japanese Emperor butterfly] use the sap of Quercus acutissima. As for the diversity of insects which feed off tree-sap, there exists a research record by Yoshimoto (30). However, many different insects attracted to the sap of Zelkova serrata have not been recorded before. On this account and the fact that our present research failed to find insects which feed on the sap, the nutritional value of Zelkova serrata may be lower than that of Quercus acutissima. At the moment we think it possible that the sap of Zelkova serrata is xylem sap, which does not have enough sugar to power the high demands of insect flight. Assuming that Primocerioides petri and Ceriana japonica became inferior in past competition among cerioidines, perhaps this explains why they now feed on Zelkova serrata sap, which, even though its nutritional value is low, constantly exudes from early spring.

Among the three cerioidines of Japan, it is known that adult *Primocerioides* petri visit Brassica rapa L. var. nippo-oleifera, Eurya japonica and Eupteleaceae (19) and Ceriana japonica visit Ligustrum obtusifolius (8), Deutzia crenata (10), Pyracantha coccinea and Elaeagnus umbellata. Here we also discovered that Ceriana japonica visit male Rhus sylvestris. Thus these two species use flowers as nutritional resources just like other syrphids. The individuals of both Primocerioides petri and Ceriana japonica found around exuding sap of Zelkova serrata did not show any feeding activity at all, proving that their main food was flowers, not tree-sap.

On the other hand, flower-visiting activities of *Monoceromyia pleuralis*, whose emergence period is much longer and number of individuals much larger compared with the other two species, have not been observed at all until now. So far, adult Monoceromyia pleuralis have been found at sapping trees of Quercus acutissima and Ulmus, and their feeding activities occasionally observed. We confirmed feeding activities in both male and female Monoceromyia pleuralis on the trunks of Quercus acutissima (Ichikawa et al., unpublished). Thus the adults of this species mainly feed on tree-sap, not flowers. As noted above, Monoceromyia pleuralis uses the highly nutritious sap of Quercus acutissima and does not have to depend on anything other than sap for food during the season; and it does not visit flowers (even though a syrphid). On the other hand, *Primocerioides petri* and *Ceriana japonica*, which use the sap of Zelkova serrata of lower nutritional value, cannot flourish without the nectar and pollen of flowers. We suppose that the nutritional value of Quercus acutissima is high from the life-style of the adults of Volucella suzukii Matsumura. So far the flowervisiting activities and the adult life of these insects have neither been observed nor at all known. However, our recent research has shown that they have a unique lifestyle: the adults use the tree-sap of *Quercus acutissima* for 15 minutes at most, just after sunset. (20). If Volucella suzukii and Monoceromyia pleuralis do not visit flowers, the ingredients of the sieve-tube sap must contain other vital nutrition in addition to sucrose in its ingredients. There was a fragmentary record that adult syrphids feeding on Quercus acutissima sap were thought to be only diurnal, but Volucella suzukii uses this tree in twilight after the diurnal *Monoceromyia pleuralis* have flown away, suggesting their lives are separated in time according to the competitive exclusion principle.

We do not think it is possible that our fragmentary research can lead to a satisfactory conclusion. However, although we do not know much about the life of the Syrphidae, we have been able to surmise that competition among species that share oviposition sites and food has a great influence on the timing of their activity, choice of oviposition site and flower-visiting behaviour. We may understand syrphid life-histories better by conducting more detailed research in the future.

Summary

Most cerioidines are rarely found, and their adult lives and larval sites have been described in only a few of the nearly 200 species. The three Japanese species are *Monoceromyia pleuralis* (Coquillett), *Primocerioides petri* (Hervè-Bazin) and *Ceriana japonica* (Shiraki). We carried out fieldwork on the adult behaviour of *Primocerioides petri* and *Ceriana japonica* in the daytime of fine days between 1999 and 2008 at Takamatsu City and Sanuki City in Kagawa Prefecture. We found adult *Primocerioides petri* on the tree trunks of *Zelkova serrata* between early and late April in 2005, 2007 and 2008. The four males were settling individually on the trunk near sap-exuding bark holes (approx. 3 mm diameter); and females were also individually remaining near sapexuding bark holes and walking with their abdomen tips extended ventrally, sometimes stopping and ovipositing. Two *Ceriana japonica* (one male and one female) were found on the flowers of the same male tree of *Rhus sylvestris* in late May. Two female *Ceriana japonica* were also found on *Zelkova serrata* trunks in the middle of May, 2007. These females were walking and ovipositing around the holes from which sap had stopped exuding for less than 15 days, behaviour similar to that of *Primocerioides petri*.

In this paper we have addressed possible factors affecting the emergence periods, selection of oviposition sites and flower visits of the two cerioidine species, with special reference to interspecific competition.

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