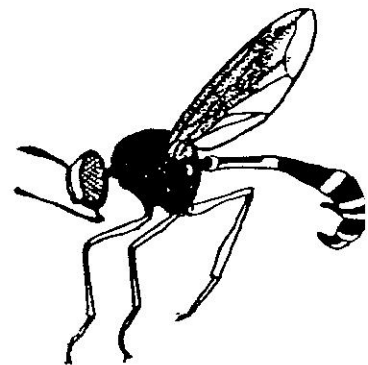


Conopid Recording Scheme

INCORPORATING THE LONCHOPTERIDAE STUDY GROUP



Newsletter No.5

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Professional duties and the birth of a second son in 1993 have, along with all the other everyday trials human flesh is heir to, conspired to keep your intrepid conopid recorder out of circulation for longer than is decent. Nevertheless, there is much to report, and I can only apologize (like all the other times, I know) for keeping it from you. What can I say? I'm sorry. Here it is. Enjoy!

Zodion notatum – Some observations on Manx specimens

Steve Crellin

On 27 May 1990, I was collecting at the western end of Glen Mooar near the village of Glen Maye on the Isle of Man. The glen runs east to west with tree-covered valley sides, and is drained by a stream flowing westwards towards the Irish sea. I was studying an area of dry mud that is the nesting site for the solitary bee *Halictus rubicundus* (Christ), when a small grey fly landed on my leg. I was fortunate enough to net the specimen, which Dave Clements subsequently confirmed to be *Zodion notatum* Meigen.

On 30 May the following year I swept another female from a low-growing willow at the edge of the mud area, close to the stream, and later a male from streamside vegetation nearby. However, it wasn't until early June 1992 that I finally discovered the species to be present in good numbers, when I captured a further male and two females. One of the females was captured as it attacked a female *H. rubicundus* at the nest site. At this time I also observed different specimens on the flowers of *Ranunculus* sp and cat's-ear (*Hypochoeris radicata*). They did not appear to be feeding, but rather waiting in ambush either for mates or hosts. The flies would sit facing outwards on the end of a petal, where they would shuffle about and rotate their heads to and fro. No successful ambushes from flowers were observed, but sometimes the flies would dart after what were evidently perceived to be suitable targets. Such targets often included other flies such as syrphids and large calypterates.

As mentioned above, one successful attack was observed and the participants captured. The female *Zodion* was first noticed on the ground amongst the nest burrows of *H. rubicundus*, acting in a manner similar to those observed earlier on the flowers. Eventually a female *H. rubicundus* returned to the nesting area, and was immediately attacked by the *Zodion* female, a few inches above the ground, where they were netted for identification.

My specimens show some variation in the coloration of the antennae and also in their overall size. My smallest specimen, a male, has entirely black antennae. The others have varying degrees of orange coloration ventrally at the apex of the second and base of the third antennal segments, contrasting with the black remainder. The first segment is always dark in coloration.

[Steve's finding of this rare (RDB 3) species is very exciting. *Z. notatum* has only otherwise been recorded four times since 1960, from sites in Wales and southern England. An association with *Halictus* has long been supposed, the somewhat commoner *Z. cinereum* having been reared from both *Halictus* and *Hylaeus*. I have also seen a specimen which I considered likely to be *Z. notatum* taken from the Isle of Man by Eileen Thorpe, although crucially this specimen had lost its antennae, so I could not be absolutely certain. This was a largish specimen, but within the size range of *Z. notatum* found by Steve.]

Observations of Conops behaviour in Kent

Eric Philp

On 7 September 1991 in Randall Wood, Shorne (TQ 6870) in West Kent, I noticed a large number (at least 40) of the large tachinid fly *Tachina fera* (L), sitting on the flowers of a large clump of water mint (*Menta aquatica*). Also present were small numbers of both *Conops ceriaeformis* Meigen and *C. quadrifasciatus* Degeer.

On most occasions when the tachinid flies took off they would be 'attacked' by a *Conops*, in much the same way as they might attack a bumblebee. Whether these were actual egg-laying attempts or whether the conopids were simply being attracted to 'bumblebee-sized' insects in general I am not sure. I now regret not taking a sample of the *Tachina* to see if eggs had actually been laid, either deliberately or in error. Although Diptera have not been recorded as hosts for any conopid species to date, there is always just a chance, so further observation would certainly be of interest.

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[There have been suggestions elsewhere in the literature that hosts other than Hymenopterans might be used by conopids in other countries, particularly Orthopterans. The non-British Stylogasterine subfamily uses a range of insect orders as hosts, but these may not be particularly closely related to the rest of the Conopidae, perhaps being better placed in a separate family.]

The taxonomy, biology and distribution of conopids in Japan.

Yasuo Maeta and Rod Macfarlane have now published results from their studies on Japanese conopids, referred to in earlier newsletters. The paper (Maeta and Macfarlane, 1993) indicates that the similarity between the Japanese fauna and that of Europe is far closer than had originally been thought. Of the 25 species now recorded only two or three are considered to be confined to Japan, with at least 10 (perhaps 12) of the remainder being synonymous with British species. The paper goes on to investigate the distribution, seasonal activity, flower-visiting preferences and hosts of Japanese conopids, and the percentage incidence of conopid parasitism in foraging bumblebees.

Five species of conopids were reared from 10 species of bee, and in all cases a single conopid pupa was found to fully occupy the abdomen of the host. Amongst these, *Zodion cinereum* was reared from *Andrena prostomias*, *Myopa buccata* was reared from *Andrena japonica* and *Physocephala obscura* (probably synonymous with *P. rufipes*) was reared from two species of *Bombus*.

Parasitism percentages in foraging worker bumblebees were found to vary at between 9–33%, and to decline as the season progresses, mirroring the decline of captured adult conopids. This level of parasitism is in accord with other studies elsewhere in the world, and the study also agrees with others in suggesting that bumblebee species which show lower percentage incidence of parasitism tend to be those which have more specialised flower-visiting habits. Parasitism of males and queens occurred at much lower frequencies than workers.

The authors consider that all of the Japanese species of *Sicus*, *Thecophora* and *Physocephala*, together with *Zodion cinereum*, *Conops flavipes* and *C. santaroi*, have two or more generations per year in Japan. Adult conopids were found to live only a few days (up to a week), and the egg and larval stages were found to last no more than 2–3 weeks, indicating long periods spent as pupae in many of the species studied. Hosts containing conopids were found to die within about 14–20 days from oviposition, representing about a halving of the usual life expectancy for the host. The reported levels of parasitism and life expectancy reductions must have a considerable impact on the foraging effectiveness and survivorship of host colonies.

Maeta, Y & Macfarlane, R P (1993): Japanese Conopidae (Diptera): their biology, overall distribution, and role as parasites of bumble bees (Hymenoptera, Apidae). *Japanese Journal of Entomology* 61: 493–509.

Studies on conopid biology – the work of the Schmid–Hemple group at the University of Basel.

In 1991, a *New Scientist* article brought the work of Paul and Regula Schmid–Hemple and their colleagues at Basel University to my attention. Since about 1988, this group has been carrying out some fundamental work on the biology of conopids as parasites of bumblebees, investigating their impact on bee foraging efficiency, behaviour and physiology. A recent summary of the work carried out by this group was given by Müller (1994).

The first paper to emerge appears to have been that of Schmid–Hemple and Schmid–Hemple (1988). This reported that, in common with the few other studies which had been done previously, investigation of bumblebee populations at two sites in Switzerland suggested parasitism rates by conopids averaged 20–30% of workers and 5–10% of males – far higher than the incidence of adult conopids in the field would suggest. Statistical analysis suggested that the actual attack rate must be even higher than this, since the parasitism rates observed were based on successful development and emergence of conopids, whilst it was obvious that some conopids did not develop and, in a few cases, more than one egg was laid into the same host ('superparasitism'). In the latter case only one larva ultimately develops. The majority of the conopids responsible were believed to be *Sicus* and *Physocephala*, infesting 5 different species of *Bombus*. Given the fatal consequences of parasitism by conopids, which cause death of the host within about 10 days of oviposition, the paper goes on to speculate that conopids must play a significant role in reducing the foraging efficiency of bumblebee colonies in the field, by substantially reducing the life expectancy of infested hosts.

This early work was then backed up by a larger study reported by Schmid–Hemple *et al* (1989). This was based on a total sample of 1740 bumblebees (*Bombus*) and cuckoo-bees (*Psithyrus*) taken at three sites in Switzerland, and confirmed once again the high incidence of conopid parasitism, to an observed maximum of 46% in the peak summer period. The

study was carried out through the period April to October, and the species responsible were once again primarily *Sicus* and *Physocephala*, identified as *S ferrugineus*, *P rufipes* and *P vittata* respectively. Both genera of bees were affected.

Parasitism by *Sicus* was more prevalent during spring, affecting the vernal bee species such as *Bombus terrestris* and *B hortorum*. Parasitism by *Physocephala* peaks in the later summer months, therefore affecting chiefly the non-vernal, long-cycle bees such as *B pascuorum* and *B lapidarius*. The probability of parasitism was found to be significantly affected by certain factors (eg species of host, sex of host and site), but unaffected by others (eg size of host, density of foraging hosts).

Schmid-Hempel and Schmid-Hempel (1989) investigated the phenomenon of superparasitism further, finding that multiple oviposition by conopids occurs regularly although only one conopid emerges per host. The successful larva apparently out-competes its rivals by consuming the host more rapidly. When parasite densities are very high there is a tendency for overall conopid emergence levels to decline, probably because superparasitism occurs at such high frequency that it reduces the chances of any larvae successfully developing at all. This mechanism probably assists in regulating parasite numbers – at one site, during one week, 74% of the foraging bees sampled were found to contain conopid larvae!

A fundamentally important finding then emerged, as reported by Schmid-Hempel and Schmid-Hempel (1990). This indicated for the first time that flower-choice by foraging bumblebees may be altered by the presence of a conopid larva. This study concentrated on the foraging behaviour of *Bombus pascuorum* in the field, a long-tongued bumblebee which is capable of collecting nectar from flowers with deep or short corollas. The study indicated that bees which were later found by dissection to contain larvae of either *S ferrugineus* or *P rufipes* were actively choosing to forage from betony (*Betonica officinalis*), which has a short corolla, whereas unparasitized bees showed no preference between this plant and large self-heal (*Prunella grandiflora*), which has a much deeper corolla. Factors such as age and size of bee were eliminated. The authors suggest that the presence of a conopid endoparasite causes stress on the host bee, which subsequently concentrates its foraging effort on short-corolla flowers which are easier to obtain nectar from and require less handling-time.

These aspects of conopid/bumblebee ecology were further investigated by Schmid-Hempel and Müller (1991), using *Bombus lucorum* in the field. Worker bees in colonies of this species gain most of their 'reproductive fitness' indirectly, by assisting the queen to rear her young (with which they share a high proportion of genes), rather than attempting to rear their own young independently. The authors looked at parasitism incidence in workers which were observed actively entering and leaving colonies ('colony foragers'), in comparison with workers of unknown origin taken from amongst the general foraging population out in the field ('field foragers'), and they found that the former showed significantly lower levels of infestation by conopids. This was supported by examination of workers taken directly from bee colonies at night, when all the members of the colony should be 'at home'. They concluded that, for some reason, infested workers avoid returning to the colony and instead spend most of their time in the field, night-time included. Why should this be? The authors were unable to suggest which might benefit most from this change in behaviour, the host or the parasite, but suggest that it might be the conopid, since the parasite will have to pupate

and overwinter wherever the bee eventually dies. Since the comb is abandoned by the bees in the autumn, and quickly becomes infected by bacteria and fungi as it decays, it might be an advantage to the conopid to ensure that the host dies outside the colony, far away from the potentially lethal pathogens of the decaying comb.

Interestingly, a subsequent investigation by Müller and Schmid-Hempel (1993) suggests that the reverse may be true, and that staying outside the colony at night is a mechanism employed by the host bee against the conopid larva inside it. Parasitized workers of *Bombus terrestris* were shown not only to stay outside the colony at night, but also to actively seek out cold sites to roost in. The reason for this appears to be that such behaviour delays the development of the conopid larvae, and may even prevent it from pupating successfully before the end of the bee's natural lifespan. By staying outside the colony at night, the parasitized bee appears to be employing a strategy designed to prolong its lifespan, and thus the length of time in which it can assist in rearing the colony offspring to which it is related.

Meanwhile, a study by Schmid-Hempel and Durrer (1991) investigated the possible impact of conopid infestation levels on bumblebee ecology, particularly the timing of reproductive stages (ie production of males and queens). Factors such as colony growth, time of appearance of male bees, duration of male emergence, numbers of males and ratio with workers were measured for selected colonies of *Bombus pascuorum*, *B. terrestris* and *B. lucorum*. In addition to parasitism by conopids (*S. ferrugineus* and *P. rufipes*), other environmental factors such as flower availability and resource demand were also measured. It was found that the timing of reproduction in particular appears to be affected by the rate of parasitism by *S. ferrugineus* and *P. rufipes*, causing a delay in reproductive onset in *terrestris* and *lucorum* and an advancement in *pascuorum*. This suggests that infestations by conopids may have a significant impact on reproductive behaviour in bumblebees, although other factors (especially flower availability) are also acknowledged to be important.

Müller and Schmid-Hempel (1992) also examined the reproductive ecology of artificially reared colonies of *Bombus lucorum*, in response to parasitism both by conopids and cuckoo-bees (*Psithyrus* spp). Previous studies have shown that bee colonies founded early in the season have a tendency to greater reproductive success later in the season, when queens and males are produced. This wide-ranging study indicated, amongst other things, that *Psithyrus* has an especially significant effect early in the season, attacking early-founded colonies and reducing their reproductive success. Parasitism by conopids, on the other hand, appears to have its greatest effect later in the season, causing high worker mortality. This again reduces reproductive success, with the production of underweight queens and males and/or a tendency to produce few or no queens at all.

Finally, a paper in press by Müller describes how conopid parasitism in *B. terrestris* apparently influences the final site which the host bee dies in. Bees containing parasites were found to die far more frequently in underground situations, rather than on the soil surface, a situation which significantly enhances the likelihood of the parasite overwintering and emerging successfully. It appears that the mature conopid larva causes the bee to actively dig itself into the soil before dying. Further experiments showed that conopids in buried hosts (as opposed to hosts on the soil surface) emerged in better condition, were less prone to being attacked by hyperparasitoids and less likely to be eaten by scavengers such as mice.

I am grateful to Dr Christine Müller for providing me with copies of the above papers and for keeping me up to date with the progress of this research.

Müller, C (1994): Behavioural changes in parasitized bumblebees: who is in control, host or parasitoid? *Antenna* 18: 62–70.

Müller, C (in press): Parasitoid induced digging behaviour in bumblebee workers. *Animal Behaviour*.

Müller, C & Schmid-Hempel, P (1992): Correlates of reproductive success among field colonies of *Bombus lucorum*: the importance of growth and parasites. *Ecological Entomology* 17: 343–353.

Müller, C & Schmid-Hempel, P (1993): Exploitation of cold temperature as defence against parasitoids in bumblebees. *Nature* 363: 65–66.

Schmid-Hempel, P & Durrer, S (1991): Parasites, floral resources and reproduction in natural populations of bumblebees. *Oikos* 62: 342–350.

Schmid-Hempel, P, Müller, C, Schmid-Hempel, R & Shykoff, J A (1990): Frequency and ecological correlates of parasitism by conopid flies (Diptera, Conopidae) in populations of bumblebees. *Insectes Sociaux* 37: 14–30.

Schmid-Hempel, R & Müller, C (1991): Do parasitized bumblebees forage for their colony? *Animal Behaviour* 41: 910–912.

Schmid-Hempel, P & Schmid-Hempel, R (1988): Parasitic flies (Conopidae, Diptera) may be important stress factors for the ergonomics of their bumblebee hosts. *Ecological Entomology* 13: 469–472.

Schmid-Hempel, P & Schmid-Hempel, R (1989): Superparasitism and larval competition in conopid flies (Dipt., Conopidae), parasitizing bumblebees (Hym., Apidae). *Mitteilungen der Schweizerischen Entomologischen Gesellschaft* 62: 279–289.

Schmid-Hempel, P & Schmid-Hempel, R (1990): Endoparasitic larvae of conopid flies alter pollination behaviour of bumblebees. *Naturwissenschaften* 77: 450–452.

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Meanwhile, I am plodding on with revisionary keys to British and Western European conopids, concentrating on *Myopa*. I now have the British *Myopa* sorted, but have feebly failed to find time to prepare the necessary figures for the paper. Male *Sicus* remains a problem, and as for *Thecophora*...! In the meantime, I am still willing to look at conopids from Britain and Europe. Keep 'em coming.

UK Conopid Recording Scheme

David Clements, 1 Quarry Close, Stratton, Cirencester, Glos GL7 2JN.