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Biology of the parasitic wasp nest beetle, Metoecus paradoxus (Coleoptera: Ripiphoridae), in Finland

Atte Komonen

Komonen, A., Department of Biological and Environmental Science, P.O. Box 35, FI-40014 University of Jyväskylä, Finland. atte.komonen @j yu.fi

Parasitoids and predators can cause marked mortality in their host species. I studied the occurrence, abundance, and biology of the wasp nest beetle *Metoecus paradoxus* (Ripiphoridae), inhabiting the nests of the common wasp *Vespula vulgaris* (Vespidae) in Central Finland. I also compiled phenological data of the species in Finland. The proportion of parasitized nests was 80%. The abundance of the beetle was generally some tens of individuals (max. = 130) per nest, and the parasitism rate 1–18% of the sealed cells, which are typical for the species in temperate Europe. The beetle occurred in several combs but was absent or rare in the oldest and newest combs. Sex ratio was female biased. Females were larger than males, and individuals from large cells were larger than from small cells. Adult beetles were observed rather steadily from early August to late September. The study shows that *M. paradoxus* is a common inhabitant of *V. vulgaris* nests in Central Finland, but due to a low frequency of parasitized cells its impact on wasp populations is likely to be minor.

Introduction

Parasitoids and predators can cause marked mortality in their host species and even regulate population dynamics. The abundance of social wasps, i.e. yellow jackets and hornets (Vespinae), is known to fluctuate yearly (Akre & Reed 1981, Pawlikowski & Pawlikowski 2006, Sorvari 2013, Lester et al. 2017). The cause of this fluctuation is unknown, but it has been hypothesised to result from weather, food availability, competition for nest sites, and parasitoids and predators. To assess the possible role of parasitism in vespine fluctuations, the occurrence and abundance of parasitoids, as well as their biology, must be documented.

Parasitic life-style is rare among Coleoptera, and in Finland endoparasitic species are only found within Ripiphoridae (formerly Rhipiphoridae): *Pelecotoma fennica* (Paykull) parasitizes Anobiidae (Coleoptera) (Svácha 1994), *Ripidius quadriceps* (Abeille de Perrin) cockroaches (Blattodea) (Batelka et al. 2021), and *Metoecus paradoxus* (L.) (Fig. 1) several social wasp species, particularly the common wasp *Vespula vulgaris* (L.) (Heitmans & Peeters 1996). To my knowledge, *M. paradoxus*, the wasp nest beetle, has only been recorded from *V. vulgaris* nests in Finland. It seems that the Finnish distribution of the wasp nest beetle has expanded northwards. In 2002, the northernmost known observation was from Ta: Tuulos (Biström & Rassi 2002), whereas currently the northernmost observation is from Obo: Oulu (Finnish Biodiversity Info Facility, laji.fi; accessed 5 October 2022).

After emergence from wasp nests in the autumn, the wasp nest beetles mate and lay eggs in crevices of living and dead trees (Chapman

Figure 1. Female *Metoecus paradoxus* has just emerged from the *Vespula vulgaris* nest in Kylmänoro. Photo: Petri Kuhno.

1891). To my knowledge, however, the evidence for this is only based on observations of captive beetles (Chapman 1891), and oviposition has not been observed in nature (Svácha 1994). Thus, the possibility that mated females overwinter and lay eggs in the spring cannot be overruled. Ovipositing in the spring would make it possible to lay eggs in those trees that are regularly visited by wasps, which would increase the chance that the triungulin larvae are carried to the nests. In any case, the 1st instar triungulin larvae attach themselves to wasps that are scraping wood for pulp, and are then carried to the nest. The 1st instar larva is an endoparasitoid, becoming an ectoparasitoid when the wasp larvae close the cell mouth and pupate (Hattori & Yamane 1975). After consuming the host, the beetle pupates in the closed wasp cell, emerges, and crawls out from the nest, typically from August to October.

The frequency of occurrence of *Metoecus paradoxus* in wasp nests has been studied with a large sample size only on few occasions, but the studies indicate that it can be as high as 67% (Spradbery 1973). In an occupied nest, the beetle is rarely numerous, usually numbering in tens (Heitmans & Peeters 1996). Yet, occasionally the proportion of sealed brood parasitized can be as high as 42% (*Vespula flaviceps*; Matsuura & Yamane 1990). This suggests that *M. paradoxus* could have a marked negative impact on colony development in some cases.

Literature on *M. paradoxus* consists mostly of observations on the occurrence, abundance and distribution of the species (but see Hattori & Yamane 1975, Van Oystaeyen et al. 2015). Most studies are from temperate regions, and I am not aware of any studies from the boreal region. Here I report the occurrence, abundance, parasitism rate, sex ratio, and body size of *M. paradoxus* in *V. vulgaris* colonies in Central Finland, and the phenology of the species in Finland, based on examined nest material, direct observations, and a museum database.

Materials and methods

Sampling

The data are based on eight parasitized *Vespula vulgaris* nests ($n_{examined}$ = 10) in Central Finland in 2020–2022 (Table 1), which belongs to the middle boreal zone. Four nests (Kylmänoro, Viitakangas 1, Keljo and Köhniö) were removed intact, so that it was possible to count the number of cells separately for each comb. All nests were put in a freezer after extraction. All nests were underground nests, except Virrat, Keljo and Köhniö, which were in human constructions. Kylmänoro nest was monitored irregularly for a month and excavated after the wasp activity ceased. Other nests were still active when removed, although Keljo was practically ceased, i.e. no adults but

Table 1. Characteristics of the *Vespula vulgaris* nests parasitized by *Metoecus paradoxus* in Central Finland; number of individuals, proportion of parasitized cells and sex ratio.

Nest	Removed	# cells (sealed)	*M. paradoxus*	Parasitism %*	Males	Females	Sex ratio
Kylmänoro	23.9.2020	1711 (0)	38	2	11	27	0.41
Viitakangas 1	15.9.2020	7260 (1937)	130	7	12	32	0.38
Viitakangas 2	15.9.2020	n.a. (251)	37	11	6	31	0.19
Pukara	6.8.2021	5076 (2381)	17	1	5	8	0.63
Virrat	4.9.2020	n.a. (1070)	26	2	4	6	0.67
Palokka	5.9.2022	n.a.	22	n.a.	8	14	0.57
Keljo	18.9.2022	337 (79)	7	9	2	4	0.50
Köhniö	26.9.2022	835 (17)	3	18	n.a.	n.a.	n.a.

* Percent parasitized sealed cells, except in Kylmänoro where parasitism is the number of adults divided by the total number of cells. n.a. = the nest was destroyed so it was impossible to count cells, or only pupae were recorded. The sum of males and females may differ from the total number of individuals, because it was not possible to determine the sex of pupae.

a few living pupae inside sealed cells. All nests were mature, i.e. they had produced males or queens, except Köhniö with only worker vells. Nest material was examined for *M. paradoxus* adults, and all sealed cells were opened to find *M. paradoxus* pupae or adults, except in Palokka. The total number of sealed wasp cells with and without *M. paradoxus* was counted.

Measurements

Parasitism was generally measured as the number of parasitized sealed cells divided by the total number of sealed cells, which can give an over- or underestimate. Only sealed cells were included because the parasitism by *Metoecus* is difficult or impossible to detect reliably after the individual has left the wasp nest. In Kylmänoro, parasitism was measured as the observed number of *Metoecus* divided by the total number of cells, which is surely an underestimate. For each adult *M. paradoxus*, the sex was determined.

Body length from the forehead to the tip of abdomen was measured with an electronic caliper with 0.01 mm accuracy; only fully pigmented individuals were measured. In two nests, the size of wasp cells was evaluated dichotomously either as large or small, which in these two nests happened to be quite clear; in one nest it was possible to distinguish the median-sized cells. Although male wasps can develop in large cells, all the individuals from the vicinity of the *M. paradoxus* from large cells were queens, whereas individuals from small cells were surrounded by male cells.

Phenology

I compiled data on the observation dates of *Metoecus paradoxus* by sex from the Finnish Biodiversity Info Facility (laji.fi; accessed 5 October 2022), Martikainen (2020) and my own data (Table 1). The species is easy to identify, so the observations in laji.fi can be considered reliable; many observations included photos, which confirmed the identification. Dates were divided in six periods: July, four 15-day periods starting from August 1, and September 30 onwards. If only time period, rather than the exact date, was available, I divided the individual between the two periods (0.5 and 0.5); if the observation period covered three time periods it was excluded (n = 2). If many individuals were reported from the same site from the same date, these were considered as one observation. Thus, the phenology included 78 observations, of which 91% were from the 21st century.

Statistics

The *Metoecus paradoxus* adults recorded from the sealed wasp cells allowed to analyse the relationship between *M. paradoxus* body size and cell size, which reflects resource quantity. Because only two males were recorded from large cells, the difference between females from large (n = 11) and small (n = 13) cells, and difference between females (n = 13) and males (n = 12) from small cells were analysed separately with one-way t-tests. One-way test was chosen, because individuals from the large cells are expected to be larger than those from the small cells (Heitmans & Peeters 1996). Because Levene's test indicated equality of variances ($F = 0.001$, $p = 0.98$, $df = 22$, and $F = 0.098$, $p = 76$, $df = 23$), t-test with equal variance assumption was conducted.

Results

Eight out of ten *Vespula vulgaris* nests were parasitized by *Metoecus paradoxus*. The beetle was recorded from large and small wasp cells, and from different combs, but was absent or very rare in the basal and outermost comb (Fig. 2). The parasitism rate was 1–18% in the sealed cells. Sex ratio was female-biased. The nest-specific male:female ratio varied from 0.19–0.67 (Table 1), and in the Finnish Biodiversity Info Facility database, the male:female ratio was 0.90 (n = 95; nests in Table 1 are not included).

Metoecus paradoxus females were larger than males, and individuals of both sexes were larger in large wasp cells (Viitakangas 1 nest; Fig. 3). Females from the large cells were an average 2.03 mm longer than from the small cells ($t = 4.51$, $df = 22$, $p < 0.001$). Females from the small cells were an average 0.97 mm longer than males from the small cells ($t = 2.05$, $df = 23$, $p < 0.026$). Only two males were recorded from the large cells, and their body length was between that of females and males from small cells. In Viitakangas 2 nest, the average size of females from the median-sized cells was 11.8 mm (n = 3) and that of females from large cells 15.3 mm (n = 10). In Virrat nest, all *M. paradoxus* were from small cells. The average size of females was 11.6 mm (n = 5) and that of males 10.6 mm (n = 4).

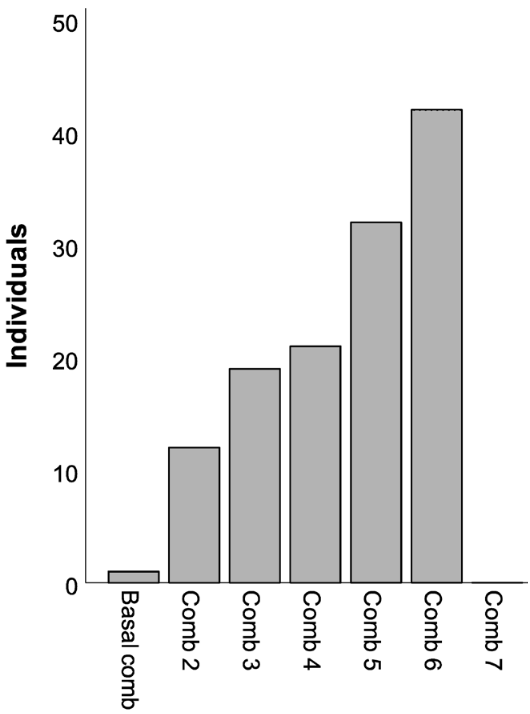

Figure 2. The number of *Metoecus paradoxus* in different combs in Viitakangas 1 nest (7 combs, of which 5, 6 and 7 contained only large cells).

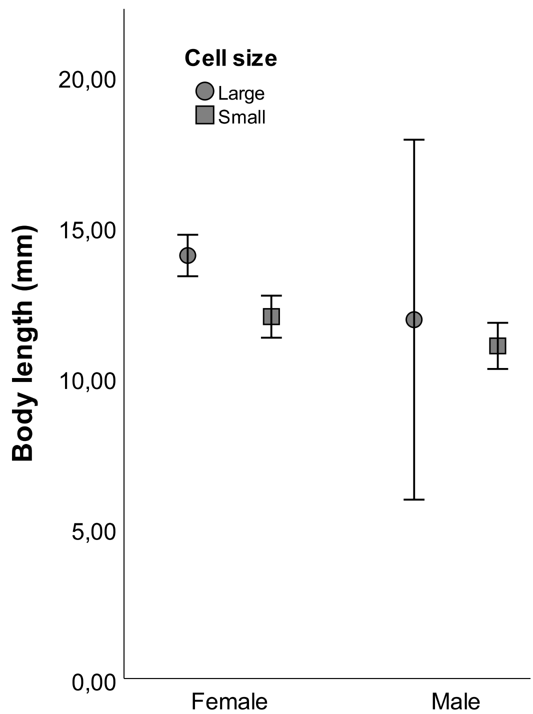

Figure 3. The mean (± 95% CI) body length of female and male *Metoecus paradoxus* from large and small cells in Viitakangas 1 nest. Only two males from the large cells were recorded, hence the wide CI.

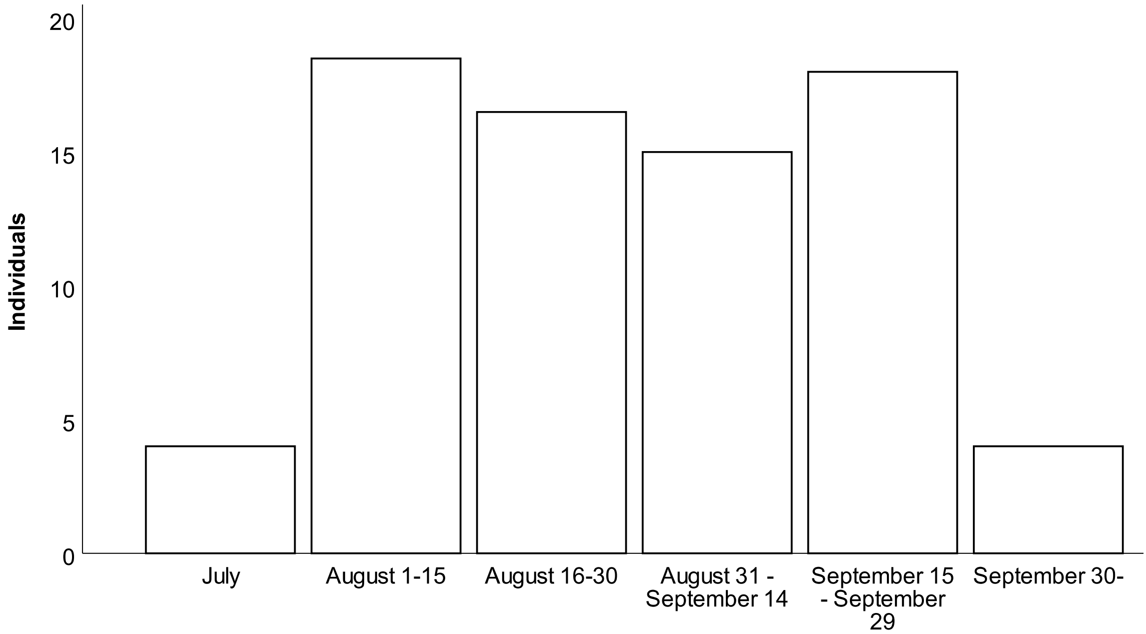

Figure 4. Phenology of *Metoecus paradoxus* in Finland, based on the observations (n = 78) in the Finnish Biodiversity Info Facility.

Metoecus paradoxus has been recorded rather steadily from early August to late September (Fig. 4). The earliest observation is July 21 and the latest October 26. 62% of males (n = 21) and 46% of females (n = 28) were observed in July or August. In Kylmänoro, the first individual was observed on August 18 (the first day of monitoring) and the last September 15 (n = 38 individuals). Individuals were seen emerging from the nest during daytime between 10:32 and 14:16. Of the 17 individuals that were seen to emerge from the nest, eleven flew away directly and six stayed on nearby vegetation up to an hour.

Discussion

Overall, 80% of the inspected *Vespula vulgaris* nests were parasitized by *Metoecus paradoxus*. In other studies, with much larger sample size, the frequency of parasitized nests was 21%, 66% and 67% (Tuck 1897 cited in Heitmans & Peeters 1996, Spradbery 1973, Van Oystaeyen et al. 2015). However, the observed frequency of parasitized nests could be too low, because of false absences that are due to difficulty in detecting parasitism in broken nests or in large nests with very few parasitoids, especially since the 1st instar larva is an endoparasitoid. Yet, one can conclude that parasitism by *M. paradoxus* is common and the species parasitises *V. vulgaris* nests both underground and in buildings (see also Heitmans & Peeters 1996).

The nest-specific rate of parasitism was rather low (1–18%), which corroborates previous studies (Heitmans & Peeters 1996). It is typical to find a few or some tens of individuals in a *Vespula* nest (Tuck 1897 cited in Heitmans & Peeters 1996, Crawley 1905, Hattori & Yamane 1975, Svácha 1994, Heitmans & Peeters 1996, Van Oystaeyen et al. 2015), but also over a hundred beetles have been occasionally counted (Reichert 1914 cited in Heitmans & Peeters 1996, this study). Consequently, also the infestation of sealed brood varies from 3% percent (*V. vulgaris*; Potter 1964) to 42% (*V. flaviceps*; Hattori & Yamane 1975). The parasitism rate calculated based on the parasitized sealed cells could be an over- or underestimate of the true parasitism rate. The most reliable but laborious way to document the true parasitism rate would be to monitor the nest for a couple of months, document all emerging *M. para-*

doxus, excavate the nest, and count the total number of cells.

Metoecus paradoxus were recorded from several combs, both from large and small cells. The basal- and outermost combs had no or very few parasitized cells. This is rational because the likelihood that the triungulin larvae are carried to the nest increases with worker numbers, and the basal cells can be empty in later stages of colony development. Similarly, the outermost comb is probably too new that the triungulin larvae would have surveyed outside the nest so long (see Heitmans & Peeters 1996). The results also confirm previous studies in that females are larger than males and that size of the host larval (queen vs. workers and males) affects the size of *M. paradoxus* (Hattori & Yamane 1975, Van Oystaeyen 2015). There was also some indication that the individuals tend to emerge a few hours before and after noon, but proving this would require full-day monitoring. Some emerging individuals took off immediately, whereas others tended to stay for up to an hour or even longer in the vegetation near the nest entrance before taking off (see also Svácha 1994).

Metoecus was observed rather evenly from the early August to late September, which corroborates previous studies (Heitmans & Peeters 1996). Because the beetle is generally observed outside the wasp nest from which they have emerged, the observations reveal not only the flight time, but also the timing of emergence. The long emergence period is not only due to the spatial variation in environmental conditions and colony development, because in Kylmänoro, which was monitored for a month, the difference between the first and last individuals was about a month. Similar nest-specific observations have been reported earlier (Langeveld 1992, cited in Heitmans & Peeters 1996). Neither the previous studies nor this study can answer, if there is yearly variation in *Metoecus* phenology or abundance.

Sex ratio was female biased, but less so than in Van Oystaeyen et al. (2015). In general, ectoparasitic insects have equal or female-biased sex ratio, which is partly due to the shorter life span of males (Marshall 1981). Because sex ratio was determined based on individuals inside a nest or emerging, longevity does not influence the observed sex ratio. Furthermore, in insects males often emerge earlier, which could bias the observed sex ratio, if the nests are removed at later developmental stages. Indeed, we found some indication that males emerge earlier than females, but due to a small sample size this conclusion is not definitive. Furthermore, the variation in the emergence times is more likely to result from variation in the timing of the triungulin larvae entering the nest, rather than sex. Yet, it is clear that a given wasp nest produces both male and female *Metoecus* throughout the autumn. The large variation in the emergence times supports the idea that the triungulin larvae are carried to the nests by wasps (Heitmans & Peeters 1996).

The number of *Metoecus paradoxus* observations has increased, and the range has expanded northwards, in Finland during past decades. This study shows that the parasitism rate of *M. paradoxus* in *V. vulgaris* nests in the boreal zone is like that in the temperate zone. The study also provides new insights about the sex ratio, comb-specific parasitism, and phenology of the species. It seems unlikely that the species could cause yearly fluctuations of *V. vulgaris*.

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