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The socially parasitic ants of the *Tetramorium caespitum/impurum* complex: an overview of the observations in Belgium (Hymenoptera: Formicidae)

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Abstract

Anergates atratulus (Schenck, 1852) and *Strongylognathus testaceus* (Schenck, 1852) are the only two parasitic ant species in Belgium to be found in the nests of their host *Tetramorium* spp. Parasitic species are increasingly less common than their hosts and their status is therefore often represented as vulnerable, endangered, or critically endangered. The two parasitic species we will discuss here also belong to this classification. The data at our disposal have enabled us to present a better picture for the current situation in Belgium. Additionally, some aspects of the biology of these parasites have been highlighted.

Keywords: parasitic ants, Formicidae, *Strongylognathus testaceus*, *Anergates atratulus*

Samenvatting

In België huisvest de gastheer *Tetramorium* spp. slechts twee parasitaire miersoorten: *Anergates atratulus* (Schenck, 1852) en *Strongylognathus testaceus* (Schenck, 1852). Een parasitaire soort is steeds minder algemeen dan de gastheer waarbij de status als kwetsbaar, bedreigd of ernstig bedreigd wordt omschreven. Ook de twee soorten die wij hier zullen bespreken, komen in aanmerking voor deze classificatie. De gegevens waarover wij beschikken, laten ons toe deze situatie voor België te beoordelen. Bovendien kunnen met deze data sommige aspecten van hun biologie worden toegelicht.

Résumé

En Belgique, on ne trouve que deux fourmis parasites dans les nids de *Tetramorium* spp.: *Anergates atratulus* (Schenck, 1852) et *Strongylognathus testaceus* (Schenck, 1852). Une espèce parasite est toujours moins commune que son hôte et son statut de conservation est dès lors souvent vulnérable, en danger ou en danger critique. Les deux espèces parasites qui font l'objet de cette discussion ont également ce statut. Les données à notre disposition permettent de se faire une meilleure idée de la situation en Belgique, et nous mettons en lumière certains aspects de la biologie de ces parasites.

Introduction

With a very few exceptions the distribution of both parasitic species *Anergates atratulus* and *Strongylognathus testaeus* seems to be restricted to the northern part of Belgium. Jean Bondroit is the only source from the beginning of the twentieth century we can consult on the presence of these species. In his first publication (BONDROIT, 1910) a single gyne of *S. testaceus* is

indicated for the village Rosières but without specification. Genval is mentioned in his second publication (BONDROIT, 1918). Rosières and Genval (Wallonia region) are neighbouring municipalities and as for none of the two locations there is a specimen available in Bondroit's collection at the Royal Belgian Institute of Natural Sciences, we conclude that it concerns one and the same observation. Bondroit additionally mentions that *A. atratulus* was not yet observed in Belgium at that time. The first observation of *A. atratulus* was made by Jos Van Brabant on 19th July 1958 in Genk where he found a nest with three functional queens (VAN BOVEN, 1977). In the southern part of Belgium, the first observation was made in September 1974 by Jacques M. Pasteels in a quarry near Marchin (Huy) (VAN BOVEN, 1977). With only two more records in Wallonia, Visé (BOER *et al*., 2006) and Ampsin (Philippe Wegnez 26th July 2009) we can claim that both, *A. atratulus* and *S. testaceus* are very rare in the south of Belgium. For the sake of completeness however, we must not overlook the observation on 21st August 2017 in the municipality Trazegnies (province Hainaut) where two nests of *A. atratulus* were found at 125 metres from each other. At both sites, about 50 winged females and at one site 2 males were counted (WEGNEZ & IGNACE, 2018). This observation offers us important information about the number of sexuals that may be present in a single nest.

There are several host species within the genus *Tetramorium* Mayr that live in a forced symbiosis with both *S. testaceus* and *A. atratulus*. The available data for *S. testaceus* within the distribution area of Belgium, mainly mention *T. caespitum* (Linnaeus, 1758) and *T. impurum* (Foerster, 1850) as the host. However, the Palaearctic range of host species can be supplemented by *T. moravicum* Kratochvil, 1941, *T. ferox* Ruzsky, 1903 and *T. brevicorne* Bondroit, 1918 after observation in Italy (SANETRA *et al*., 1994, 1999). Except in nests of *T. caespitum* and *T. impurum*, the workerless parasite *A. atratulus* has been found in nests of *T. chefketi* Forel, 1911, *T. diomedium* and *T. moravicum* Kratochvil, 1941 (SANETRA & BUSCHINGER, 2000; LAPEVA-GJONOVA *et al*., 2012).

The potential hosts for Belgium are limited to *T. caespitum* and *T. impurum*. Most of our data are the result of long-term surveys using mainly pitfall traps and the observation from those series show a simultaneous presence of *T. caespitum* in the sites where the two parasitic species were detected. However also *T. impurum* is a dominant species in certain regions in Flanders (loamy soils and some calcareous grasslands), and therefore we will refer only to *Tetramorium* spp. as the host in Belgium.

Observations in Belgium

The analysis presented in this paper is based on the data entered in the Belgian database FORMIDABEL (BROSENS *et al*., 2013). As there are no specimens available for the data mentioned in the literature, we will notice these records as observations. Most of the records in the database were collected during field surveys where various trapping techniques were used, such as light traps, window traps and especially pitfall traps. These techniques, often applied during long-term surveys, allow us to better estimate the richness of ant diversity and ant distribution over time and inform us on the activity of the sexuals. It should be emphasized that the long-term investigations were mainly limited to Flanders and that most of the areas surveyed correspond to sandy xerothermous habitats, characteristic of the large heathland situated predominantly in north-eastern Belgium and to a lesser extent the dune vegetation on the coast.

The observed absence or rarity of both *A. atratulus* and *S. testaceus* in Wallonia cannot be associated with the occupancy of the host species since the latter are commonly present (DEKONINCK *et al*., 2012). In the south of Belgium, ants' nests were searched for during excursions, but were not always intensively checked for parasites. Only three long-term studies have been performed in Wallonia. During a study in Visé, 23 different ant species were

collected with pitfall traps between the end of June and the end of October, and it is here that a single female of *A. atratulus* was found (Table 1) (BOER *et al*., 2006). In another survey using pitfall traps, 26 different ant species were captured in 2003 from April to October (DEKONINCK *et al*., 2010). Finally, 30 different species were collected in Viroinval by pitfall trapping between September 2002 and October 2003 (DEKONINCK *et al*., 2007). Although the presence of both *T. impurum* and *T. caespitum* was demonstrated during these last two studies, the two parasitic ant species were not observed. In order to form a picture of the lifestyle and periods of the nuptial flight of both *A. atratulus* and *S. testaceus*, we are therefore mainly dependent on the data from Flanders.

Table 1. List of sites where long-term studies have been conducted with the number of individuals of *Anergates atratulus* and *Strongylognathus testaceus* captured with various trapping techniques. The time interval usually ran from early spring to late autumn, with a few exceptions. * Two more alate gynes were captured with a light trap respectively in 2012 and 2014.

municipality	toponym	year	*Anergates atratulus*		*Strongylognathus testaceus*		
			males	females	workers	males	females
Adinkerke	Cabourduinen	2006	-	1	-	-	-
Balen	Keiheuvel	2014	-	3	3	-	13
Balen	Keiheuvel	2018	-	-	2	6	3
Dessel	NIRAS	2008	-	-	-	-	3
Genk	highway E314	1999	-	1	1	-	-
Hasselt	sod roofs	2020	-	1	-	-	-
Hechtel	Kamert	2003	-	-	1	-	7
Hechtel-Eksel	Pijnven	2020*	-	-	-	9	7
Houthalen	Tenhaagdoornheide	1999	-	-	-	-	5
Houthalen	Tenhaagdoornheide	2020	5	32	-	-	8
Kalmthout	Kalmthoutseheide	2005	-	3	1	-	35
Kalmthout	Zoom	2017	-	3	6	-	13
Lanklaar	Teutelberg	2010	-	-	-	-	23
Lombardsijde	dunes	2010	-	1	-	-	-
Lommel	Balimheide	2018	-	-	-	-	3
Maasmechelen	FRC	2017	-	-	-	-	1
Maasmechelen	FRC	2020	-	4	-	-	-
Meeuwen-Gruitrode	Monnikswijer	2012	-	2	-	-	-
Meeuwen-Gruitrode	Oudsberg	2000	-	1	-	-	2
Neerpelt	Hageven	2000	-	3	-	-	2
Oostmalle	airport	2005	-	-	-	-	40
Oostmalle	airport	2008	-	2	3	8	12
Oostmalle	Bruulbergen	2005	-	-	1	-	34
Opglabbeek	Zwarte berg	2019	-	-	-	-	2
Postel		2016	-	2	-	-	-
Visé	Thier de Lanaye	2005	-	1	-	-	-
Zonhoven	highway E314	1999	-	-	1	-	3
Zonhoven	Teut	1999	-	1	3	-	2
Zonhoven	Teut	2000	-	2	-	-	9
Zonhoven	Teut	2020	-	3	-	-	6

Anergates atratulus (Schenck, 1852)

Anergates Forel, 1874 is a monotypic genus with *A. atratulus* as the only species and as the genus name indicates, this parasitic ant has no workers of its own.

Native in the Palaearctic region, its range extends from Great Britain in the west to Central Siberia in the east. Travelling with the settlers, this species has managed to establish itself in the north-east of the United States where a single specimen was described in 1934 by William Creighton as *Anergates friedlandi* sp. nov., later referred to as a synonym of *Anergates atratulus* (CREIGHTON, 1934; 1950) (Fig. 1). Despite this extensive range, this parasite is in no case common.

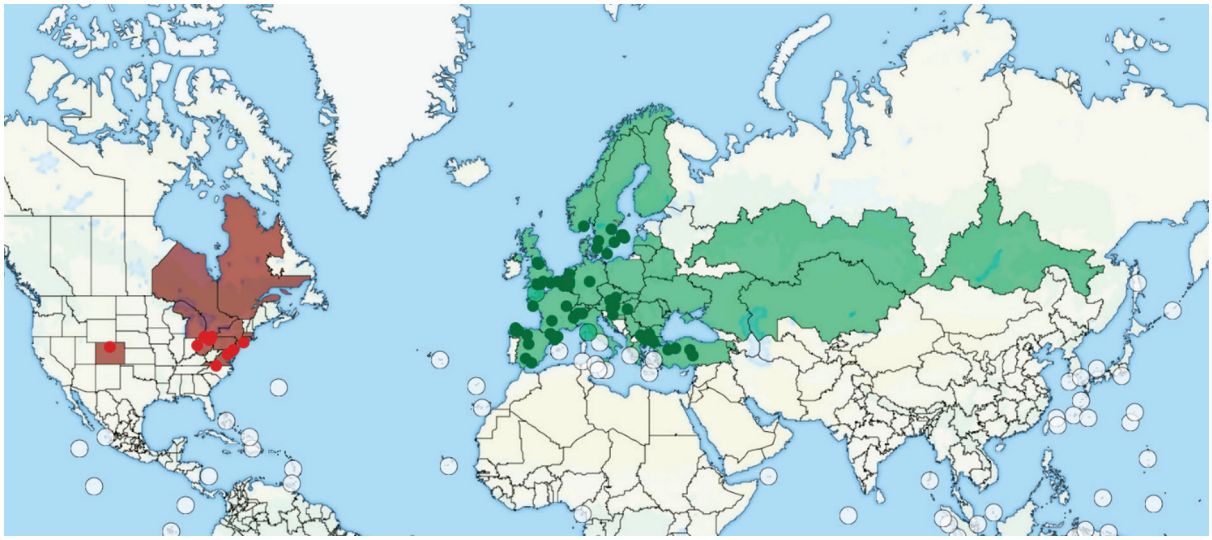

Fig. 1. Worldwide distribution of *Anergates atratulus* (Schenck, 1852); green = native, brown = exotic - © antmaps.org

Whereas the number of males produced by the host species *Tetramorium* spp. is much higher than the number of queens (ratio 0.14; VAN BOVEN, 1977), *A. atratulus* is characterised by a ratio whereby many more females are produced than males. In several examined samples, the sex ratio of this parasitic species was found to be between 0.67 and 0.98 (HEINZE *et al*., 2007). Also, in the nest that was examined in Trazegnies, where 50 females were counted and only 2 males, the sex ratio was set at 0.96 (WEGNEZ & IGNACE, 2018).
Before mating, the female's gaster shows a clear depression that runs across all segments. Once a female has been fertilized and succeeds in entering and taking over a host nest, the gaster swells enormously. From that moment on, this queen will produce as many males and females as possible that will later mate among themselves in the nest (SEIFERT, 2018).
This ant has no typical nuptial flight with males and females finding each other in a flight outside the nest. Mating occurs on the ground, mainly in the nest and results in the dispersion of the fertilized gynes looking for an improved site for the foundation of a new colony. The males of *A. atratulus* conduct intranidal mating with their own sisters (adelphogamy). The males are wingless, not very mobile, giving the impression that they have not reached full maturity (Fig. 2). But on the contrary, they have highly developed gonads and in their pupoidal form they copulate with multiple females, barely 24 hours after hatching. This reproductive behaviour does not allow males to be observed outside the nest, especially as their inhibited development means they are barely able to move around (FRANCOEUR & PILON, 2011). It was therefore surprising to find 1 and 4 males respectively in a pitfall trap during a survey in 2020 at Tenhaagdoornheide in Houthalen on two different dates. However, this does not appear to be a unique finding since, during an observation of a nest in Canada in August/September 2007, a dozen males were observed outside the nest (Fig. 2). Here it was found that the males were carried outside by the workers of the host species *Tetramorium caespitum*, and barely moved away from the place where they were deposited (FRANCOEUR & PILON, 2011).

Distribution and outdoors activity of sexuals of *Anergates atratulus*

In our database currently 87 specimens of *A. atratulus* are listed which were effectively collected during several projects. Of these, 52 are dealate females, 28 alate females and 7 males (all specimens from long-term studies and other samplings). With a few nest observations and 3 historical references to the literature (VAN BOVEN, 1977), we will note 29 squares of 1x1 km in which *A. atratulus* was observed (Fig. 3).

Fig. 2. Pupoidal male of *Anergates atratulus* observed outside the nest. © Claude Pilon

Besides the observations in the literature and during field trips, we collected 1 individual with a window trap, 1 specimen with a colour trap and 69 with pitfall traps.

To link the activity of the sexuals to a possible nuptial flight with dispersal of the gynes, only the observations obtained with trapped specimens (pitfall traps, colour traps, window traps i.e., out of the nest) were included. Bernhard Seifert (SEIFERT, 2018) reports two periods in the year when new sexuals are present in the nest: a period from April 30th to July 6th and a period from July 22nd to September 16th. With an interval of a fortnight these periods strongly lean against each other, from which we may conclude that males and females can be found in the nest from early spring to the end of summer. From our observations, we find that from April 10th to October 14th females are found outside of the nest, which virtually excludes a typical short period of nuptial flight (Fig. 4). Except for the capture of a single alate female on the 6th of September 2010 (Lombardsijde) all the alate gynes are noticed during summer between May 13th and August 4th. Before and after this period, only dealated gynes were found outside the nests.

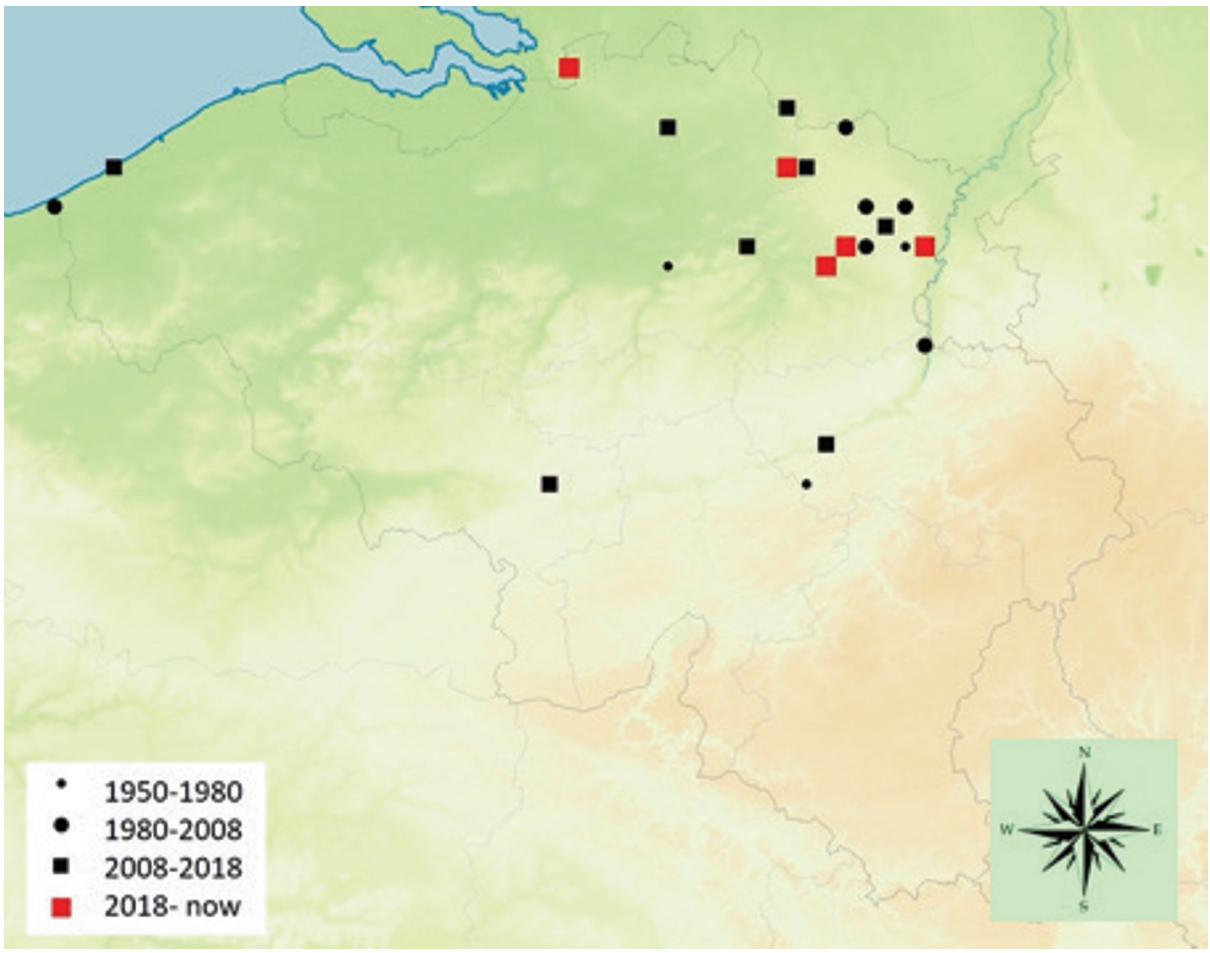

Fig. 3. Locations with the presence of *Anergates atratulus* displayed within UTM grids of 5 x 5 km in Belgium.

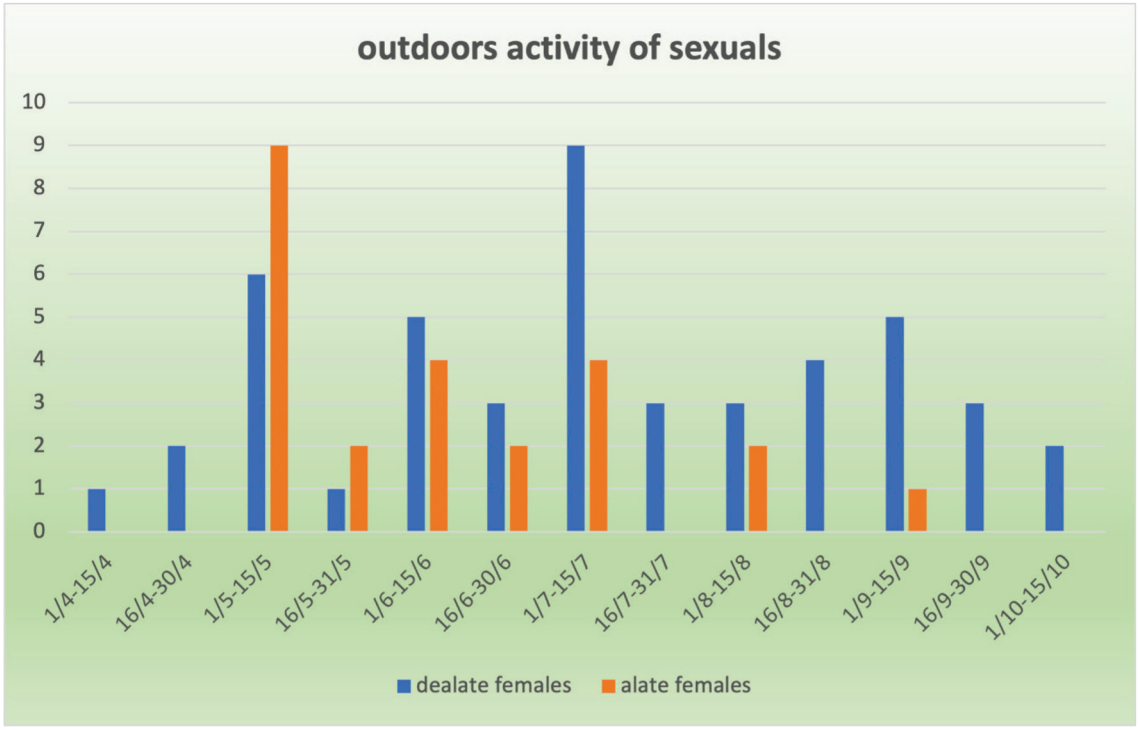

Fig. 4. Presence of females (alate and dealate) outside the nest. Observations of at least one female of *Anergates atratulus* outside the nest were used.

***Strongylognathus testaceus* (Schenck 1852)**

The pair of pointed falcate mandibles of *S. testaceus* (Fig. 5) call to mind comparisons with the dulotic *Polyergus rufescens* (Latreille, 1798), which supplement their potential for slaves with regular raids. Other species of the genus *Strongylognathus* are known to undertake raids as well.
August Forel reports on a raid by *S. huberi* Forel, 1874 workers that he observed in the Canton of Valais (Swiss Confederation) on the 23rd of June 1871 (FOREL, 1874). The fact that it is not always easy to determine predatory behaviour in nature is endorsed by *S. alpinus* Wheeler, 1909. There are indications that this *Strongylognathus* spp. also undertakes raids to neighboring nests of *Tetramorium* spp., but this dulotic parasite would forage underground at night, using existing corridors (KUTTER, 1969).

Fig. 5. Lateral and frontal view of a dry mounted specimen of *Strongylonathus testaceus*. © M. Borowiec

However, at the foundation of a new colony of *S. testaceus*, a fertilised female enters the host's nest and coerces the foreign workers to adopt her as queen. In this way of founding, the queen of the host is left alive and continues to replenish the potential of her own workers but at the same time ceases to produce sexuals of her own kind. From this point of view, there is no need for the prospective workers of this parasitic ant to carry out raids on other nests. The sickle-shaped jaws, which gives them the ability to conduct raids, can be seen here as a rudiment of an abandoned behaviour. Taking care for the colony, nest construction and foraging, is carried out by the workers of the host species (KUTTER, 1969).

Comparing the universal range of the two parasitic species we are discussing here, we find that they overlap, with a few exceptions (Figs 1, 6). Since they both use the same host, this is an expected pattern and the difference in coverage is probably due to the intensity of research. The colonisation of the United States leaves two options open. Unlike *A. atratulus*, *S. testaceus* has not yet been imported or the latter is also present but has not yet been observed.
After the first mention in 1910 of the presence in Belgium (Rosières, Wallonia), the first observations of *S. testaceus* in Flanders were made by Jos Van Brabant in the oriental part of Flanders: Diest, Dilsen, Engsbergen, Koersel, Overpelt and Rothem (VAN BOVEN, 1977).

Distribution and outdoors activity of sexuals of *Strongylognathus testaceus*

We entered 329 specimens of *S. testaceus* in our database divided over 60 squares of 1x1 km: 37 workers, 235 dealate females, 34 alate females and 23 males (all specimens from long-term studies and other samplings). Besides the records from literature and field observations, 18 specimens were collected with a light trap (Hechtel-Eksel, Pijnven – Table 1), 1 individual captured with a window trap, and an overwhelming quantity of 285 specimens collected by

pitfall traps. The distribution map (Fig. 7) indicates that their presence is mainly confined to the large heathland areas of north-eastern Belgium. As is the case for the Palaearctic region, here too we see an overlap with *A. atratulus*.

Fig. 6. Palaearctic distribution of *Strongylognathus testaceus*. - © antmaps.org

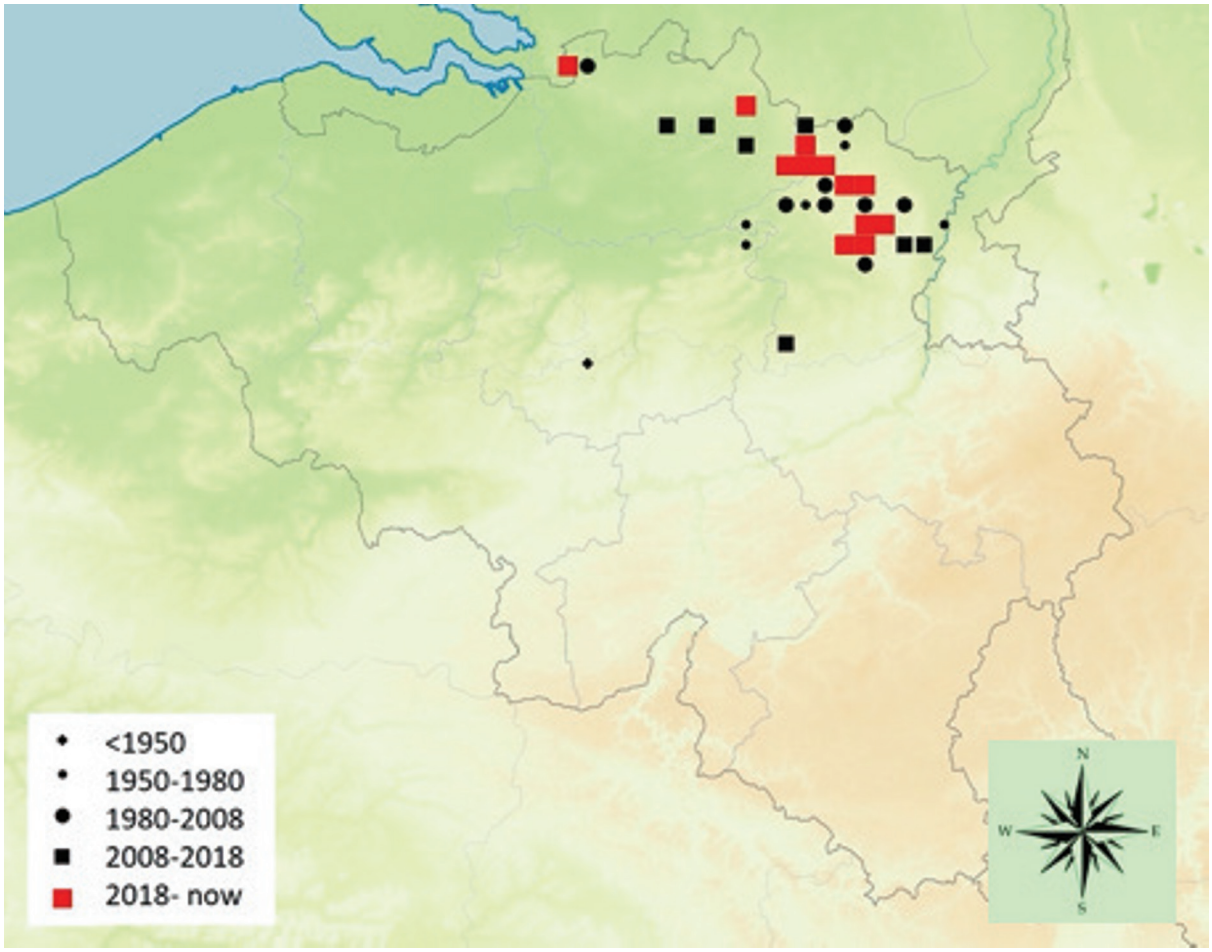

Fig. 7 Locations with the presence of *Strongylognathus testaceus* displayed within UTM grids of 5 x 5 km in Belgium.

Collecting females and males with pitfall traps allows us to show the most favourable period of the nuptial flight of ants. In compiling the data to give us an impression of the sexual activity of this parasite, we have not included four dates which were way out of range. They relate to sexuals (6 dealate females and 1 male) that were noted on the following dates: 6-04-1999, 21-01-2010, 21-09-2018, and 31-12-1987, with the clarification for the latter date that it only indicates that the species was observed in 1987. These are therefore exceptional observations that do not add significant value to the general picture of mating and subsequent nuptial flight. Our data indicate that *S. testaceus* shows the greatest activity of mating and swarming in search of a new host between early July and mid-August (Fig. 8). In only 6 of the 58 squares of 1x1-km, 28 workers were collected, mostly synchronous with the appearance of the gynes. This prompts questions about the activities of these parasitic workers in the mixed colony. Their rarity outside the nest certainly does not argue for a foraging behaviour and their extranidal activity can coincide with the period of a nuptial flight of the sexuals. According to the observations of J. van Boven a sex ratio of 0.63 calculated for *S. testaceus* characterises the colony structure less female-biased than for *A. atratulus* (VAN BOVEN, 1977).

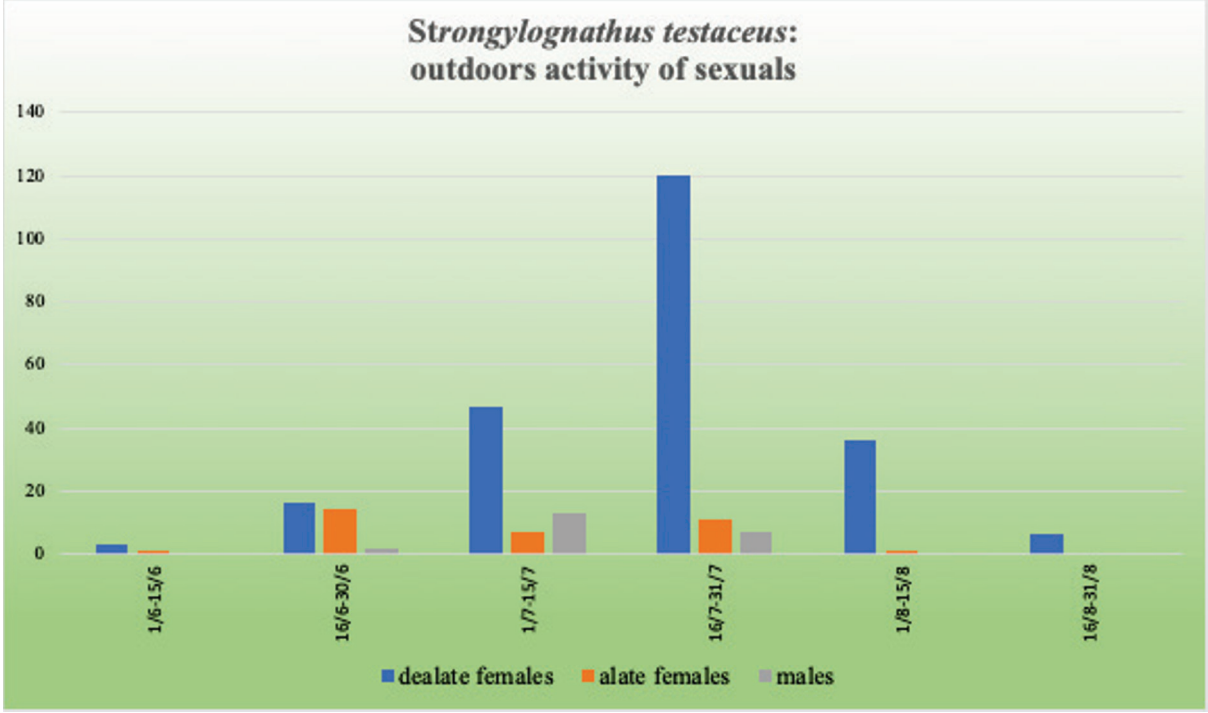

Fig. 8. Presence of females (alate and dealate) and males outdoors. In the period between 16/7 and 31/7, a total of 120 dealate females were collected. The capture of 4 dealate females on 21th Januari 2010, 1 dealate female on 6th April 1999, 1 male on 21th September 2018 and 1 dealate female on 31th December 1987 are not included in this chart.

Discussion

In 2003 we noticed *A. atratulus* as threatened with extinction and *S. testaceus* as critically endangered in Flanders (DEKONINCK *et al*., 2003). Unlike *A. atratulus* which is listed on the IUCN Red List of Threatened Species as vulnerable, there is no mention of *S. testaeus* on that list. After intensively monitoring ants in Flanders over a period of more than two decades, it may be appropriate to reconsider their conservation status.

As far as Flanders is concerned, the value of this criterion is certainly not determined by the low presence of its host species *T. caespitum*, as this is a very common species and to a lesser extent *T. impurum*. The habitat of the main host, the xerothermophilous *T. caespitum*, is

preferably located in sandy soils typical of the Limburg and Antwerp Campine. It is here in the north-east of Belgium that both *A. atratulus* and *S. testaceus* are found with a certain regularity during long-term surveys. Without these investigations, we would have to rely on intensive searching and sorting of the nests of *Tetramorium* spp. in order to gather distribution data of these parasitic species. Given the labour-intensive nature of such observations, this is an almost impossible task and the number of individuals of these parasites that would be found, would be extremely low. Just as a predator is increasingly rarer than its prey, parasitic species will also be much less common and, by definition, more vulnerable than the host species. Sufficiently large numbers of colonies of the host species in the suitable habitat offer a certain guarantee for the survival of the parasites. Perhaps we should differentiate between *A. atratulus* and *S. testaceus* when assigning a status despite both depending on the abundance of the same host species. In contrast to our assignment in 2003 (DEKONINCK *et al*., 2003), we propose for Flanders and by extension Belgium, that both *A. atratulus* and *S. testaceus* are vulnerable in their existence, when assessed by the presence of the host species. But, for *A. atratulus* this may be a bit more up for debate if we consider a possible impoverishment of the genetic potential due to the reproductive behavior between siblings. Only a thorough genetic study of this species can show whether inbreeding here can be detrimental to survival. We can presume that 80 observations of dispersing females are a considerable number but spread over 21 years and linked to large-scale surveys, this offers little perspective for the long-term conservation of the species.

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