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Odonate wing vein preferences in haemolymph sucking *Forcipomyia paludis* (Diptera: Ceratopogonidae; Odonata)

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Abstract

In summer 2020, the Odonata fauna in the Weerribben-Wieden National Park was examined at various localities for the Odonata parasite *Forcipomyia paludis*. This park is currently one of the localities in the Netherlands where the species is found every year. Five localities in the area have been surveyed and many of the Odonata species were found to be infected by biting midges. The parasites have been studied in more detail on photos of the Odonata species and an accurate overview was obtained on which wing veins they sucked. The highest numbers of biting midges were observed on the Cubitus vein. Furthermore, 91% of all observed midges sucked on the lower wing veins of the dragonflies and 9% on the upper ones. Biting midges were not observed in all of the sites surveyed in the park.

Zusammenfassung

Analyse der vom Libellenparasiten *Forcipomyia paludis* bevorzugten Flügeladern (Diptera: Ceratopogonidae; Odonata) – Im Sommer 2020 wurde die Libellenfauna an verschiedenen Orten im Nationalpark Weerribben-Wieden auf den Libellenparasiten *Forcipomyia paludis* untersucht. Dieser Park ist derzeit einer der Orte in den Niederlanden, an denen die Art jedes Jahr gefunden wird. Fünf Standorte in der Region wurden auf ihre Libellenfauna untersucht, und eine große Anzahl der Libellen war von Gnitzen parasitiert. Die Gnitzen wurden auf Fotos der Libellen genauer untersucht, und dabei ergab sich ein genaues Bild, auf welchen Flügelvenen sie parasitierten. Die meisten Gnitzen wurden an den Cubitus-Adern der Libellenarten beobachtet. Darüber hinaus wurde festgestellt, dass 91 % aller beobachteten *F. paludis* auf den niedrig stehenden Flügeladern der Libellen saugten und 9 % an den höher stehenden. Gnitzen wurden nicht in allen Gebieten des Nationalparks beobachtet.

Introduction

Currently nine localities are known in the Netherlands where *Forcipomyia paludis* is found as an Odonata parasite. In this study, peat bogs in the Weerribben-Wieden National Park were examined for the presence of *F. paludis* on Odonata

species. The area is a large fenland and is located in the North-East of the Netherlands. In 2008, *F. paludis* has been discovered in this area in the Netherlands for the first time (Manger & Martens 2013).

New in this research is the determination of the degree of contamination of *F. paludis* on Odonata species at various locations in a large swamp area. It is also new to determine what preference these Diptera have for certain wing veins. The position and quantity of the midges were recorded. The question was also whether biting midges in the research area show local differences and whether certain Odonata species are more parasitized.

Methods and study area

In 2020, five peat bogs in the Weerribben-Wieden National Park (52.78316° N, 5.94065° E) were investigated in June and July. The area is located in the province of Overijssel in the northeast of the Netherlands. With over 10,000 hectares, the Weerribben-Wieden National Park is the largest continuous peat bog area in northwestern Europe. Previous peat extraction and reed cultivation have created a labyrinth of ponds, lakes, ditches, swamp forests, extensive reed plots, and flowery hay meadows. The Weerribben-Wieden are among the best Odonata areas in Europe. In the last ten years, 50 Odonata species have been observed in the area, including some that are very rare in the rest of Europe. Especially in spring, the numbers of dragonflies are quite impressive. The five sites examined are scattered in an area of approximately 3,500 hectares. Two locations have been examined at different times (Table 1).

By slowly walking several hundred meters along the bank and taking pictures of the dragonflies, an inventory of the Odonata population was made. Most of the Odonata were territorial males perched on the bank edge or individuals photographed in flight. The others were females, mating wheels and tenerals (Table 2). The photos were later analysed and recorded. The position on the wing was determined for each *F. paludis*.

In this research, the Odonata species from the family Libellulidae were studied in more detail. The Odonata species in this group were the most represented, as they usually sit on the water side for a long time and the wing position is quite easy to capture photographically. *Forcipomyia paludis* was also found in the Zygoptera, but this Odonata group was not included in the study.

One day, a male *Aeshna isoceles* sat on my head and I was able to gently grab it (Fig. 1). Eventually, almost all midges left the wings, presumably due to the violent movement of the wings while holding. Catching dragonflies with biting midges with an insect net is not very successful, because the biting midges fly away due to the stress (Martens et al. 2008).

Specific parts of the wings of the different Odonata species have been examined for biting midges. For example, it was investigated how many midges sucked on the upper or the lower side of the wings and how many on the forewings or

Table 1. Study sites in the Weerribben-Wieden National Park, The Netherlands, inventory data and number of *Forcipomyia paludis* and dragonflies. – **Tabelle 1:** Untersuchungsgewässer im niederländischen Weerribben-Wieden Nationalpark und ihre Maße sowie Anzahl der Gnitze *F. paludis* und der Libellen.

Date	Locality name	Width [m]	Length [m]	# *F. paludis*	# Dragonflies
03-vi-2020	Jurriës 1	16	400	4	26
03-vi-2020	Groot erve 1	15	700	70	48
12-vi-2020	Jurriës 1	16	400	24	41
12-vi-2020	Groot erve 1	15	700	147	114
12-vi-2020	Groot erve 2	3	400	44	38
17-vi-2020	Woldlakebos	4	1500	0	138
12-vii-2020	Jurriës 2	2	1000	45	140

Table 2. Total and parasitised number of Anisoptera species and number of *Forcipomyia paludis* in the Weerribben-Wieden National Park. – **Tabelle 2:** Gesamtzahl und Zahl der von *F. paludis* parasitierten Libellenarten (Anisoptera) sowie die Zahl der erfassten Gnitzen im Weerribben-Wieden Nationalpark.

Species	Total number	parasitised	# *F. paludis*
Aeshna grandis	3	3 (100%)	7
Aeshna isoceles	5	3 (60%)	10
Somatochlora flavomaculata	1	1 (100%)	4
Leucorrhinia caudalis	76	34 (45%)	76
Leucorrhinia pectoralis	203	75 (37%)	141
Libellula fulva	45	3 (7%)	4
Libellula quadrimaculata	88	21 (24%)	60
Orthetrum cancellatum	22	2 (9%)	2
Sympetrum danae	19	1 (5%)	1
Sympetrum sanguineum	55	16 (29%)	23
Sympetrum vulgatum	23	7 (30%)	8

hindwings. The distribution of the biting midges on the Odonata wings was also determined from the wingbase to the wingtips. So the question is which wing veins biting midges prefer. Odonata wings have an aerodynamic construction with lower and upper wing veins (Fig. 2). To clarify on which wing section the midges preferably suck, I partitioned the wings into 13 sections (a–m). Each section is based on a lower wing vein framed by higher veins (Fig. 6) and looks like a little gutter (central inset Fig. 2).

Figure 1. *Aeshna isoceles* with four *Forcipomyia paludis* on the right hindwing. Because the individual sat on my head, I could grab it and realised that the *F. paludis* specimens remained on the wing veins. Weerribben-Wieden National Park, 03-vi-2020. – **Abbildung 1:** *Aeshna isoceles* mit vier *F. paludis* auf dem rechten Hinterflügel. Da das Tier auf meinem Kopf saß, konnte ich es greifen und erkannte, dass *F. paludis* auf den Flügeladern sitzen geblieben war. Weerribben-Wieden Nationalpark, 03.06.2020.

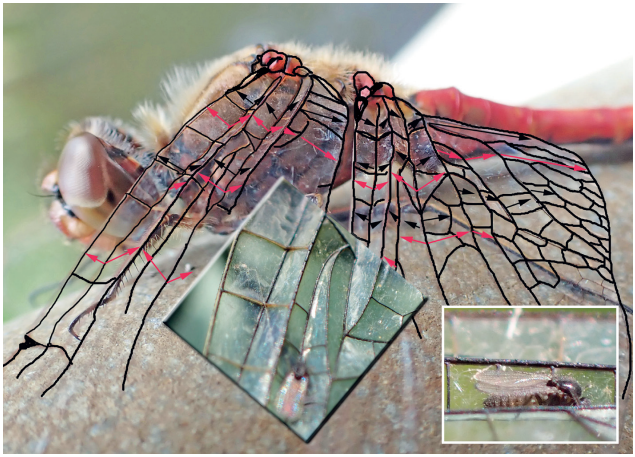

Figure 2. Wing profile in *Sympetrum vulgatum*. One female *Forcipomyia paludis* (see inserts) sucks on a lower wing vein (Arculus). Weerribben-Wieden National Park, 12-vii-2020. – **Abbildung 2:** Flügelprofil von *S. vulgatum*. Eine weibliche *F. paludis* (Einschübe) saugt an einer tief verlaufenden Flügelader (Arculus). Weerribben-Wieden Nationalpark, 12.07.2020.

Results

Twelve Odonata species (Anisoptera) were observed (Table 2). Nine species belonged to the Libellulidae family, of which, relatively speaking, *Leucorrhinia caudalis* and *L. pectoralis* were seen the most with *F. paludis* on the wings and, during the early season, *Libellula fulva* the least (Table 2). Also few individuals of the genera *Aeshna* and *Somatochlora* were listed. More than 75% of infected Odonata had one or two parasites on the wings, and the minority had more than two of them (Fig. 3). The highest number of ten *F. paludis* were seen on an imature *Leucorrhinia caudalis* male (Fig. 4). Many young dragonflies carried biting midges, but also old worn individuals were sometimes found with them.

In this study, *F. paludis* was recorded on the dragonfly wings only and not on other body parts. There were more of them on the forewings (58.7%) than on the hindwings (41.3%). A clear difference could be seen in the ratio with the number of biting midges on the upper or lower side of the wings. There were about three times as many midges on the upper side of the wings (262 individuals) than on the lower side (72 individuals). Furthermore, all *F. paludis* turned out to be frontally orientated towards the dragonfly's body.

Number of *F. paludis* from wingbase to nodus

During the study, 334 biting midges on 169 dragonfly hosts were observed. From four Odonata species the location of the biting midges is determined from wingbase to nodus (Fig. 5). The wing is divided into five parts, in four quarters from the wingbase to the nodus. The fifth part is from nodus to wingtip. Four species,

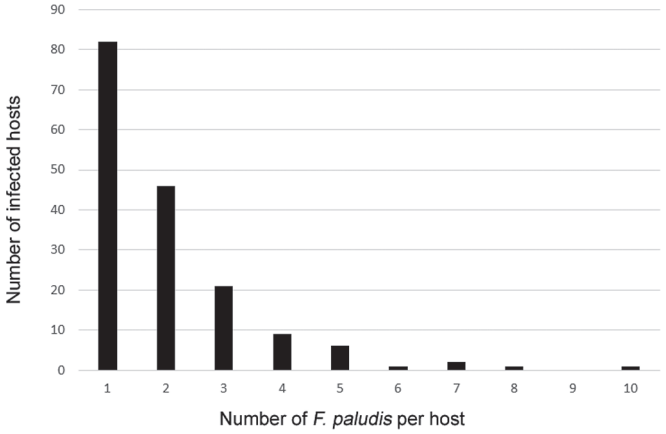

Figure 3. Intensity of infestation of *Forcipomyia paludis* (n = 334) on anisopteran wings in the Weerribben-Wieden National Park; number of infected dragonflies: n = 169. – **Abbildung 3:** Befallsstärke durch *F. paludis* (n = 334) auf Anisopterenflügeln im Weerribben-Wieden Nationalpark; Zahl der parasitierten Libellen: n = 169.

Leucorrhinia pectoralis, L. caudalis, Libellula quadrimaculata, and *Sympetrum sanguineum* were the most common and have been compared. Of all Odonata species, these four species contributed 42% of the total number of midges on the wings. Most biting midges were observed at the basal part of the wings (Fig. 5).

Upper or lower wing veins

Figure 2 shows the construction of an Odonata wing. Differences in height level between adjacent wing veins create little gutters in the wings and ensure the right aerodynamics. Such a slot is formed by upper and lower wing veins. *Forcipomyia paludis* was seen on both types of veins, however most midges (91%) sucked on the lower veins (Fig. 6), which obviously were especially suitable for a safe attachment (insets Fig. 2).

Number of *F. paludis* per wing section

Table 3 shows the number of biting midges observed on all Odonata species per wing section (cf. Fig. 7). Most parasites were found on the Cubitus veins (sections c and i), which are running in the center of the wing base. Wing sections (a, b, f, g, and m) on the front of the wings were found to contain fewer biting midges. Midges were missing in the middle of the forewings (e) and on the front of the hindwings (h).

Figure 4. Young *Leucorrhinia caudalis* male with the highest number of ten *Forcipomyia paludis* found during this investigation. Weerribben-Wieden National Park, 12-vi-2020. – **Abbildung 4:** Junges *L. caudalis*-Männchen mit der höchsten Anzahl von zehn *F. paludis*, die während dieser Studie gefunden wurde. Weerribben-Wieden Nationalpark, 12.06.2020.

Discussion

About three-quarters of the biting midges were located on the upper side of the wings. Furthermore, most of them appeared to be at the wing base (Fig. 7). This corresponds to previous studies (Martens et al. 2008; Černý 2014; Vinko et al. 2017; Boudot et al. 2019; Cordero-Rivera et al. 2019; Wildermuth et al. 2019).

In Anisoptera, forewings have a smaller wing area than hindwings. However, in this study, more parasites were found on the forewings than on the hindwings (196/138). In a recent study in Belgium, *F. paludis* also shows a slight preference for the forewings (De Knijf 2021). Martens et al. (2008) have found almost equal numbers on the forewings and hindwings of Anisoptera.

In the same study about twice as many biting midges have been observed on the upper side of ansopteran wings (180/95) than on the underside (Martens et al. 2008). In this Weerribben-Wieden study about three times as many midges have been recorded on the upper side of the wings than on the lower side (262/81).

The observed orientation of *F. paludis* towards the dragonfly's body is probably a case of random orientation as in 2016 in the same area midges sucked with their heads directed towards the wing tip (Manger & Van der Heijden 2016). In previous research in Europe, only a very small proportion of the parasites was

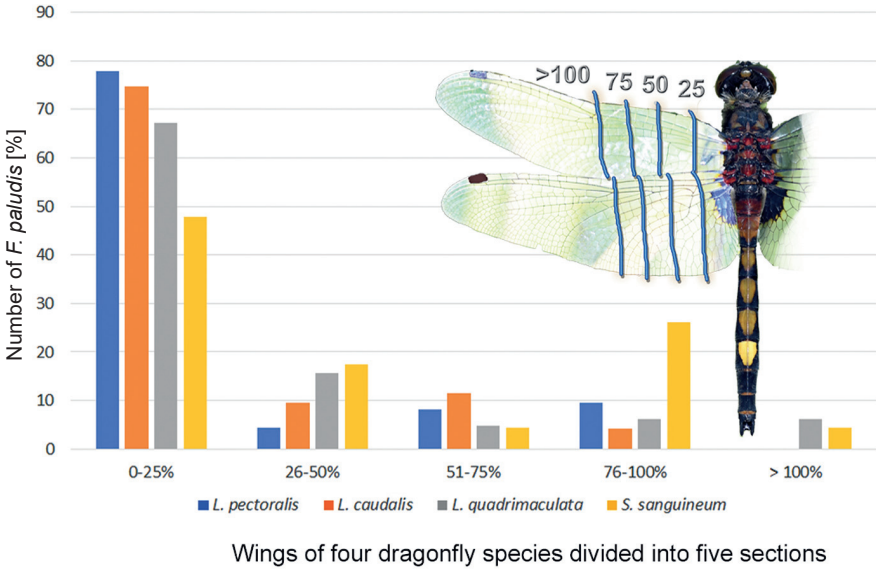

Figure 5. Relative distance of *Forcipomyia paludis* from the wing base to the nodus on the wings of four Odonata species. Biting midges between the nodus and wing tip are indicated as > 100. – **Abbildung 5:** Relativer Abstand von *F. paludis* von der Flügelbasis zum Nodus auf den Flügeln von vier Libellenarten. Gnitzen zwischen Nodus und Flügelspitze werden als > 100 angezeigt.

Table 3. Number of *Forcipomyia paludis* per wing section (cf. Fig. 7) of the observed anisopteran species in the Weerribben-Wieden National Park. Infected dragonfly individuals = 169. – **Tabelle 3:** Anzahl der *F. paludis* pro Flügelteil (Abb. 7) der im niederländischen Weerribben-Wieden Nationalpark beobachteten Anisopterenart. Infizierte Libellenindividuen = 169.

	Forewing sections						Hindwing sections						
Species	a	b	c	d	e	f	g	h	i	j	k	l	m
Aeshna grandis	0	0	1	0	0	0	1	0	5	0	0	0	0
Aeshna isoceles	1	0	2	0	0	3	0	0	3	0	0	1	1
Somatochlora flavomaculata	0	0	2	0	0	0	1	0	1	0	0	0	0
Leucorrhinia caudalis	12	0	18	2	0	7	2	0	24	2	2	3	0
Leucorrhinia pectoralis	14	0	53	0	0	16	4	0	37	9	2	6	0
Libellula fulva	1	0	0	0	0	1	0	0	2	0	0	0	0
Libellula quadrimaculata	5	0	35	1	0	8	0	0	4	5	1	3	0
Orthetrum cancellatum	0	0	0	0	0	0	0	0	1	0	0	1	0
Sympetrum danae	0	0	0	0	0	0	0	0	1	0	0	0	0
Sympetrum sanguineum	0	1	6	0	0	3	2	0	6	1	1	3	0
Sympetrum vulgatum	0	0	4	0	0	0	0	0	0	3	0	0	0
Total	33	1	121	3	0	38	10	0	84	20	6	17	1

observed facing the wing tip. In contrast with the present study midges are sometimes seen on the abdomen or thorax of Odonata (Martens et al. 2008; Cordero-Rivera et al. 2019).

This investigation has shown that there are differences in the infestation by *F. paludis* on Odonata species. *Leucorrhinia caudalis* was most frequently seen with *F. paludis,* followed by *L. pectoralis*, *Sympetrum sanguineum*, and *Libellula quadrimaculata. Libellula fulva* was found to be the least infected by the biting midges (Table 2). This is striking because in the Weerribben-Wieden *L. pectoralis* and *L. fulva* live in the same habitat, emerge in the same period and have the same flying season. Both species would therefore have the same chance of becoming infected by biting midges. It is difficult to understand why there is such a difference between these two species. It could be that the moment of emerging determines the degree of parasitism on the dragonflies. Much remains unclear about *F. paludis*. How does this species reproduce? It is suspected that the females deposit eggs in moist soil close to water where the larvae develop. The hatched females then attack their host near the water (Wildermuth et al. 2019).

Most biting midges have been observed at the basal part of the wings close to the thorax. They were mainly observed in the central part of the wing base (Fig. 8). Here are lower veins (Rajabi et al. 2016), where the midges find sufficient firm-

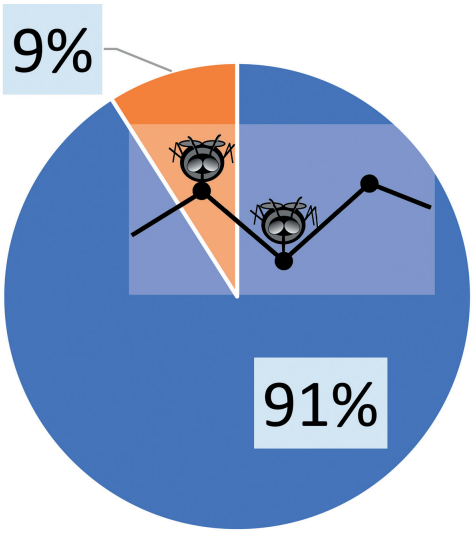

Figure 6. Number of *Forcipomyia paludis* (n = 334) in percentages that were observed on lower or upper veins of all infected Odonata recorded in the Weerribben-Wieden National Park. – **Abbildung 6:** Prozentualer Anteil von *F. paludis*-Individuen (n = 334), die an tief oder hoch verlaufenden Adern der Libellenflügel im Weerribben-Wieden Nationalpark beobachtet wurden.

Figure 7. Wings of *Sympetrum vulgatum* divided into 13 wing sections (a–m). Each wing section is based on one or more lower wing veins. The number of biting midges observed is divided into four frequency classes. – **Abbildung 7:** Flügel von *S. vulgatum*, unterteilt in 13 Sektionen (a–m). Jede Sektion basiert auf einer oder mehreren tiefer gelegenen Flügeladern. Die Anzahl der beobachteten Gnitzen ist unterteilt in vier Häufigkeitsklassen.

ness and shelter. On the Cubitus vein (Cu) (Figs 7, 8) most parasites have been observed. None was seen on the Costa (front vein). Presumably this vein at the front of the wings is too strongly sclerotised, so that the midges cannot get into the vein with their mouth parts (Wildermuth & Martens 2007). Biting midges on the upper wing veins appear more vulnerable, as they are probably more at risk of falling off the wings. Previous research has suggested that the high proportion of biting midges at the basal half of the wing is related to the increased circulation of haemolymph. On that part of the wing, the centrifugal forces to which they are exposed during wing strokes will be less (Wildermuth & Martens 2007).

No midges were found at the Woldlakebos site on 17 June (Table 1). Also, in this best researched part of the Weerribben-Wieden, the species has only been found once in the past. This area in the east of the National Park is separated about five kilometers from the other locations. The Woldlakebos has its own water management and the area is lower than the other examined locations in the park. Water is only let in from the Weerribben-Wieden during the vegetative growing season. The water in Woldlakebos is more basic compared to the rest of the National park. For example, there are less reed stands with peat moss and there are fewer acidophilic plants in this area. Furthermore, all Odonata species known

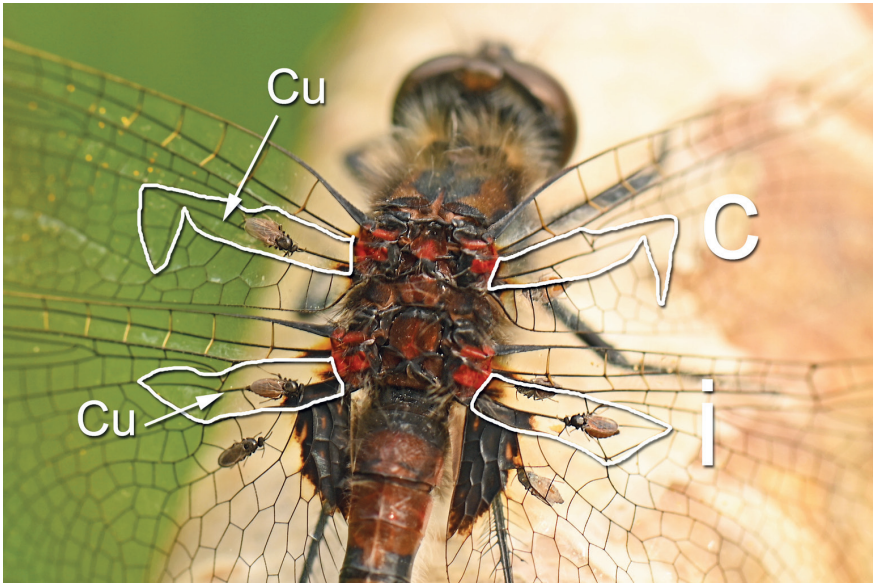

Figure 8. Wing sections c and i, on which most *Forcipomyia paludis* were found on the Cubitus veins (Cu). The photo shows a male *Leucorrhinia pectoralis* with eight midges. Weerribben-Wieden National Park, 03-vi-2020. – **Abbildung 8:** Flügelsektoren c und i, auf denen die meisten *F. paludis* auf den Cubitus-Adern (Cu) gefunden wurden. Das Foto zeigt ein *L. pectoralis*-Männchen mit acht Gnitzen. Weerribben-Wieden Nationalpark, 03-06-2020.

from the park also occur in the Woldlakebos, except *Coenagrion armatum*. The occurrence of *F. paludis* could depend on several factors such as water quality, water level, and vegetation, but more specific research has to to be done to gain a better understanding. In a Belgian study on *F. paludis*, it is suggested that there may be a link between the occurrence of *F. paludis* and the plant species *Cladium mariscus.* Localities in Western Europe, where *C. mariscus* is growing, might be a suitable larval habitat for *F. paludis* (De Knijf 2021). In the Weerribben-Wieden National Park *C. mariscus* is widely distributed and biting midges are abundant. In the Woldlakebos only a few *C. mariscus* plants were present and biting midges were not observed (Table 1).

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