

# Comparative study of courtship and copulation in five *Oedothorax* species

Liesbeth Maes<sup>1</sup>, Danny Vanacker<sup>1</sup>, Sylvia Pardo<sup>1</sup> and Jean-Pierre Maelfait<sup>1,2</sup>

<sup>1</sup> Research Group of Terrestrial Ecology, Ghent University, Ledeganckstraat 35, 9000 Gent, Belgium

<sup>2</sup> Institute of Nature Conservation, Kliniekstraat 25, 1070 Brussels, Belgium

Corresponding author : L. Maes, e-mail : [liesbethmaes83@hotmail.com](mailto:liesbethmaes83@hotmail.com) (or [danny.vanacker@rug.ac.be](mailto:danny.vanacker@rug.ac.be))

**ABSTRACT.** *Oedothorax gibbosus* (Blackwall, 1841) is a dwarf spider restricted to oligo- and mesotrophic alder carrs. This dwarf spider is distinguished from other *Oedothorax* species by its male dimorphism; *gibbosus* males are characterised by a hunch and a hairy groove on their carapace, *tuberosus* males do not have these features. The hairy groove is important during gustatorial courtship behaviour; this is the uptake of secretions by the female from a male body part during courtship. Another remarkable difference between *O. gibbosus* and its sister species is that courtship and copulation duration is much longer in this species. The rare *O. gibbosus* spiders also seem to be less active than common spiders of *O. fuscus* (Blackwall, 1834), *O. retusus* (Westring, 1851) and *O. apicatus* (Blackwall, 1850). In that way common spiders raise their chances of survival in the open field. A more active lifestyle seems to be related to a shorter, heavier courtship and copulation. It is also possible that the longer courtship and copulation time, useful for male competition and sperm competition, results from the male dimorphism in this species. The web has an important function in the reproduction of *Oedothorax* spiders : it is necessary during gustatorial courtship, other courtship activities and copulation, and it is also probably important for the distribution of contact pheromones. The copulation of *Oedothorax* species differs from that of *Erigone* : instead of two continuous insertions, we observed, in this case, a series of very short insertions, which can be linked to one other to make up longer periods.

**KEY WORDS :** *Araneae*, *Erigoninae*, *Oedothorax*, *Erigone*, gustatorial courtship, courtship, copulation, comparative study.

## INTRODUCTION

The dwarf spider *O. gibbosus* (Blackwall, 1841) is a rather rare spider in Flanders. It can be found in wet to very wet habitats, such as oligo- and mesotrophic alder carrs (DE KEER & MAELFAIT, 1989; ALDERWEIRELDT, 1992). Besides *O. gibbosus*, other representatives of the genus *Oedothorax* are present in Belgium : *O. apicatus* (Blackwall, 1850), *O. agrestis* (Blackwall, 1853), *O. fuscus* (Blackwall, 1834) and *O. retusus* (Westring, 1851). *O. agrestis* is even more rare than *O. gibbosus*, and is also restricted to wet to very wet habitats (DE KEER & MAELFAIT, 1989). The other three species on the other hand are among the most common spider species in Belgium. They frequently occur in enormous numbers in various types of habitats (ALDERWEIRELDT, 1992).

Only one representative of the genus *Oedothorax*, *O. gibbosus*, is characterised by male dimorphism (DE KEER & MAELFAIT, 1989). The genetically dominant (MAELFAIT et al., 1990; VANACKER et al., 2001b) *gibbosus* morph possesses a large protuberance on the last third of the carapace, preceded by a hairy groove. The *tuberosus* morph on the other hand does not possess such a groove and its carapace is smooth and convex.

In *O. fuscus* the highest point of the male carapace is situated in the anterior part, and there is typically a pale region in the middle of the abdomen of the female. On the clypeus there are two long hairs (ALDERWEIRELDT, 1992). This last feature is also typical for *O. agrestis* males.

However, the cephalic part of an *O. agrestis* male is very similar to that of the *tuberosus* morph of *O. gibbosus*; the posterior part of the carapace of *tuberosus* is slightly higher than that of *O. agrestis* males. In *O. retusus*, the anterior part of the carapace is strongly raised and there is only one hair on the clypeus (ALDERWEIRELDT, 1992). On both sides of the carapace, there are grooves with pores (SCHAIBLE et al., 1986). *O. apicatus* also possesses lateral grooves (SCHAIBLE et al., 1986) and only one hair on the clypeus (ALDERWEIRELDT, 1992). Typical for this species is the presence of a narrow protuberance on the highest part of the male carapace (SCHAIBLE et al., 1986; ROBERTS, 1987).

Dwarf spiders of the genus *Oedothorax* are approximately 3 mm long and the females are bigger than the males. Most of the time, copulation takes place upside down in the web. In this way, the male finds itself above the female and inserts a palp in the epigyne. Each time a small quantity of sperm is transmitted from the palp into the female spermathecae, by means of a hydraulic pumping system of the haematodoch-bladder (FOELIX, 1996). In many cases, copulation is preceded by courtship, which can have a gustatorial character and can be considered as 'nuptial feeding'. The term 'nuptial feeding' refers to any form of offering food by the male to the female, during or immediately after the courtship or (and) copulation (VAHED, 1998). The phenomenon of secretion in cephalothoracic protrusions is not an exclusive character of the family Linyphiidae. Such secretions are also found in other

families, for example in *Argyrodes antipodiana* O.P.-Cambridge, 1880 (Theridiidae) (WHITHOUSE, 1987).

VANACKER et al. (in press) mentioned several interspecific gustatorial courtships by a *gibbosus* male, and a male or female of the closely related species *O. fuscus*. These interspecific interactions suggest that the hairy groove in the *gibbosus* male morph is a nuptial feeding device possibly under the influence of sexual selection. The interspecific interactions can possibly be interpreted as 'robbings' of the nuptial feeding (VANACKER et al., in press). Histological data (VANACKER, unpubl.) confirm that *gibbosus* males secrete a nuptial gift in their groove; the hunch of *gibbosus* is filled with gland cells with different kinds of secretions.

Here we describe intraspecific courtship behaviour in the different *Oedothorax* species. Because only *O. apicatus* males have a clearly distinct protuberance on the carapace comparable with the hunch of *gibbosus* males, we assume that the possibility of the occurrence of a gustatorial courtship is higher in *O. apicatus* than in *O. fuscus*, *O. retusus* and *O. apicatus*.

We also describe copulation behaviour of the different *Oedothorax* species. The copulation of *Erigone atra* (Blackwall, 1833) is also taken into account, because *E. atra* is closely related to the *Oedothorax* species according to the phylogenetic trees of HORMIGA (2000). *E. atra* is, like *O. fuscus*, *O. retusus* and *O. apicatus*, a very common species of open habitats. It can be supposed to be very active to increase its chances of survival in the open field by evading natural predators. This active behaviour can have consequences for the duration of copulation. *O. gibbosus* and *O. agrestis* on the other hand are rare species, which are restricted to a very specific habitat. Such species probably have the opportunity to copulate more slowly and for longer.

Here, we investigate the hypothesis about the occurrence of gustatorial courtship as well as the hypothesis about copulation duration. Also the function of the web during courtship and copulation is described. The litera-

ture about the courtship and copulation behaviour of other spider species is reviewed as well.

## MATERIALS AND METHODS

The dwarf spiders were captured manually. *O. gibbosus* spiders were caught in the nature reserve Het Walenbos at Tielt-Winge, 30-km northeast of Brussels. Representatives of *O. fuscus* and *O. retusus* came from the military domain de Yzermonding at Lombardsijde. *O. apicatus* spiders were from the first generation of spiders coming from the same domain. The *O. agrestis* spiders were caught in Het Krawaalbos at Asse. The *E. atra* spiders were collected in the nature reserve De Westhoek at De Panne.

To keep the collected spiders alive as well as to breed them, the spiders were put into separate plastic cups (diameter : 4 cm and height : 2.5 cm), with a bottom of plaster and a piece of moss. Young animals were fed every two days with four springtails (*Isotoma spec.* among others). After the second moult the spiders received each time three fruit flies. At the same time three drops of water were added to maintain a relative humidity near 100%. The spiders were kept in a climatic chamber at a temperature of circa 20°C and a photoperiod L :D of 16 :8. We opted for 20°C because this is the best temperature to rear this dwarf spider species (ALDERWEIRELDT & DE KEER, 1988; VANACKER et al., 2001a).

Copulations were observed with a WILD-binocular dissecting microscope and a cold light source. Each couple was observed for at least one hour and, in case of copulation until at least half an hour after the copulation. To take pictures of the courtship and copulation of *Oedothorax gibbosus* during our observations, we used a digital camera (Nikon).

We observed 81 copulations of *O. gibbosus*, 16 of *O. fuscus*, 22 of *O. retusus*, 24 of *O. apicatus*, 19 of *O. agrestis* and 12 of *E. atra*. Table 1 gives a complete survey of the total number of gustatorial courtships and copulations that were observed for each species.

TABLE 1

The observed numbers of courtships and copulations in five *Oedothorax* species and *Erigone atra*.

Species	Gustatorial courtship	Incomplete copulation	Complete copulation	Studied couples	Couples with 1 copulation	Couples without copulations	Couples with multiple mating
<i>O. gibbosus</i>							
<i>gibbosus</i> male	41	23	16	28	18	4	6
<i>tuberosus</i> male	not observed	23	19	98	37	59	2
both males	41	46	35	126	55	63	8
<i>O. fuscus</i>	not observed	6	10	26	13	12	1
<i>O. retusus</i>	not observed	4	18	24	13	7	4
<i>O. apicatus</i>	18 'mini- courtships'	8	16	27	8	12	7
<i>O. agrestis</i>	not observed	6	13	13	9	0	4
<i>E. atra</i>	not observed	not observed	12	32	0	20	12

## RESULTS

### *Oedothorax gibbosus* (Blackwall, 1841)

The reproductive behaviour of *O. gibbosus* is first of all characterised by a pronounced courtship behaviour,

which contains two phases. During the first phase the male approaches the female, both of the partners pump with the abdomen, the male cleans its palps or does up-and down movements with the forelegs, and some males make a specific dance to seduce the female. Such a dance

consists of movements in '8' or '0' forms, which they execute while approaching the female.

During the second phase, physical contact is made between both partners. In the *gibbosus* morph the second phase is characterised by a gustatorial courtship (HEINEMANN, 1998) (Table 3). The female brings her chelicerae into the hairy groove and takes up the secretions (Fig. 1).

Such a gustatorial courtship continues on average  $9.53 \pm 8.68$  min ( $n=19$ ) (Table 2). During the second phase of the courtship, the couple gets into copulation position and the male tries to insert a palp. Courtship behaviour of the *tuberosus* morph was also observed. Because this morph does not possess a groove that is filled with a secretion, this courtship is not gustatorial. *Tuberosus* can thus only perform the aforementioned courtship acts of the first phase. Most of the observed couples courted, but in some cases, they immediately started to copulate.

Mostly the copulation itself took place upside down in the web in such a manner that the male was above the female (Fig. 2). The web has an important function in reproduction of this dwarf spider not only during gustatorial courtship, but also during normal courtship and copulation, and probably also for the distribution of contact pheromones. When copulation starts, the female chelicerae mostly stop making contact with the groove of her partner. Sometimes the transition from courtship into copulation proceeds fluently; sometimes there are interruptions. In some cases the male is dragged by the female, while its palp is still inserted. Other positions are also possible: on the bottom of the cup, on the moss or against the wall.



Fig. 1. – Gustatorial courtship of *Oedothorax gibbosus* (female left, *gibbosus* male right). Note that the picture is turned 180° to be more clear; the normal courtship posture is male as well as female upside down, male above female.

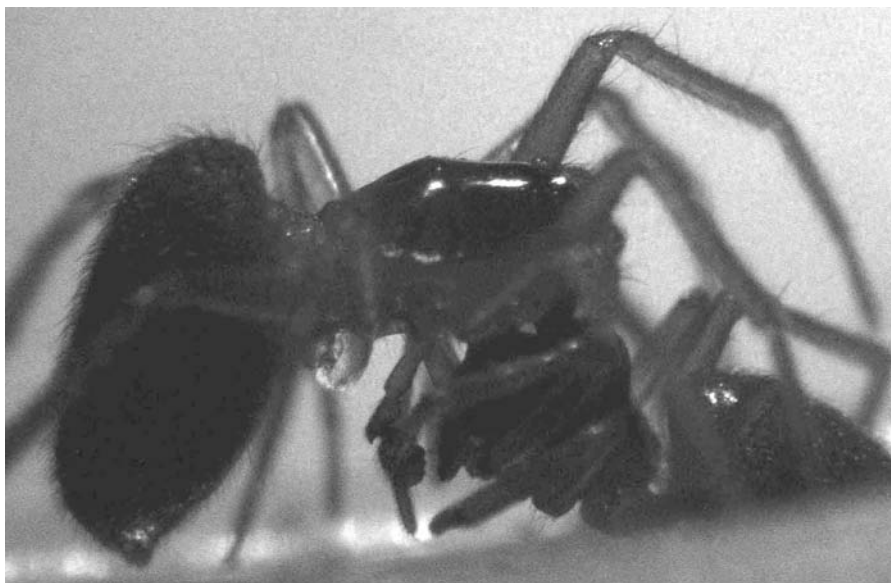


Fig. 2. – Copulation of *Oedothorax gibbosus* (*gibbosus* male right, female left). The haematodoch-bladder is also visible in the picture; the normal courtship posture is male as well as female upside-down, male above female.

During an insertion, sperm is pumped into the epigyne by means of swelling and shrinking of the haematodoch, a bladder that is part of the male palp. Insertion of the palps occurs successively; a copulation with both palps is called a 'complete copulation', while if only one insertion takes place we refer to an 'incomplete copulation' (HEINEMANN, 1998). Complete as well as incomplete copulations

occur in this spider species; we observed 46 incomplete and 35 complete copulations (Table 1).

In *O. gibbosus*, one insertion takes on average about  $34.05 \pm 1.68$  min and the second insertion about  $33.39 \pm 0.09$  min (Table 2). In eight studied couples 'multiple mating' was noticed.

TABLE 2  
Duration of courtship and copulation of *Oedothorax* species.

	Duration of courtship	Duration of copulation
<i>Oedothorax gibbosus</i>	9.53 ± 8.68 min (n=19) (gustatorial courtship)	1 <sup>st</sup> palp : $\bar{x}$ = 34.05 ± 1.68 min, n= 81; 2 <sup>nd</sup> palp : $\bar{x}$ = 33.39 ± 0.09 min, n= 35
<i>Oedothorax fuscus</i>	not observed	1 <sup>st</sup> palp : $\bar{x}$ = 4.09 ± 1.78 min, n= 16; 2 <sup>nd</sup> palp : $\bar{x}$ = 6.60 ± 0.96 min, n= 10
<i>Oedothorax retusus</i>	a few seconds	1 <sup>st</sup> palp : $\bar{x}$ = 4.09 ± 0.97 min, n= 22; 2 <sup>nd</sup> palp : $\bar{x}$ = 2.61 ± 0.61 min, n=18
<i>Oedothorax apicatus</i>	a few seconds ('mini-courtships')	1 <sup>st</sup> palp : $\bar{x}$ = 5.67 ± 1.74 min, n= 24; 2 <sup>nd</sup> palp : $\bar{x}$ = 7.63 ± 1.41 min, n= 16
<i>Oedothorax agrestis</i>	not observed	1 <sup>st</sup> palp : $\bar{x}$ = 6.95 ± 1.81 min, n= 19; 2 <sup>nd</sup> palp : $\bar{x}$ = 4.31 ± 0.75 min, n= 13

### *Oedothorax fuscus* (Blackwall, 1834)

Besides trilling of the forelegs, *O. fuscus* performed no form of courtship behaviour in the 17 studied couples (Table 3). Copulation in this species is not preceded by a gustatorial courtship, or if it takes place it is very short. We observed 16 copulations (Table 1).

Copulation position is comparable with that of *O. gibbosus*, but copulation duration is remarkably shorter (First palp : 5.88 ± 1.78 min, n=16; Second palp : 6.60 ± 0.96 min, n=10) (Table 2). The web is also very important for

copulation. *O. fuscus* spiders are usually much more active than *O. gibbosus* spiders. This could possibly explain the fact that there is no courtship and that the copulation is much shorter. Another difference between the species is that *O. gibbosus* uses its head structures only during the courtship and not while copulating, whereas the *O. fuscus* female is in contact with the male cephalic structures during copulation. The head structures of *O. fuscus* are only used to force the spider into a better position. Multiple mating was noticed in one couple.

TABLE 3  
Contact of the female chelicerae with the male head structures in the five *Oedothorax* species.

Species	Contact during courtship	Contact during copulation	Type of courtship
<i>Oedothorax gibbosus</i>	X	/	Pronounced courtship Gustatorial courtship ( <i>gibbosus</i> morph)
<i>Oedothorax fuscus</i>	/	X	No pronounced courtship No gustatorial courtship observed
<i>Oedothorax retusus</i>	/	in some cases	Pronounced courtship No gustatorial courtship observed
<i>Oedothorax agrestis</i>	/	in some cases	Distinct courtship No gustatorial courtship observed
<i>Oedothorax apicatus</i>	X	X (hunch)	Mini-courtships No gustatorial courtship observed

### *Oedothorax retusus* (Westring, 1851)

In this species there is, in most cases, a courtship (Table 3). The most common courtship acts are trembling with the first pair of legs, plucking on the web with the forelegs, cleaning the palps, etc. In one case, the male executed some kind of dance; by sinking a few times through its legs, alternating with raising itself, it worked itself up and down. This behaviour took place while it stood erect in the web, and was combined with trembling of the opisthosome. In the second phase of the courtship, both partners touched each other with the forelegs and put themselves into copulation position. Meanwhile the male attempted to insert a palp.

The copulation itself usually takes place upside down under the web, although one copulation took place on the

bottom and another one against the wall of the cup. The position is comparable with that of *O. gibbosus*. Like *O. fuscus*, copulation duration of *O. retusus* is much shorter than that of *O. gibbosus* (First palp : 4.09 ± 0.97 min, n=22; Second palp : 2.61 ± 0.61 min, n=18) (Table 2). In four studied couples, multiple mating was noticed. In most cases, the female mouthparts were situated above the head structures of the male during copulation.

### *Oedothorax agrestis* (BLACKWALL, 1851)

In *O. agrestis* no obvious courtship behaviour was noticed (Table 3). The copulation position was comparable with that of *O. gibbosus*. Although this species behaves rather calmly, the copulation duration was remarkably shorter than that of *O. gibbosus* (First palp : 6.95 ± 1.81 min, n=19; Second palp : 4.31 ± 0.75 min,



n=13) (Table 2). One couple copulated twice. These results are in a way different from those formulated by SCHLEGELMILCH (1974) who mentioned an average duration of insertion of 7.5 min.

According to SCHAIBLE et al. (1986), there is no contact between the female chelicerae and the male head structures. In one case we observed, however, that the female mouthparts were situated above the male head structures. In the other cases there was no contact during the copulation. In four studied couples, multiple mating was noticed.

### *Oedothorax apicatus* (Blackwall, 1850)

This representative of the *Oedothorax* genus is remarkable for its short, nervous and fierce copulation (First palp :  $5.67 \pm 1.74$  min, n=24; Second palp :  $7.63 \pm 1.41$  min, n=16) (Table 2). In many cases the female held the protuberance (hunch) of the male between the chelicerae (seven observations). Both partners trilled a lot while copulating and the female usually dragged the male violently and over long distances.

The presence of the hunch as well as the solid stitch between the palp and the epigyne, assures that the copulation is not interrupted. The copulation position is strongly comparable with that of *O. gibbosus*, with exception of the continuing contact between hunch and chelicerae. Because of the nervous copulation, the function of the web is apparently of less importance for copulation in *O. apicatus*.

Analogously with the courtship of other more active spiders, such as *O. fuscus* and *O. retusus*, the courtship of *O. apicatus* is very short and nervous. Moreover, several times so-called "mini-courtships" were executed; the female held the male hunch by means of her chelicerae, in addition to which the female touched the head of the male with the first pair of legs (Table 3). During this "mini-courtship", however, the female did not make sucking or biting movements with the mouth, as was the case in *O. gibbosus*. In seven studied couples 'multiple mating' was noticed.

### *Erigone atra* (Blackwall, 1833)

An elaborate courtship was not observed in *E. atra*. While approaching the female, the male moved its palps up and down, trembled briefly with its forelegs and pumped a single time with its abdomen.

The copulation is different from that of the *Oedothorax* species: instead of two continuous insertions we observed, in this case here, series of very short insertions ( $9.81 \pm 5.32$  min, n=93), which could be linked to one another to form longer periods. During such a series, the male inserts one pedipalp, pumps once (haematodoch swells and shrinks one time), removes the palp, cleans it, inserts the other (in some cases the same) palp, etc. The aforementioned longer periods continued for about  $83.42 \pm 5.99$  min (n=12) and embraced, in four couples seven, in one couple eight, in six couples nine and in the other couple eleven series of insertions.

## DISCUSSION

The majority of the erigonine males carry head structures of various kinds: elevations, accretions, notches, grooves and hair fields. SCHAIBLE & GACK (1987) mentioned that all species possessing such structures, have in common that the chelicerae of the female makes contact with the male head structures during copulation. This statement appears not to be true; with *E. atra*, for example, there was no contact observed, neither during courtship, nor during copulation (SCHAIBLE et al., 1986). SCHAIBLE et al. (1986) did not observe any contact of the female mouthparts with the male head structures. Our observations, however, showed one case in which the female chelicerae were above the head structures of the male.

Although many dwarf spiders court before copulating, we found mention in the literature of few dwarf spider species that make physical contact during courtship: *Baryphyma pratense* (Blackwall, 1861) and *Ceratinella brevipes* (Westring, 1851) (SCHLEGELMILCH, 1974; SCHAIBLE et al., 1986). Other spider species which make chelicer contact during courtship are *Atypus muralis* Bertkau, 1890 and *Atypus piceus* (Sulzer, 1776) (Atypidae), *Avicularia avicularia* (Linnaeus, 1758), *Grammostola mollicoma* (Ausserer, 1875) and *Phormictopus canceridis* (Latreille, 1806) (Therophosidae), *Scytodes thoracica* (Latreille, 1802) and *Scytodes velutina* Heineken & Lowe, 1832 (Scytodidae), *Holocnemus pluchei* (Scopoli, 1763), *Pholcus phalangoides* (Fuesslin, 1775) (Pholcidae), *Segestria bavarica* C. L. Koch, 1843, *Segestria florentina* (Rossi, 1790) and *Segestria senoculata* (Linnaeus, 1758) (Segestriidae), *Pachygnatha clercki* Sundevall, 1823, *Pachygnatha degeeri* (Sundevall, 1830) and *Pachygnatha listeri* (Sundevall, 1830), *Tetragnatha extensa* (Linnaeus, 1758), *Tetragnatha montana* Simon, 1874 and *Tetragnatha nigrita* (Lendl, 1886) (Tetragnathidae), *Nigma walckenaeri* (Roewer, 1951) (Dictynidae), *Clubiona germanica* (Thorell, 1871) and *Clubiona terrestris* (Westring, 1851) (Clubionidae) (HUBER, 1998).

The copulation duration of *Oedothorax gibbosus* is comparable with that of *Ceratinella brevipes* (Westring, 1851), *Diplocephalus latifrons* (O.P.-Cambridge, 1863), *Gonatium rubellum* (Blackwall, 1841) (SCHLEGELMILCH, 1974; SCHAIBLE et al., 1986). In other spider families, for example *Dysdera erythrina* (Walckenaer, 1802) (Dysderidae), *Oonop placidus* Dalmas, 1916 (Oonopidae), *Pisaura mirabilis* (Clerck, 1757) (Pisauridae), *Xysticus cristatus* (Clerck, 1757) (Thomisidae) and *Heliophanus cypreus* (Walckenaer, 1802) (Salticidae) have similar copulation duration to *Oedothorax gibbosus* (HUBER, 1998).

Our results show that, within the genus *Oedothorax*, *O. gibbosus* differs from its sister species by executing a longer courtship, certainly in the case of the *gibbosus* male, as well as a longer copulation. We observed gustatorial courtship only in *O. gibbosus*, although we also observed "mini-courtships" in *O. apicatus*.

The *gibbosus* morph has a hairy groove in which a nuptial gift and/or pheromones are secreted (VANACKER et al., in press). The *tuberosus* morph, on the contrary, has no distinct head structures. They have few cephalic gland

cells (VANACKER, unpublished results) and probably this is also the case in the males of *Oedothorax* species without distinct cephalic structures. *O. apicatus* can be regarded as taking an intermediate position: an *O. apicatus* male is characterised by one narrow hunch on its cephalothorax. The possible occurrence of a few gland cells could explain the appearance of the “mini-courtships” in this species. The results of MEIJER (1976) indirectly confirm this hypothesis; the author found remnants of secretions on spiders that were caught in pitfalls, including on *O. apicatus*. This article also mentions possible secretions in *Troxochrus scabriculus* (Westring, 1851), which is also known for its male dimorphism. Further histological and TEM research will study the occurrence of such cells.

Probably most erigonine males possess gland cells (some species more than others). The gustatorial courtship is most pronounced in *O. gibbosus* (probably linked to the male dimorphism of this species), but the mini-courtships of *O. apicatus* also have in most cases a ‘gustatorial’ character (MEIJER, 1976). It is possible that the biting movements only appear in *O. gibbosus*, because the substance, in that species, is secreted in a groove. In this way, heavier sucking movements are necessary for the female to reach the secretion. Another possibility is that because of this groove, the female first places some saliva into the groove and then sucks up (SCHAIBLE & GACK, 1987). We have observed this several times (VANACKER, unpubl.). Because the possible secretions in the other *Oedothorax* species are superficial (i.e. not in a groove), females of this species do not have to execute pronounced bite and suck movements. Courtship of the kind seen in *O. apicatus* or simple contact during copulation as in *O. retusus* and *O. agrestis* could also have a gustatorial character. Gustatorial contact in these last species is not so obvious, because the contact is much shorter and the secretions are probably less. In *O. fuscus*, this contact is probably so short that it almost cannot be observed during copulation. It is also possible that there are secretions in *E. atra*. Superficial contacts between female mouthparts and male head structures to exchange secretions remain a possibility.

If we compare courtship and copulation behaviour of *Oedothorax* species with the other dwarf spiders, we can conclude that the courtship behaviour is comparable within the subfamily Erigoninae. *Oedothorax* species are characterized by a copulation of two insertions, which is typical for most dwarf spiders. This also appears in some other dwarf spider species, but there are also species whose copulations contain several series of insertions, such as *Erigone* species, *Tmeticus graminicolus*, etc. We observed in *E. atra* series of very short insertions, which can be linked to each other to form longer periods. SCHLEGELMILCH (1974) also mentioned this, but he claims an increasing duration of insertion; we found on the contrary more or less regular insertion times. The copulation duration, according to SCHLEGELMILCH (1974) is 100-150 minutes; in our results we found an average duration of  $83.5 \pm 7.78$  min ( $n=12$ ) per longer period. *Erigone dentipalpis* (Wider, 1843) and *Erigone longipalpis* (Sundevall, 1830) seem to have similar copulation behaviour to that of *E. atra* (SCHLEGELMILCH, 1978).

The copulation of many species in which the male possesses head structures, is characterised by an anchorage of the male head structures by the female chelicerae (*Hypomma bituberculatum* (Wider, 1834), *Walckenaeria corniculans* (O.P.-Cambridge, 1875): SCHLEGELMILCH, 1974). *O. gibbosus* only shows physical contact of the female chelicerae with the groove and hunch of the *gibbosus* male, during gustatorial courtship. SCHAIBLE & GACK (1987) suggested that the function of the male head structures is to fix the copulation posture. This is probably not the most common function, because there is, for example, in most cases no retained contact between the chelicerae and the male head structures during copulation of *O. gibbosus*.

*Oedothorax* species have a relatively short copulation duration, excepted for *O. gibbosus*, where average copulation duration is strikingly longer than that of the other *Oedothorax* species. The longest copulation duration belongs to *Erigone atra* (50'-75' / insertion) – but this last species has another copulation technique – and the shortest to *Tmeticus graminicolus* (5' per insertion). The extremely high copulation duration of *O. gibbosus* is very remarkable. Why, however, is such a long copulation necessary, if closely related species can achieve sperm transfer in a much shorter time? A longer copulation time leads to a higher risk of being caught by a predator. Possibly this risk is more pronounced for species living in open habitats than in more rare ones. There is for example no specific natural predator of *O. gibbosus* in the studied population in the public nature reserve Het Walenbos; the lycosid spider *Pirata hygrophilus* Thorell, 1872 occurs at high density but does not predate on *O. gibbosus* (VANACKER, unpubl.). That the copulation of the rare *O. agrestis* is short is in disagreement with the above-mentioned hypothesis. However, this species behaves rather calmly, which is comparable to the activity of the also rare *O. gibbosus*.

Multiple mating occurs very frequently in *Oedothorax* and *Erigone*. The number of couples that performed multiple mating in *O. gibbosus* was not very high in the described experiment, but in other experiments with longer observation periods multiple mating was also very frequent in both male morphs of *O. gibbosus* (VANACKER, unpubl.). The web has an important function in the reproduction of *Oedothorax* spiders. It seems reasonable to assume the importance of the web in reproduction decreases with the activity of the spiders.

The longer courtship and copulation time could also be a consequence of the occurrence of male dimorphism in this species caused by male competition and sperm competition. More ethological and genetic research, such as construction of a phylogenetic tree of *Oedothorax* on the basis of DNA, is necessary to give a decisive answer about this.

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