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# DIPLOMARBEIT

Titel der Diplomarbeit

## The spider *Heteropoda venatoria* and its visual system

Verfasser

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# Abstract – English

*Heteropoda venatoria* (Sparrasidae), like *Cupiennius salei* (Ctenidae), belongs to the Huntsmen spiders. They do not build any webs but live as sit-and-wait predators. Beyond that, with some exceptions on habitus and lifespan, there is no other information on *Heteropoda* in contrast to *Cupiennius* on which, thanks to numerous studies, huge knowledge could be gained during the last decades.

Therefore, but also because these two spiders live in similar habitats and in general show similar lifestyles and though have exceptional differences in size and position of their eyes, it is of great interest to take a closer look on the visual system of *Heteropoda*.

In two behavioural experiments and by measuring the visual fields, first data should be gained.

Using a goniometer we measured the expansions of the visual fields of the secondary eyes. It could be shown, that the secondary eyes cover almost all of the spiders surrounding with the AL eyes perceiving the very front of the spider, the PM eyes covering almost the entire upper hemisphere and the PL eyes covering great parts of the spiders' side, especially the backside. As the AM eyes do not reflect incident light, due to the lack of a tapetum, these eyes could not be investigated in this study. Only minor differences in size and form of the visual fields between males and females have been detected. All eyes show overlapping areas between and within the different eye types.

In the first behavioural experiment we wanted to find out if *Heteropoda* shows a visual stimulated behaviour and if it can distinguish between different targets, if it is able to perceive them at all. The spiders were set free in an experimental arena in which, in a first series of experiments, two black paper targets with different widths were simultaneously presented. It could be shown that the wider ones were preferred and that when targets of similar width were presented, an equal number of runs headed towards each. In a second series of experiments only one target was presented. As the number of runs heading towards them was decreasing the slender they became, one can say, that the eyes of *Heteropoda venatoria* allow a spatial resolution of at least 4-8°.

In the second behavioural experiment we took a closer look at the walking paths of *Heteropoda venatoria* and compared them with the walking paths of *Cupiennius*

*salei.* In numerous observations *Cupiennius* showed some kind of zigzagging on its way towards a target. It had been assumed that this way of running is a method to distinguish between targets at different distances and in general gives information about the foreground and background by using motion parallax. In this trial both spiders had to do 25 runs each in which no such zigzagging could be noticed for *Heteropoda venatoria,* which showed very direct and linear running paths. This suggests that *Heteropoda* uses other ways to gain distance information than *Cupiennius*, if it does at all.

Finally, in this study, first information on the visual system of *Heteropoda venatoria* could be gained and it could be shown, that the eyes of *Heteropoda venatoria* and *Cupiennius salei* are more alike as could have been expected by the size and the arrangement of their eyes.

# Abstract – German

*Heteropoda venatoria* (Sparrasidae) gehört wie auch *Cupiennius salei* (Ctenidae) zu den Jagdspinnen. Sie bauen keine Netze sondern ergreifen ihre Beute als sogenannte Lauerjäger. Drüber hinaus gibt es bis heute, mit Ausnahme von einigen wenigen Informationen bezüglich Körperbau und Lebensdauer, kaum Informationen zu *Heteropoda venatoria* im Gegensatz zu *Cupiennius salei*, über welche man in den letzten Jahrzehnten, dank zahlreicher Studien, großes Wissen erlangen konnte.

Auf Grund dieser Tatsache, aber auch auf Grund dessen, dass diese beiden Spinnenarten ein ähnliches Leben führen und in ähnlichen Habitaten vorkommen, und dennoch völlig unterschiedlich sind was die Größe und die Anordnung ihrer Augen anbelangt, ist es von großem Interesse das visuelle System von *Heteropoda venatoria* näher zu beleuchten. Mit Hilfe zweier Verhaltensexperimente und dem Vermessen der Sehfelder sollten erste Daten gewonnen werden.

Hierzu wurden mit Hilfe eines Goniometers die Ausmaße der Sehfelder der Sekundäraugen näherungsweise ermittelt um so auf die Gesichtsfelder schließen zu können. Es konnte gezeigt werden, dass diese einen Großteil der Umgebung der Spinne abdecken, wobei die AL Augen die Front betrachten, die PM Augen nahezu die gesamte obere Hemisphäre abdecken und die PL Augen für die Abdeckung der Seite, vor allem der hinteren Seite, verantwortlich sind. Die AM Augen konnten auf Grund des Fehlens eines Tapetums mit der hier angewandten Methode nicht untersucht werden. Weiters zeigten die Ergebnisse nur geringe Unterschiede zwischen den Augenfeldern der Weibchen und der Männchen, wobei erstere die etwas kleineren haben. Sowohl zwischen als auch innerhalb der einzelnen Augentypen gibt es Überlappungen der Gesichtsfelder.

Im ersten Verhaltensexperiment sollte herausgefunden werden ob *Heteropoda* ein visuell gesteuertes Verhalten zeigt und ob sie, sofern sie Objekte überhaupt wahrnimmt, zwischen verschiedenen Objekten unterscheiden kann. Die Spinnen wurden in eine Laufarena gesetzt in welcher in der ersten Versuchsreihe gleichzeitig zwei unterschiedlich breite schwarze Papierrechtecke präsentiert wurden. Es hat sich gezeigt, dass die breiteren bevorzugt wurden und, dass, bei ähnlich breiten Objekten, beide ähnlich oft angelaufen werden. In einer zweiten

Versuchsreihe wurde nacheinander immer nur ein Objekt, mit unterschiedlichen Breiten, präsentiert. Je schmäler diese waren umso weniger oft wurden sie angelaufen woraus geschlossen werden kann, dass die Augen von *Heteropoda venatoria* zumindest eine räumliche Auflösung von 4-8° erreichen.

Im zweiten Verhaltensexperiment wurden die Laufspuren von *Heteropoda venatoria* mit denen von *Cupiennius salei* verglichen. *Cupiennius* hat in zahlreichen Beobachtungen ein Art Zick-zack-Lauf gezeigt wenn sie sich auf ein Objekt zubewegt. Es wird angenommen, dass dieses Verhalten dazu dient, besser zwischen Objekten in unterschiedlichen Entfernungen unterscheiden zu können und so eine Art Tiefensehen auf Grund von Bewegungsparallaxe zu ermöglichen.

In diesem Experiment, in welchem beide Spinnen je 25 Läufe auf ein präsentiertes Objekt machen mussten, konnte gezeigt werden, dass *Heteropoda venatoria* keine Zick-zack- sondern vielmehr sehr geradlinige und direkte Läufe macht. Daraus kann geschlossen werden, dass sie, wenn überhaupt, auf eine andere Art Distanz- und Tiefeninformationen gewinnt.

In dieser Studie konnten erste Informationen über das visuelle System von *Heteropoda venatoria* gewonnen werden und in einem Vergleich mit *Cupiennius salei* gezeigt werden, dass die Funktion der Augen dieser Spinnen ähnlicher zu sein scheinen als deren Position und Größe dies vermuten ließen.

# Table of content

# 1. Introduction

## 1.1. *Heteropoda venatoria*

### 1.1.1. Heteropoda venatoria – systematics

The hunting spider *Heteropoda venatoria* (Linnaeus 1767) belongs to the family of Sparassidae – previously Heteropodidae. Sparassidae, sometimes referred to as huntsmen spiders (Australia and the United States of America), banana spiders (New Zealand and the United Kingdom) or giant crab spiders are distributed worldwide in temperate and tropical regions (Ibister & Hirst 2003). The cosmotropic Sparassidae include over 80 genera and about 700-800 species (Ibister & Hirst 2003; Jäger 1998). A more up to date source even claims that Sparassidae are the ninth largest spider family with more than 1100 species (Platnick 2010).

### 1.1.2. *Heteropoda venatoria* – habitus

*Heteropoda venatoria* is a large brown spider with a depress body and a decent dorsal pattern. Adult males have a smaller body, especially the opisthosoma, and longer legs than the females. In contrast to the females, the males have a black longitudinal stripe on the opisthosoma and a black area encircled by a light border on the prosoma (Fig. 1). Females and males have black dots all over their legs from which bristle like structures arise.

**Fig. 1:** *Heteropoda venatoria* male (top), female (bottom).

The mean body length of an adult spider is 2.2- 2.8cm and they have a leg span of 7-12cm (Edwards 2000). The name „giant crab spider" describes the alignment of the legs during resting position, that resembles that of crab spiders.

Although *Heteropoda venatoria* is similar in size to *Cupiennius salei* concerning leg span, the Sparassidae are far lighter due to their much more frail, even filigree, legs und body. Whereas an adult female of *Cupiennius salei* can weigh up to 5g the heaviest spider in this study of *Heteropoda venatoria* only weight 1.35g.

### 1.1.3. *Heteropoda venatoria* – life cycle

*Heteropoda venatoria,* as a vagrant species, does not build any webs to catch prey but is a sit-and-wait predator. Due to its ability to run very fast and because of its strong chelicerae (Edwards 2000) this spider is an effective hunter. The spider is not known to be specialized on certain prey but to feed on whatever comes along and whatever fits and can be overcome, even scorpions and bats (Bhattacharya 1941) – although it is questionable that these are common prey. Moreover, *Heteropoda sp.* is told to feed on a great variety of prey in some areas on the one hand but also reported to prefer certain prey, in other areas, on the other hand (Harries et al. 2008).

Despite the fact that *Heteropoda venatoria* can be found throughout tropic and subtropic regions of the world, this spider is often found associated with human settlements. This might be explained by the amount of prey that can be found next to human beings (Subrahamanyam 1944, Edwards 2000), which makes it therefore quite easy to find this spiders.

When mating and a successful insemination occurred in *Heteropoda venatoria,* it lasts between 12-14 days before a flat, disc-like egg sac is produced by the female (Ross et al. 1982). As the egg sac, which is on average 2cm in diameter, is carried around under the body with the help of the pedipalps the female stays relatively immotile (Biswas 2009). During this time it had been observed that the female does not feed. Usually this stage lasts 8-14 days. Ross et al. (1982) states an average number of 163 eggs per egg sac in laboratory and up to 400 eggs per egg sac in field. The first molt occurs inside the egg sac and the spiders reach adulthood after about 8-10 instars (males) and 9-12 instars (females) (Ross et al. 1982).

Ross and colleagues (1982) reported that the total life span of spiders of the species *Heteropoda venatoria* from egg to death is 1.4 years in average. In laboratory, as we observed in our own stock as well, females of this spider species were even found to survive for three years as adults (Rovner per com. in Ross et al. (1982)).

### 1.1.4. *Heteropoda venatoria* – poisonousness

Ibister & Hirst (2003) studied the poisonousness of spiders of the family Sparassidae. They reported that bites of spiders of this family were characterized by immediate pain lasting for about five minutes, associated with bleeding and or punctuate marks and redness. Although there are no confirmed bites of *Heteropoda venatoria* recorded, but only of *Heteropoda ssp*., and despite the fact, that there seem to be slight differences in the effects of bites between the different genera (Ibister & Hirst 2003), it is stated that these Huntsmen spiders cause only minor effects as described above.

### 1.1.5. *Heteropoda venatoria* – the eyes

Like most other spiders *Heteropoda venatoria* has eight simple camera-type eyes that can be distinguished according to their position (Fig. 2). They are arranged in two rows and can be categorized in principal eyes and secondary eyes. The principal eyes contain the anterior median eyes (AM) and the secondary eyes contain the posterior median (PM), the posterior lateral (PL), and the anterior median eyes (AM).

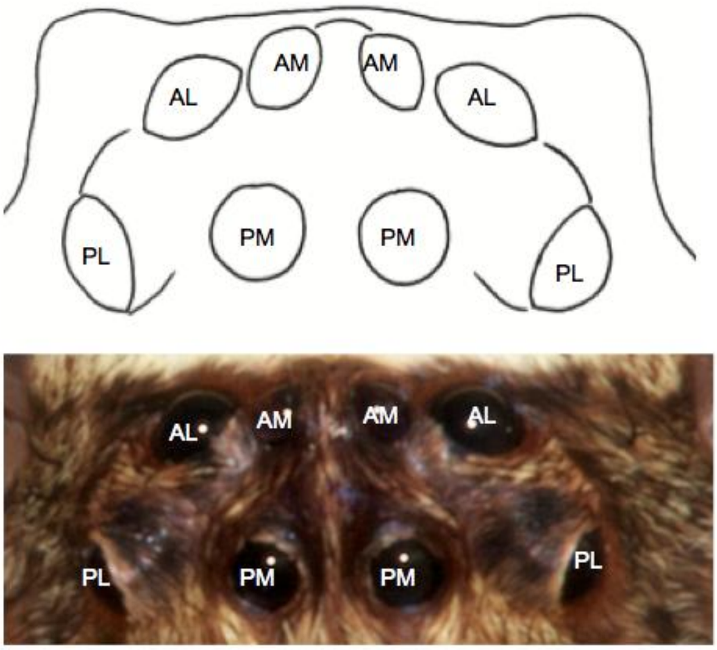


**Fig. 2**: Looking from above onto the dorsal Prosoma with the spider‘s front at the top. *Heteropoda venatoria* has eight eyes arranged in two rows, which are classified in principal eyes (Anterior median eyes, AM) and secondary eyes (Anterior lateral eyes, AL; Posterior median eyes, PM; Posterior lateral eyes, PL). Drawing (top; modified after Jäger 1998).

No information on retinae, possible tapeta or the visual fields can be found for *Heteropoda venatoria* and only very little knowledge on these can be found for other Sparassidae like *Leucorchestris arenicola* for example. What we do know about the eyes of this spider, and what is assumed for *Heteropoda venatoria*, too, is that the AM eyes have no tapetum and everted retinae (Norgaard et al. 2008, Blest 1985) which means that their rhabdomers point towards the incident light and the cell nucleus is situated proximal (Land 1985) (Fig. 3).

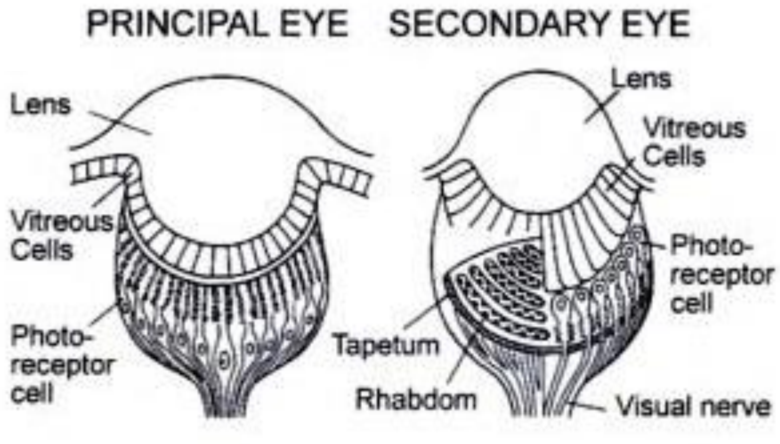


**Fig. 3:** Organisation of principal (AM) and secondary eyes (AL, PM, PL): The principal eyes consist of a lens, vitreous cells and photoreceptor cells with their cell nuclei proximal to the rhabdomers, which are pointing towards the incident light (everted eyes). The secondary eyes also consist of a lens and a cellular vitreous body. The cell nuclei is situated distal and the rhabdomers are turned away from the incident light (inverted eyes) (Grusch et al. 1997).

The secondary eyes on the other hand have no tapetum and inverted retinae with their rhabdomers turned away from the incident light and their cell nucleus being located distal (Land 1985).

A study by Fenk & Schmid (2010a) shows that there are four muscles attached to the eye tubes of the AM eyes of *Heteropoda venatoria.* These are thought to be used to move the retinae of these eyes as it is known in other spiders like *Cupiennius salei* or jumping spiders. In *Heteropoda venatoria* four eye muscles can be found whereas in *Cupiennius* only two (Kaps & Schmid 1996) and in Salticidae six eye muscles can be found (Land 1969).

### 1.1.1. Visual fields

An approximate estimation of the visual fields of the eyes of *Heteropoda venatoria* was one major goal of this investigation.

For some other spiders, like for example *Leucorchestris arenicola* and *Olios sp.,* two other members of the family of Sparrasidae, or *Cupiennius salei*, these are already known.

For *Cupiennius* an almost all-around view, except a posterior gap of about 10-15° (Land & Barth 1992) has been measured. The fields of view of the PM and PL eyes cover almost the entire upper hemisphere and about 40° of the lower hemisphere with only a small gap between the visual fields. The AL eyes cover the field directly in front of the chelicerae. The visual field of the two AM eyes allow binocular vision as they are the only eyes whose visual fields overlap and cover the areas directly in front of the spider. Furthermore the visual fields of the AM eyes overlap almost completely with the ones of the PM eyes (Land and Barth 1992; Kaps 1998) (Fig. 4).

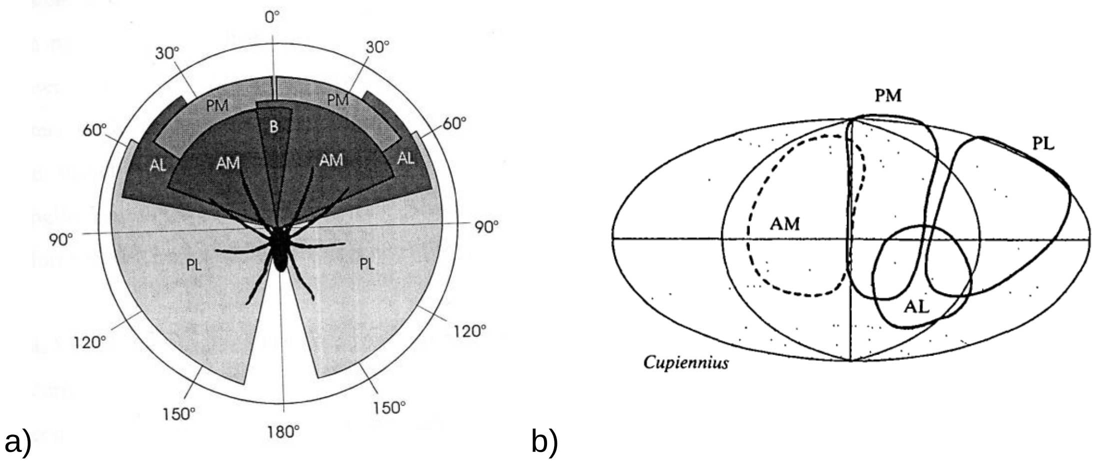


**Fig. 4:** Visual fields of *Cupiennius salei*. The fields of view of AM and PM eyes overlap for a large extent, whereas the AM eyes show a small area of overlapping visual fields. PM and PL eyes cover a large area in front of the spider and beside the spider with a small gap between them. The AL eyes have the smallest visual fields in front of the chelicerae. **a)** Scheme of Kaps after Land & Barth (1998). **b)** Drawing of Land and Barth (1992).

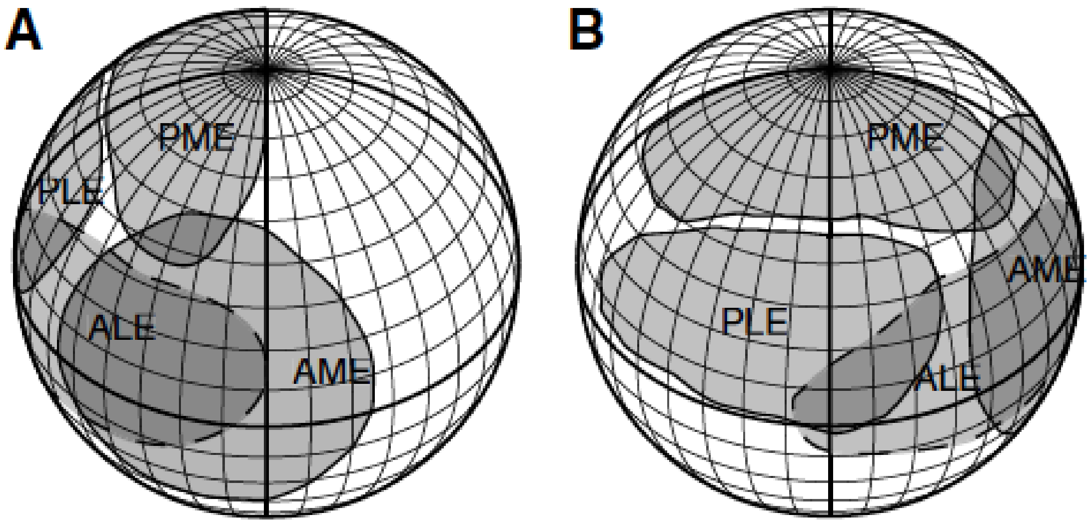


**Fig. 5:** (A) Frontal view of the visual fields of the four eyes on the right side of *Leucorchestris arenicola*. (B) Lateral view of the right-side visual fields. The equator defines the horizontal plane with the spider exhibiting its typical body posture. The dashed lines mark the boundaries of the AL eyes' visual fields (averages from five spiders, goniometric measurements). The visual fields of the principal eyes are based on histological measurements of the shape of the retina (averages from two spiders) (Norgaard et al. 2008).

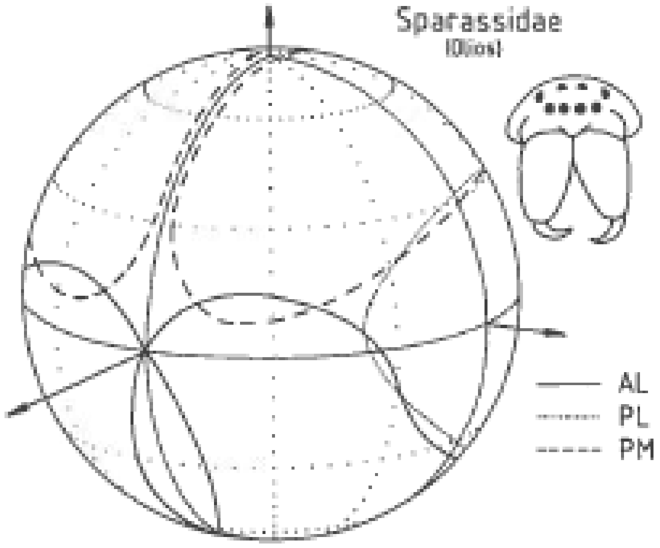


**Fig. 6:** Fields of view of the secondary eyes of *Olios sp.* plotted onto a globe with the spider at the centre. The globe is viewed from 15° above the equator, and 30° to the spider's longitudinal axis (Land 1985).

The visual fields of *Leucorchestris arenicola* have quite recently been investigated by Norgaard et al. (2008). The visual fields of the AL and PL eyes turned out to be similar in shape, both being horizontally elongated. They are slightly overlapping but provide an extended view of the surroundings along the horizon with only a gap of 40–50° at the rear in their combined visual fields. The visual fields of the PM eyes cover the remaining upper part of the hemisphere and the visual fields of the AM eyes were nearly circular and overlapping and show a distinct binocular overlap at almost 50° slightly above the horizon. Their visual fields also overlap considerably with the visual fields of the AL eyes (Fig. 5).

In *Olios sp*. the visual fields of the secondary eyes are similar in size and shape with the AL eyes looking forward and down, the PM eyes looking up and the PL eyes looking laterally with their visual field extending to the very rear (Fig. 6). Due to the fact that the AM eyes have no tapetum and therefore do not reflect any light the used method did not work for the AM eyes which is the reason why visual fields of these eyes could not be measured (Land 1985).

## 1.2. Aim

There is only little knowledge concerning *Heteropoda venatoria* and even on Sparassidae, in contrast to *Cupiennius salei.* Besides the mechanosensory system also the visual system of *Cupiennius* was focus of a great number of investigations and as *Cupiennius salei* seems to have a similar lifestyle as *Heteropoda venatoria* it seems to be interesting to study the visual system of *Heteropoda* as well and to compare it to the one of *Cupiennius*. Spiders of the Ctenidae and those of the Sparassidae, are nocturnal and most likely can be found on leaf litter. Therefore, because of their coexistence, it seems plausible that the spiders of these two families compete for food and shelter for example (Rego et al. 2005). Whereas it is well known, that *Cupiennius salei* lives on bromelias and banana plants, which are important plants as substrata for hunting and courtship behaviour (Barth 1993), we do not know that for *Heteropoda venatoria*.

What we do know is that both spiders live in similar habitats and have similar lifestyles. They are both nocturnal, do not build any webs but catch their prey as sit-and-wait predators and are of similar body size. Nevertheless, the arrangement of their eyes and the size of the different eyes are completely different. The difference in body structure and habitus suggests that *Heteropoda venatoria* uses other substrate for its activities. The depress body of this species seems to be a perfect adaptation for living in small cracks and crevices and indeed Edwards (2000) states, that spiders of this species usually can be found in such places and along with its adaptability to human habitations even in houses, barns, sheds, under boards, on the ground, and in other sheltered areas. These places and structures provide them a suitable alternative like dry vertical surfaces on which to hunt during the night and crevices which they can use to hide during the day (Ibister & Hirst 2003).

Nevertheless, these two families coexist and their members often live similar lives and, considering *Cupiennius salei* and *Heteropoda venatoria*, still differ completely in the arrangement and the size of the eyes (Fig. 7 and Fig. 8).

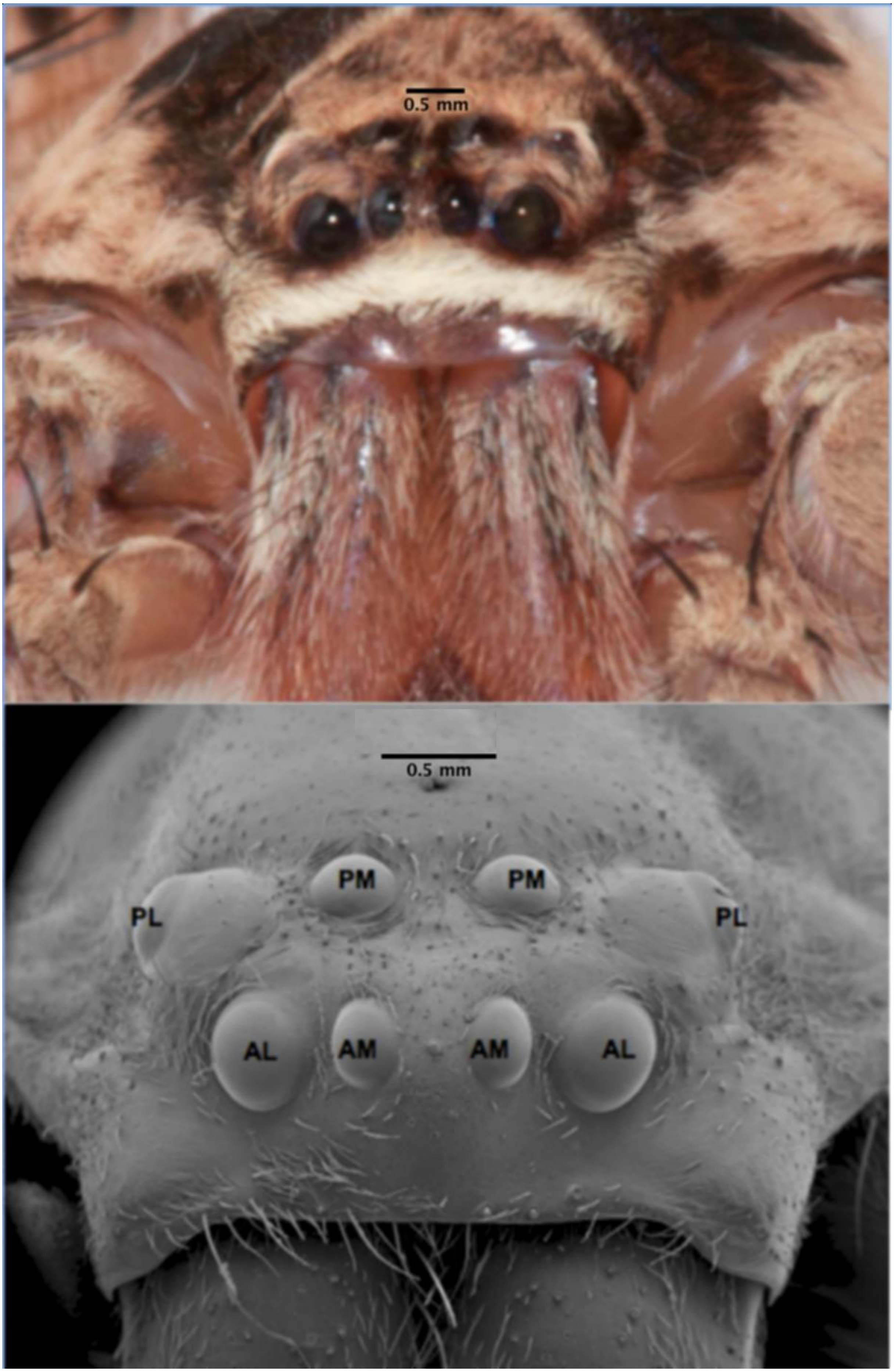


**Fig. 7:** A foto (top) and a REM picture (bottom) of *Heteropoda venatoria*: Anterior median eyes, AM; Anterior lateral eyes, AL; Posterior median eyes, PM; Posterior lateral eyes, PL.

**Fig. 8:** A foto (top) and a REM picture (bottom) (Zopf 2010) of *Cupiennius salei*: Anterior median eyes, AM; Anterior lateral eyes, AL; Posterior median eyes, PM; Posterior lateral eyes, PL.

Therefore the question arises whether these differences of eye position and eye size have a functional background and if so, what that might be.

As a consequence of their similar lifestyle and their different visual systems the aim of this study was to make first investigations on the eyes of *Heteropoda venatoria*. In detail, the aim was first of all to find out whether *Heteropoda venatoria* shows any visual guided behaviour when presented black targets in an experimental arena. If they do, and if they run towards them, do they also perform a simultaneous twofold choice between two different targets?

Another goal of this study was to determine the visual fields of the different eyes of this spider. Additionally, the visual fields of *Heteropoda venatoria* shall be compared with the ones of *Cupiennius salei*.

In a last experiment the walking paths of *Cupiennius* and *Heteropoda,* towards a target, shall be observed and compared to each other.

By these investigations we expect to gain information about the visual system of *Heteropoda venatoria* and to get an idea of whether the visual system of this spider is indeed that different from the one of *Cupiennius salei,* like the size and the position of the eyes would suggest.

# 2. Material and Methods

## 2.1. Animals

**Fig. 9:** *Heteropoda venatoria* male (left), female (right).

All experiments were carried out with adult females and males of the species *Heteropoda venatoria* (Sparassidae). The spiders were bred at the Department of Neurobiology of the Faculty of Life Sciences of the University of Vienna, Austria.

All spiders were bred at 25-28°C at a relative humidity of 70-80% under a 12:12 h light:dark cycle in individual glass jars and fed on flies (*Calliphora spp.)* once a week.

Males weighed from 0.777g to 1.350g and females weighed from 0.847g to 1.227g. There was no obvious difference in weight between males and females. The similar weight despite the bigger body of females is due to the longer legs of the males.

# 2.2. Investigations

## 2.2.1. Arena experiments

### 2.2.1.1. Arena

The spiders were set free in an experimental arena made of Styrofoam, which was 180cm long, 150cm wide and 90cm high. The arena furthermore was covered with a mosquito net for the spiders not being able to leave it in vertical direction. The mosquito net was of exceptional importance due to the ability of *Heteropoda venatoria* to run very fast. The colour of the arena which was situated in a homogenously white painted room was white. At the backside of the arena two targets made from black paper that differed in size were presented
The brightness in the arena was at any point between 630 – 730 Lux.

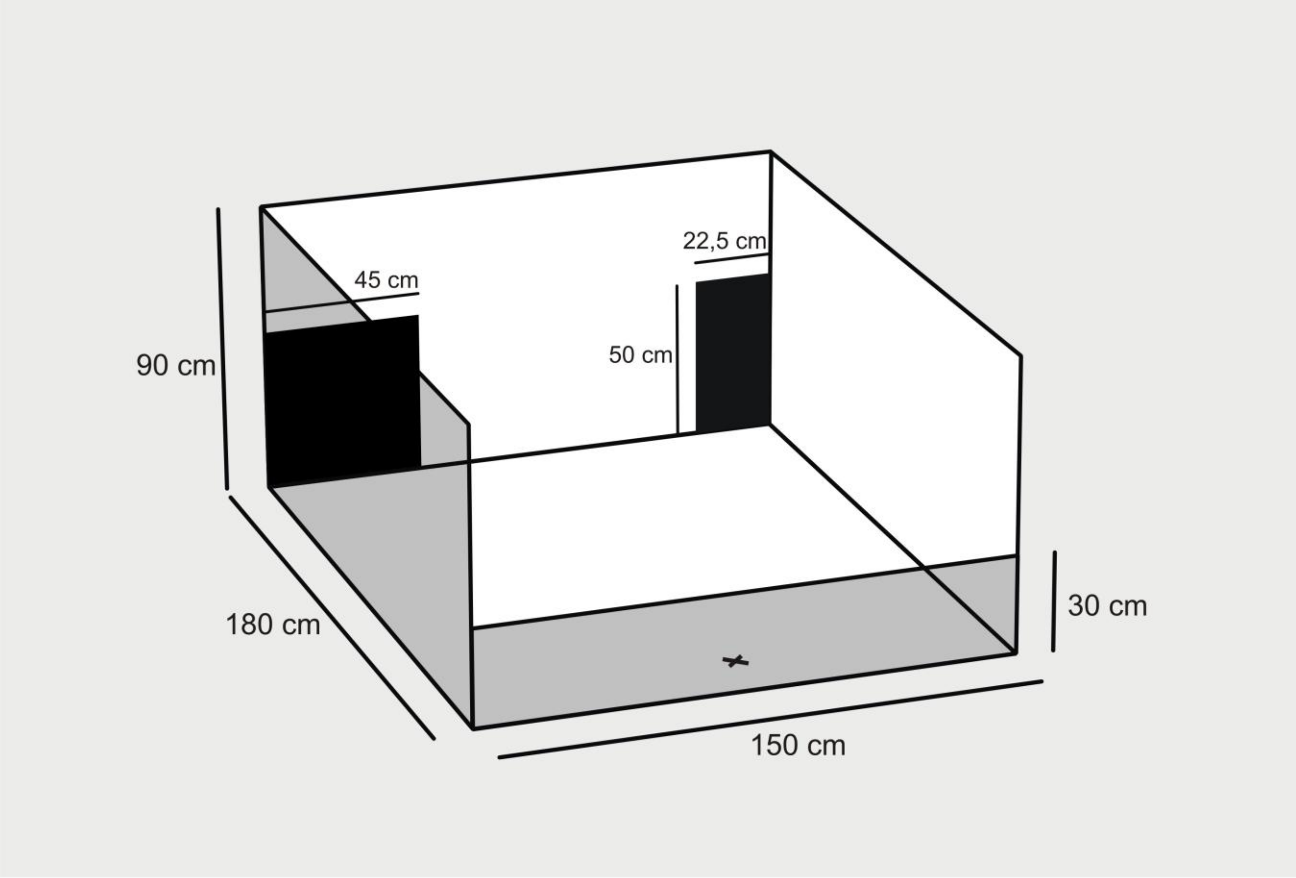


**Fig. 10**: Illustration of the experimental arena used in all experiments (size: 150cm wide, 180cm long and 90cm high). The spiders being released at the X and two black paper rectangles (50x45cm and 50x22.5cm) are presented at the back wall.

For the illumination of the arena three daylight fluorescent tubes had been used which were fixed above the arena. The starting point where the spiders were set free was at a distance of 170cm from the presented targets. Only vertical rectangles were used because they show a greater attractiveness at least for *Cupiennius salei* (Schmid 1998).

For setting free the spiders out of their glass jars a long iron stick with a soft pillow-like end was used. The animals were slightly touched until they left the jar. They were touched again when not immediately running towards a target or any other direction. All animals were released at the start point facing the presented targets.

After a run the animal was caught again and another spider was tested. Every spider had a pause of at least one hour between its runs.

In some cases a camera at the front of the arena, right behind the starting point, was installed to film the spiders’ runs.

The room temperature where the arena was situated was constant between 25°C – 28°C and the relative humidity was 36%.

#### 2.2.1.2. Target discrimination

The aim of this experiment was to measure the spatial resolution of the eyes of *Heteropoda venatoria*. Ten spiders did a total of 330 runs. This amount of runs was assembled in 11 different tests. In each test six spiders were used to perform five runs each. Therefore a total of 30 runs for each test was carried out. During these runs both sexes were used in a 50:50 ratio. Due to different reasons like death some of the spiders had to be replaced by new spiders of the corresponding sex.

In six of the 11 tests two targets were presented. During one run test no target at all was presented and in the remaining 4 tests only one target was presented.

Table 1 gives an overview of the runs and the corresponding size and number of targets.

**Table 1:** During 11 run tests the amount as well as the size of the presented targets varied.

| Test | Number of targets | Size of targets in cm |
|---|---|---|
| 1 | 2 | 45x50 vs. 22.5x50 |
| 2 | 2 | 22.5x50 vs. 45x50 |
| 3 | 2 | 28x50 vs. 45x50 |
| 4 | 2 | 45x50 vs. 34x50 |
| 5 | 2 | 40x50 vs. 45x50 |
| 6 | 2 | 45x50 vs. 40x50 |
| 7 | 1 | 22.5x50 |
| 8 | 1 | 17x50 |
| 9 | 1 | 11.5x50 |
| 10 | 1 | 6x50 |
| 11 | none | |

The spiders were released at the starting point and the different targets were presented at a distance of 170 cm. The targets had a height of 50cm and a variable width of 6-45cm, which corresponds to visual angles of 2° to 15° seen from the starting point (Table 2).

The amount of runs towards these different targets indicates their respective visibility.

**Table 2:** Width of the presented targets and their angular extension seen from the start point, 170cm away.

| Width of presented targets | Angular extension from 170cm |
|---|---|
| 45cm | 15° |
| 40cm | 14° |
| 34cm | 12° |
| 28cm | 10° |
| 22.5cm | 8° |
| 17cm | 6° |
| 11.5cm | 4° |
| 6cm | 2° |

To exclude possible side effects the presented targets had been changed in position after every test.

The experimenter watched and documented the runs and some of them were filmed.

### 2.2.1.3. The way of running

As the runs of *Heteropoda venatoria* and *Cupiennius salei* towards a target seemed to be different concerning the walking style, another aim of this investigation was to take a closer look onto these.

Before that any side preference was tested and eliminated in another extra trial by presenting only one target and changing the presentation side in two tests and as in each test an equal number of runs headed towards the different sides no side effects could be examined.

For the actual test 20 runs of *Cupiennius salei* and 20 runs of *Heteropoda venatoria* towards a target have been watched. The target had a width of 45cm and was placed on the left side of the rear arena wall, for *Heteropoda*, and on the right side for *Cupiennius*.

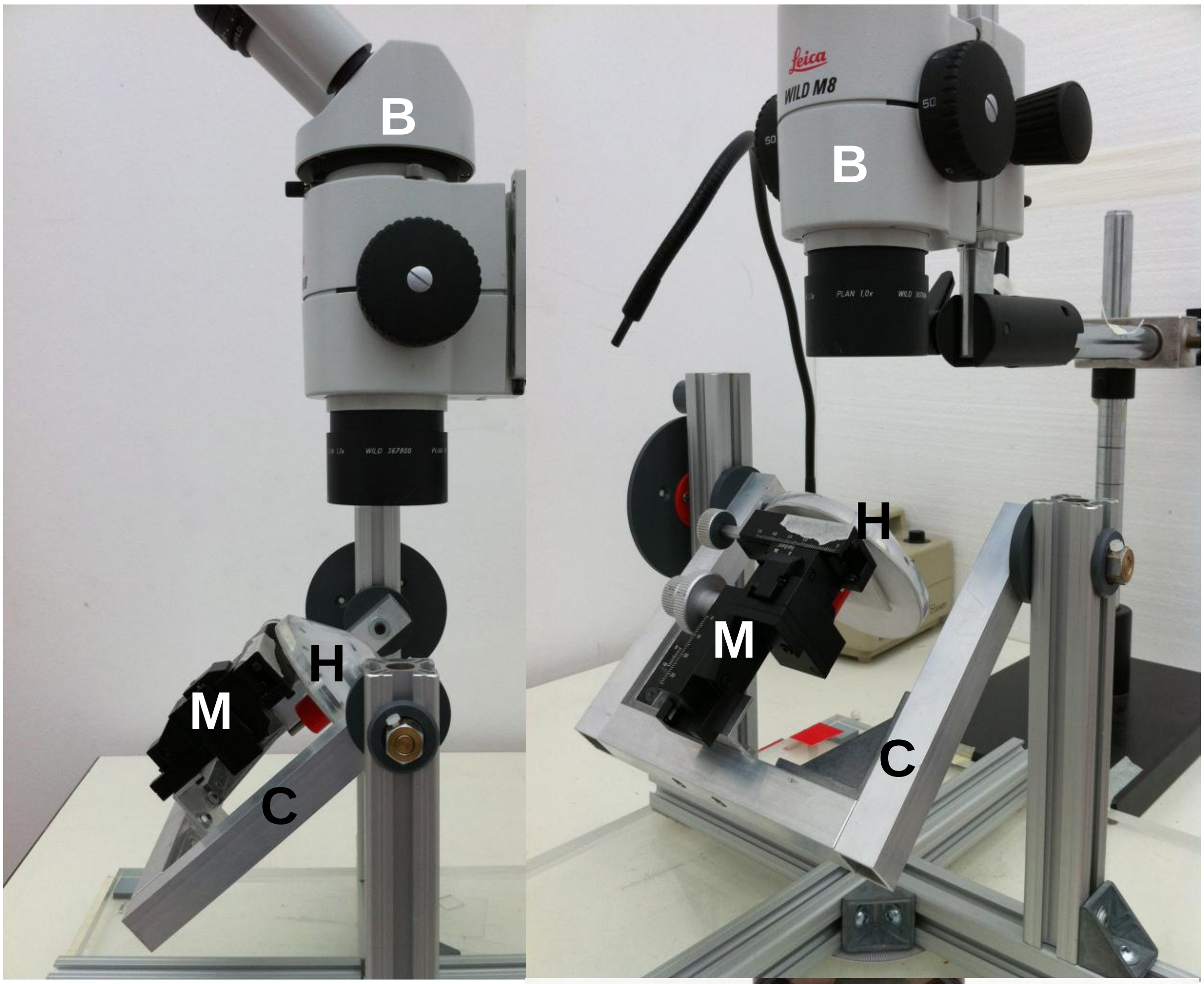
As soon as the spiders were released out of their glass jars they were observed very exactly and the investigator charted their line of running simultaneously.

### 2.2.2. Visual field

For measuring the visual fields, the spiders were immobilized by narcotizing them with $CO_2$. Therefore a tube connected with a $CO_2$ container was held into the glass jars of the spiders and due to the fact, that $CO_2$ is heavier than the surrounding air, it falls to the ground and after some seconds, when the spiders had stopped moving, the tube was removed and the narcotized spiders were taken out. Afterwards they were fixed with parafilm on the plastic hemisphere. First the whole body and the legs were fixed. Then the parafilm covering the eyes and the opisthosoma was removed in order to let the spider breath and to have free sight onto the eyes.

**Fig. 11:** Lateral (left) and top view (right) of a prepared *Heteropoda venatoria.* The animal was fixed on a plastic hemisphere with stripes of parafilm. Prosoma and Opisthosoma were kept free of parafilm in order to let the spider breath and to have a clear view onto the eyes.

After a few minutes the spiders were conscious again but unable to make the slightest move, which would have made it impossible to measure the size of the visual fields accurately. The spiders were examined with a goniometer using the fact, that in a well-focused eye with a reflecting tapetum, light which enters the eye will be reflected out almost exactly along its original direction of incidence (Land 1985).



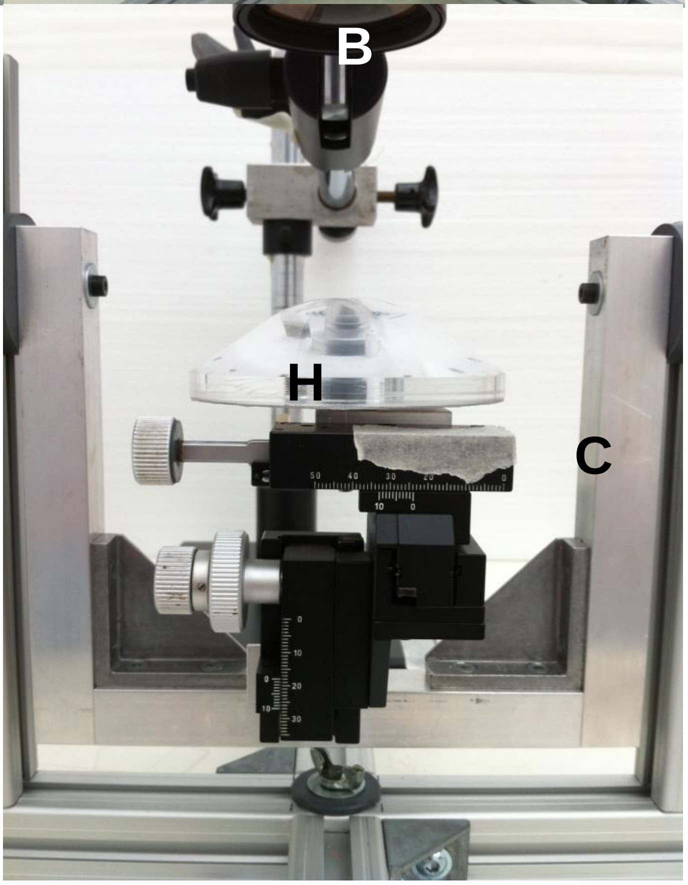


**Fig. 12:** Three different views of the used Goniometer: **B:** Binocular eyepiece for watching the reflections of the retinae when illuminated via a light guide. **H:** Hemisphere on which the spiders were fixed. It can be rotated for 360°. **M:** Micromanipulator, which was used to put the hemisphere into the correct position. **C:** Compensator, which can be swung forwards and backwards. It was used to swing the hemisphere forwards and backwards till no more light reflections out of the spiders' eyes could be seen. This was done in steps of 30°.

By using a binocular eyepiece, the light of a light guide and a micromanipulator, which was fixed into the goniometer, it was possible to estimate the angular extend of the retinae. The plastic hemisphere was fixed onto the micromanipulator and by rotating it with the fixed spider in steps of 30° and by swinging the hemisphere forwards and backwards it was possible to estimate the angular extend of the retinae. More exactly it is the extend of the tapetum that is estimated but retina and tapetum are usually coextensive (Land 1985). All but the AM eyes had been measured. This was due to the fact that these eyes have no tapetum and therefore the method used here was not working (Land 1985). Nevertheless, in order to guess the area, around which their visual fields extend, the centre of the AM eyes was appraised.

After the measurements, the parafilm was carefully removed and the spiders were, without any harm or injury, put back in their glass jars again.

The goniometer (Fig. 12) used for these measurements was built in the workshop at the department.

The values for each eye were gained by rotating the hemisphere with the fixed spider horizontally in steps of 30° from 0° (360°) to 330°, in 12 positions. In every of these positions the hemisphere, which was fixed on the micromanipulator in the goniometer, was swung forwards and backwards till no more light reflections out of the eyes could be seen. The values of the degrees for these two positions were noted. This was done twice for all 12 positions for every eye and two individuals of each sex. The results of both ratings were averaged for each sex. Afterwards the values of the left eyes and the values of the right eyes were averaged, too. Furthermore the values of each eye from 0°-150° and from 180°-330° were mirrored and averaged as the forward values for 0° are equivalent to the backward values for 180°, 30° are equivalent to 210°, 60° are equivalent to 240° and so on. The averaged and final gained data are illustrated in Table 3.

## 2.3. Data acquisition

### 2.3.1. Target discrimination

Each run was protocolled by the experimenter. Different parameters of each run, as to be the direction of the run and the walking path, were recorded. Some runs, for further investigations and presentation, had been filmed by a camera.

In order to correctly collect the data of the walking paths the spiders were set free and the experimenter simultaneously drew the path into an arena illustration.

### 2.3.2. Goniometer

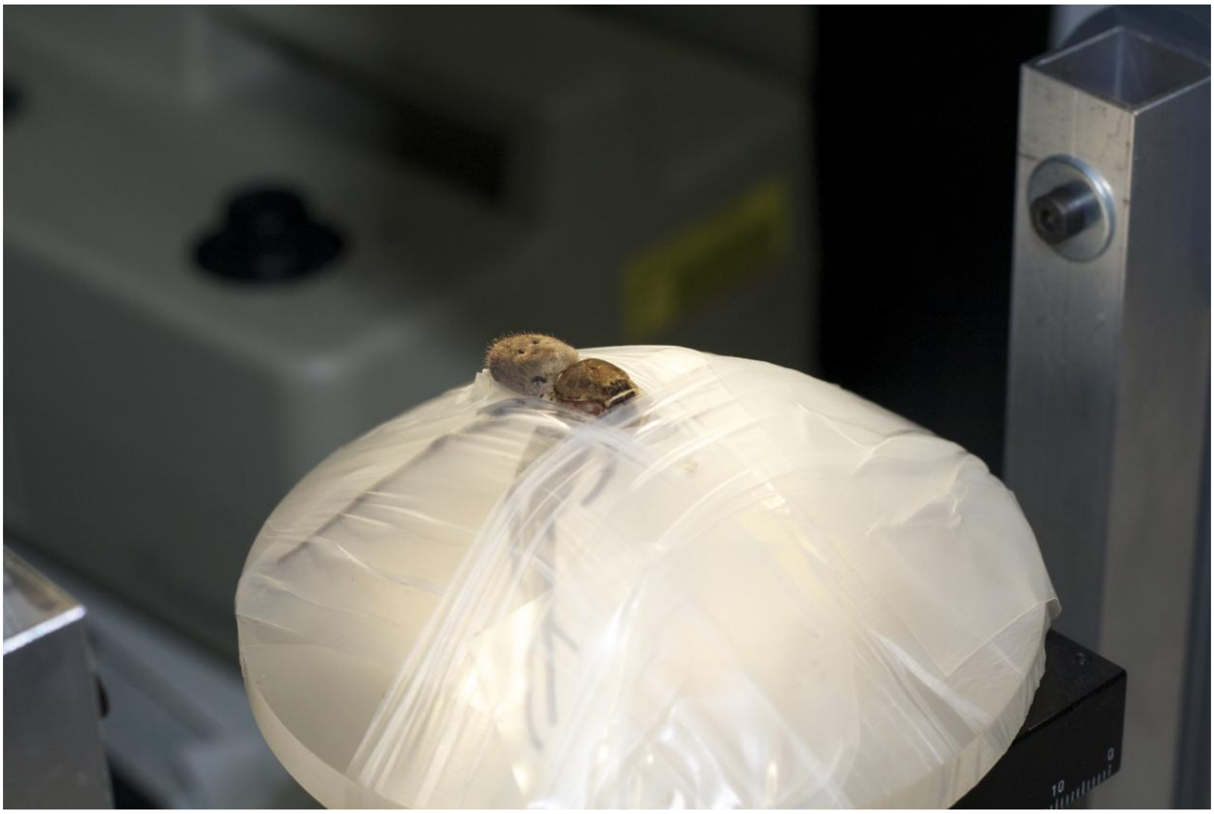


**Fig. 13:** *Heteropoda venatoria* (female) fixed on a plastic hemisphere and positioned in the goniometer device. Light from above illuminates the spider. A micromanipulator on which the hemisphere was installed allows moving the spider in any position needed.

The method used to measure the size of the visual fields, a tapetum presupposed, makes use of the fact that light, which enters the eye, will be reflected out almost exactly along its original direction of incidence (Land 1985). By using a goniometer, a binocular eyepiece, a light source, and by rotating the spider it is possible to estimate the angular extend of the tapetum which is supposed to be coextensive with the retina (Fig. 12). For further details on how the values of the visual fields were estimated see “2.2.2 Visual Field”.

## 2.4. Analysis and statistics

All statistical analysis where carried out with “SPSS Statistics” (Version 19, IBM, New York, USA).

As there had been at least one hour of time between the runs of the same spider, and it had not been acted on the assumption that *Heteropoda venatoria* is able to remember its runs, the arena and the presented targets, the runs of each spider were treated as independent trials. Using $\text{Chi}^2$ test $P$ is the significance of the $H_o$ expectation.

# 3. Results

## 3.1. Target discrimination

A total of 330 runs with 10 animals were carried out. Eleven different target combinations were used, summed up in 10 experiments, in which the width of the presented targets varied. Although six spiders had to run five times at every combination, four of them had to be replaced by new spiders of the corresponding sex, due to death – their adult life expectancy had been reached - which summed up to 10 spiders.

In Fig. 14 the results as well as the experimental arena of one of the run setups is shown in a figurative display.

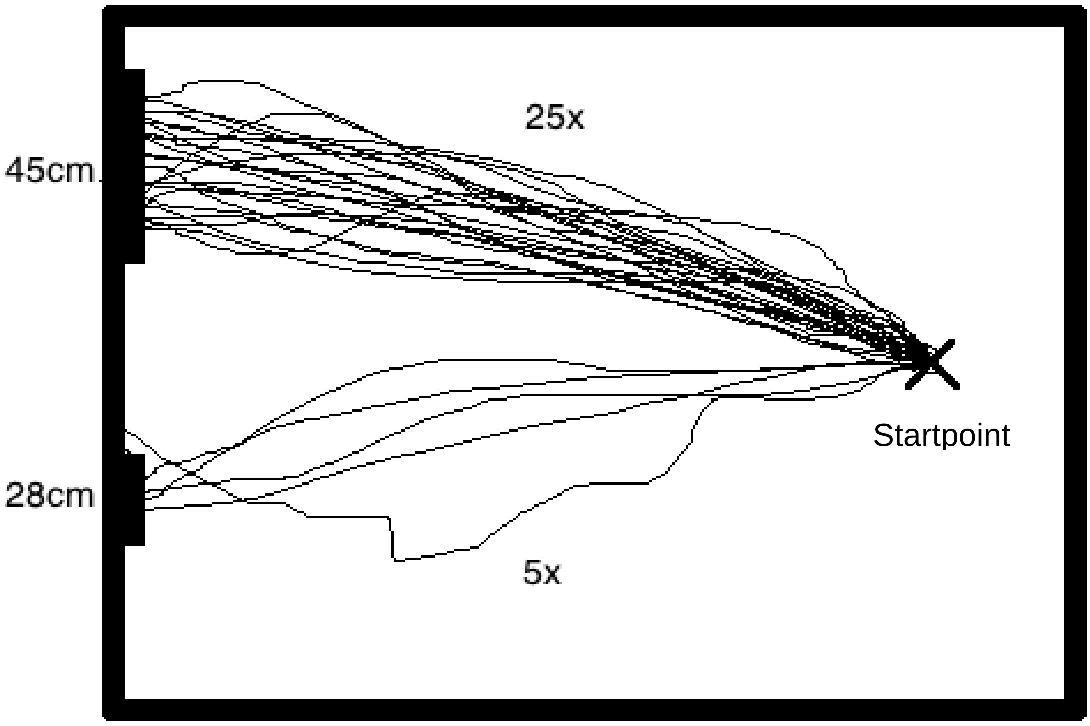


**Fig. 14:** Schematic illustration of the experimental arena and two targets presented at the distal arena wall. 25 out of 30 runs pointed towards the bigger target. X= Start point, where the spiders had been released out of their glass jars with the targets being 170cm away.

All targets presented in this study had been of equal height and differed only in width.

In the first experiment two targets, 45cm and 22.5cm, were presented and 26 out of the 30 runs headed towards the wider target whereas the remaining 4 runs headed anywhere in the arena. In order to exclude possible side effects the second experiment was performed with the same targets but changed positions. A similar result was obtained with only two runs towards the slender target, three runs heading beside the target at the wall of the arena and the rest heading to the wider target. The data gained in these two experiments were merged referred to as experiment 1 with 60 runs in which 2 runs headed towards the slender target, 51 headed towards the wider target and 7 runs going anywhere in the arena (Fig. 15). Leaving out the runs that headed anywhere this is a highly significant result ($P<0.001$).

In the second experiment a 45cm wide and a 28cm wide target were presented. In this trial 25 out of 30 runs aimed towards the wider target whereas five pointed towards the 28cm wide one (Fig. 15). Again, the spiders significantly ($P<0.001$) distinguished between the presented targets.

In the third experiment the targets were 45cm and 34cm. This time only a small majority, 16 runs, headed towards the wider target and no significance between the two targets could be measured ($P=0.102$). The other runs, 14 out of 30, aimed either towards the slender target, eight runs, or anywhere in the arena, six runs.

In the fourth experiment 40cm and 45cm targets were used. The majority of runs headed towards the wider target even though they represented only 40% of the total runs. The other 60% equally aimed either towards the slender target, nine runs, or anywhere, nine runs. No significance was found here ($P=0.513$).

In the fifth experiment the targets were of equal size in order to see whether this constellation would show an equal distribution. In fact, the results of this showed an almost equal number of runs towards the targets presented - 16 runs towards one and 13 runs towards the other target, out of 30. The remaining run headed anywhere at the arena wall.

In the experiments 6-9 it should be determined if the spiders run towards the wider targets, being able to perceive and discriminate both, or whether they cannot see the slender targets. Therefore only one target was presented in any of these experiments.

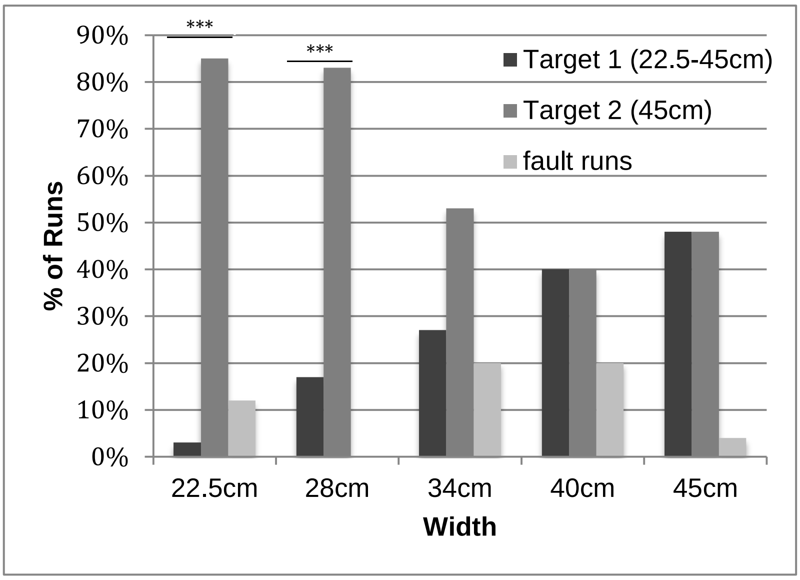


**Fig. 15:** The percentage out of 30 runs (except: 60 runs in 22.5cm) towards different targets presented. X-axis: The width of the presented targets. Dark grey: representing the "Target 1"; Grey: representing the "Target 2" (45cm); Light grey: representing the "fault runs" in the arena. Y-axis: The percentage of the total number of runs towards either the "Target 1", the "Target 2" or "fault runs" in five different setups. These differ only in the width of the "Target 1" (22.5; 28cm; 34cm; 40cm; 45cm). $^*P<0.05$; $^{**}P<0.01$; $^{***}P<0.001$

In the sixth experiment one 22.5cm wide target on the right side of the rear arena wall was used. 22 out of the 30 runs, 73.4%, headed anywhere whereas the remaining runs, 26.6%, pointed towards the target.

In the experiments seven to nine the target presented was continuously reduced in size so that the width of the target contracted from 22.5 to 17cm in the seventh, to 11.5cm in the eighth and to 6cm in the ninth experiment.

The seventh experiment showed a similar result like the sixth. Only this time 21 runs headed anywhere and one run more than in the previous trial, 9, 30%, aimed towards the target (Fig. 16).

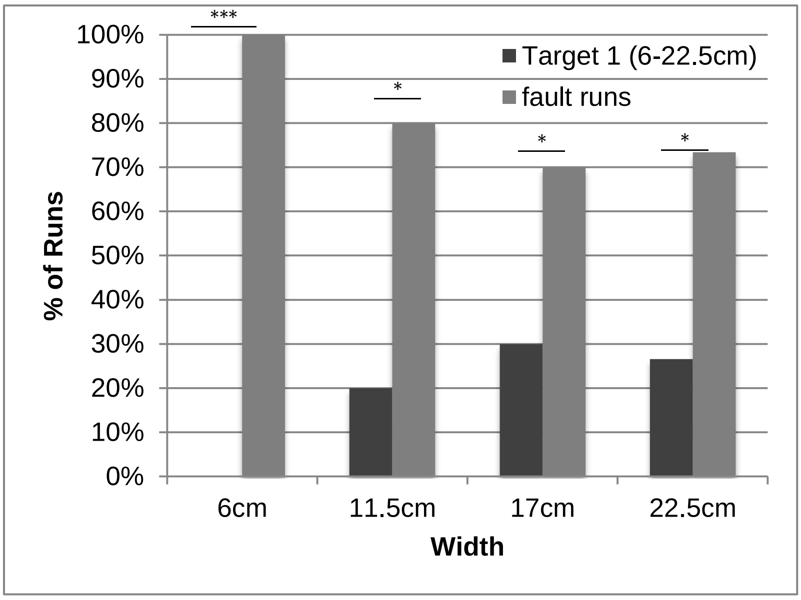


**Fig 16:** The percentage out of 30 runs towards different sized targets when only one target was presented. X-axis: The width of the presented target. Light grey: representing the "fault runs". Y-axis: The percentage of the total number of runs towards either the "Target 1" (dark grey) or "fault runs" (light grey) in four different setups. These differ only in the width of the targets (6cm; 11.5;cm 17cm; 22.5cm). $^*P<0.05$; $^{**}P<0.01$; $^{***}P<0.001$

In the last two experiments, in which only one target was presented, similar results have been gained.

As can be seen in Fig. 16 only six runs, i. e. 20%, of the eighth experiment headed towards the target whereas the vast majority of runs, 24 out of 30, headed anywhere. In the experiments 6-8 the spiders significantly (*P*<0.05) more often ran anywhere in the arena.

In the ninth experiment, in which only one target was presented the target only had a width of 6cm. The results in Fig. 16 show that none of the runs performed by the spiders aimed this target but all went anywhere, which results in an utmost significance (*P*<0.001).

Finally in the tenth and last experiment no target at all was presented. The results of this trial show that all runs headed towards different points in the arena. There was no point in the arena towards which a majority of runs headed to.

## 3.2. The way of running

As can be seen in Fig. 17 the walking paths differ between *Heteropoda venatoria* and *Cupiennius salei.* The first tends to run in a direct, straight way towards the target whereas the walking path of *Cupiennius salei* shows a zigzagging style. In this trial, 20 runs had to be performed by two spiders of both spider families. All of the 20 runs of *Heteropoda* were almost linear whereas all of the 20 runs of *Cupiennius* showed at least at the beginning of their walking paths zigzagging.

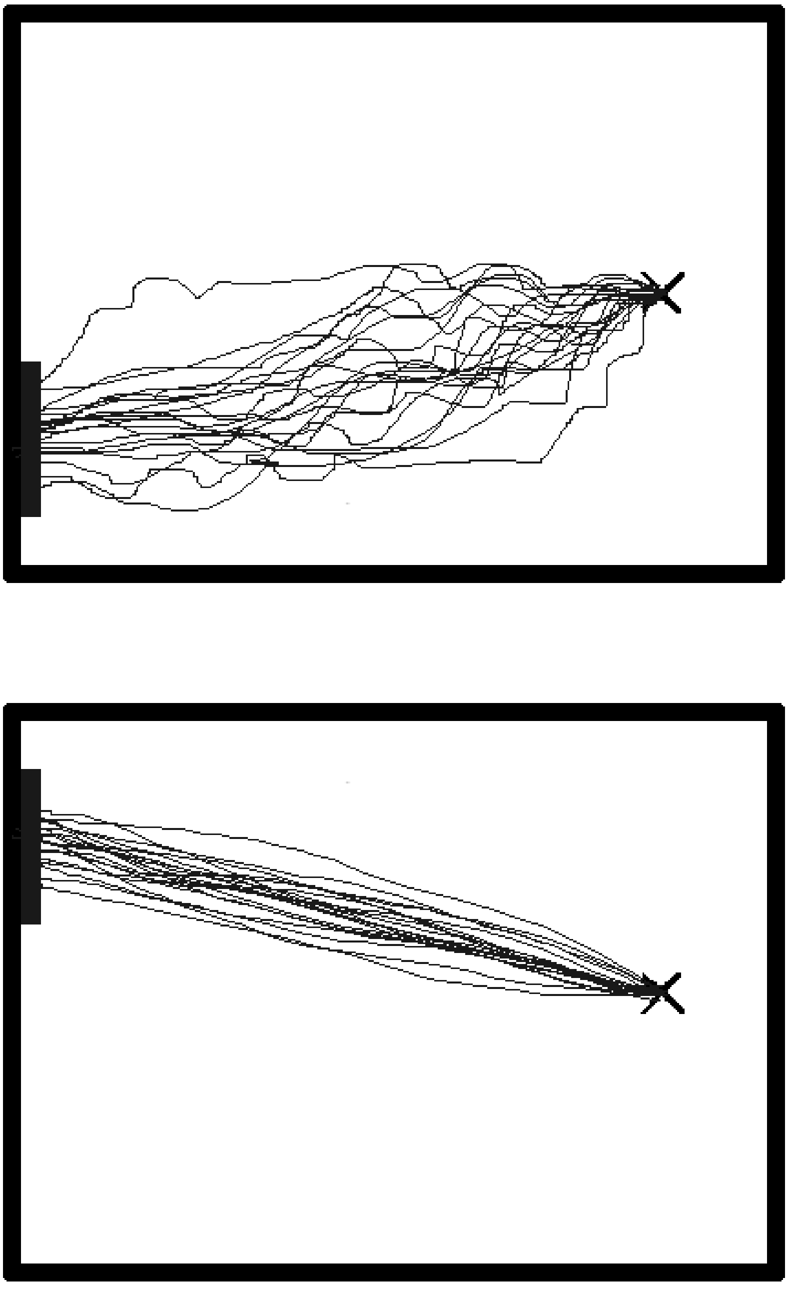


**Fig. 17**: The walking paths of *Cupiennius salei* (top) and *Heteropoda venatoria* (bottom). *Cupiennius* shows some kind of zigzagging towards the target whereas *Heteropoda* shows a more direct, linear walking path towards the target.

## 3.3. Visual fields

Two female and two male *Heteropoda venatoria* have been used to measure the visual fields. For both sexes two measurements have been done whose results have been averaged. Afterwards, data of the corresponding counterpart eyes have been mirrored and averaged again. Finally we got the very simplified Table 3, which shows the averaged data that were used to design the visual field illustrations (Fig. 18 and Fig. 19).

**Table 3:** Data of the visual field measurements averaged from four animals. For each sex two individuals had been used and the results of both ratings were averaged. A further, more detailed explanation is to be found in "Visual Fields" (2.2.2.).

| Male | | | | | | Female | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **AL Position** | left | | **AL Position** | right | | **AL Position** | left | | **AL Position** | right | |
| | forewards | backwards | | forewards | backwards | | forewards | backwards | | forewards | backwards |
| **0°** | 53 | 41 | **0°** | 53 | 41 | **0°** | 38 | 38 | **0°** | 38 | 38 |
| **30°** | 79 | 21 | **30°** | 27 | 53 | **30°** | 54 | 19 | **30°** | 21 | 53 |
| **60°** | 78 | 12 | **60°** | 14 | 68 | **60°** | 71 | 12 | **60°** | 13 | 67 |
| **90°** | 73 | 11 | **90°** | 11 | 73 | **90°** | 70 | 11 | **90°** | 11 | 70 |
| **120°** | 68 | 14 | **120°** | 12 | 78 | **120°** | 67 | 13 | **120°** | 12 | 71 |
| **150°** | 53 | 27 | **150°** | 21 | 79 | **150°** | 53 | 21 | **150°** | 19 | 54 |
| **180°** | 41 | 53 | **180°** | 41 | 53 | **180°** | 38 | 38 | **180°** | 38 | 38 |
| **210°** | 21 | 79 | **210°** | 53 | 27 | **210°** | 19 | 54 | **210°** | 53 | 21 |
| **240°** | 12 | 78 | **240°** | 68 | 14 | **240°** | 12 | 71 | **240°** | 67 | 13 |
| **270°** | 11 | 73 | **270°** | 73 | 11 | **270°** | 11 | 70 | **270°** | 70 | 11 |
| **300°** | 14 | 68 | **300°** | 78 | 12 | **300°** | 13 | 67 | **300°** | 71 | 12 |
| **330°** | 27 | 53 | **330°** | 79 | 21 | **330°** | 21 | 53 | **330°** | 54 | 19 |
| **PL Position** | left | | **PL Position** | right | | **PL Position** | left | | **PL Position** | right | |
| | forewards | backwards | | forewards | backwards | | forewards | backwards | | forewards | backwards |
| **0°** | 48 | 45 | **0** | 48 | 45 | **0°** | 43 | 27 | **0°** | 43 | 27 |
| **30°** | 44 | 55 | **30** | 54 | 35 | **30°** | 35 | 48 | **30°** | 48 | 26 |
| **60°** | 37 | 65 | **60** | 69 | 34 | **60°** | 28 | 54 | **60°** | 66 | 27 |
| **90°** | 34 | 75 | **90** | 75 | 34 | **90°** | 27 | 60 | **90°** | 60 | 27 |
| **120°** | 34 | 69 | **120** | 65 | 37 | **120°** | 27 | 66 | **120°** | 54 | 28 |
| **150°** | 35 | 54 | **150** | 55 | 44 | **150°** | 26 | 48 | **150°** | 48 | 35 |
| **180°** | 45 | 48 | **180** | 45 | 48 | **180°** | 27 | 43 | **180°** | 27 | 43 |
| **210°** | 55 | 44 | **210** | 35 | 54 | **210°** | 48 | 35 | **210°** | 26 | 48 |
| **240°** | 65 | 37 | **240** | 34 | 69 | **240°** | 54 | 28 | **240°** | 27 | 66 |
| **270°** | 75 | 34 | **270** | 34 | 75 | **270°** | 60 | 27 | **270°** | 27 | 60 |
| **300°** | 69 | 34 | **300** | 37 | 65 | **300°** | 66 | 27 | **300°** | 28 | 54 |
| **330°** | 54 | 35 | **330** | 44 | 55 | **330°** | 48 | 26 | **330°** | 35 | 48 |
| **PM Position** | left | | **PM Position** | right | | **PM Position** | left | | **PM Position** | right | |
| | forewards | backwards | | forewards | backwards | | forewards | backwards | | forewards | backwards |
| **0°** | 44 | 74 | **0°** | 44 | 74 | **0°** | 43 | 63 | **0°** | 43 | 63 |
| **30°** | 49 | 19 | **30°** | 25 | 70 | **30°** | 48 | 13 | **30°** | 16 | 64 |
| **60°** | 54 | 8 | **60°** | 11 | 60 | **60°** | 55 | 8 | **60°** | 10 | 58 |
| **90°** | 56 | 7 | **90°** | 7 | 56 | **90°** | 55 | 7 | **90°** | 7 | 55 |
| **120°** | 60 | 11 | **120°** | 8 | 54 | **120°** | 58 | 10 | **120°** | 8 | 55 |
| **150°** | 70 | 25 | **150°** | 19 | 49 | **150°** | 64 | 16 | **150°** | 13 | 48 |
| **180°** | 74 | 44 | **180°** | 74 | 44 | **180°** | 65 | 43 | **180°** | 65 | 43 |
| **210°** | 19 | 49 | **210°** | 70 | 25 | **210°** | 13 | 48 | **210°** | 64 | 16 |
| **240°** | 8 | 54 | **240°** | 59 | 11 | **240°** | 8 | 55 | **240°** | 58 | 10 |
| **270°** | 7 | 56 | **270°** | 57 | 7 | **270°** | 7 | 55 | **270°** | 55 | 7 |
| **300°** | 11 | 60 | **300°** | 54 | 8 | **300°** | 10 | 58 | **300°** | 55 | 8 |
| **330°** | 25 | 70 | **330°** | 49 | 19 | **330°** | 16 | 64 | **330°** | 48 | 13 |

Due to the fact that the principal eyes, the AM eyes, do not have a tapetum and therefore could not be used for this kind of measurement to estimate the visual field, no data was gained for these eyes, which is to be done in another investigation. However, the positions of the central points of the AM eyes were investigated to be at 33° to the right and to the left, respectively, with 0° being at the very front of the spider between the AM eyes.

The maintained data suggest that *Heteropoda venatoria* is able to perceive almost 360° of its surroundings. Moreover, the different eyes have different fields of view and cover different parts of the environment. There are only minor differences between males and females in the form of the visual fields but little more differences in the size with the females showing a bit smaller visual fields (Fig. 18 and Fig. 19).

The PM eyes cover almost the entire upper hemisphere with a relatively large overlap at the upper backside and an uncovered area at the upper frontside. The maximal extend of the visual fields of these eyes towards the side is around 70° (Fig. 18).

In both, females and males, the PL eyes cover a large part of the back hemisphere with the bigger part covering the upper backside. In males there is a small overlap of about 10° whereas the females showing a gap of about 10° between the PL eyes. Furthermore the males PL eyes cover the lower backside to a greater extend (Fig. 18 and Fig. 19).

The AL eyes are the ones responsible for covering the spiders' front. There is a gap between them in the very front of about 20° in both sexes. The AL eyes are those eyes which show the greatest extend towards the ground with over 50° towards the ground in females and over 60° in males, measured from the equator.

All secondary eyes show areas of overlapping visual fields with a small area where all three cover the same environmental surrounding (Fig. 18 and Fig. 19).

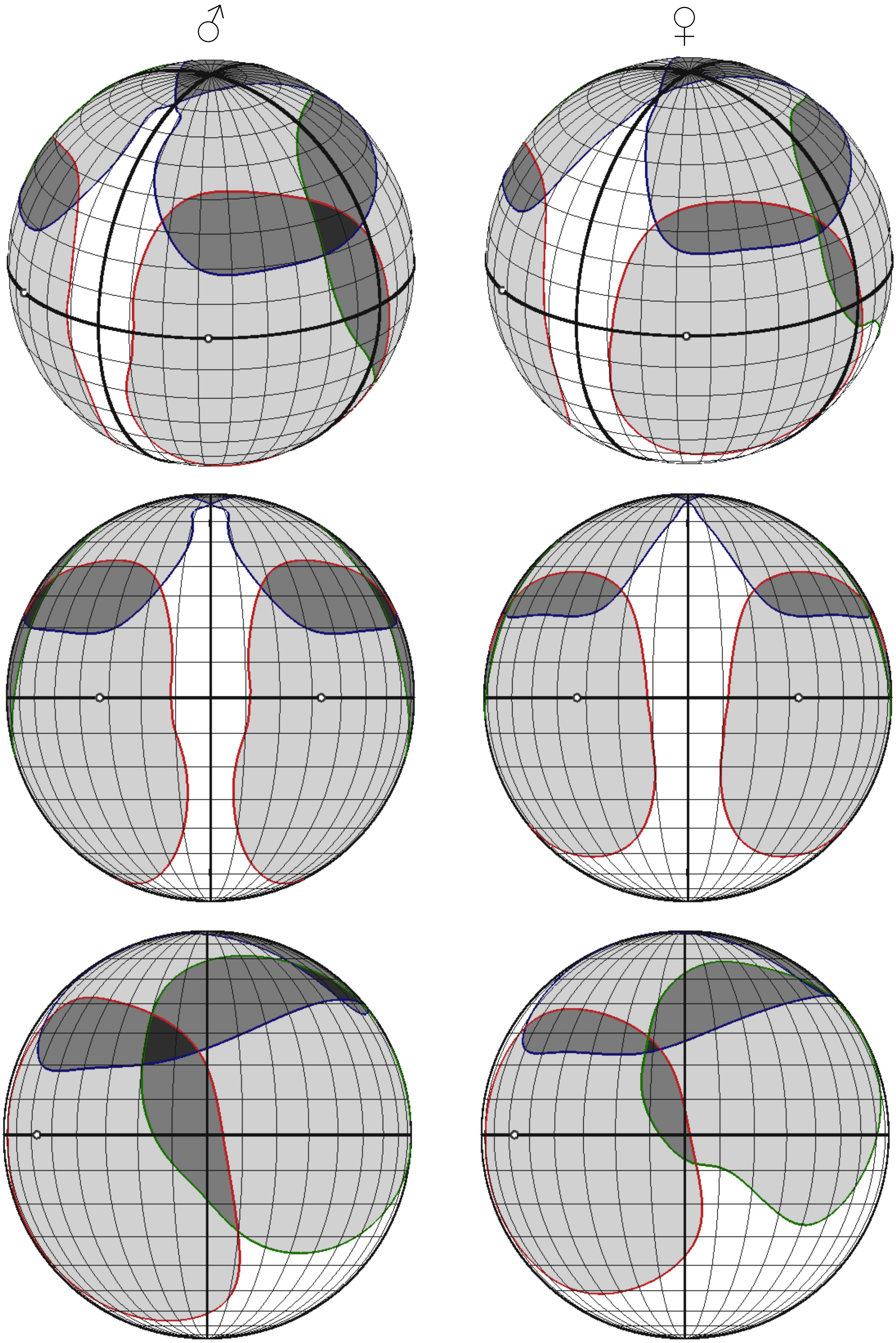


**Fig. 18:** Visual fields of *Heteropoda venatoria* plotted onto a globe with the spider sitting in the centre. Looking onto the left front side (top), the very front (middle) and the left side (bottom). The different eyes are encircled in different colours (AL red, PM blue, PL green). The small circles indicate the centre of the AM eyes. Right-hand-side: female; Left-hand-side: male.

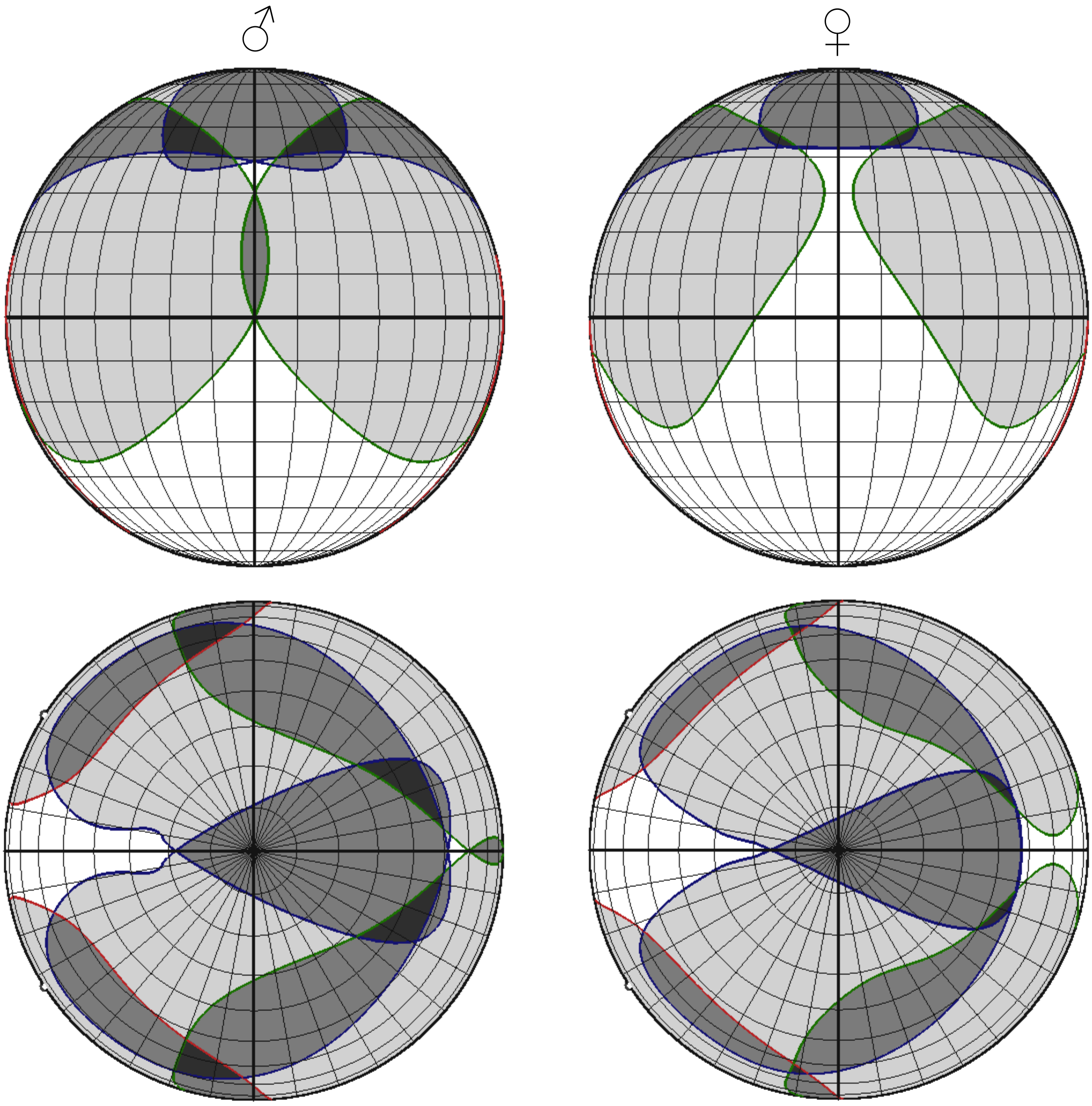


**Fig. 19:** Visual fields of *Heteropoda venatoria* plotted onto a globe with the spider sitting in the centre. Looking onto the back side (top) and the top with the front side being on the left (bottom). The different eyes are encircled in different colours (AL red, PM blue, PL green). The small circles indicate the centre of the AM eyes. Right-hand-side: female; Left-hand-side: male.

# 4. Discussion

## 4.1. Target discrimination

In this first experiment the aim was to find out if *Heteropoda venatoria* can see at all and if it shows visual guided behaviour. Therefore two black targets made from paper, which differed in width, were presented at the rear wall of an experimental arena. A black target is likely to be interpreted as some kind of retreat or hideout. In nature trunks of trees, stones, crevices and other similar retreats are always darker than the surrounding or at least show great difference in contrast concerning the surroundings. The black targets used here show great contrast and seem to be darker and less illuminated than the surrounding arena and therefore seem to be acceptable retreats.

In all these tests the wider targets were favoured in comparison to the slender targets. When two targets of similar size were presented the number of runs towards each of them was almost the same. A reason for this might be that a wider target is interpreted as a better and more secure hideout and a slender target probably is not worth running towards it.

As *Heteropoda* showed visual guided behaviour the aim of the next experiment was to find out about the quality of its visual system. Therefore only one target, which varied from 22.5cm to 6cm, was presented. As can be seen in Fig. 16, the slender the targets became the less runs headed towards them. Whereas 26.6% of all runs headed towards a single target with a width of 22.5cm none of the runs headed towards a single target when it was only 6cm wide. This suggests that a target 22.5cm wide, which had a spatial expansion of about 8° (Table 2), concerning the target being at a distance of 170cm, seems to be within the spatial resolution of the spiders. This size may be perceived by all of the spiders but only seemed attractive to a minority of them as a “retreat” because that size may not be interpreted as good enough.

Nevertheless, taking into account a spatial resolution of about 8° this only seems to be an average value in comparison to other spiders’ spatial resolution, down to 1° for *Cupiennius salei* (Fenk & Schmid 2010), 0.18° for a common jumping spider

(Land 1969a), 0.04° for *Portia sp*. (Jackson & Blest 1981) or, as an unusual comparison, humans' spatial resolution of about 0.016° (Land & Barth 1991).

## 4.2. The way of running

There are different cues for animals to obtain distance information and to distinguish between foreground and background. So-called depth cues like for example oculomotorical, monocular, motion-induced and binocular depth cues (Goldstein 1997) enable the perception of distances. These cues differ in the kind of information that is used for distance discrimination like for example the position and movement of eye muscles that move eyes, perspective and texture gradients, movement of either the observer or the target in reference to each other or the information of slightly different images on the retinas of two eyes (Goldstein 1997).

Even though there is no literature that deals with the way of running of a spider towards a target, certain observations on this have been made by several people of our working group on behalf of the spider *Cupiennius salei.* Kosenburger (2006) could observe in her diploma thesis that *Cupiennius* tends to run in a zigzag way towards a target. The more difficult it is to discriminate the target from the background the more the spider tends to zigzag. In an investigation by Lehnert (2011) similar observations have been made. Because of the morphology of the eyes and the zigzagging towards a target, it can be suggested that motion parallax might play a significant role in the depth perception of *Cupiennius salei.*

Because of the similar lifestyles of *Heteropoda venatoria* and *Cupiennius salei* the aim of this experiment was to find out if *Heteropoda* shows similar walking paths. If so, it might be suggested that motion parallax also for *Heteropoda* might play a significant role in gaining distance information.

Therefore the walking paths of both spiders towards a target were observed. In contrast to *Cupiennius salei* the walking paths of *Heteropoda venatoria* towards the target had always been in a very direct and linear way without any zigzagging. This suggests, that motion parallax does not play a role for *Heteropoda* to gain distance information as it does for *Cupiennius*. If Heteropoda is able to distinguish between targets at different distances, at all, this is still to be found out as there are a number of other methods to gain distance information. Mantids and locusts, for example, use lateral peering movements of the head to produce motion parallax (Wallace 1959; Sobel 1990; Walcher and Kral 1994; Proteser and Kral 1995; Kral and Proteser 1997).

## 4.3. Visual fields

As the lifestyles of *Heteropoda venatoria* and *Cupiennius salei* are similar in so many ways and though they show exceptional differences in the size and the arrangement of their eyes the aim of this investigation was to measure the visual fields of *Heteropoda* and to compare them to the ones of *Cupiennius*, which are already known (Land and Barth 1992; Kaps 1998).

With the exception of the AM eyes, the visual fields of all the other eyes, the secondary eyes, have been investigated. The AM eyes do not have a tapetum and therefore do not reflect incident light, which made it impossible to measure these eyes with our method. Nevertheless, the position of the centre of the AM eyes was estimated (Fig. 18 and Fig. 19).

There were only minor differences between the visual fields of males and females. In all three secondary eyes females tend to have a bit smaller visual fields with very small differences in form in comparison to the males. The most obvious sex related difference concerning the visual fields could be found in the PL eyes (Fig. 19). A reason for the bigger gap between the left and the right PL eye of females in contrast to the males could be the larger opisthosoma that limits the females' visual fields (Fig. 9 and Fig. 13).

Both sexes show a visual gap between the AL eyes of about 20° (Fig. 18). This gap most likely will be covered by the AM eyes (Fig. 7 and Fig. 18) and should be investigated in a follow-up study.

The visual fields of *Heteropoda venatoria* are quite similar to those found by Land (1985) in *Olios sp*. (Fig. 6). In another Sparassidae, *Leucorchestris arenicola,* likewise visual fields in terms of position and form could be found (Norgaard 2008, Fig. 5). The size, on the other hand, seems to be smaller in *Leucorchestris arenicola*, especially at the bottom of the side and at the backside, where a bigger gap between the right and the left eye avoid covering as much of the spiders' surrounding as they do in *Heteropoda.*

Most interesting, according to the aim of this study, seems to be the comparison of the visual fields between *Heteropoda venatoria* and *Cupiennius salei*. In this context one major difference is the form of the visual fields of the different eyes. Whereas in *Cupiennius* they are vertically elongated the opposite is the case in

*Heteropoda* where they seem to be horizontally elongated (PM) or almost circle like (PL, AL, Fig. 18 and Fig. 19). Moreover the eyes of the sparassid spider seem to cover a slightly greater extend of the surroundings than the eyes of the ctenid spider.

Finally it can be stated, that despite the found differences, the visual fields of these two spiders are more alike than the size and the position of their eyes would have made us guess.

## 4.4. Conclusion

When assembling the results of the investigations done in this study it can be stated that *Heteropoda venatoria* is able to perceive visual stimuli and that it shows visual guided behaviour. In detail, this spider has shown to differentiate in a twofold simultaneous choice between different sized targets and that a target must have a certain expansion in order to be run to. Nevertheless the exact spatial expansion which a target has to have in order to be perceived by the spider and to elicit visual guided behaviour is not known yet.

Furthermore, as *Heteropoda* shows different, very straight, walking paths in comparison to *Cupiennius* and therefore does not seem to use motion parallax, it is uncertain whether *Heteropoda* is able to gain distance information at all.

In a last experiment the visual fields of *Heteropoda venatoria* were measured and the results indicate that the spider is able to perceive almost all of its surrounding with the different eyes covering different parts and only little differences between males and females, which have smaller ones. In comparison to *Cupiennius salei*, which's eyes also cover most of the surrounding, one major difference is the direction of the eyes and therefore of the visual fields. In *Cupiennius* other eyes than in *Heteropoda* cover certain areas of the surrounding.

In summary, it can be stated, that despite the differences in size and position of the eyes of *Heteropoda venatoria* and *Cupiennius salei* they seem similar, at least in some aspects.

On the other hand, the spatial resolution of the eyes of these two spiders seems to be different with *Cupiennius* being able to resolve objects down to 1° whereas *Heteropoda* is only able to resolve objects down to 4-8°. Nevertheless, one must not forget that in this study, this data only was gained by behavioural experiments whereas in *Cupiennius* data was gained by electrophysiological measurements by Fenk & Schmid (2010).

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# 6. Appendix

## 6.1. Curriculum vitae

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