A behavioural investigation into *Eristalis tenax*

Pursuit, approach estimation, locomotor activity and rearing

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Abstract

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Hoverflies are suggested to be the 2nd most important pollinator group after bees and bumblebees, and with the changing climate and dwindling numbers of pollinators it might never have been more important understanding our pollinators. Given the hoverflies' small brains, beautiful aerial acrobatics, good temporal resolution, but limited spatial resolution, these flies make interesting study animals for flight behaviour and vision research. *Eristalis tenax* hoverflies are globally spread generalist pollinators, thus well suited for studies internationally. However, due to weather and behavioural seasonality, the hoverflies can be hard to access all year round. Furthermore, only observational studies have been performed to investigate their activity rhythm, and neither pursuit behaviour nor interactions with other insects are well studied. We therefore developed a new protocol for rearing *E. tenax*, and by adding artificial hibernation we managed to get the hoverflies to survive up to a year – making the hoverflies accessible all year round. Using LAMS, we confirmed earlier suggestions that *E. tenax* are diurnal, and also showed that they are active during the entire light phase of an LD cycle. We also found that the hoverflies locomotor activity is remarkably robust – it was not affected by age, diet or starvation. However, an accompanying conspecific did affect the locomotor activity. Using high speed videography in the field we found that female *Eristalis* are affected by the presence of other insects outdoors as well. The females escaped their food flowers 94 % of the times they were approached, even though only 16 % of the incomers were potentially dangerous wasps. Interestingly, the females seemed to be able to distinguish between wasps and other incomers, leaving the flowers earlier and at a higher speed when approached by wasps. Bringing our high-speed cameras indoors we developed a flight arena, allowing for studies of eristaline flight behaviour all year round. Using this setup, we found that male *E. tenax* pursue beads 6 - 38.5 mm in diameter traveling at 0 - 1.8 ms-1. Fascinatingly, we found that the flies pursued the beads from both below and above, often keeping the target outside their bright zone.

Keywords: Eristalis tenax, Insect rearing, Hoverflies, Pollinators, Circadian rhythm, Target detection, Motion vision, Pursuit, LAMS, Flight arena

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Till Moa,
du gör allting möjligt.

Till våra fina barn,
ni är framtiden och min största inspiration.

Och till Hanna, vi ses i Nangijala.

"Jag blev rätt nöjd ändå.
Jo, jag blev det.
Det är inte alltid."

Barbro "Babben" Larsson

List of Papers

This thesis is based on the following papers, which are referred to in the text by their Roman numerals.

I Nicholas, S., **Thyselius, M**., Holden, M., Nordström, K. (2018) Rearing and long-term maintenance of *Eristalis tenax* hoverflies for research studies. *Journal of Visualized Experiments,* 135(e57711): 1-6.

II **Thyselius, M**., Nordström, K. (2016) Hoverfly locomotor activity is resilient to external influence and intrinsic factors. *Journal of Comparative Physiology A*, 202(1): 45–54.

III **Thyselius, M**., Gonzalez-Bellido, P., Wardill, T., Nordström, K. (2018) Visual approach computations in feeding hoverflies. *Journal of Experimental Biology,* 221(10): 1-9.

IV **Thyselius, M**., Ogawa, Y., and Nordström, K. "Target pursuits in male hoverflies". *Manuscript*

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Additional publications

1. Shirazi Fard, S., **Thyselius, M**., All-Ericsson, C., Hallböök, F. (2014) The terminal basal mitosis of chicken retinal Lim1 horizontal cells is not sensitive to cisplatin-induced cell cycle arrest. *Cell Cycle*, 13.23 (2014): 3698-3706.

2. Dahlbom, J., **Thyselius, M**. (2015) Vad gillar blomflugor?. *Bi-lagan*, (2015): 16-17.

3. van der Bijl, W., **Thyselius, M**., Kotrschal, A., Kolm, N. (2015) Brain size affects the behavioural response to predators in female guppies (*Poecilia reticulata*). *Proceedings of the Royal Society of London Series B*, 282(1812): 20151132.

4. **Thyselius, M**., Nordström, K. (2018) Forskning på blomflugors seende. *Yrfän*, 1(2018): 23.

Contents

Abbreviations

°/s	Degrees per second
β	Bearing angle
ε	Error angle
φ	Retina speed
θ	Retina size
τ	Retina size change or angular increment
#	Number
♀	Female
♂	Male
A. mellifera	*Apis mellifera*
COM	Centre of mass
C. megacephala	*Chrysomya megacephala*
d	Distance
D. melanogaster	*Drosophila melanogaster*
DAMS	*Drosophila* activity monitor system
E. balteatus	*Episyrphus balteatus*
E. nemorum	*Eristalis nemorum*
E. tenax	*Eristalis tenax*
fly^{-1} min^{-1}	Per fly per minute
fps	Frames per second
GPS	Global positioning system
h	hours
IR	Infrared
LAMS	Locomotor activity monitor system
LD	Light:Dark
LoS	Line of Sight
L. sericata	*Lucilia sericata*
min^{-1}	Per minute
ms^{-1}	Meters per second
RT	Room temperature
S. pipiens	*Syritta pipiens*
sd	Standard deviation
SEM	Standard error of the mean
sp.	*Species*, the genus is known but not the species
V. inflata	*Volucella inflata*
V. bombylans	*Volucella bombylans*

1 Introduction

1.1 Hoverflies and their usefulness

1.1.1   General information

The order of Diptera (flies and mosquitoes) consists of more than 150 000 species, of which roughly 6000 are hoverflies (Syrphidae) who are divided into 209 genera (Pape et al. 2011). Hoverflies are abundant and many, including the genus *Eristalis*, can be found all around the globe (Hull 1937; Francuski et al. 2013; Nationalnyckeln 2009; Sengupta et al. 2016; Thompson 1997; Bańkowska 2000; Van Veen and Moore 2004; Stubbs and Falk 2002).

The hoverfly lifecycle differs between the different genera of Syrphidae, but all go through the following stages: egg, larva, pupa and imago (adult) (Ball and Morris 2015). There are variations in many parts of the cycle, a few examples being in larval food preference (Nationalnyckeln 2009), egg laying sites (Nationalnyckeln 2009), egg number (Van Veen and Moore 2004; Nationalnyckeln 2009), timing of adult emergence (Nationalnyckeln 2009) and morphological differences of larva and imago (Rotheray 1993;
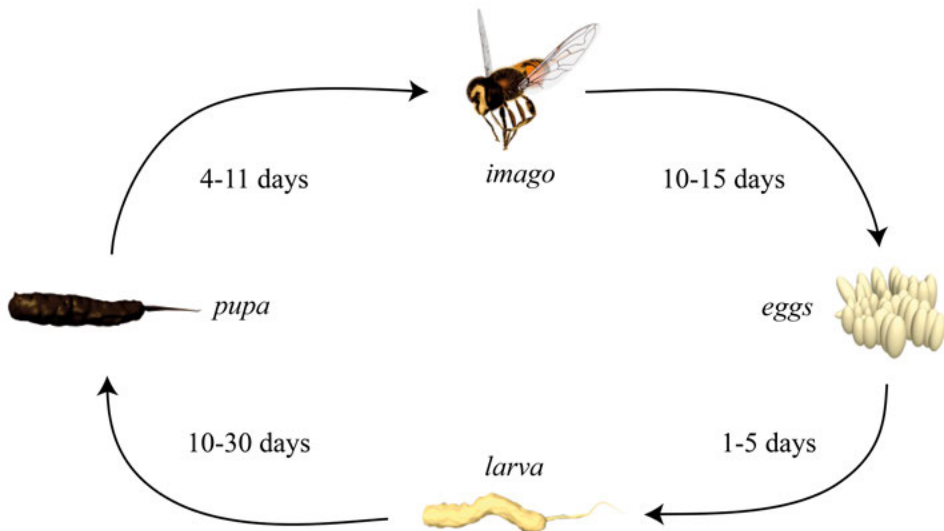

Figure 1. Lifecycle of *Eristalis tenax.*

Nationalnyckeln 2009; Ball and Morris 2015; Stubbs and Falk 2002; Van Veen and Moore 2004).

The lifecycle of the genus *Eristalis* takes roughly two months to complete (figure 1). In most of Europe the genus *Eristalis* has two generations, one summer generation with territorial males and one autumn generation where males are not territorial (Fitzpatrick 1981). The autumn generation will hibernate through the cold winter months and emerge with the warmth of spring (Kendall and Stradling 1972; Morley 1941; Timms 1946; Ellis 1937; Dennys 1927) to be the founders of next year's summer generation (Kendall and Stradling 1972). Females brought out of hibernation will lay eggs after approximately 15 days (Kendall and Stradling 1972). The larvae of *Eristalis* are aquatic and saprophagous, feeding on rotting organic matter in liquid or semiliquid environments (Nationalnyckeln 2009). The larvae complete two moults before seeking a dry and dark place to pupate. The length of the larval state depends on food, sex and temperature, and lasts somewhere between 10-30 days, followed by 4-11 days in the pupal state (Ottenheim and Holloway 1994; Pérez-Bañón et al. 2013). The hoverfly then emerges as an imago. If the hoverfly is female she can start to lay eggs 10 days later (Dolley et al. 1933) and the cycle starts again (figure 1).

As their name implies, hoverflies are good at hovering near motionless in the air (Nationalnyckeln 2009; Ball and Morris 2015; Stubbs and Falk 2002; Fitzpatrick 1981). Hoverflies of the *Eristalis* genus use hovering for territorial guarding (Wellington and Fitzpatrick 1981; Fitzpatrick 1981) and males of the species *Eristalis nemorum* can be seen forming courtship towers (figure 2), where up to four males hover over a single female (Wijngaard 2014; Heal 1987; Iliff 2003).

The resemblance of hoverflies to insects of the order Hymenoptera is another distinguishing feature (Ball and Morris 2015; Stubbs and Falk 2002; Van Veen and Moore 2004). Most hoverflies are considered batesian mimics of Hymenoptera, i.e., they belong to a harmless species copying a harmful species in order to avoid predation (see e.g., figure 3 comparing a honeybee worker and an *E. tenax* female). It has for example been shown that toads that have been stung by honeybees are less inclined to eat the *E. tenax* hoverflies afterwards (Brower and Brower 1962). Another predator having a hard time differentiating between Hymenoptera and mimetic-hoverflies are pigeons. When trained to identify wasps and

Figure 2. Courting tower of *E. nemorum* here with two males above a female feeding on a flower.

Figure 3. *Apis mellifera* worker (left) and female *Eristalis tenax* (right).

non-mimetic flies the pigeons reaction to mimetic-hoverflies were closer to their reaction to wasps if the hoverfly was classified as a better mimic, and closer to that of non-mimetic flies if the hoverfly was classified as a poorer mimic. (Dittrich et al. 1993). Naïve human subjects also have a hard time differentiating between different Hymenoptera and their hoverfly mimics (Golding et al. 2005a). Indeed, the hoverfly *E. tenax* looks so much like its hymenopteran counterpart the honeybee *Apis mellifera* (figure 3) that in ancient times (Fallon 2006; Atkins Jr 1948) and up until around the mid 17th century (Osten-Sacken 1893) it was believed that honeybees spontaneously arose from the carcasses of dead oxen, when it was in fact newly emerged hoverflies of the genus *Eristalis*. This phenomenon is called bugonia, from the Greek words for oxen and progeny (Osten-Sacken 1893), and is also briefly mentioned in the bible (Book of Judges 14.8). These kinds of mix ups between hoverflies and bees can still be seen, for example at Virgin.org where the hoverfly *Eristalinus* is showcased in a guest blog about bee tourism (McGuire 2015). Even honey-producers seems to struggle with the mimicry, as can be seen on their social media pages where *Eristalis* hoverflies are shown on flowers with captions suggesting they are bees in mid honey production (Island Beehive 2019; Svensk Honungsförädling AB 2021). In a video from the European Parliament about bee protection an *Eristalis* female can be seen in place of a bee worker (European Parliament 2018).

Some hoverflies mimic both the morphology (including colour and size) as well as the behavioural traits of their models. When comparing the drone flies of the *Eristalis* genus to their model, the honeybee *A. mellifera*, one can see that the drone flies perform similar movements around flowers and have similar flight speed as honeybees (Golding and Edmunds 2000; Golding et al. 2001). However, the behavioural mimicry is not correlated with the morphological mimicry in all hoverflies. For example, when comparing flight similarities between wasps and a few hoverflies deemed to be wasp mimics,

the poorer mimics *Syrphus* (Dittrich et al. 1993) had more similar flight patterns to the wasp than the larger, more morphologically similar hoverflies *Sericomyia, Hellophilus* and *Myathropa* (Golding et al. 2005b). Thus, it seems as if some hoverflies have developed either a morphological or a behavioural mimicry, whereas others are using both simultaneously.

When trying to explain why not all mimics are good copies of their models Edmunds (2000) argues that by looking a little like several different models a poor mimic can live in more areas than a good mimic, since a good mimic has to live in the same area as its model to remain protected. Penney et al. (2012) disagrees with Edmunds hypothesis since in their study no hoverfly could be found that was an intermediate mimic between several hymenopteran. They did however show that mimetic fidelity is not correlated with how abundant a species is, but instead correlated with the hoverfly's size, where larger hoverflies are better mimics (Penney et al. 2012). They argue that since a larger hoverfly is a more valuable meal than a small one, the evolutionary pressure on large hoverflies to become good mimics is higher.

1.1.2   Use in agriculture and as a food source

With the changing climate the need to understand our pollinators has maybe never been greater. Hoverflies are important pollinators together with bees and bumblebees (Rader et al. 2016; Jauker et al. 2012; Ssymank et al. 2008; Doyle et al. 2020). Unfortunately, the number of bees and bumblebees have been reported to decline across the globe (Potts et al. 2010; Goulson et al. 2015; Zattara and Aizen 2019). In 2017 Hallmann et al. (2017) reported an alarming general decline in pollinator biomass and in 2018 the EU Pollinators Initiative communicated that all kinds of European pollinators (including hoverflies) are in decline (European Commission 2018). Indeed, Powney et al. (2019) showed a general decline of hoverflies in the UK between 1987 and 2012. However, Wotton et all (2019) show that the numbers of migrating hoverflies over the UK between 2000 – 2008 was in fact not in decline, but rather that the numbers fluctuate a lot. By modelling how climate change might affect hoverfly distributions Miličić et al. (2017) agrees that the hoverfly population might not be in decline but rather move from low lands to alpine regions across Europe over the coming 30 to 50 years.

Even though hoverflies are not as effective pollinators as honeybees (Jauker et al. 2012), in some settings they can be of equal importance (Gladis 1997; Gladis 1994a; Rader et al. 2016). Hoverflies or solitary bees might even be better options in some instances, e.g. closed greenhouses where an entire honeybee colony cannot be sustained (Gladis 1997; Gladis 1994a). Furthermore, for pollination of some plant combinations a mix of hoverflies and solitary bees has proven to be most effective (Gladis 1997; Gladis 1994a).

For the purpose of crop pollination mass rearing protocols exist (Gladis 1994b; Francuski et al. 2014). However, these protocols do not share the

mating selection pressure that wild hoverflies endure. Wild hoverfly males often guard territories and chase both intruders and potential mates (Fitzpatrick and Wellington 1983a; Fitzpatrick and Wellington 1983b; Fitzpatrick 1981; Wellington and Fitzpatrick 1981; Ball and Morris 2004; Rotheray et al. 2014), a behaviour that puts selective pressure on both motor skills and sensory systems. This selective pressure is important as Francuski et al. (2014) showed that genetic heterogeneity can be quickly lost in mass rearing protocols. Protocols for smaller scale rearing also exist (Dolley Jr et al. 1937), but they fail to comply with today's sanitary standards.

Not only adult hoverflies can be of use to humans, but the larvae as well, especially in agriculture. For example the larvae of some species are aphidophagous (eating aphids) (Nationalnyckeln 2009) and can be used as organic pesticides (Ankersmit et al. 1986). Other dipteran larvae are saprophagous (eating degrading organic matter) (Nationalnyckeln 2009; Čičková et al. 2012) and protocols exist for their use in degradation of manure and other bioorganic waste (Čičková et al. 2012; Van Huis 2013). Additionally, dipteran larva have been suggested as food for livestock (Van Huis 2013) and in some parts of the world insects are already used as a human food source (Ramos-Elorduy 2009). Successful trials have also been made to introduce insects as a food source to populations where entomophagy (the eating of insects) is not common (Caparros Megido et al. 2014). Insects has also recently made its way into the popular Swedish TV-programme "Hela Sverige bakar" as both a bread- and cake-ingredient (Meter Television AB 2017, 2021). "Worm-tacos" containing mealworms with toasted crickets as a side snack also made an appearance in "Klimatkampen", a program using celebrities to teach swedes how to live more environmentally friendly (Utbildningsradion 2022). Sveriges Television AB (SVT) even provides the recipe for the "worm-tacos" (https://www.svt.se/recept/tacos-pa-insekter). It has also recently become legal in all of EU to sell insects as food (Livsmedelsverket 2020). This gives hope for a wider spread of insects as a food source for both humans and animals which, given that breeding insects require very little space (Čičková et al. 2012) and that the insect generation time is relatively short (Nationalnyckeln 2009; Ball and Morris 2015; Čičková et al. 2012), makes them a good food alternative to mammals (Van Huis 2013).

1.1.3 Use in the lab
Hoverflies have also proven to be great for laboratory experiments, since they are easily available (Nationalnyckeln 2009) and require very little space for housing (Dolley Jr et al. 1937). They have been used in numerous field and laboratory experiments, a selection of these are presented below. The hoverfly *Syritta pipiens* has been extensively studied in terms of its optics and visually mediated behaviour (Collett and Land 1975a). The motion vision of the drone fly *E. tenax* has been studied at a neuronal level with electrophysiology

(Nordström and O'Carroll 2006), its lift force during take-off has been determined (Chen et al. 2013), and even more recently the floral preferences it possesses and how that differs globally was examined (Nordström et al. 2017). Studies of flying insects can easily be translated to robotics (Floreano et al. 2009; Finio et al. 2010). In addition, knowledge gained in insect vision can, as Cajal stated already 1915 (1915), help us understand vision in more general terms, since the visual system of insects share many features with ours, even though it seems so very different at a first glance (Cajal and Sanchez 1915; Sanes and Zipursky 2010).

1.2 Diurnal activity and locomotion

Locomotion in ethology, the study of animal behaviour, is defined by Encyclopædia Britannica as "any of a variety of movements among animals that results in progression from one place to another" (Zug 2018). Locomotor activity, or performing the action of locomotion, is a useful tool when studying an animal's circadian rhythm, i.e. a rhythm with a cycle length of roughly 24 hours. Most animals are mainly diurnal (active during the day), nocturnal (active during the night) or crepuscular (active at dusk and dawn) (Mistlberger 1994; Lewis and Taylor 1965). Therefore, studying when an animal is most active will tell a researcher which of these categories it belongs to and thus when it is prudent to perform experiments on said animal. These sorts of locomotor studies can be undertaken using activity monitoring, which record an animal's movements, often walking (Bahrndorff et al. 2012; Fernandez et al. 1999) or running (Abe et al. 1989). Different methods for this are further described in section 3.1.4 of this thesis. Locomotor activity can also be studied by simply observing when animals are actively moving during the day (Gilbert 1985), often complemented by trapping the animals (Ottenheim 2000).

In flies, circadian rhythms and the hormonal control thereof, have been extensively studied in *Drosophila* (Tataroglu and Emery 2014; Pfeiffenberger et al. 2010). Circadian activity rhythms have also been studied in other flies, such as blowflies (Cymborowski et al. 1994) and houseflies (Bahrndorff et al. 2012). The activity rhythm of hoverflies has only been studied by means of observation and trapping (Ottenheim 2000; Kikuchi 1962a; Gilbert 1985), and they have been shown to be diurnal (Ottenheim 2000). Most diurnal animals, including flies, maintain a circadian rhythm if kept in complete darkness, but get a strange rhythm or go into constant activity when exposed to constant light (Green 1964). Many adult flies are phototactic (Meyer 1978), i.e. attracted to or prone to move towards light, which should not be confused with their activity rhythm that can be set to a light/dark (LD) cycle and is more of an anticipatory behaviour (Green 1964).

1.3 The visual system in relation to behavioural output

1.3.1 Spatial resolution

The fly visual system is several magnitudes smaller than that of humans. The brain of the housefly *Musca domestica* weighs about 0.4 mg (Strausfeld 1976) and contains about 300 000 neurons (Strausfeld 1976), which is a vast difference to the human brain where the average weight is ca 1.5 kg and the neuronal count is around 85 billion (Azevedo et al. 2009). Due to the similarities in size between hoverflies and houseflies (Nationalnyckeln 2009; Landin 1974) it is likely that the neural count of hoverflies are within the same magnitude as that of houseflies. Even so, hoverflies are able to perform amazing flight manoeuvres in complex visual surroundings (Fitzpatrick 1981; Collett and Land 1978), at speeds reaching 10 ms^{-1} (Collett and Land 1978). These findings become even more incredible if one considers their compound eyes and the resulting limited spatial resolution.
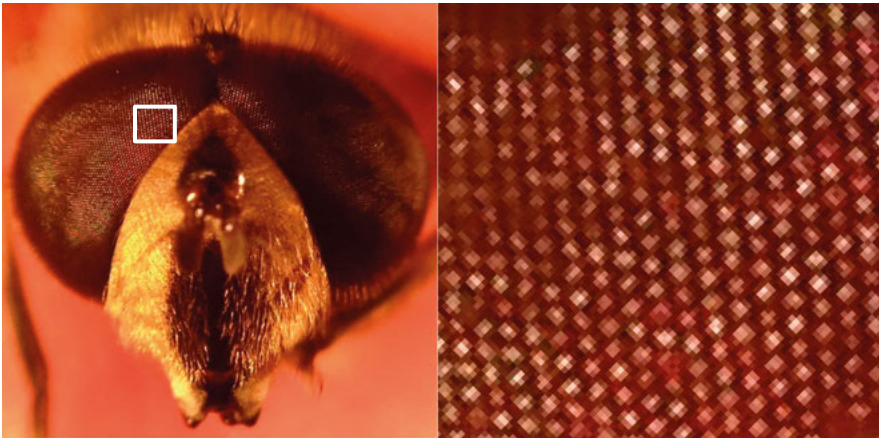
Figure 4. Head of male *Eristalis tenax* (left) and zoom in of white square (right) illustrating the ommatidial patterning of the compound eye.

A compound eye is divided into sections called ommatidia or facets (figure 4), where each facet provides one pixel of the image. The entire compound eye thus forms one image (Land and Nilsson 2012), just as a camera type eye (the type of eyes humans possesses, with only one lens), not to be confused with some fictional ideas (Cronenberg 1986; Gordon 1977) that each facet forms its own complete image (see figure 5 for a comparison between movie ideas, human vision and insect vision). The spatial resolution of the image generated by the compound eye depends on the number of ommatidia it

encompasses, so that the maximum amount of pixels is equal to the amount of ommatidia (Land and Nilsson 2012). This arrangement gives the hoverfly a spatial resolution of 0.5 - 1° (Collett and Land 1978, 1975a; Land and Nilsson 2012), which corresponds to the width of your thumb at an arm's length. If humans would have compound eyes, but still keep our spatial resolution of 0.016°, our eyes would need to be about 20 m in diameter (Land and Nilsson 2012). Incredibly enough, hoverflies can still detect small targets at a distance of approximately 1 m, when the target subtends about 1° (Collett and Land 1978).
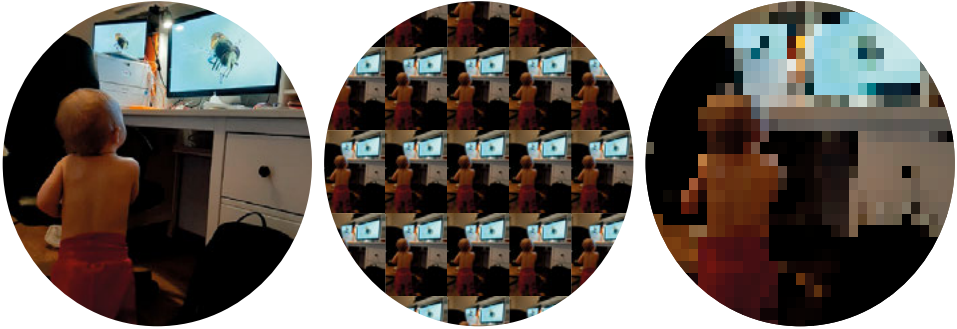
Figure 5. My oldest daughter looking at my *Eristalis* 3D model as seen by a human (left), an insect from a 1970s or1980s horror film (middle) and a real insect (right), with each facet giving a pixel of the picture mosaic. Note that the different color vision of insects is ignored here.

1.3.2 Temporal resolution
Humans have better spatial resolution than flies, but we are no match for their temporal resolution. The reaction time, i.e. time between visual input and motor output, of hoverflies is around 20 ms (Collett and Land 1978), whereas in humans this is around 400 ms (Thorpe 1996). It is argued that the human neural processing of vision, excluding the motor output, might only take 150 ms (Thorpe 1996), but this is still nowhere near the reaction time of flies. To illustrate just how big a difference it is, in 400 ms the housefly *Fannia canicularis* (with a reaction time of 30 ms) has during a conspecific pursuit already completed two changes in flight direction (Land and Collett 1974). In a human sprint race, starting less then 100 ms after the start signal is considered a false start (cheating by starting to early, IAAF 2017), in which time a fly has had well enough time to both observe and react to a stimulus (Collett and Land 1978). One explanation for the higher temporal resolution in insects can be found in the photoreceptors and the phototransduction cascade. Flies have most of the proteins necessary for phototransduction (light input to electrical signal output) collected in a big complex and this complex has a direct effect on the ion channels that control the electrical signalling of

the photoreceptor (Yau and Hardie 2009; Fain et al. 2010). In contrast, the proteins involved in vertebrate phototransduction need to find each other and act via second messengers to affect the ion channels to start a neural signal (Yau and Hardie 2009; Fain et al. 2010).

1.4 Pollination, flower interactions and escape responses

1.4.1 Pollination and foraging

In the field hoverflies are known to feed on pollen and nectar from different flowers (Gilbert 1985; Gilbert 1981), with females eating more pollen than males. Females also spend more time feeding than males do (Maier and Waldbauer 1979b). It has been suggested that hoverflies chose flowers based on the morphology of their mouthparts (Gilbert 1981). There is likely some truth to this since too short of a proboscis will make feeding from deep floral tubes hard or even impossible (Rijn and Wäckers 2016). However, this is unlikely to be the entire truth as it has been noted that hoverflies seem to feed on any available flower and thus will be more likely to feed on the most abundant flowers (Branquart and Hemptinne 2000). This goes well in line with the mentioning of hoverflies as generalist pollinators (Rader et al. 2016; Nationalnyckeln 2009; Stubbs and Falk 2002; Ball and Morris 2015; Van Veen and Moore 2004; Branquart and Hemptinne 2000). Hoverflies have indeed been shown to feed on a variety of flowers and can even be fooled to visit artificial flowers that offer no reward (Nordström et al. 2017). So even though food is necessary for survival and mouthpart morphology likely plays a part in the choice of foraging site, hoverflies do not seem to be very selective.

1.4.2 Flower interactions and the escape responses

There are, however, other things than flower morphology to consider for a feeding hoverfly. Hoverflies might meet many other insects when foraging, both non-harmful insects, such as other hoverflies (Ball and Morris 2015; Nationalnyckeln 2009), and potentially harmful insects, such as wasps, or arachnids that may also visit flowers to forage (Akre 1982; Harris and Oliver 1993; Morris and Reader 2016). The hoverfly *Sphaerophoria* shows a hesitant behaviour before landing on flowers, which could potentially be a way to deal with the threat of crab spiders (Yokoi and Fujisaki 2009). Bees have been shown to be less prone to land on flowers occupied by crab spiders or those flowers that show signs of a potential crab spider meal (Reader et al. 2006). However, interactions with other insects are in most cases unavoidable. In the 1960s Kikuchi described dominance hierarchies formed between insects on flowers, and noted that *Eristalis* not readily shares a flower with another insect

(Kikuchi 1962b, a), unless the flower is large (Kikuchi 1963). However, *Eristalis* hoverflies have also been seen to huddle together with conspecifics in groups when hibernating through the winter (Kendall and Stradling 1972), so there are occasions when they will consider sharing their space with others.

For most animals there is a trade-off between staying in a potentially dangerous situation and leaving it (Cooper and Frederick 2007). Water striders will wait longer before leaving a bigger prey, arguably because it is a bigger loss than a smaller prey would be (Ydenberg and Dill 1986). Guppies have even devised a strategy to figure out if a predator poses a big enough treat for them to leave their foraging and escape: One or a few guppies from a school will perform an inspection of the predator to assess whether the school can stay or needs to escape the threat (Dugatkin and Godin 1992).

Escaping a hostile situation is one of the actions an animal can take to protect itself from injury or death (Blanchard et al. 1998; Cooper and Frederick 2007; Hemmi 2005a; Card 2012). Escape is defined by the Cambridge Dictionary (Cambridge Dictionary, English Dictionary 2018) as: "to get free from, or to avoid something". The behaviour has been well studied in *Drosophila* (Card and Dickinson 2008a; Card and Dickinson 2008b). Card and Dickinson (2008) showed that the escape from a looming stimulus, i.e. a stimulus that approached an animal or is perceived to do so, consists of a cascade of behavioural events that are different from voluntary take-offs (Card and Dickinson 2008a). Escape take-offs are faster but less stable than voluntary take-offs (Card and Dickinson 2008a). The behavioural escape cascade shown in *Drosophila* can also be stopped at any point (Card and Dickinson 2008b). The speed and size of the looming stimuli has also been shown to be encoded by different neuronal groups (Ache et al. 2019). The approach direction of the threatening stimulus also affects the escape of *Drosophila*, with direct approaches from the front or back eliciting an escape in a 180° angle away from the threat, whereas side approaches gives an escape angle closer to 90° (Card and Dickinson 2008b). The most effective stimulus angle is 90 ° azimuth and 30 ° elevation, giving an escape response close to 80 % of the time (Williamson et al. 2018). Also, crabs are affected by the approach angle of a threat, responding later but more likely when approached directly (Hemmi 2005b). However, this was only true in a lab environment (Oliva et al. 2007). In the field the crabs ignored the threat direction and rushed straight to their burrows, even if that meant running towards the threat (Hemmi 2005b, a). The escape response of the crabs were also heavily affected by the distance to the crabs' burrows, the crabs responded faster and with an increased speed and acceleration the further away they were from their burrows (Hemmi 2005b, a). The speed of the stimulus had, however, only a small effect on the crabs' escape response, though Hemmi (2005) suggested that some of the effect might be lost due to the constraints of the setup. Indeed, Oliva and Tomsic (2012) found that in a laboratory setting crabs match their

speed to the expansion rate of the threatening stimulus (Oliva and Tomsic 2012).

Different triggers have been reported for escape responses. Card and Dickinson (2008) showed that for *Drosophila* a visual stimulus is enough to alone elicit an escape response and that the trigger for take-off is the size of the visual stimulus (Card and Dickinson 2008b). Also, locusts seem to base their take-off decision on stimulus size (Fotowat and Gabbiani 2007). However, for crabs the trigger for starting the escape has been shown to be the stimulus' angular increment, i.e. how fast the stimulus grows in retinal size (Oliva and Tomsic 2012).

1.5 Territoriality and pursuit behaviour

1.5.1 Territoriality

A territory is a defended area (Britannica 1998; Fitzpatrick 1981), whereas a home range is an often larger area that the animal do not defend but still lives in (Britannica 1998; Fitzpatrick 1981). A territory either makes up the entire home range or comprises a part of it (Britannica 1998; Wellington and Fitzpatrick 1981). Many animals as different as flies (Wellington and Fitzpatrick 1981), fish (Sowersby et al. 2018) and lions (Mosser and Packer 2009) keep territories. Even the innocent looking butterflies show territoriality. (Woodruff et al. 1989; Hayes et al. 2019). Some animals, like wolfs and lions, keep territories throughout the year, albeit with some variation in territory size (Brandell et al. 2021). Other animals keep territories only during certain periods of the year, for example *Eristalis* hoverflies who defend territories in the spring but not during late summer and autumn (Wellington and Fitzpatrick 1981; Fitzpatrick 1981). Furthermore, *Eristalis, Volucella* and *Merodon* hoverflies only maintain territorial behaviour during warm sunny weather, and takes breaks or delay start of the territorial behaviour when the weather is to cold or cloudy (Wellington 1976; Wellington and Fitzpatrick 1981; Ball and Morris 2004; Fitzpatrick 1981; Grayson 2003). Some animals only upkeep territories during special circumstances, such as the ayu fish, that only keep single-fish territories during low fish densities, but school during high densities (Katsumata et al. 2017). For some species males and females keep separate territories, like snow leopards (Johansson et al. 2018) and some species of frog (Wells 1980). Some species also keep territories together in parental units (Sowersby et al. 2018), e.g. the cichlid fish *Hypsophrys nematopus,* or as an entire pack, such as lions do (Mosser and Packer 2009). There are also several cases where only one sex keeps territories, which is true for several hoverfly species, where only

the males keep territories (Fitzpatrick 1981; Ball and Morris 2004; Rotheray et al. 2014).

Territories are often kept to obtain food (Pompozzi and Simó 2020; Katsumata et al. 2017; Mosser and Packer 2009), increase mating opportunities (Fitzpatrick 1981; da Rocha et al. 2018; Ball and Morris 2004), secure a space for offspring rearing or egg laying (Sowersby et al. 2018; Souza et al. 2021) or some combination of the three. For example, the ayu fish keep feeding territories as long as defending the territory does not take away too much time from feeding (Katsumata et al. 2017), some frog species with parental behaviour keep territories with good egg laying sites (da Rocha et al. 2018), and hoverfly males keep territories at locations desired by females to increase their chances of finding a receptive female (Fitzpatrick 1981; Maier and Waldbauer 1979b).

So, what can territorial behaviour look like? Amongst the dragonflies, who mainly keep territories for mating purposes (Lohmann et al. 2019) but might also keep them for better feeding opportunities (Williamson 1899), there are perchers and hawkers (or fliers). Perchers sit and wait on a perch, whereas hawkers patrol their territory on the wing (Corbert 1962; Dannelid and Sahlén 2008; Olberg et al. 2005). These distinctions also exist in other insect orders, e.g. Syrphidae, with some hoverflies perching on vegetation, observing their territories (Fitzpatrick and Wellington 1983a), whereas other hoverflies combine the percher and hawker behaviours, hovering still in the air monitoring their territory (Fitzpatrick 1981; Collett and Land 1975b)

The male *Eristalis* hoverflies form territories ranging from size 0.22 m^3 – 2 m^3 or 0.36 m^2 – 3.6 m^2 depending on species (Wellington and Fitzpatrick 1981; Fitzpatrick 1981). Males will pursue conspecific males and females, chasing the former out of the territory and the latter will be stalked to a landing spot where the male will try to mate with the female (Fitzpatrick 1981). Heterospecific insects will often also be pursued, the more restless the males gets the wider the range of pursued targets he will have and the more aggressive his approaches will be (Wellington and Fitzpatrick 1981). Male *Eristalis* will have resting periods interspacing periods of territoriality, often located in the home range but outside the territory (Wellington and Fitzpatrick 1981). If a male is unable to get rest, if for example there are too many other male territories flanking his territory, the male will increase its aggressiveness (Wellington and Fitzpatrick 1981). A relaxed male will wait for a bee worker to exit a flower and then chase it for a little while, whereas an aggressive male will repeatedly strike (with its body since hoverflies lack the stinger of bees) a bee worker, till she stops her pollen collection. The male might even go so far as to violently tackle bee workers to the ground, sometimes stunning the bee (Wellington 1976; Wellington and Fitzpatrick 1981). Aggressive males might attack passing butterflies, leaves and even hornets, something that might have deadly consequences for the territorial hoverfly (Wellington and Fitzpatrick 1981; Fitzpatrick 1981). Small falling flower petals, pebbles or

small dipterans might also be pursued by *Eristalis* males (Wellington 1976; Wellington and Fitzpatrick 1981), as well as pinecones, cheery seeds or strawberry hats thrown by an exasperated PhD student (personal observation).

Thus, for an *Eristalis* male, territoriality is expressed by hovering, screening the territory for intruders and potential mating partners, pursuing said intruders or mating partners, and can in some cases end in clasping, tackling, mating or in some rare cases even death.

1.5.2 Pursuit strategies

3D pursuit (such as e.g. aerial pursuit) can be performed in several ways (Shaw 1985; Pembury Smith and Ruxton 2020). Here four such techniques (figure 6) utilized by flying insects will be briefly presented. The first is smooth pursuit (figure 6a), where the pursuer continuously moves towards the current position of its target (Boeddeker et al. 2003; Gonzalez-Bellido et al. 2016);
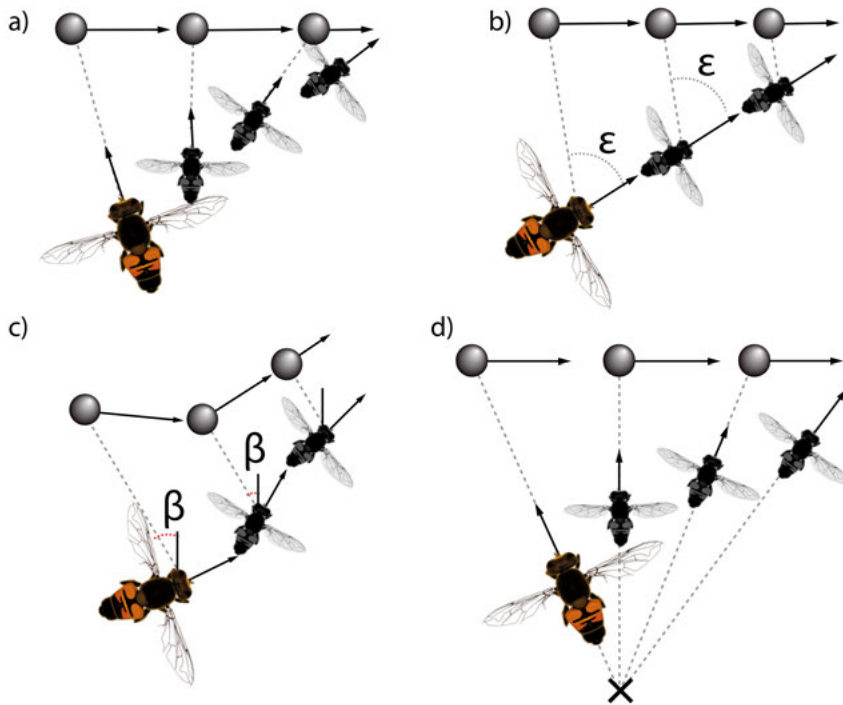
Figure 6. Pursuit styles illustrated with hoverflies and beads. **a**) smooth pursuit, were the fly continuously flies towards the current position of the bead. **b**) Interception with constant error angle, the hoverfly flies towards a future position of the bead by keeping the error angle fixed. **c**) Interception with constant bearing, the fly flies towards a future position of the bead by keeping the bearing angle constant. **d**) Shadowing, the fly has a constant angle towards a point behind itself, so it appears motionless when viewed from the bead. Adapted from *Paper IV* figure 5a.
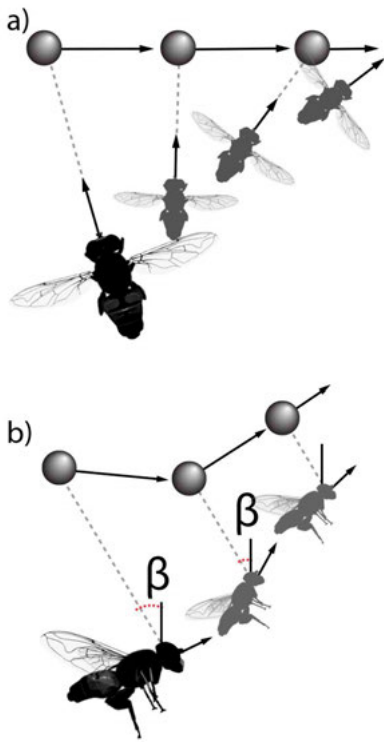
Figure 7. Illustration of pursuits in the horizontal and vertical plane. **a)** Smooth pursuit in the horizontal plane. **b)** Interception with proportional navigation in the vertical plane.

Interception, is where the pursuer predicts and flies towards a future position of the target. There are several ways the pursuer can achieve this. One is by keeping the error angle (ε, figure 6b) constant, where the error angle is the angle between the fly's heading (black arrows connected to flies, figure 6b) and a line connecting the fly and the target, often called the line of sight (LoS, straight dashed grey lines, figure 6). Another way to perform interception is by keeping the bearing angle constant (β, figure 6c). The bearing angle is the angle between the LoS and an external point. Another way a pursuer can approach a target is by using shadowing (figure 6d and Pembury Smith and Ruxton 2020; Srinivasan and Davey 1995), where the pursuer keeps itself on a line crossing the target and an external point, thereby appearing motionless when viewed from the target. All these pursuit styles have many names, for example smooth pursuit can also be called pure pursuit (Varennes et al. 2020; Fabian et al. 2018; Shaw 1985), classical pursuit (Pembury Smith and Ruxton 2020), tracking or target tracking (Varennes et al. 2020). Interception with constant error angle is sometimes only called interception (Collett and Land 1978) but has also been called biased pursuit (Varennes et al. 2020), deviated pursuit (Fabian et al. 2018) or constant error model (Gonzalez-Bellido et al. 2016). Interception with constant bearing has also been called proportional navigation (pro-nav) (Varennes et al. 2020; Fabian et al. 2018; Shaw 1985), constant bearing angle model (Wardill et al. 2017), constant bearing, constant absolute target direction (Gonzalez-Bellido et al. 2016), or constant bearing decreasing range (Hobbs 2009). Shadowing can also be called motion camouflage (Mizutani et al. 2003).

Blowflies and houseflies have generally been believed to use smooth pursuit (figure 6a and Trischler et al. 2010; Land and Collett 1974; Boeddeker et al. 2003), but recent research suggest that blowflies only use it in the horizontal plane (figure 7 for illustration of pursuit in different planes),

whereas in the vertical plane they seem to use interception with constant bearing (figure 6d & Varennes et al. 2020). Killer flies, robber flies and Dragonflies are all known to use interception with constant bearing (Olberg et al. 2000; Wardill et al. 2017), killer flies even use the same tactic to pursue targets both from bellow and above (Rossoni et al. 2021; Wardill et al. 2015)., Some dragonflies have also been shown to utilize shadowing (Mizutani et al. 2003). The hoverfly *S. pipiens* has been recorded to use a multitude of tracking strategies, including smooth pursuit, interception with constant error angle and shadowing (Srinivasan and Davey 1995; Collett and Land 1975a). In contrast, *Eristalis* hoverflies are thought to use only interception with constant error angle to track targets (Collett and Land 1978).

1.5.3 Target location on the pursuer's retina

When pursuing targets many insects, such as dragonflies (Dickinson 2015), male *S. pipiens* hoverflies (Collett and Land 1975a), drone bees (Praagh et al. 1980) and male houseflies (Burton and Laughlin 2003), keep their targets in the area of the eyes with the highest visual acuity. This area is called acute zone, fovea or love spot (Ignatova et al. 2021; Burton and Laughlin 2003; Land 1997). This is similar to eye tracking behaviour in humans, with a small target receiving more corrective eye-movements than a larger target to keep it foveated (Heinen et al. 2018). The human fovea has a high density of photoreceptor-cells to increase the spatial resolution (Hirsch and Curcio 1989; Kolb 2012; Land 1997). For the same purpose insects has large facets and small interommatidial angels (Land 1997). Male *Eristalis* hoverflies and male *Chrysomya megacephala* blowflies do not have an acute zone, but instead an area in their eyes with increased facet size called a bright zone (Straw et al. 2006; Badenhorst and Villet 2018). The bright zone is suggested to be good for target tracking, possibly through an increase in light capture leading to better signal-to-noise-ratios (Van Hateren et al. 1989; Straw et al. 2006). However, performed studies on *Eristalis* pursuits (Collett and Land 1978; Fitzpatrick 1981) do not show whether or not the *Eristalis* males keep their target in the bright zone during pursuits, and no helpful parallels can be drawn from the *C. megacephala* males since their pursuit behaviour is yet to be studied.

2 Aims

The overall aims of these studies have been to develop techniques and subsequently use them to investigate the behaviour of the important alternative pollinators, the *Eristalis* hoverflies, to increase their effectivity as model animals, and to further understand their visual behaviour during pursuits as well as on and around flowers.

Paper I

The aims of *Paper I* were to establish a protocol for effectively rearing hoverflies from eggs or 3rd instar larvae, to ensure year-round access to experimental wild type animals, and to prolong the survival time of the hoverflies in the lab.

Paper II

The aims of *Paper II* were to set up a locomotor activity system and use it to investigate the activity of *Eristalis* hoverflies. In addition, the aim was to determine whether the rhythm was diurnal or a response to light, and to characterize how intrinsic and extrinsic factors affect hoverfly locomotor activity.

Paper III

The aims of *Paper III* were to develop and use a method to study the interactions of female hoverflies around flowers in the field and the outcome of these, as well as to describe available visual cues during the interactions.

Paper IV

The aims of *Paper IV* were to construct an indoor flight arena that would allow for studies of male hoverfly pursuits of artificial targets, to describe these pursuits and to characterize the target range of male hoverflies in terms of target size and speed.

3 Methods

3.1 Behavioural studies

The behaviour of animals can be studied using a number of different methods, including but not limited to, locomotor activity monitoring systems (Catterson et al. 2010; Bahrndorff et al. 2012), videography (Zimmerman et al. 2008; Wardill et al. 2017), GPS tracking (Wilson et al. 2013), trapping (Karlsson et al. 2005) and observations (Gilbert 1983; Kikuchi 1962b), each with their own advantages and disadvantages, which are discussed in more detail below.

3.1.1 Behavioural patterns

Observational studies, where an observer, often with the help of a tape recorder, documents a behaviour while it is performed, are good for studying general behavioural patterns since they do not require an extensive equipment setup, and can additionally allow the observer to study the behaviour without interfering with the animal. These kinds of studies have, for example, been used to study time budgets of hoverflies (Fitzpatrick 1981; Alderman 2010), to perform comparative behavioural studies between bees and their hoverfly mimics (Golding and Edmunds 2000), and to study more specific behaviours, such as insect movements on flowers while feeding (Gilbert 1983) and dominance hierarchies around flowers (Kikuchi 1962b). Observational studies are, however, heavily observer biased and may generate data that can be both hard to quantify and to compare between studies.

3.1.2 Geographic spread and quantification of animals

Manual trapping, where insects are hand netted (Ottenheim 2000), generally shares the same problems as observational studies, since the method is dependent on the experimenter's ability to spot and identify the animal. Traps, such as the Malaise trap (Karlsson et al. 2005) or sticky traps (Atakan and Pehlivan 2015), circumvent such experimenter bias and allow for a high amount of data to be collected quickly. However, the temporal resolution decreases significantly compared to observational studies, since it will only be as high as the frequency with which the traps are emptied, which can vary between every few days (Atakan and Pehlivan 2015), to every other week (Karlsson et al. 2005). Nevertheless, trapping studies have been used to determine the geographic spread of different insects (Karlsson et al. 2005), and also the annual (a yearlong rhythm) and diurnal rhythms of different insect species (Ottenheim 2000; Karlsson et al. 2005).

Another way to study the geographic spread of animals, their annual numbers, and also their migratory behaviour is marking studies, successfully used in birds (e.g. bird ringing, Bergner et al. 2021) and monarch butterflies (Taylor Jr et al. 2020). The tags used on the butterflies weighed 10 mg and accounted for 2 % of the butterflies' body weight, which is a similar amount to the radio tags used for birds (Naef-Daenzer et al. 2001), but heavier than bird rings (<0.5 %, Hawk Conservancy Trust 2021). This method might work well with animals as large as birds or for larger insects, but for the smaller *Eristalis* hoverflies weighing only around 15 mg themselves (*Paper I*, figure 3) 10 mg is a significant weight.

Markings using ink have been used on hoverflies with variable success to study territory and home range usage. Some hoverflies left the study area immediately after being marked whereas others stayed and was identifiable up to nine days later (Fitzpatrick and Wellington 1983a). Small tags (2 x 2 mm, Modlmeier et al. 2019) have been used on ants to study activity rhythms (Mildner and Roces 2017) and interactions during different ant densities (Modlmeier et al. 2019). Metal tags have been used on bumblebees to attach them to flight mills (a way to study tethered flight), the authors found that the tags placement affected several aspects of the bumblebees flight performance (Kenna et al. 2019). There have also been some effort with mark-recapture studies in *Drosophila* to study dispersal using protein markers (Vacas et al. 2019). Mark-recapture studies have also been performed on hoverflies such as *Volucella pellucens, V. inflata, V. bombylans* (Ball and Morris 2004) and *Hammerschmidtia ferruginea* (Rotheray et al. 2014) using enamel paint, where recapture rates varied between 7 % and 16 % and were affected by experimenter effort. In conclusion, studying hoverflies using individual makers is feasible, but the time restraint and experimenter bias is an important factor.

3.1.3 GPS tracking and migration

GPS tracking, which sometimes combines a GPS tracker and accelerometers (Wilson et al. 2013), offers an often detailed temporal resolution of animal behaviour and has been used to study movements of larger animals such as cheetahs (Wilson et al. 2013) or the migratory behaviour of birds (Klaassen et al. 2008), and can even be used to track pets such as cats and dogs (Aqraldo et al. 2021). GPS tracking can, however, pose a limit on the number of animals studied, since like with the marking techniques mentioned above each animal has to be individually tagged. In addition, GPS trackers are currently too large for mounting on insects, as the one Klaassen et al. (2008) used on birds weighed 45 g. Bouten et al. (2013) managed to shrink a GPS tracker down to 12 g. However, this is still very heavy for an insect like *Eristalis,* which weighs only 0.1-0.2 g. Some efforts are being made with arthropod tracking, however,

this is mostly to track big populations or breeding sites (Thomson and Connor 2000).

3.1.4 Locomotor activity measuring

Locomotor activity monitors, such as the *Drosophila* activity monitoring system (DAMS) or the larger Locomotor activity monitoring system (LAMS), do not offer the detailed view of observational studies, but are high throughput systems that allow for a high temporal resolution, as well as objective data collection. Both the LAMS and the DAMS record the locomotion of insects using infrared (IR) beams. An insect is placed in a glass tube sealed at both ends. The tube is then placed in the activity monitor so that one or several IR beams passes through the centre of the tube. The number of beam breaks are then recorded over a fixed time interval of seconds to days (for a more detailed description see Pfeiffenberger et al. 2010; Chiu et al. 2010).

DAMS is a commonly used method when studying *Drosophila* and especially their sleep-wake behaviour. The method has been used to study e.g. the connection between sleep- and starvation-pathways (Keene et al. 2010), the sexual differences in locomotor activity (Helfrich-Förster 2000) and the effect of temperature on circadian rhythm (Glaser and Stanewsky 2005). The larger LAMS has been used to study behavioural rhythms in larger insects, such as bees (Giannoni-Guzmán et al. 2014), true bugs (Pivarciova et al. 2016), houseflies (Bahrndorff et al. 2012) and ants (Mildner and Roces 2017).

3.1.5 Videography

Videography has been used to study, among other topics, aerial chases of insects (Wardill et al. 2015; Collett and Land 1978), predator inspection behaviour in fish (van der Bijl et al. 2015), snake predatory behaviour (Clark 2006) and the mating dances of male peacock spiders (Girard et al. 2015) and birds of paradise (Scholes and Laman 2018). Like locomotor activity monitors, videography offers a high temporal resolution and often the possibility to study behaviour in great detail, similar to observational studies but with less, or no, observer bias. The analysis time is, however, often much longer than that of observational studies and locomotor activity monitors. Thus, if the research question does not require the high detail that videography can provide, data analysis time can be greatly shortened by usage of another method.

To study flight behaviour in dipteran flies, videography has for several decades, with the more recent addition of high-speed videography, been used as an addition to, or as a replacement for, observational studies (Collett and Land 1975a; Geurten et al. 2010; Boeddeker et al. 2003; Chen et al. 2013; Wardill et al. 2015). Importantly, videography circumvents many of the problems with observational studies while maintaining the capability to

distinguish behavioural patterns. Different behaviours require different temporal resolution and thus different frame rates are required from the camera. A high frame rate of 5000 frames per second (fps) can showcase individual wing beats (Chen et al. 2013), whereas a slower frame rate of e.g. 50 fps can be enough for a broader behavioural overview (Collett and Land 1975a). This is important to keep in mind, as there is a trade-off between the temporal resolution (frame rate) and the spatial resolution (number of pixels per image) (Nayar and Ben-Ezra 2004). For example, using the camera EX-FH25 (Casio, Tokyo, Japan) one can film at 120 fps or 1000 fps, but at 120 fps each frame is 640 x 480 pixels, whereas at 1000 fps this has shrunk to 224 x 64 pixels (Digital Camera EX-FH25 User's Guide). Thus, if high temporal resolution is needed the spatial resolution usually has to be compromised. This is an issue in some cases, such as when studying the lift force generated from wing beats, which needs high temporal resolution as well as high spatial detail (Chen et al. 2013). This can be solved by increasing the percentage of the frame covered by the insect, thus increasing the number of pixels the insect occupies and thereby the available detail, by e.g., moving the camera closer to the insect. To practically move the camera closer to the insect the space available to the insect might have to be restricted (Geurten et al. 2010; Chen et al. 2013). This in turn might generate a trade-off between the size of the area the animal can move in and the behaviour, with larger movement space likely giving a more natural behaviour since it is less constrained. A larger filming area results in less available detail but more natural behaviour and one thus has to decide what is most important for the study question at hand, great spatial detail or a more natural behaviour.

Another factor to consider in videography is the size of the files, since large quantities of data, taxing to analyse, can be rapidly generated, as higher frame rates and/or higher spatial resolution generates larger files. To keep the file size down the film time can be decreased, but this will in turn put a limit on the length of the behaviour to be studied. Another solution to maintaining a high frame rate and/or spatial resolution while saving data storage space is to only save the interesting frames, e.g. using a system that triggers data recording when a behaviour is initiated (Chen et al. 2013), or to only save the flight path and not the entire movie (Maimon et al. 2008).

Many studies on hoverfly flight behaviour have been performed in 2D (Collett and Land 1975a; Alderman 2012; Golding et al. 2001). Later studies on other dipterans have been performed in 3D (Wardill et al. 2015; Geurten et al. 2010; Bomphrey et al. 2009), allowing more detailed studies of the flight behaviours. Land & Collett (1974) studied the chasing behaviour of houseflies in 2D and acknowledged that there are parts of the behaviour that cannot be seen while studying in 2D, though they argued that this would not have a great effect on the behaviour covered by their study. This might indeed be true for studying e.g. the optomotor response (Collett and Land 1975a), a reflex for course or gaze stabilization where the fly follows the motion of its surrounding. However, when looking at chases of beads (see e.g. figure 1 in Collett and Land 1978), it is impossible to know if the fly approached the bead from above, below, or in line with the bead just from looking at the 2D tracks. When looking at a track in 2D it can indeed be hard to differentiate between the fly flying slowly or at an angle, in the same way that it is hard to differentiate between a small object at a close distance and a large object further away without 3D information (figure 8 and Wardill et al. 2015). Since flies move in a 3D space, studying them in 3D will likely give a more complete picture of their flight behaviour than restricting the study to 2D.
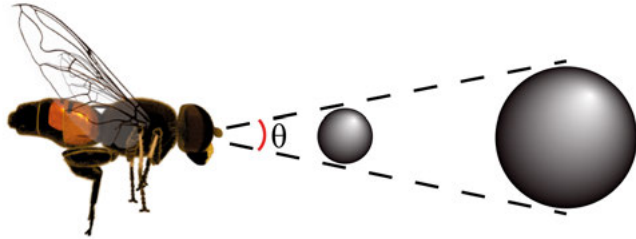
Figure 8. Perspective, a big bead far away appears to be the same size as a small bead close by.

3.1.6 Indoors or outdoors

Studying animals indoors in a lab environment or outdoors in the animals' natural habitat pose different challenges (Calisi and Bentley 2009) and can sometimes (Hemmi and Tomsic 2015), however not always (Butterworth et al. 2019), give different results. Take for example fiddler crabs who in the lab on a Styrofoam ball always run away from an approaching threat (looming stimuli, Oliva et al. 2007) whilst in the field the running direction is also tied to the distance and direction to the crabs burrow (Hemmi 2005a). In contrast, the blowfly *Chrysomya flavifrons* perform more similarly in a lab and field situation executing the same steps, however with some variation in time spent on each step, in its complex mating ritual in both locations (Butterworth et al. 2019).

Studying animals in the field gives the most natural response but environmental factors might cause the results to be hard to obtain or interpret (Calisi and Bentley 2009). In a lab setting many environmental factors can be

controlled and thus make the results easier to interpret, however, one risk is oversimplifying or over-extrapolating results so that they are no longer meaningful to the animal. Another risk is oversimplifying the environment so that it starts to affect the animals performance, one example comes from Roy et al. (2016) that showed how juvenile zebrafish reared in a bare environment fared worse in memory tests than relatives reared in a more complex environment. A trait of the animal might also be hard to interpret out of its original setting (Neff 2020). In some cases the animals might even have been used so long in the lab so that the their behaviour have started to diverge from the wild population, for example Russell and Kurtz found significant differences in three different behavioural assays for the extensively used model organism *D. melanogaster* (Russell and Kurtz 2012). The question then arises if the lab populations still provide a good representation of wild type behaviour.

3.1.7 Arenas and artificial targets

3.1.7.1 Arenas

Behavioural arenas have been used to study a number of flight behaviours in flies and other insects. Some examples of behaviours studied in hoverflies are their optomotor reflex (*S. pipiens*, Collett and Land 1975a), the effect of background on freefall (*Episyrphus balteatus*, Goulard et al. 2016), their prototypical movements (*E. tenax*, Geurten et al. 2010) and target pursuit (*S. pipiens*, Collett and Land 1975a). Target pursuit have also been studied in many other insects using arenas, for example in killer flies (Wardill et al. 2015), blowflies (Boeddeker et al. 2003), and dragonflies (Lin and Leonardo 2017).

Arenas are one way to solve the problem of how to limit an animal's available space to better be able to capture a behaviour on film (as mentioned in section 3.1.5 Videography). However, caution is needed when choosing arena size seeing as some behaviours requires a certain amount of space to take place. For example *Eristalis* territories are said to have a minimum size (Wellington and Fitzpatrick 1981), suggesting that the flies might not perform territorial pursuits in too small a space. Indeed for *E. tenax* Geurten et al. (2010) has shown that arena size affects the flight speed, number of saccades and to some extent also the prototypical behaviours. The flies flew slower but used more saccades and also spent more time flying backwards in a small arena compared to a larger one (Geurten et al. 2010). A larger arena might thus be better, and Mischiati et al. (2015) therefore converted an entire room into a mini outdoors for their dragonfly pursuit studies. However, larger arenas might, as during field studies, force the experimenter to limit where to film and important bits of the behaviour studied risk falling outside the range of the cameras (Lin and Leonardo 2017; Mischiati et al. 2015).

Not all animals perform well in captivity, for example Olberg et al. (2007b) found that their dragonflies did not feed well and quickly died when brought indoors. In order to study their pursuit behaviour, they instead constructed a mech cage outdoors, allowing for all the natural stimuli the dragonflies seem to need but still limiting the study area. However, this setup restricted the experimental period to when daylight shone on the cage (Olberg et al. 2007b). The setup of Mischiati et al. (2015) beautifully solves this problem with their effective naturalistic environmental factors, such as light, temperature, humidity and visual texture. Their background scenery, even though it provides the dragonflies with naturalistic visual cues (Lin and Leonardo 2017), is however a picture made for human eyes. Printed pictures are often photographed with cameras optimised for the human visual system, often with more green added (Tabora 2019). Many animals have vision quite different from human vision (Land and Nilsson 2012). A special camera was recently developed to help understand the vision of birds, allowing us to get an idea of how they experience a dense tree canopy (Tedore and Nilsson 2019). However, to not only photograph, but to also print pictures that will appear natural to animals, one might also need a printer that takes their vision into account, since even humans perceive colours differently when printed on different printers (with the same red-green-blue-values, Stevens and Cuthill 2005).

Another problem with backgrounds is that they might affect tracking (discussed in further detail bellow), either by creating low contrast between the insect and background or by restricting the filmable part of the arena. Some ways to try and solve the issue of the background occluding the camera view is by making a hole in the background (Geurten et al. 2010), not cover all sides (Geurten et al. 2010; Baird et al. 2021; Lecoeur et al. 2019) or film from inside the arena (Bomphrey et al. 2009; Lin and Leonardo 2017). However, the problem with low contrast between insect and background might still prevail, depending on the camera angle. One can try and solve this problem by using a background that gives a higher contrast to the insects being tracked, such as different red/white patterns (Geurten et al. 2010; Luu et al. 2011; Lecoeur et al. 2019), or by not having a background at all, using a mech (Olberg et al. 2007a; Hateren and Schilstra ; Schilstra and Van Hateren ; Schilstra and Hateren) or Perspex arena (Rossoni et al. 2021).

3.1.7.2 Artificial targets
Target tracking in insects have been studied at the neuronal level (Nordström et al. 2006; Nicholas et al. 2018), as well as the behavioural level (Wardill et al. 2015; Collett and Land 1978; Boeddeker et al. 2003). When studied at the behaviour level living targets can be used, for example *Drosophila* as prey for killer flies (Wardill et al. 2015) and dragonflies (Lin and Leonardo 2017), or conspecific males as targets for hoverfly and housefly males (Collett and Land 1975a; Wehrhahn et al. 1982). These naturalistic targets comes with its own

set of variables due to the unpredictability of living organisms (Mcelroy and Mcbrayer 2021; Domenici et al. 2008). One way to gain more predictability and thus eliminating some variables, so that the study questions can remain in focus, is to use artificial targets. The artificial targets can be physical objects such as beads (Wardill et al. 2015; Boeddeker et al. 2003), peas (Collett and Land 1978), wooden blocks (Collett and Land 1978), model preys made of clay (Morris and Reader 2016) or even dead conspecifics (Maier and Waldbauer 1979a) or prey animals (Morris and Reader 2016). The artificial targets can also be digital, shown on a computer screen (Nicholas et al. 2018) or with a LED setup (Keleş and Frye 2017).

Clearly an artificial target cannot mimic all the features of a naturalistic target, however great efforts are made to replicate naturalistic stimuli when the study question requires it. Eichorn et al. (2017) found that blowfly *Lucilia sericata* have age and sex specific wing flash frequencies (how the flies' wings reflect light during wing beats) that are differently attractive for males. They managed to get male alighting responses towards acrylic spheres using flashing LEDs replicating the wing flash frequencies of young females (Eichorn et al. 2017). However, the setup was constructed for stationary targets so the technique might be more difficult to use if one would like to use a moving target. Lin et al (Lin and Leonardo 2017) showed that dragonflies readily pursue both living *Drosophila* and artificial prey moved by an artificial prey presentation system in their arena, and argued that the artificial preys allowed them to study a much broader range of target variables than those accessible to them using only the *Drosophila*.

The motion paths of artificial targets, such as straight horizontal (Lin and Leonardo 2017; Collett and Land 1978), straight vertical (Wardill et al. 2015) or circular (Boeddeker et al. 2003) paths, are quite simple (Wardill et al. 2015; Lin and Leonardo 2017; Boeddeker et al. 2003; Collett and Land 1978) compared to flight paths of target conspecifics (Collett and Land 1978) or prey (Van Breugel and Dickinson 2012). However, methods for more varied target paths are being developed, such as the novel arena set up by Varennes et al. (2019) allowing for more complex 2D paths of an artificial target.

The use of artificial targets allows the experimenter to control one or several variables of the target, such as speed (Boeddeker et al. 2003), direction of movement (Wardill et al. 2015), size (Olberg et al. 2005) and colour (Morris and Reader 2016) just to name a few. Artificial targets have been used with killer flies (Wardill et al. 2015), robber flies (Wardill et al. 2017), blowflies (Boeddeker et al. 2003), dragonflies (Olberg et al. 2005; Lin and Leonardo 2017), hoverflies (Collett and Land 1978) and spiders (Morris and Reader 2016) to determine the target range pursued in terms e.g. size and velocity of the target (Wardill et al. 2015; Boeddeker et al. 2003), pursuit style (Collett and Land 1978; Wardill et al. 2017; Wardill et al. 2015), where the insects keep the target on their retina during pursuit (Lin and Leonardo 2017) and mimetic effect of target coloration (Morris and Reader 2016). Artificial targets thus allow an experimenter to isolate target variables. However, as with

artificial environments in the lab, caution needs to be taken not to over extrapolate results or simplify the target situation so that it no longer can represent a natural situation.

3.2 Flight path tracking

When studying flight behaviour, one might want to track the flying insect under study. Depending on the exact behaviour to be studied different parts of the fly might need to be tracked. For studies of flight trajectories one point on the fly is enough if one assumes that the fly does not fly backwards (Buelthoff et al. 1980; Schilstra and Hateren 1999). If one wants to include the body orientation two points on the fly needs to be tracked (Geurten et al. 2010; Hateren and Schilstra 1999), and to address the lift force during take-off a model of the wings may need to be fitted to each frame (Chen et al. 2013). This might in turn impose different requirements on the spatial resolution, as well as the tracking software.

Analysis of flight tracks, especially if manual, is often time consuming. This time can be decreased with automated tracking (Wardill et al. 2017; Dell et al. 2014). However, automated tracking might not be possible if the contrast between the insect to be tracked and the background is too low, e.g. if the insect is flying in a complex or moving environment, or if the insect to be tracked covers too few pixels (see Dell et al. 2014 for a detailed review)

There are a number of commercially available software solutions for animal tracking with different requirements on hardware and animal resolution, though most of these only perform tracking in 2D (Dell et al. 2014). Recently, software tracking animals in 3D has also started to become available (e.g., 3Dtracker (3dtracker.org), Track3D (noldus.com), DeppLabCut (mackenziemathislab.org)), though most of these require better resolution of the animal than is often possible for e.g., field studies (Nakamura et al. 2016; Stewart et al. 2015). Therefore, custom written software that matches specific study questions and settings are common (Wardill et al. 2017; Chen et al. 2013; Geurten et al. 2010). The benefits with automated tracking in 3D using commercially available software is that comparison between different studies can be easily done, though there is yet to be developed a software that can handle enough settings to be useful for this purpose (Dell et al. 2014).

3D tracking is usually performed with 2 cameras (Wardill et al. 2015; Boeddeker et al. 2003), but can be performed with as little as one camera if a mirror is used (Buelthoff et al. 1980; Bomphrey et al. 2009). If one has access to high computational power an array of cameras can be used for a potentially more accurate tracking or tracking over a larger area (Chen et al. 2013; Maimon et al. 2008; Dell et al. 2014).

To be able to perform 3D tracking, the cameras used for recording need to be synchronized, so that the same point can be tracked for each frame by

both/all cameras (Wardill et al. 2017; Stewart et al. 2015; Chen et al. 2013). Many cameras can be synchronized automatically (Stewart et al. 2015), but if this feature is not available cameras can also be synchronized manually. Manual synchronization is more time consuming than automatic but does allow for the usage of 3D tracking in field settings where automatic synchronization might be hard.

Another essential part of 3D tracking is the calibration, giving the software information about the size of the setting to be filmed. This can be done by e.g. using a checker pattern of known size that is filmed by both cameras simultaneously (Wardill et al. 2017).

Placing the cameras for tracking can sometimes be tricky (Dell et al. 2014), especially when in the field. When using two cameras a 90-degree angle between the cameras is common (Wardill et al. 2017; Geurten et al. 2010; Stewart et al. 2015), though in the field this might not always be achievable due to obstruction from e.g., foliage. Since tripods or other camera stances are required to not let camera movement affect the subsequent 3D tracking, the terrain on which to put the camera stance might also pose a problem (Dell et al. 2014).

3.3 Short description of methods employed in Paper I, II, III and IV

The methods used in *Paper I, II, III* and *IV* will be described briefly below. For a more detailed description please see the methods section in each paper.

3.3.1 Paper I

In *Paper I* rearing methods for the hoverfly *E. tenax* were developed, inspired by previously described protocols for hoverfly rearing. Protocols were tested against each other, evaluated for sanitary standards and user friendliness. Artificial hibernation was introduced to prolong the life of the hoverflies, in order to negate the effect of seasons that might otherwise make hoverflies hard to obtain from the wild. LAMS was used to confirm that the hoverflies' activity did not diverge from that of wild caught hoverflies. The weight of males and females was determined and the sex ratio of the hatched hoverflies investigated for a potential sex bias.

3.3.2 Paper II

In *Paper II* the locomotor activity of *E. tenax* and what affects it was studied. The different external factors studied were diet, starvation and company; the intrinsic factors studied were age and sex. For all

experiments, but the starvation experiment (that lasted 7 days), hoverflies were kept in a LAMS for 54 h. Hoverflies were kept individually in each tube, except when the effect of a conspecific companion was investigated, then the hoverflies were kept in pairs. Hoverflies were randomly assigned to slots in the LAMS. The light cycle was set to a 12:12 LD regime and the temperature was 19-25 °C. The circadian rhythm of the hoverflies was also investigated and by performing an additional experiment where the light was turned on for 4 hours during the 2nd night of the experiment, we could determine if the rhythm was a light response or a circadian rhythm.

3.3.3 Paper III
In *Paper III* the interactions between hoverflies (*Eristalis sp.* and *E. balteatus*), bees (*A. mellifera*) and wasps (*Vespula sp.*) around flowers were studied in 3D using high-speed videography with two cameras (120 fps) placed at least 30° apart. The data were collected July – September 2015 between 10 am and 5 pm on calm sunny days. The hoverfly sitting on the flower at the start of the interaction was classified as the occupant and was always a female *Eristalis*. The approaching insect was defined as an incomer. Definitions were made after Kikuchi (1962b). Calibration and 3D reconstruction was done as previously described (Wardill et al. 2017). Briefly, the centre, which is roughly similar to the centre of mass (COM, Chen et al. 2013) of both interactants were located for each frame and both cameras. These 2D coordinates were translated to 3D using custom written Matlab software. The movies were manually synchronized using a cell phone flashlight, or at instances where the flash was not visible in both cameras a distinct motion (e.g., a flower petal flick) was used. The movies were then manually checked for 10 frames to ensure correct synchronization. From the 3D coordinates visual variables such as speed, distance between the interactants, and angular information available to the occupant, were calculated.

3.3.4 Paper IV
In *Paper IV* an indoor flight arena (1 m^3, clear plexiglass) was developed and subsequently used to study male *E. tenax* pursuits of artificial targets. The artificial targets were fours sizes of black painted beads (6 mm - 38.5 mm) attached to a horizontal fishline. A stepper motor was programmed to continuously run a bead back and forth across the length of the arena (similarly to Wardill et al. 2017) alternating between seven different speeds

of the beads (0.1 ms^{-1} - 1.8 ms^{-1}), pausing briefly between each speed. 10 males and 8 females were kept in the arena at all times. New flies replacing old or dead flies were taken from the hibernation stock developed in *Paper I*. The females were only in the arena to encourage the male's pursuit behaviour and were not the focus of this study. Interactions between the male flies and the beads were filmed and reconstructed similarly to the occupant-incomer interactions in *Paper III*. The variables studied where also similar to *Paper III* with the addition of error angle to see where in the visual field the male keeps the target during pursuit. As well as pursuit length and some relationships between bead speed, pursuit probability and pursuer speed to investigate pursuit style and target range of the male hoverflies. The light and temperature conditions were the same as in *Paper II*.

4 Results and Discussion

4.1 *Eristalis* as study animals

4.1.1 Accessibility

Hoverflies are used more and more in laboratory studies (Chen et al. 2013; Nordström et al. 2008; Geurten et al. 2010; Nicholas et al. 2020; Ouattara et al. ; Khan et al.), making yearlong access to adult hoverflies important. One way of obtaining adult hoverflies is to catch them in the field. This method can be rather time consuming as the right species, and sometimes sex, of hoverfly needs to be seen, identified and caught. In Europe the flight period of hoverflies does not include the cold winter and the highest number are generally seen during the summer (Ottenheim 2000; Nationalnyckeln 2009). However, hoverflies are most active between 15 and 25 °C (Gilbert 1985) and some species will not fly in rain, cold or cloudy weather (Fitzpatrick 1981; Ball and Morris 2004; Grayson 2003), narrowing the window of easy access further.

Figure 9. Head of male *Eristalis tenax*. Photo of dead specimen from the Swedish museum of natural history. Depicting the large eyes.

Another way to access adult hoverflies is to breed them and some protocols already exist for this purpose (e.g., Gladis 1994b; Dolley Jr et al. 1937). However, these protocols either do not live up to current sanitary standards or are focused on mass rearing. During mass rearing the selective pressure on aerodynamic skills and vision is relaxed or non-existent compared to the situation in the wild (Fitzpatrick 1981), opening up for less fine tuning of these qualities, as well as a potential risk of a quick loss of genetic heterogeneity (Francuski et al. 2014). This would be unfortunate given that vision and flight behaviour are two of the most prominent traits of the hoverflies, named after their ability to hover and with large eyes covering a big portion of the flies head (figure 9 and Nationalnyckeln 2009; Ball and Morris 2015). We therefore set out to create a protocol that lives up to today's sanitary standards and allows for mating selection pressure (*Paper I*). Our

protocol uses either eggs from wild females or 3rd instar larvae collected from the wild, thus keeping the selective pressure in the field. We also further increased the previously recorded survival times for adult hoverflies in rearing situations from around 4 months (Heal 1989; Dolley Jr and Golden 1947; Gladis 1994b) to over a year, effectively combating the low to non-existent access during the winter months. We did this by introducing an artificial hibernation, were we kept the flies in 8 °C taking them out in room temperature to feed and groom every three to four days. The hoverflies were successfully used in experiments up to 7 months (*Paper II,* figure 2) and lay fertile eggs up to 5 months (*Paper II*). Thus, our breeding protocol ensures wild selection and access to adult hoverflies that can be used in experiments all year round.

4.1.2 Circadian rhythm

Only observational studies have been done when investigating the circadian rhythm of *Eristalis* hoverflies (Ottenheim 2000; Kikuchi 1962a), possibly introducing a bias towards the time of the day where a human observer would be most likely to spot the hoverflies. To remove this potential bias we used a LAMS setup, which allows for more objective measurements, to quantify the circadian rhythm. Our data confirmed that *E. tenax* are diurnal in their activity rhythm and we showed that they are equally active throughout the entire light phase of an experimenter set LD cycle (*Paper II,* figure 1). This fits well with what can be seen for other dipteran flies (Bahrndorff et al. 2012; Green 1964; Cymborowski et al. 1994), as well as some hymenopterans (Giannoni-Guzmán et al. 2014), but is in contrast to the bimodal activity pattern *Drosophila* shows in a 12:12 LD lab setting (Schlichting 2020).

The constant activity of *Eristalis* in the lab, that could effectively be set after an LD cycle, allows for experiments to be carried out during the entire day (light phase of the flies) and at a time suiting the experimenter. This, together with our finding in *Paper I* that activity does not differ between lab reared and wild caught flies (*Paper I*, figure 3b), as well as our finding that cruising flight speed does not differ between field (*Paper III*, figure 2, black and purple box plots) and indoor recordings (*Paper IV*, figure 3b, pink violin plots), gives a great flexibility that makes these hoverflies well suited as study subjects.

4.1.3 Age

Age is another factor that has been shown to affect activity in many animals (Rakshit et al. 2013). For example, Fernández et al. (1999) showed that the locomotor activity of some *Drosophila* strains is affected by aging (Fernandez et al. 1999). *Eristalis* has previously been shown to survive about 4 months (Heal 1989; Dolley Jr and Golden 1947; Gladis 1994b) in the lab, whereas

some hoverflies species are only known to live a few days (Stubbs and Falk 2002; Conn 1976). Using artificial hibernation, we managed to extend the life of *E. tenax* hoverflies to just over a year (*Paper I*). Age could thus be an important factor to consider for laboratory experiments with hoverflies. In *Paper II* we therefore looked at the activity of *E. tenax,* from newly hatched flies to 7-month-old flies, and found no difference in activity level (*Paper II,* figure 2a), showing that *E. tenax* have a stable locomotor activity throughout their lifetime, allowing them to be studied during their entire life. However, age might be of importance if a less general behaviour should be studied, as we in *Paper IV* noted that male *E. tenax* started mating tries at around two weeks of age and pursuits of an artificial target after two months (*Paper IV*, Materials and methods, Hoverflies). The onset of the mating tries could be understood by the timing of the sexual maturation of the females (figure 1 and Dolley et al. 1933) as well as the age dependent territorial settlement of the males (Fitzpatrick and Wellington 1983a).

4.1.4 Food type and starvation
It is known that food can affect the activity level in animals (Abe et al. 1989; Green 1964). *Eristalis* is known to feed from pollen and nectar in the field (Gilbert 1985; Gilbert 1983; Golding and Edmunds 2000). However, the use of pollen as a food additive for lab reared hoverflies has been discussed: some believe it to be important for oviposition and sexual maturation (Rijn and Wäckers 2016), whereas others believe that bee collected pollen cannot be ingested properly by the hoverflies and that only fresh pollen from flowers work as a food source (Gladis 1994b). To this day many different kinds of food combinations have been used for *Eristalis* in different studies, including e.g. honey and pollen (de Haan et al. 2013; Heal 1979), sugar (Horridge et al. 1975), honey (Wacht et al. 2000) and pollen and sugar (Dolley Jr et al. 1937). In some studies, it is not even disclosed what food, if any, was given to the hoverflies (Chen et al. 2013; Geurten et al. 2010). Therefore, we determined how different food combinations affected the activity levels of *E. tenax* and noted that their activity level was not affected by the food type used (*Paper II,* figure 4), making it unlikely that food affected the results of previous studies. However, we did note that *Eristalis* males could not survive on a pollen only diet (*Paper II,* fig. 4b black), whereas females could (*Paper II,* figure 4b grey). This could indicate that previous studies suggesting pollen not being a suitable food source could have been looking mainly at the male population. Thus, a carbohydrate source seems to be needed, at least for the males. In *Paper I* and *Paper II* we showed that females, both wild caught and bred from 3rd instar larvae, successfully lay fertile eggs on a pollen (bee collected, dry) and honey diet at 5 months of age. On the coloration of the fly droppings, which neatly matched that of the different pollens, in the home cages or bags (*Paper I,* figure 1 for graphics on the flies housing

arrangements) we could ensure that pollen had indeed been ingested. This does not confirm that pollen is needed for oviposition, however excluding it might be risky if oviposition is required for the study, since the blowfly *L. sericata* have been shown to need a protein food source to produce mature eggs (Alqurashi 2020) and the hoverfly *E. balteatus* does not seem to produce eggs on a sugar-water diet (van Rijn 2013).

In *Paper II* we also found that not even the absence of food (*Paper II*, figure 5) had any effect on the hoverflies' activity. The hoverflies instead had a very even activity till they died of starvation, with females surviving longer than males (*Paper II*, figure 5c, compare grey and black data). This finding is confusing since most animals, including many Diptera, increase their activity when starved (Scharf 2016; Yang et al. 2015; Grettenberger and Joseph 2019; Vera et al. 2007; Mistlberger 1994; Patton and Mistlberger 2013) until they find a new food source or die trying (Green 1964). One suggestion for this might be that *Eristalis* are always equally active. However, since their activity could be affected by a conspecific (*Paper II*, figure 3) and field studies show that male *Eristalis* tend to have both active periods patrolling their territory as well as resting periods where they are performing less-active tasks (Fitzpatrick 1981; Wellington and Fitzpatrick 1981), this is not likely. The lack of increase in activity during starvation could however be in line with our findings in *Paper III*, where we saw that 94 % of female *Eristalis* escape from their food flowers when approached (*Paper III*, figure 1a). Even though only 16 % of the approaching insects were wasps, who are potentially dangerous to the hoverflies, the female hoverflies also most often did not return to the flower within our study window (*Paper III*, figure 1a, 72 % have not returned after 2 s). We first found it a bit strange that the females neither stayed on the flowers nor returned to them, since foraging is a task generally important to animals and female *Eristalis* spend more time feeding than males do (Maier and Waldbauer 1979b). However, one explanation for the females escaping their food flowers could be high food supply, since this has been seen to affect the behaviour of other animals, such as lizards and spiders. Both male (Ducey and Heuer 1991) and female (Wu et al. 2019) lizards decrease their interspecific aggression when food supply is high, and the dessert spider *Seothyra henscheli* makes its web larger or smaller depending on food supply, spending less energy when supply is high (Lubin and Henschel 1996). It might be that *Eristalis* hoverflies are accustomed to a high food supply, and since they are generalist pollinators mostly active during blooming season (Nationalnyckeln 2009; Stubbs and Falk 2002) that might not be too far a stretch. Gilbert (1983) also suggested that when visiting *Aster novae-angliae* flowers, *Eristalis* hoverflies only needs to feed from three florets to justify its visit energetically, something that only takes roughly 0.3 s. Thus, it might not be a problem for the females to quickly abandon a food source, even if the hoverflies most often stay much longer, with the mean visiting time being around 20 s (Gilbert 1983). Being solitary insects (Nationalnyckeln 2009) *Eristalis* are not

confined to one location either, hence increasing their opportunities for finding food.

Thus, it might be that female *Eristalis* hoverflies living in a world of plentiful food, with little attachment to a single location, and being quick to replenish their flight energy, see no point in the potential risk of an interaction with another insect.

4.2 Flight behaviours

Flies use their ability to fly in several different ways. Some of them are hovering, where male hoverflies monitors their territory looking out for intruding insects (Fitzpatrick 1981); pursuit, where a male fly chases a conspecific male or female (Wagner 1986; Land and Collett 1974; Collett and Land 1975a; Fitzpatrick 1981; Maier and Waldbauer 1979b); escape, where flies move away from a potential threat (Card and Dickinson 2008b); landing, where the flies deaccelerate as they move closer to the landing substrate (Collett and Land 1975a; Balebail et al. 2019; Eckert 1983; Wagner 1982). Some flight styles have distinguishing features, and I will discuss two of them, escape and pursuit, bellow.

4.2.1 Escape

Kikuchi have shown that *Eristalis* hoverflies do not readily share their flowers with other insects (Kikuchi 1962a), something we confirmed for female *Eristalis* hoverflies in *Paper III*. The females left their flowers 94% of the time when approached by another insect and had 72% of the time not returned after 2 s (*Paper III,* figure 1), a time range long enough for an *Eristalis* hoverfly to complete an entire pursuit (Collett and Land 1975b; Maier and Waldbauer 1979b). The hoverflies left the flowers faster when approached by another insect compared to during spontaneous take-offs (*Paper III*, figure 3a and b). The spontaneous take-off flight speed we measured matched those already recorded for *Eristalis* hoverflies of around 0.1-0.2 ms^{-1} (Golding et al. 2001), whereas the take-off speed with another insect present was around 0.5 ms^{-1}, with a maximum of 1.5 ms^{-1}. The higher speed when another insect is present might indicate that the female hoverflies performed an escape when approached. A similar difference in take-off speed can also be seen in *Drosophila* during escape and voluntary take-offs (Card and Dickinson 2008a).

Another interesting aspect of the take-off behaviour of the female *Eristalis* is that the take-off speed by far is the fastest when they are approached by wasps (*Paper III*, figure 3a and b). The females also took off earlier, i.e., when the distance to the intruder were farther (*Paper III*, figure 4a), if the incoming insect was a wasp, in comparison to other intruding insects. This indicates that

the female hoverflies might be able to distinguish wasps, who predates on hoverflies (Akre 1982; Richter 2000; Harris and Oliver 1993), from the less harmful intruding bees and hoverflies. If this is done visually, that is an impressive feat, given the hoverflies spatial resolution.

Many animals, such as fish (Domenici and Blake 1997), birds (Tätte et al. 2018), Kangaroo rats (Freymiller et al. 2019) and fruit flies (Card and Dickinson 2008a; Williamson et al. 2018) escape at an angle away from an artificial or real threat. Depending on the approach angle of the threatening stimulus fruit flies have even been shown to alter both their escape azimuth (Card

Figure 10. Azimuth and elevation.

and Dickinson 2008a; Williamson et al. 2018) as well as their escape elevation (Williamson et al. 2018, see figure 10 for a graphic representation of elevation & azimuth). We could see the *Eristalis* females behave similarly, taking off away from intruders (*Paper III*, figure 3c), with the direction being upwards or to the sides (*Paper III*, figure 3d). Our findings thus suggest that flower take offs with an incomer present is indeed escapes.
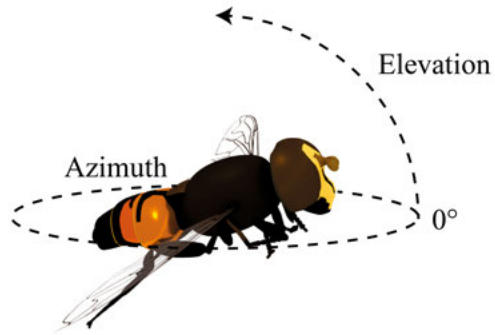
An incomer can be perceived as a looming stimulus. In *Drosophila* a looming stimulus can elicit an escape response (Card and Dickinson 2008a; Fotowat et al. 2009), and the escape starts when the looming stimulus reaches an angular width threshold (Fotowat et al. 2009). Looming stimuli can also elicit escape responses in goldfish, and even though the angular size and speed effects their escape probability, the stimulus contrast is the variable found to best predicts the fish escape response (Otero Coronel et al. 2020). In birds the flight initiation distance, i.e., the distance between the threat and the bird at take-off, is an important measuring tool (Tätte et al. 2018). The same type of studies has also proven useful when studying escape behaviour in dragonflies, showing that larger dragonflies escape when the predator is further away (Bell et al. 2019). For female *Eristalis* neither distance to the incomer (*Paper III*, figure 4a), angular width of the incomer on the retina (*Paper III*, figure 4b), angular speed of the incomer on the retina (*Paper III*, figure 4c) or angular increment (*Paper III*, figure 4d), could alone predict the start of the females escape response from the flowers.

Even though the females seem to be performing an escape response, the approaching insects might not perform an active attack since the incomers did not accelerate during the approach (*Paper III*, figure 2a) – something many animals do during pursuit (Collett and Land 1978, 1975a; Bomphrey et al. 2016; Wardill et al. 2017; Fiehler et al. 2019). The flight speed we measured

for the *Eristalis* incomers (*Paper III*, figure 2, black and purple data) instead matched the cruising flight speed previously measured in the field (Golding et al. 2001) and in our indoor flight arena (*Paper IV*, figure 3b, pink data). The cruising flight speed measured in *Paper III* was also lower than the flight speed measured during male hoverfly pursuit (*Paper IV*, figure 3, orange and blue), adding to the likelihood that the incomer was not in active pursuit of the occupant females.

4.2.2 Pursuit

Eristalis pursuit behaviour has previously only been studied outdoors, using observation (Fitzpatrick 1981; Wellington and Fitzpatrick 1981) or one camera (Collett and Land 1978). In fact, all syrphid pursuit studies, including Collett and Lands (1975a) arena study of *S. pipiens* pursuit behaviour, have so far been performed outdoors (e.g. Ball and Morris 2004; Rotheray et al. 2014; Alderman 2010; Collett and Land 1975a, 1978; Fitzpatrick 1981; Wellington and Fitzpatrick 1981). In *Paper IV* it is shown for the first time that eristaline hoverflies can pursue artificial targets in an indoor flight arena (*Paper IV*, figure 1).

The target range of *Eristalis* males have been suggested to be focused around that of a conspecific in terms of size and speed (Collett and Land 1978). However, observational studies suggest that the males can, during special circumstances, also pursue both much larger and smaller targets (Fitzpatrick 1981; Wellington and Fitzpatrick 1981). We therefore gave the males four different target sizes to pursue: 6 mm, 8 mm, 10 mm and 38.5 mm. The *E. tenax* hoverflies has a length of 14 – 16 mm (Nationalnyckeln 2009) and males have been shown to pursue targets with a 7 mm diameter (Collett and Land 1978), thus the 8 and 10 mm beads were expected to lay within their target range. The 6 mm bead, which is slightly smaller than the previously shown target diameter, and the 38.5 mm bead, which is much larger, would thus not be pursued if Collett and Lands (1978) suggestion would hold true.

We found that the males only rarely pursued the 6 mm bead, but readily pursued all the other bead sizes (*Paper IV,* table 2). Thus, our findings suggests that if the flies would have a target range centred around conspecific size they are using the length rather than width, which is ca 5.5 mm for *E. tenax* (Gilbert 1981), of their conspecifics. However, newly settled territorial males have been observed to pursue small targets in the field, but this is only a short phase of the male's territorial period (Fitzpatrick 1981; Wellington and Fitzpatrick 1981) and would thus be observed more rarely. The fact the flies pursue the largest bead support the observations of males pursuing large targets, such as leaves, butterflies and hornets (Fitzpatrick 1981; Wellington and Fitzpatrick 1981), but is in direct contrast to the conspecific centred target range suggested by Collett and Land (1978). In *Paper I* we found that female *Eristalis* are larger than males (*Paper I*, figure 4) and since male territorial

behaviour, including their pursuit behaviour, have been suggested to be focused on finding a mating partner (Fitzpatrick 1981) a target range shifted to larger sizes would thus make sense for the males. Blowflies, killer flies and dragonflies all pursue targets their own size (Boeddeker et al. 2003; Wardill et al. 2015; Khelifa 2021; Lohmann et al. 2019). However, blowflies and killer flies also pursue larger targets (Boeddeker et al. 2003; Wardill et al. 2015), and dragonflies and killer flies also pursue smaller targets (Wardill et al. 2015; Lin and Leonardo 2017). Thus, *Eristalis* is indeed not the only flying insect with a wide size target range.

In *Paper IV* we also found that *E. tenax* males pursue target speeds well below the previously suggested 8 ms^{-1} (Collett and Land 1978), namely 0 ms^{-1} – 1.8 ms^{-1} (*Paper IV*, figure 2b). In view of Collett and Lands (1978) suggestion that target speeds matches the speed of a conspecific, these lower speeds could stem from the fact that the flies were restricted to a flight arena (*Paper IV*, figure 1a), instead of being able to fly freely outdoors. Indeed, Geurten et al. (Geurten et al. 2010) showed that the size of a flight arena does affect the flight speed of *E. tenax*. However, there is another possible explanation: Collett and Land (1978) might have given *Eristalis* hoverflies a to narrow flight speed range to begin with. The bead speeds chosen for our experiments are more in line with the results from Golding et al. (Golding et al. 2001), who showed that *Eristalis* hoverflies in the field have a cruising flight speed of 0.2 ms^{-1}. We confirmed this cruising speed in both *Paper III* (figure 3, 0.34 ms^{-1}) and *Paper IV* (0.35 ms^{-1}, figure 3b, pink data). The speed of escaping female *Eristalis* (*Paper III*, figure 3a-b) also lays within the pursued bead speed range in *Paper IV* (*Paper IV*, figure 2b). It is also very likely that territorial male *Eristalis* hoverflies encounter females cruising or escaping from flowers in their territories centred around flower beds or flowering bushes (Wellington and Fitzpatrick 1981; Fitzpatrick 1981). Thus, the suggestion that male *Eristalis* hoverflies pursue targets flying at conspecific speed (Collett and Land 1978) might still hold true, but the speed range might be wider than first suggested.

Something interesting in the distribution of pursued speeds per target size (*Paper IV*, figure 2b) is that the largest bead is pursued almost exclusively at the two lowest speeds as well as when stationary. The pursuits of the largest bead were also longer than the pursuits of the smaller beads (*Paper IV*, figure 2a). It could be that the hoverflies sometimes react to the largest bead as they would to a passing butterfly or hornet, or possibly seeing it as a big conspecific (Fitzpatrick 1981; Wellington and Fitzpatrick 1981). This should interest the males since females in general are larger than males (*Paper I*, figure 4). Another possibility is that the large bead looks like a flower from a hoverfly point of view, since Collett and Land (Collett and Land 1975a) showed that male *S. pipiens* hoverflies would land on stationary flowers and also argues that flowers moving in the wind might give raise to some tracking behaviour before landing.

The majority of the pursuits of the three smaller beads were performed at the four or five highest speeds (*Paper IV*, figure 2b). Looking closer at the pursuits of the 8 and 10 mm beads we found that the speed of the bead did not have much effect on the flight speed of the pursuing males (*Paper IV*, figure 3b). This, together with the broad ranges of the four variables that we found in *Paper IV* (figure 4): pursuit distances to the target, retina size of target, retina speed of target and retina size change of target, suggest that the males do not have as fixed a pursuit model as suggested by Collett and Land (Collett and Land 1978). Instead, they seem to have a broader pursuit range, possibly arising from a different end goal with pursuit than catching the target. Doing so otherwise seems to be the goal of pursuit for both dragonflies and blowflies, who have been shown to have catch rates as high as 97 % and 95 % respectively (Olberg et al. 2000; Boeddeker et al. 2003).

Could it be that instead of catching their target hoverflies tries to get close to, but not in physical contact with, their target? Field observations might suggest so, since *Eristalis* males rarely make contact with an intruder if they are not in a heightened aggressive state (Wellington and Fitzpatrick 1981; Fitzpatrick 1981). Indeed, many animals do not choose physical contact as their first response in a conflict. For example, dolphins display before contact in both inter- and intraspecific conflicts (Volker and Herzing 2021) and cichlid fish do the same with an artificial conspecific (Cobey et al. 2020). Furthermore, mountain gorillas also choose non-physical interactions the majority of times when two groups meet (Mirville et al. 2018). This behaviour can also be seen in the insect world with e.g. hornets clicking their jaws before attacking (Ros et al. 2006), or dragonflies who pursue conspecifics and prey in different ways – overshooting much more frequently during territorial conspecific pursuits (Lohmann et al. 2019). Lohmann et al. (Lohmann et al. 2019) suggested that this could be because the dragonflies tried to avoid contact during territorial pursuits.

Another indicator that the flies' main goal might not be catching the target is that they do not only pursue targets in their dorso-frontal bright zone (*Paper IV*, figure 5), which is suggested to be good for target pursuit (Straw et al. ; Van Hateren et al.). Many insects do keep their target foveated during pursuit, including dragonflies (Lin and Leonardo 2017), some hoverflies (Collett and Land 1975a) and houseflies (Burton and Laughlin 2003).

In summary, the *Eristalis* hoverflies may track targets outside their bright zone, and have a broad target range in terms of size, speed and visual variables, as adaptive features to get close to, but not in contact with, their targets.

5 Conclusions

In *Paper* I we developed a protocol allowing us to breed hoverflies of the species *E. tenax* in the lab and, with the use of artificial hibernation, keep them alive for up to a year, mitigating the effects of weather and season on hoverfly availability. We also confirmed that the lab reared flies' weight and activity was not different from wild caught flies and that we do not get a sex bias in the hatched flies.

In *Paper II* using LAMS we concluded when during the day it is best to perform experiments on *E. tenax*. We show that the flies are diurnal and active during the entire light phase of an experimenter set LD cycle. We also showed that *E. tenax* are remarkably robust, with neither food, starvation, age or sex affecting their activity. However, the presence and sex of a conspecific did affect their activity.

In *Paper III* we show that female *Eristalis* hoverflies leave from their food flowers 94 % of the times she was approached and 72 % have not returned after 2 s. We concluded that the take offs when another insect is present seem to be escape responses even though the incomer does not seem to be performing an attack, but rather just cruse around nearby. Interestingly the females left the flowers at the highest speed and with the incomer at the farthest distance when the incomer was a wasp, suggesting that the hoverflies can somehow differentiate between wasps and less dangerous insects. We believe that the trigger for take-off is visual, but we were unable to conclusively determine which visual cue(s) contribute most to the take-off decision.

In *Paper IV* we developed an indoor flight arena for studies of eristaline flight behaviour. We thereby circumvent the seasonality of the hoverflies flight activity patterns and remove some of the hardships of performing videography in the field. Using the arena, we show that male *Eristalis* hoverflies pursue artificial target their own size, as well as much larger targets. On the contrary, they rarely pursue targets smaller than themselves. We saw a difference in pursuit of the largest bead compared to the others. The pursuits were longer and the largest bead was mainly pursued at slow speeds or when stationary. Looking at the smaller targets, the speed of the targets had little effect on the flies' speed and the range of visual variables were large. The males did also surprisingly perform pursuits both from below but also above the target, putting many targets outside the dorso-frontal bright zone of the hoverflies. All together this might suggest that the males end goal is not to catch the target but only to get close to it.

6 Future perspectives

6.1 Alterations of Paper I protocol for genetic studies

A possible future direction on the research presented in this thesis is to develop the breeding protocol of *Paper I* in such a way that it can be used for genetic studies. Both genomic and mitochondrial sequences are available for *Eristalis* hoverflies (Li et al. 2017; Hawkes et al. 2021a, b, 2022; Wiegmann and Richards 2018) and in view of how genetic tools, e.g. the CRISPR/Cas9 system (Cui et al. 2018), have been used in previous research on *D. melanogaster* (e.g. Kohsaka and Nose 2021; Smylla et al. 2021) the possibilities seems endless.

We have noted that *E. tenax* hoverflies readily mate with their siblings and produce viable offspring in the lab so similar crossing schemes as used with *Drosophila*- (Brown 2021) or *Lucilia*- (Linger et al. 2016) mutant flies could indeed be set up within our protocol. Depending on the study questions one might however need to take some care not to lose too much genetic heterogenicity over time (Francuski et al. 2014; Eusebi et al. 2019), and actively test against wild type flies produced with the original protocol to see so that no key behavioural traits are lost. Protocols for blowfly breeding regularly mix fly cages (Nasoori and Hoomand 2017) and introduce new individuals from the wild, into the established colonies, to reduce inbreeding (Magni et al. 2021; Nasoori and Hoomand 2017). The usage of a large starting population have also been shown to help slow down loss of genetic diversity in *Drosophila* (Montgomery et al. 2000), and back crossing with founder sperm when breeding endangered frogs can mitigate some of the effects of a small starting population (Howell et al. 2021).

In order to use the protocol for genetic research the larval diet might need to be changed to accommodate an eventual higher sanitary standard. It has been shown that the blowfly *C. megacephala* can be bred on both a meet (Smith et al. 2015; Reddy et al. 2014) and meet free larval diet (Reddy et al. 2014). This blowfly shows similarities with *E. tenax* hoverflies in several ways. For example, their larvae feed on similar substrate, however the *E. tenax* larvae needs a more aquatic setting (Nationalnyckeln 2009; Hobson 1932; Shah et al. 2015; Ireland and Turner 2006). If the larval diet in the study by Reddy et al. (2014) could be given a slightly more liquid character there might be a potential also for *Eristalis* larvae to successfully develop within it. Early

protocols for *Eristalis* breeding offer some larval diets free from animal waste, including rotting plant material (Ottenheim and Holloway 1994), soil soaked cereal (Gladis 1994c), hay infusion (Dolezil 1972), a sawdust-grass mixture with additives (Kobayashi 1972), wet oats (Gladis 1994b) or oat seeds (Gladis 1997). However, the meet free *C. megacephala* larval diet might be more user friendly and sanitary. A more sanitary protocol could also open up for use of *Eristalis* as a food substrate for humans or animals.

6.2 Potentials for genetically engineered hoverflies

Eristalis hoverflies are globally spread pollinators (Nationalnyckeln 2009). With genetic tools it would thus be possible to study how their genetics varies around the globe. It would also be possible to study how morphology are affected by different climates and living environments of the flies.

It is already known that the season affects both the behaviour (Fitzpatrick 1981; Wellington and Fitzpatrick 1981) and sometimes morphology of *Eristalis* (Mielczarek et al. 2016). Temperature is also known to affects wing length in *E. arbustorum* (Ottenheim and Volmer 1999). Thus, a morphological difference across the globe is indeed possible. With the excellent collections at the Swedish natural history museum, and other similar museums across the world, even a longitudinal look at how climate change has affected the flies is possible.

Another great possibility could be to genetically engineer the flies to help figure out which genes are important for the on switch (sexual maturation of spring generation or indoor raised flies) and off switch (autumn generation) of territoriality. With new videography methods arising, with AI controlled cameras (Pannequin et al. 2020) and cameras mounted on the insects themselves (Iyer et al. 2020), comparing lab data to field studies of unrestricted animals could also soon be possible. Furthermore, the rise of VR arenas (Kaushik and Olsson 2020) could open up for more well controlled settings to test flies, possibly with a combination of behavioural and neuronal techniques (fluorescent neurons, Schnell et al. 2010; optogenetics, Kohsaka and Nose 2021; Smylla et al. 2021).

7 Svensk sammanfattning (Swedish summary)

Blomflugor har föreslagits vara den näst viktigaste gruppen pollinatörer efter bin och humlor, och klimatförändringar samt oroande rapporter om minskande antal pollinatörer gör att det kanske aldrig varit viktigare att förstå våra pollinatörer. Med sina små hjärnor, sin fantastiska flygförmåga, goda temporala optiska upplösning, men mer begränsade spatiala optiska upplösning, är blomflugor också intressanta att studera för sin flygförmågas och syns skull. *Eristalis tenax* är globalt spridda generalist-pollinatörer, vilket gör att de enkelt kan studeras internationellt. Blomflugornas tillgänglighet påverkas dock av väder och årstid, vilket gör att de kan vara svåra att tillgå under vissa delar av året. Dessutom är inte deras jaktbeteende samt interaktioner med andra insekter särskilt välstuderat, och vidare har deras aktivitetsrytm enbart studerats genom observationsstudier. För att kunna fylla i dessa kunskapsluckor började vi med att utveckla ett nytt protokoll för uppfödning av *E. tenax,* och genom att införa en period av dvala i 8 - 10 °C kunde vi få blomflugorna att överleva i upp till ett år – vilket gör att vi nu har tillgång till dem hela året. Vi kunde också, med en LAMS, bekräfta tidigare påståenden om att *E. tenax* har en dygnsrytm där de är aktiva under hela ljusperioden. Vidare upptäckte vi att *E. tenax* aktivitet är oerhört robust – varken ålder, diet eller svält påverkade aktiviteten nämnvärt. Däremot påverkades aktiviteten av närvaron av en artfrände. Genom att använda höghastighetskameror fann vi att *Eristalis*-honor också i fält påverkas av närvaron av en annan insekt. Vi såg att honorna lämnar sina blommor 94 % av gångerna då en annan insekt närmar sig, trots att bara 16 % av dessa insekter var potentiellt farliga getingar. Intressant nog verkade *Eristalis*-honorna kunna särskilja getingar från andra insekter som de interagerade med – de lämnade sina blommor mycket tidigare och med en högre hastighet om det var en geting som närmade sig jämfört med om det var en annan blomfluga eller ett bi. För att kunna studera flygbeteendet för *E. tenax* året runt utvecklade vi en inomhusarena, och med hjälp av höghastighetskamerorna upptäckte vi att *E. tenax*-hanar jagar kulor med en diameter på 6 - 38.5 mm som rör sig i hastigheterna 0 - 1.8 ms^{-1}. Fascinerande nog upptäckte vi att hanarna jagar kulorna både när de är ovanför och under flugorna, vilket gör att kulorna ofta placeras utanför det område på näthinnan som tros vara viktigt för att spåra mål i luften (bright zone).

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"O little fly! Delightful fly! Perch on my wrist again: Then rub your legs and dry your eye, And climb my wrist again: For surely here, the atmosphere Is somehow right and good for you I love you most when as your host I'm in the mood for you."

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