



UPPSALA  
UNIVERSITET

The relationship between body size and dry weight in hoverflies (Syrphidae), and their movements along an urban linear landscape element

Amanda Folkö

---

Degree project in biology, Bachelor of science, 2014

Examensarbete i biologi 15 hp till kandidatexamen, 2014

Biology Education Centre, Uppsala University, and Biology Education Center at the University of Bern, Switzerland

Supervisors: Myles Menz and Anna Jakobsson

## **Abstract**

Pollination constitutes a fundamental ecosystem service for humankind. The most important order of pollinating insects is the bees (Hymenoptera) followed by the flies (Diptera), in particular hoverflies (Syrphidae). Given the recent global concern over pollinator declines, it is crucial to extend our knowledge of pollinator ecology, both for the conservation of pollinators and conservation of the plants that rely on them. One of the major causes of this decline is habitat loss and fragmentation. Linear Landscape Elements (LLEs) have been shown to act as corridors and facilitate the movement of insects between habitat patches. Thus, LLEs could be used to counteract some effects of fragmentation and isolation. Since foraging distance of bees has been shown to correlate with body mass the present study contains two parts: a morphometric analysis and a mark-recapture study. First I investigated the relationship between body size and dry weight in three common hoverfly species. I aimed to find a body size metric which easily could be used in the field for prediction of dry weight. No general correlations were found between the body size metrics and dry weight within the five groups. A stronger and general pattern of correlations were found between the body size metrics studied. Thus, IT-span was chosen as the measurement used in the mark-recapture study, also due to its simplicity to measure in the field. The mark-recapture study was performed along a linear strip of ruderal vegetation following an urban river to investigate the relationship between movement distance and body size. Despite marking 46 hoverflies, only one individual was recaptured, giving a movement distance of 8 m. This low recapture rate (2%) could be due to animals moving beyond the extent of the study area. Finding a study area with higher recapture probability would likely give this method good potential for further work in the future.

## **Introduction**

### **Pollination and pollinator decline**

Pollination constitutes a fundamental ecosystem service for humankind. Primary data from 200 countries have shown that 87 of the 115 leading global food crops (including fruits, vegetables and seeds) rely upon animal pollination (Klein *et al.* 2007). Thus, it is likely that a pollinator decline could have great impacts on food production. Ollerton *et al.* (2011) estimated the global number of animal pollinated angiosperms to 308 006, which corresponds to 87.5% of the diversity of flowering plant species. This provides further evidence about the important role of animal pollination, not just for food production, but also for ecosystem functioning. In some European countries where pollinator population status has been thoroughly evaluated, up to 65% of the bee species are red-listed (Patiny *et al.* 2009). Further, studies from pre- and post-1980 have shown that bees are declining in both Britain and the Netherlands (Biesmeijer *et al.* 2006). Kearns *et al.* (1998) concluded that the "pollination crisis" most evident in the decline of honeybees and native bees possibly could be ameliorated, but more knowledge is required to make the optimal decisions for conservation.

### **Fragmentation and isolation**

The four most likely causes for this pollinator decline are suggested as: fragmentation of habitats and changes in land use, decreases in flower diversity and quantity, insecticides and the direct or indirect toxicity of other agricultural inputs, and physical barriers, such as roadways and highways (Patiny *et al.* 2009). Stenhouse (2004) showed that remnant habitat patches tend to be smaller in highly populated metropolitan areas and that these patches also show a higher level of fragmentation. This has implications for conservation, since negative effects on biodiversity can occur when fragments are too small to sustain populations and too isolated to receive colonists from other patches (Ricklefs 2008). Steffan-Dewenter and Tscharntke (1999) showed that increased isolation of small habitat islands resulted in both decreased abundance and species richness of flower-visiting bees. They also found a positive correlation between seed set per plant and the number of flower-visiting bees. The seed set per plant was halved at a distance of 1000 m for mustard (*Sinapis arvensis*) and at 250 m for radish (*Raphanus sativus*). This indicates that isolation not only can cause pollinator decline but also affect plant-pollinator interactions. Further, Bates *et al.* (2011) showed that the diversity and abundance of both bees and hoverflies were significantly negatively associated with higher levels of urbanization in the city of Birmingham in the UK. Thus, it is essential to consider conservation of biodiversity in urban planning.

### **Corridors, linear landscape elements and barriers**

Habitat corridors, which are typically linear strips of habitat that can facilitate movements of organisms between habitat fragments, are one landscape structure that may mitigate the negative effects of habitat fragmentation (Ricklefs 2008). Using fluorescent powder to track pollen, Townsend and Levey (2005) demonstrated that pollen transfer by butterflies, bees and wasps between patches connected by a corridor was significantly higher than pollen transfer between unconnected patches.

Linear landscape elements (LLEs) such as rivers, railways, hedges and ditches all provide semi-permanent structures where wild vegetation is able to grow. LLEs have been shown to act as biological corridors for pollen dispersal between fragmented populations of two insect-pollinated herbs (*Primula vulgaris* and *Primula elatior*). The dispersal of the fluorescent dye, used as a pollen analogue was found to be significantly higher between populations of *P. vulgaris* connected by an LLE, than between unconnected populations (Van Geert *et al.* 2010). Further, populations of *P. elatior* connected by LLEs exchanged dye up to 602 m, whereas populations not connected (and separated by distances of at least 249 m) did not (Van Rossum and Triest 2012). This suggests that LLEs can serve as corridors counteracting the negative effects of fragmentation and isolation. Further, Jauker *et al.* (2009) showed that the abundance of hoverflies along transects of semi-natural habitat (field margins) increased with the distance to the source habitat, while the abundance of wild bees decreased.

By studying the pollen-specialist solitary bee *Hoplitis adunca*, Zurbuchen *et al.* (2010) found that a motorway with intense traffic and a wide river did not represent barriers for foraging by this species. However, by using the pollen of *Phacelia tanacetifolia* as a marker, Wratten *et al.* (2003) showed that the proportion of three hoverfly species (*Ephisyrrhus balteatus*, *Metasyrrhus corollae* and *Melanostoma fasciatum*) containing *P. tanacetifolia* pollen was significantly reduced by poplar (*Populus* spp.) boundaries. Another study of barrier effects on the movements of hoverflies showed that hoverflies tend to avoid flying over dirt tracks, asphalt roads and ploughed fields (Lövei *et al.* 1998). Further studies on the impact of barriers on the movement of hoverflies would be important for the facilitating dispersal and colonization in fragmented landscapes.

### **Hoverflies and their interactions**

The most important order of flower-pollinating insects is the Hymenoptera, although the second most important order is the Diptera, and especially important are Syrphidae, Bombyliidae, and Muscoidea (Larson *et al.* 2001). In European countries, hoverflies (Syrphidae) have been found to visit more than 70% of the animal-pollinated wild flowers (Rotheray and Gilbert 2011). With the decline of bees in mind (Biesmeijer *et al.* 2006; Patiny *et al.* 2009), it has been suggested that hoverflies potentially could take over in situations where bees have been lost (Rotheray and Gilbert 2011). However, studies on pollination efficiency of wild bees and hoverflies in oilseed rape (*Brassica napus*) show that the solitary red mason bee (*Osmia rufa*) is more efficient than the hoverflies (Jauker *et al.* 2012). For example, approximately a five-fold density of the two hoverfly species *Eristalis tenax* and

*Episyrphus balteatus* was required to achieve similar levels of fruit set and yield compared to the red mason bee.

Hoverflies are a diverse family, with approximately 6000 species worldwide, which are abundant in many different habitats (Ball and Morris 2013). Their ecological role is varied and includes pollination and predation on aphids, caterpillars, and larvae of mosquitoes, leaf beetles, ants, bees and wasps (Rotheray and Gilbert 2011). Pollination and pest control (Francis *et al.* 2005; White *et al.* 1995) are two ecosystem services provided by hoverflies that directly can benefit agriculture. Hoverflies also play important roles as decomposers and provide prey for a variety of natural enemies, mostly for other insects like wasps, spiders and beetles (Rotheray and Gilbert 2011). Due to the following properties, hoverfly communities are predicted to be useful for evaluation of environmental health at a larger scale: The larval habits are highly diverse (phytophagous, mycophagous, saprophagous and zoophagous), hoverflies are common and easy to find in almost all terrestrial ecosystems including urban and rural landscapes and identification is not difficult for many genera (Sommaggio 1999). All these potential uses and their important roles in many ecosystems should make hoverflies a study object of high priority, although much knowledge is still missing. Action to conserve and benefit from hoverflies would probably be more common if their ecological roles and properties became better understood.

### **Aim and scientific questions**

The present study consists of two parts; a morphometric study and a mark-recapture study. In the morphometric part wing length, intertegular span (the shortest linear distance measured between the wings tegulae across the thoracic dorsum), head width and dry weight were measured on individuals from three common hoverfly species to investigate the relationships between body size and weight. This was done to determine a simple, reliable body size metric for use in the field for investigating relationships between body size and movement distance. Since it has been shown that IT-span (intertegular span) and head width can serve as reliable predictors for dry- and fresh weight, in different *Bombus* species (Hagen and Dupont 2013), and that body length and mass are positively correlated with foraging distance of bees (Gathmann and Tschardt 2002; Greenleaf *et al.* 2007), similar studies on hoverflies could prove useful for the knowledge of their life history traits, and thus contribute to the conservation work. Therefore a mark-recapture study with hoverflies in a linear strip of ruderal vegetation along an urban river was performed.

I investigated following questions: **(1)** what is the relationship between body size metrics and dry weight in *E. tenax*, *E. balteatus* and *M. florea*? **(2)** Does the size of the hoverflies affect the distance of their linear movements? **(3)** Do hoverflies cross the river, or does the river represent a barrier to movement? **(4)** What is the pattern of movement of hoverflies along linear strips of ruderal vegetation?

### **Material and methods**

## **Morphometric study**

The following measurements were taken from pinned specimens of hoverflies, by using a digital caliper (precise to 0.01 mm): right- and left wing length, IT-span, head width and pin diameter (pin diameter since the pins could not be removed due to the risk of damaging the specimens). All specimens originated from Switzerland, but were caught at different times and in different areas. A total of 195 specimens from three common species were measured: 64 individuals of *E. tenax* (31 males and 33 females), 82 individuals of *E. balteatus* (43 males and 39 females) and 49 males of *M. florea*. After the measurements were taken, the specimens were put into a drying cabinet and dried at 45°C for five days to reduce the water content (Cane 1987). After drying, the pinned specimens were weighed with an analytical balance (precise to 0.001 g). Pins of the commonly used diameters were then weighted separately (the pin length was standardized). The average pin weight was calculated from three to five pins of each diameter and subtracted from the total dry weight to obtain the dry weight of each specimen. The mean wing length was then calculated for further use in the statistical analysis.

## **Mark-recapture study**

The fieldwork was carried out along a transect following the river Aare in Bern, Switzerland. The transect consisted of an approximately 2 m wide and 300 m long strip of ruderal vegetation in-between the river and a walking path (46°57'27.08"N, 7°26'30.42"E and followed the river 300 m south)(Figure 1). The study was conducted from 9 May to 3 June 2014, on days with very low or no precipitation and a daily temperature above 15°C.

A total of 47 hours were spent (by one person) walking along the transect to capture and recapture marked and unmarked hoverflies. A total of five hours were spent searching for marked flies on the opposite side of the river, to study barrier effects. This area was similar to the transect also consisting of a strip of ruderal vegetation in-between the river and a walking path. All hoverflies encountered were captured by net and marked individually on the thorax using waterproof color pens, using a combination of three colors, where each color represented a number from zero to nine. Marking continued for the duration of the study. The IT-span was measured for each individual by using a digital caliper (precise to 0.01 mm). The location of each capture and recapture was recorded using a GPS with an accuracy of  $\pm 3$  m. Recaptured individuals that couldn't be identified in the field were brought to the lab for identification.



**Figure 1.** The approximately 2 m wide and 300 m long transect of ruderal vegetation in Bern, Switzerland where the field work was conducted.

To control for the effects of varying flower density and species composition on movements and abundance of hoverflies, flower heads were counted before the start of the study. Every 20 m a 2 x 2 m square was searched, and all flowering species within the squares were identified and all flower heads were counted.

To calculate the distance moved by recaptured individuals, the GPS-coordinates (from the mark- and the recapture events) were used to calculate the difference in x- and y-direction. Then Pythagoras' theorem ( $a^2 + b^2 = c^2$ ) was used to calculate the distance between the two points.

### **Statistical methods**

Linear regression analysis was conducted to test for correlations between dry weight and the body size metrics. The data fitted to the assumptions without any need of transformation. The program R 3.0.3. (R Core Development Team, 2014) was used for the statistical analysis.

## Results

### Morphometric study

In the intraspecific analysis, no general correlations were found between the body size metrics and dry weight within all the five groups (Tables 1, 2, 3, 4 and 5). However, head width and IT-span were found to be significantly correlated to dry weight in all male groups (Tables 1, 3 and 5). In contrast, wing length was the only significant correlation to dry weight found within the female groups (Tables 2 and 4). The correlations between the body size metrics were generally stronger than the correlations to dry weight. Head width was found to be significantly correlated to wing length within all the five groups (Tables 1, 2, 3, 4 and 5). Further, head width and IT-span was found to be correlated ( $R^2 = 0.42-0.69$ ) within all groups (Tables 2, 3, 4 and 5) except within the males of *E. tenax* (Table 1). A significant correlation between IT-span and wing length was also found in all groups (Tables 2, 3, 4 and 5) except within the males of *E. tenax* (Table 1). The body size metric which correlated most strongly to dry weight in each group was either head width or wing length (Figures 2, 3, 4, 5 and 6).

As there was a general pattern of correlation between the body size metrics studied, IT-span was chosen as the measurement used in the mark-recapture study, due to its simplicity to measure in the field.

**Table 1.** Body size metrics- and dry weight correlations from linear regression analysis of male individuals ( $n = 31$ ) from the hoverfly species *Eristalis tenax*.

Y	X	P	R <sup>2</sup>
Wing length	Dry weight	0.051	0.09
IT-span	Dry weight	0.039*	0.11
Head width	Dry weight	0.003*	0.25
Head width	IT-span	0.067	0.08
Head width	Wing length	<0.001*	0.33
IT-span	Wing length	0.534	-0.02

\*  $P < 0.05$

**Table 2.** Body size metrics- and dry weight correlations from linear regression analysis of female individuals ( $n = 33$ ) from the hoverfly species *Eristalis tenax*.

Y	X	P	R <sup>2</sup>
Wing length	Dry weight	0.010*	0.17
IT-span	Dry weight	0.099	0.06
Head width	Dry weight	0.067	0.08
Head width	IT-span	<0.001*	0.42
Head width	Wing length	0.024*	0.13
IT-span	Wing length	0.003*	0.23

\*  $P < 0.05$

**Table 3.** Body size metrics- and dry weight correlations from linear regression analysis of male individuals ( $n = 43$ ) from the hoverfly species *Episyrphus balteatus*.

Y	X	P	R <sup>2</sup>
Wing length	Dry weight	<0.001*	0.28
IT-span	Dry weight	<0.001*	0.26
Head width	Dry weight	<0.001*	0.28
Head width	IT-span	<0.001*	0.55
Head width	Wing length	<0.001*	0.63
IT-span	Wing length	<0.001*	0.51

\*  $P < 0.05$

**Table 4.** Body size metrics- and dry weight correlations from linear regression analysis of female individuals ( $n = 39$ ) from the hoverfly species *Episyrphus balteatus*.

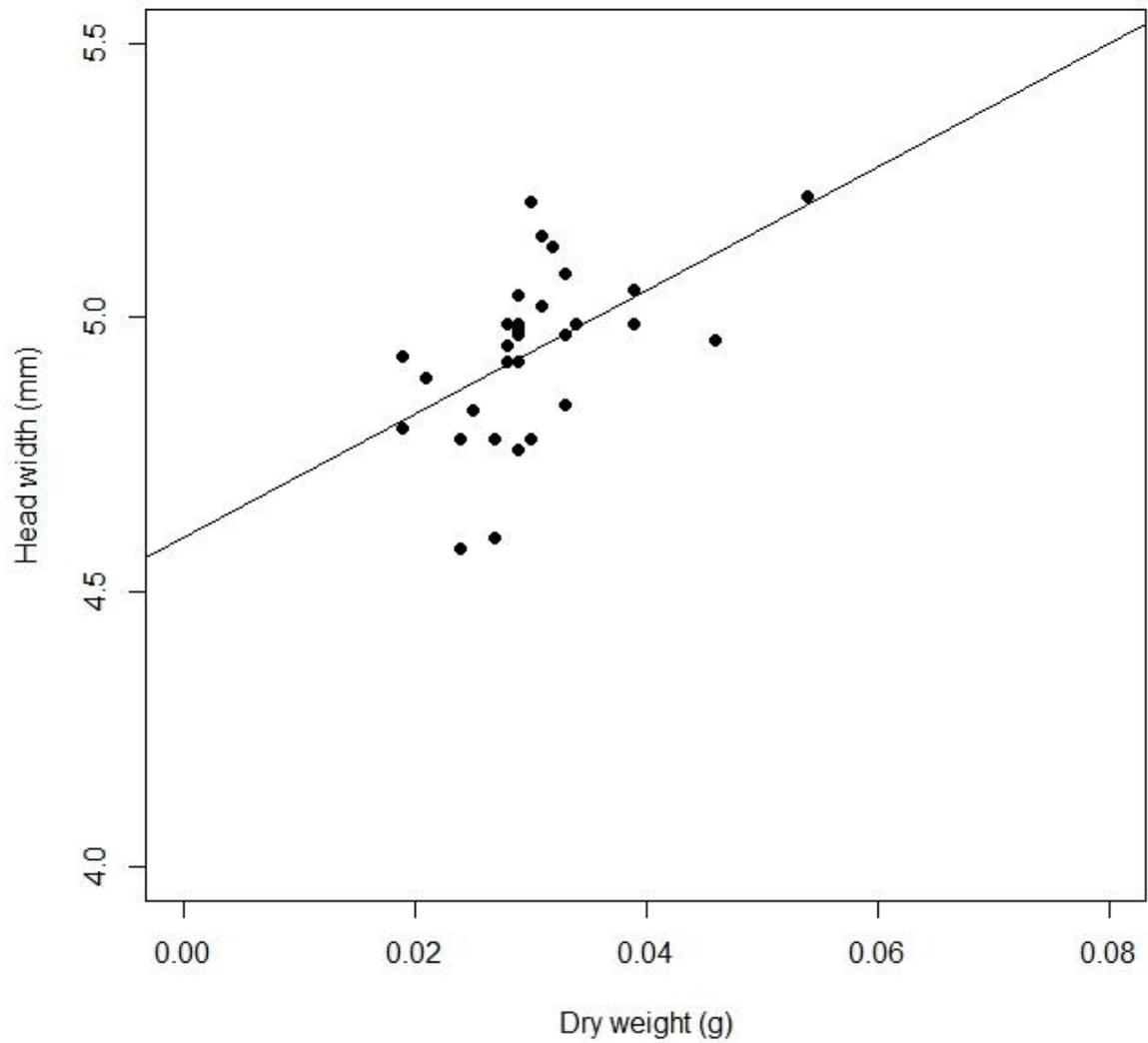
Y	X	P	R <sup>2</sup>
Wing length	Dry weight	0.017*	0.12
IT-span	Dry weight	0.051	0.07
Head width	Dry weight	0.063	0.07
Head width	IT-span	<0.001*	0.68
Head width	Wing length	<0.001*	0.80
IT-span	Wing length	<0.001*	0.57

\*  $P < 0.05$

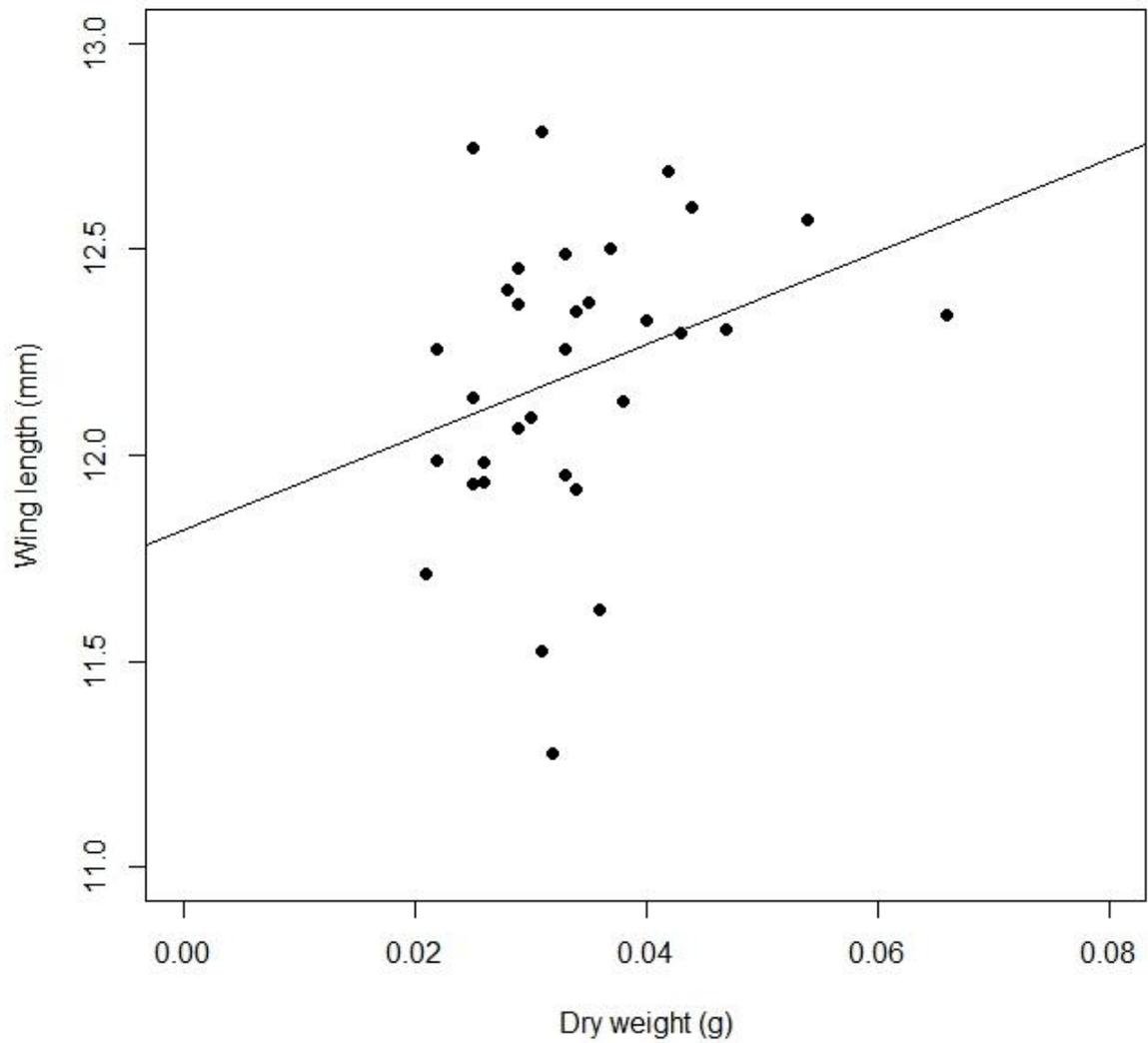
**Table 5.** Body size metrics- and dry weight correlations from linear regression analysis of male individuals ( $n = 49$ ) from the hoverfly species *Myathropa florea*.

Y	X	P	R <sup>2</sup>
Wing length	Dry weight	0.001*	0.20
IT-span	Dry weight	0.018*	0.10
Head width	Dry weight	0.005*	0.14
Head width	IT-span	<0.001*	0.58
Head width	Wing length	<0.001*	0.50
IT-span	Wing length	<0.001*	0.45

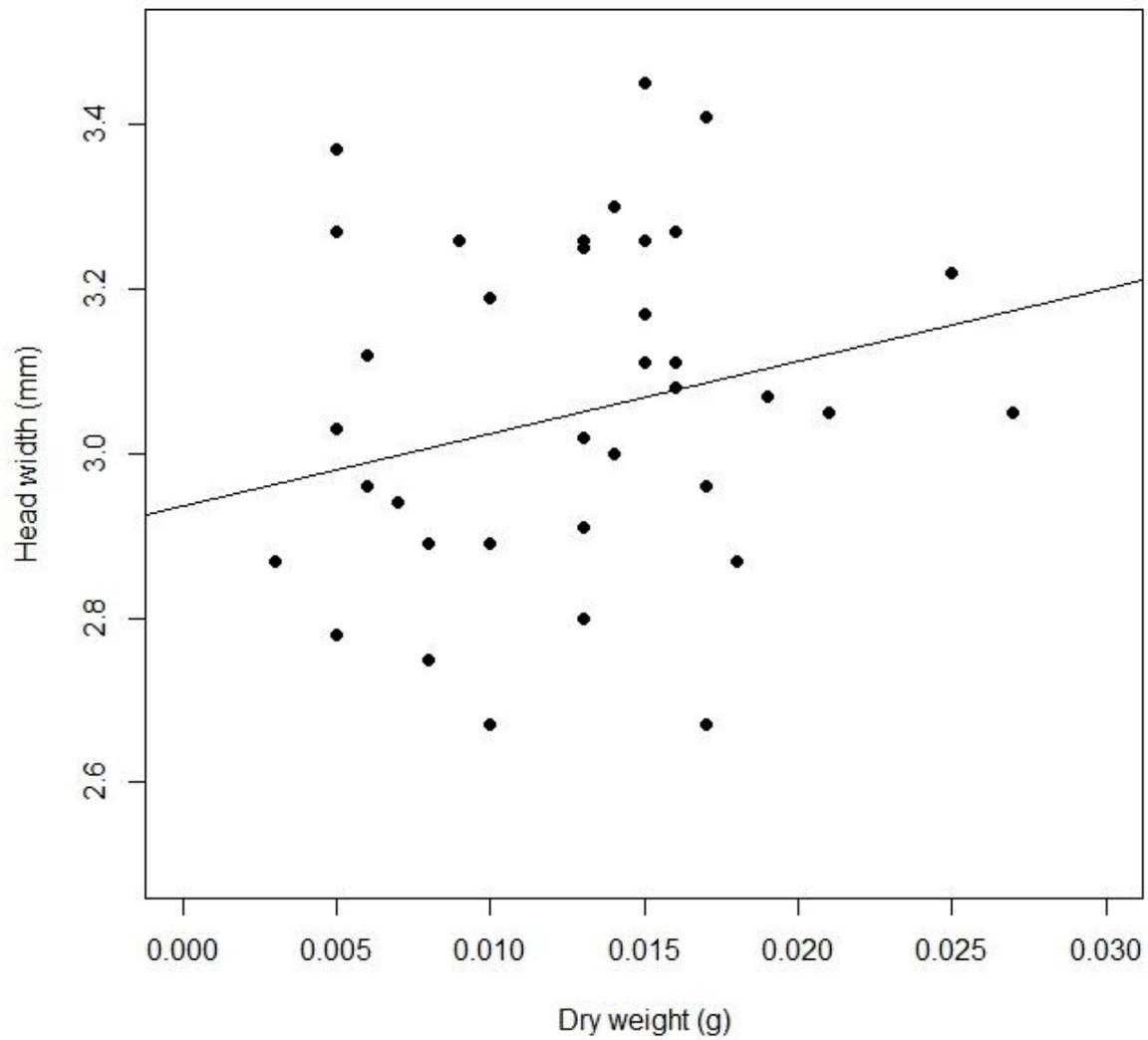
\*  $P < 0.05$



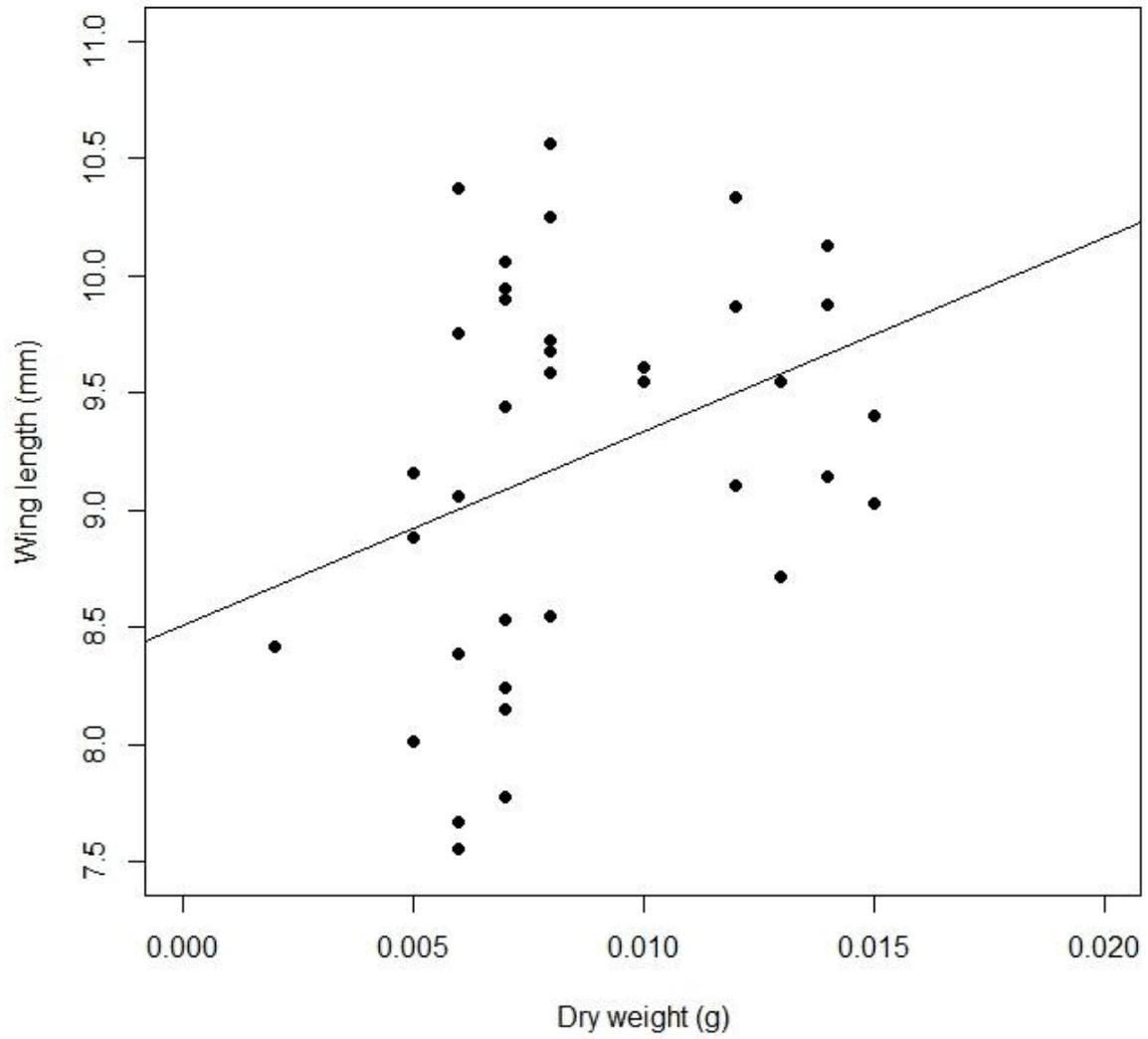
**Figure 2.** The strongest correlation between a body size metric and dry weight for males of *Eristalis tenax*,  $R^2=0.25$ ,  $P = 0.003$  and  $n=31$ .



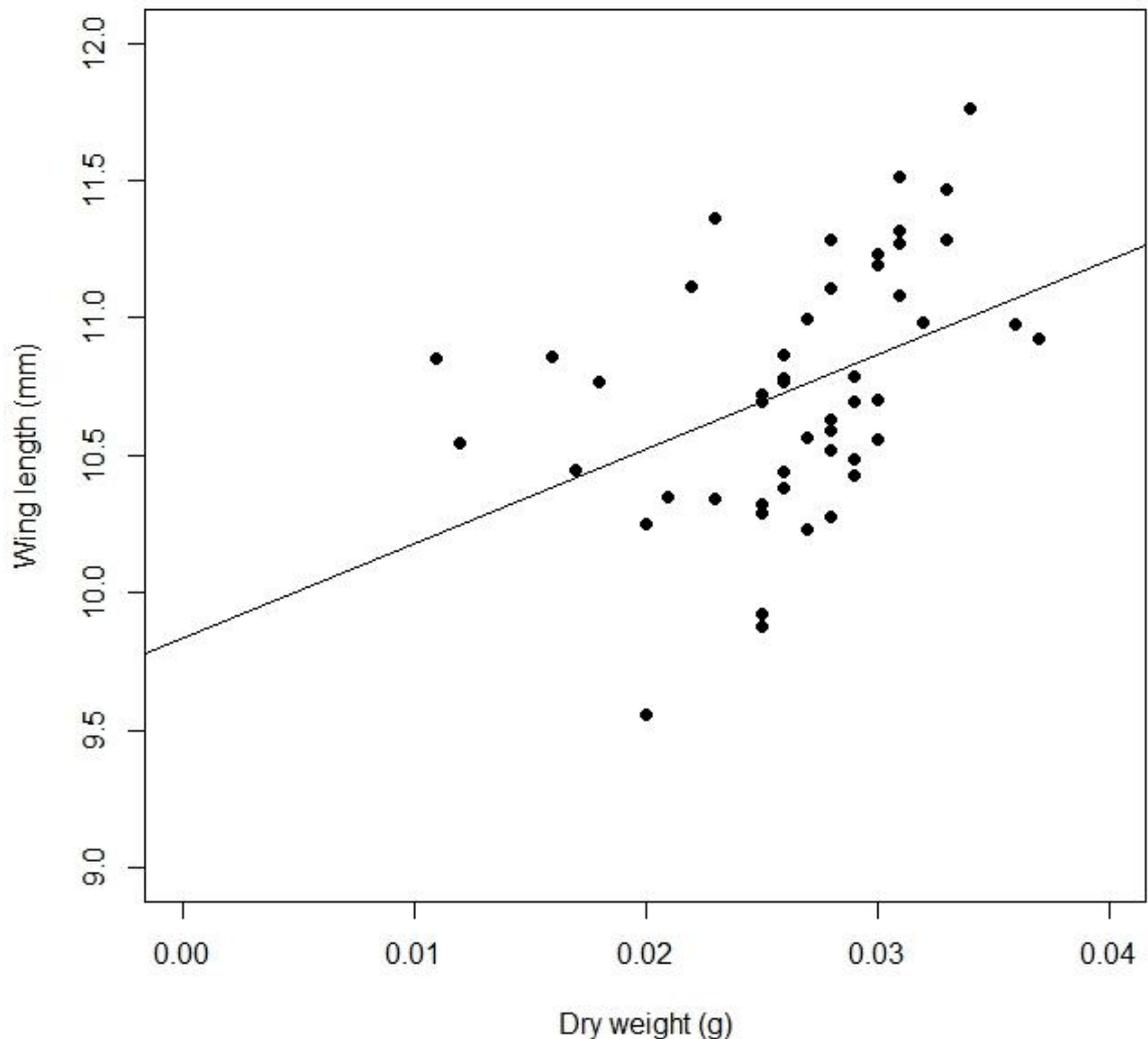
**Figure 3.** The strongest correlation between a body size metric and dry weight for females of *Eristalis.tenax*,  $R^2=0.12$ ,  $P = 0.017$  and  $n=39$ .



**Figure 4.** One of the strongest correlations between a body size metric and dry weight for males of *Episyrphus balteatus*,  $R^2=0.28$ ,  $P = <0.001$  and  $n=43$ , (wing length was equally correlated to dry weight).



**Figure 5.** The strongest correlation between a body size metric and dry weight for females of *Episyrphus balteatus*,  $R^2=0.17$ ,  $P = 0.010$  and  $n=33$ .

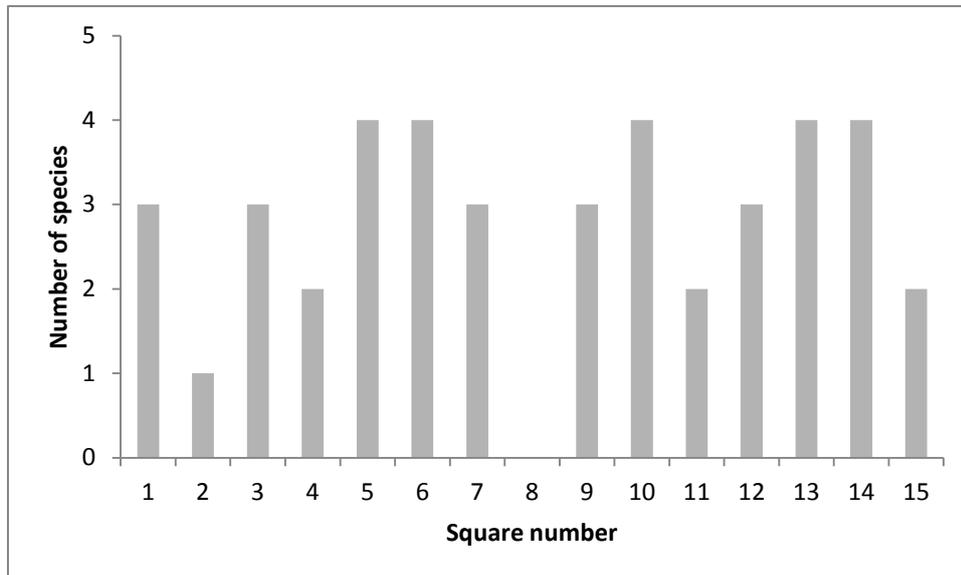


**Figure 6.** The strongest correlation between a body size metric and dry weight for males of *Myathropa florea*,  $R^2=0.20$ ,  $P = 0.001$  and  $n=49$ .

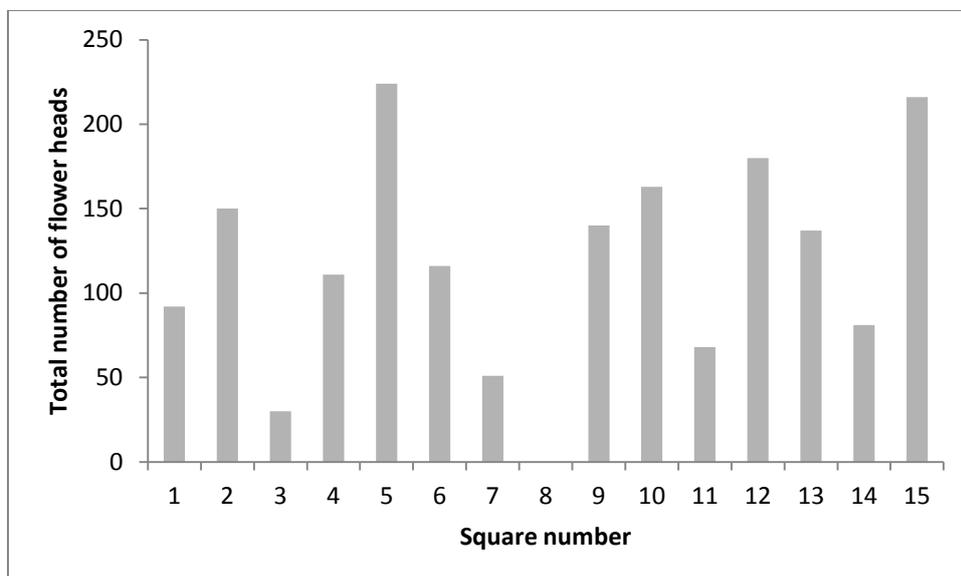
### Mark-recapture study

Out of 46 marked individuals (15 individuals of *Xanthogramma*, 21 of *Syrphus* and 10 of *E. balteatus*) one female *Syrphus ribesii* was recaptured, which gave a recapture rate of approximately 2%. The movement distance was approximately 8 m ( $\pm 3$  m) and the IT-span was 3.42 mm. The recapture occurred during the same day as the individual was marked. No recaptures were made on the corresponding area on the opposite side of the river. Six flowering species were detected within the 15 squares and out of these four were dominant (*Ranunculus acris*, *Taraxacum sp.*, *Trifolium pratense* and *Galium album*). The number of flower species varied from one to four in all squares, except for in the middle (the 8th square) where some meters only consisted of different species of grass and nettles (*Urtica dioica*)

(Figure 7). The total number of flower heads decreased in the third square and also in the middle, in the remaining squares the total number of flower heads was at least 51 (Figure 8).



**Figure 7.** The number of flowering plant species in each of 15 squares (of 2 x 2 m), counted every 20 m along the transect.



**Figure 8.** The total number of flower heads in each of 15 squares (of 2 x 2 m), counted every 20 m along the transect.

## Discussion

Regarding the first question (What is the relationship between body size metrics and dry weight in *E. tenax*, *E. balteatus* and *M. florea*?), the main findings is that the correlations between the body size metrics and dry weight is generally weak, for both males and females

of all species studied. This is in contrast to the results of Cane (1987), who showed that IT-span is a reliable predictor of dry weight for female solitary bees ( $P < 0.01$ ,  $R^2 = 0.945$ ). He considered that the thorax volume, which contains the flight muscles, should directly translate into the lift required for flight by a bee of a specific weight.

One possible explanation for the weak correlations in the interspecific analysis, might be the standardization of the pin weight. It has been shown that pin weight can be subtracted from total specimen weight, allowing estimation of dry specimen weight (Gilbert 2011). Nevertheless, it is possible that the variation in pin weights in this case were too large and that small specimens with relatively heavy pins became unreliable data points. Further, Gilbert (2011) also showed that this method is unsuitable for specimens below a length of 11 mm. Since Greenleaf *et al.* (2007) showed that body mass is positively correlated with foraging distance of bees, body mass could be a strong correlate of important life history traits. It is thus useful to be able to estimate the body mass from a body size measurement that could be easily measured in the field without causing the animals too much harm. I consider that further work is needed to study the relationship between body size and dry weight in hoverflies, taking the pin weight standardization into account.

Correlations between the different body size metrics were typically stronger than compared to dry weight. This is also consistent with the results of Gilbert *et al.* (1985), which showed that ten common species of hoverflies tend to have a constant ratio between proboscis length and body size. However, both the males and females of *E. tenax* differ from the other three groups (Tables 1 and 2), which could be due to the smaller sample sizes. However, head width and IT-span is significantly correlated to dry weight in all male groups. In contrast, wing length is the only significant correlation to dry weight within the female groups. This could be due to sexual differences in behavior such as territorial behavior performed by the males (Fitzpatrick *et al.* 1983).

The recapture rate found in the present study (2 %) is below rates of recaptures for similar mark-recapture studies of other insect groups in search of their key resources (Follett *et al.* 1996; Toepfer and Dorn 1999; Zurbuchen *et al.* 2010). In these studies the recapture rate ranged from 5-30%. However, it is not possible to tell whether the low recapture rate is due to the low probability of recapture or to the lack of linear movements. Another possible explanation could be that the hoverflies have been moving linearly, but beyond the study area. The present study shows an indication of a short linear movement (8 m) through this LLE but since the sample size is relatively small (Toepfer and Dorn 1999; Zurbuchen *et al.* 2010) further studies are needed to answer the third and fourth questions (Do hoverflies cross the river, or does the river represent a barrier to movement? and What is the pattern of movement of hoverflies along linear strips of ruderal vegetation?). Also, it is not possible to answer the second question (Does the size of the hoverflies affect the distance of their linear movements?), based on one recaptured individual. Since the number of flowering flower species along the transect was few and largely the same along the whole transect, and that there were at least 51 flower heads in all squares (except for one), I assume that the transect

was quite homogenous and that the flower density should not have had a major impact on the results.

## **Outlook**

One way to improve the method of the morphometric analysis would be to weight the pins before pinning the insects, or to remove the insects from the pins if possible. That should make the weights more precise which is needed to be able to detect if there is any correlations.

Another suggestion of improvement could be to find a Linear Landscape Element with higher recapture probability, for instance a hedge of a common species, which is more frequently visited by hoverflies. That could also help to avoid any effects of varying plant species composition. Some other suggestions could be to run the study at a different time of the year or to use traps to recapture marked individuals.

## **Acknowledgments**

I wish to express my sincerest thanks to Myles Menz for his enthusiastic supervision and great support during the whole process. Further, I want to thank the whole Institution of Community Ecology at the University of Bern and in particular professor Wolfgang Nentwig for giving me this great opportunity. I also wish to thank Anna Jakobsson for useful feedback and support.

## **References**

- Ball S, Morris R. 2013. Britain`s hoverflies: an introduction to the hoverflies of Britain. Princeton University Press, Singapore.
- Bates AJ, Sadler JP, Fairbrass AJ, Falk SJ, Hale JD, Matthews TJ. 2011. Changing Bee and Hoverfly Pollinator Assemblages along an Urban-Rural Gradient. PLOS One, doi 10.1371/journal.pone.0023459.
- Biesmeijer JC, Roberts SPM, Reemer M, Ohlemüller R, Edwards M, Peeters T, Schaffers AP, Potts SG, Kleukers R, Thomas CD, Settele J, Kunin WE. 2006. Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. Science **313**: 351-354.
- Cane JH. 1987. Estimation of Bee Size Using Intertegular Span (Apoidea). Journal of the Kansas Entomological Society **60**: 145-147.
- Fitzpatrick SM and Wellington WG. 1983. Contrasts in the Territorial Behavior of three species of Hoverflies (Diptera: Syrphidae). The Canadian Entomologist **115**: 559-566.

- Follett PA, Cantelo WW, Roderick GK. 1996. Local Dispersal of Overwintered Colorado Potato Beetle (Chrysomelidae: Coleoptera) Determined by Mark and Recapture. *Environmental Entomology* **25**: 1304-1311.
- Francis F, Martin T, Longay G, Haubruge E. 2005. Role of (E)- $\beta$ -farnesene in systematic aphid prey location by *Episyrphus balteatus* larvae (Diptera: Syrphidae). *European Journal of Entomology* **102**: 431-436.
- Gathmann A and Tschardt T. 2002. Foraging ranges of solitary bees. *Journal of Animal Ecology* **71**: 757-764.
- Gilbert FS, Harding EF, Line JM, Perry I. 1985. Morphological Approaches to Community Structure in Hoverflies (Diptera, Syrphidae). *Proceedings of the Royal Society B* **224**: 115-130.
- Gilbert JDJ. 2011. Insect Dry Weight: Shortcut to a Difficult Quantity using Museum Specimens. *Florida Entomologist* **94**: 964-970.
- Greenleaf SS, Williams NM, Winfree R, Kremen C. 2007. Bee foraging ranges and their relationship to body size. *Oecologia* **153**: 589-596.
- Hagen M and Dupont YL. 2013. Inter-tegular span and head width as estimators of fresh and dry body mass in bumblebees (*Bombus* spp.). *Insectes Sociaux* **60**: 251-257.
- Jauker F, Bondarenko B, Becker HC, Steffan-Dewenter I. 2012. Pollination efficiency of wild bees and hoverflies provided to oilseed rape. *Agricultural and Forest Entomology* **14**: 81-87.
- Jauker F, Diekötter T, Schwarzbach F, Wolters V. 2009. Pollinator dispersal in an agricultural matrix: opposing responses of wild bees and hoverflies to landscape structure and distance from main habitat. *Landscape Ecology* **24**: 547-555.
- Kearns CA, Inouye DW, Waser NM. 1998. Endangered Mutualisms: The Conservation of Plant-Pollinator Interactions. *Annual Reviews of Ecology and Systematics* **29**: 83-112.
- Klein AM, Vaissière BE, Cane JH, Steffan-Dewenter I, Cunningham SA, Kremen C, Tscharntke T. 2007. Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society B* **274**: 303-313.
- Larson BMH, Kevan PG, Inouye DW. 2001. Flies and flowers: taxonomic diversity of anthophiles and pollinators. *The Canadian Entomologist* **133**: 439-465.

- Lövei GL, Macleod A, Hickman JM. 1998. Dispersal and effects of barriers on the movement of the new Zealand hoverfly *Melanostoma fasciatum* (Dipt., Syrphidae) on cultivated land. *Journal of Applied Entomology* **122**: 115-120.
- Ollerton J, Winfree R, Tarrant S. 2011. How many flowering plants are pollinated by animals? *Oikos* **120**: 321-326.
- Patiny S, Rasmont P, Michez D. 2009. A survey and review of the status of wild bees in the West-Palaeartic region. *Apidologie* **40**: 313-331.
- Ricklefs RE. 2008. *Landscape Ecology. The Economy of Nature*. 6<sup>th</sup> edition. W. H. Freeman and Company, New York.
- Rotheray GE and Gilbert F. 2011. *The Natural History of Hoverflies*. Forrest Text, London.
- Sommaggio D. 1999. Syrphidae: can they be used as environmental bioindicators? *Agriculture, Ecosystems and Environment* **74**: 343-356.
- Steffan-Dewenter I and Tscharntke T. 1999. Effects of habitat isolation on pollinator communities and seed set. *Oecologia* **121**: 432-440.
- Stenhouse RN. 2004. Fragmentation and internal disturbance of native vegetation reserves in the Perth metropolitan area, Western Australia. *Landscape and Urban Planning* **68**: 389-401.
- Toepfer ST, Gu H, Dorn S. 1999. Spring colonisation of orchards by *Anthonomus pomorum* from adjacent forest borders. *Entomologia Experimentalis et Applicata* **93**: 131-139.
- Townsend PA and Levey DJ. 2005. An experimental test of whether habitat corridors affect pollen transfer. *Ecology* **86**: 466-475.
- Van Geert A, Van Rossum F, Triest L. 2010. Do linear landscape elements in farmland act biological corridors for pollen dispersal? *Journal of Ecology* **89**: 178-187.
- Van Rossum F and Triest L. 2012. Stepping-stone populations in linear landscape elements increase pollen dispersal between urban forest fragments. *Plant Ecology and Evolution* **145**: 332-340.
- Wratten SD, Bowie MH, Hickman JM, Evans AM, Sedcole JR, Tylianakis JM. 2003. Field boundaries as barriers to movement of hover flies (Diptera: Syrphidae) in cultivated land. *Oecologia* **134**: 605- 611.
- White AJ, Wratten SD, Berry NA, Weigmann U. 1995. Habitat Manipulation to Enhance Biological Control of Brassica Pests by Hover Flies (Diptera: Syrphidae). *Journal of Economic Entomology* **88**: 1171-1176.

Zurbuchen A, Bachofen C, Müller A, Hein S, Dorn S. 2010. Are landscape structures insurmountable barriers for foraging bees? A mark-recapture study with two solitary pollen specialist species. *Apidologie* **41**: 497-508.