— Review —

FLIES AND FLOWERS III: ECOLOGY OF FORAGING AND POLLINATION

David W. Inouye[1,2]*, Brendon M. H. Larson[3], Axel Ssymank[4], Peter G. Kevan[5]

[1]*Department of Biology, University of Maryland, College Park, Maryland, USA, 20742-4415*

[2]*Rocky Mountain Biological Laboratory, Crested Butte, Colorado, USA 81224*

[3]*Department of Environment and Resource Studies, University of Waterloo, Waterloo, Ontario, Canada, N2L 3G1*

[4]*Bundesamt für Naturschutz, Konstantinstrasse 110, 53179 Bonn, Germany*

[5]*School of Environmental Sciences, University of Guelph, Guelph, Ontario, Canada, N1G 2W1*

Abstract—Diptera are important flower visitors and pollinators for many plant species and in a variety of habitats. Although Diptera are not as well studied as other groups of pollinators, there is a growing literature that we review here about the ecology of their foraging behaviour and their effectiveness as pollinators. We consider (1) how their foraging is constrained by the interaction among body size, colour, and environmental factors such as temperature, humidity, wind, and light; (2) what is known about their foraging at scales ranging from their movements between flowers on a plant, between individuals in a population, and among species in a community (i.e., constancy); and (3) the evidence for effects of intra- and interspecific competition on foraging. We conclude with a discussion of the effectiveness of Diptera as pollinators. The available data suggest that Diptera exhibit many of the same foraging behaviours as other flower visitors and that they are effective pollinators in both natural and agricultural ecosystems.

Keywords: Diptera, ecology, fly, foraging, pollination

INTRODUCTION

Flies are common flower visitors. Species from at least 86 families of Diptera have been observed visiting flowers, and over eleven hundred species of plants from 172 families have been reported as having their flowers visited by flies (Kearns 2002; Inouye, unpublished[1]; this is undoubtedly an underestimate of the actual number). Flowers of some species of plants are visited by a huge diversity of flies (not all of which may be pollinators); for example, *Saxifraga hirculus* L. (Saxifragaceae) in Switzerland was visited by 57 species of Diptera from 16 families (Larson et al. 2001; Warncke et al. 1993). In addition to drinking nectar, some flies also eat pollen (Larson et al. 2001; Woodcock et al. 2014), especially Syrphidae (Haslett 1989a; Haslett 1989b; Irvin et al. 1999; Rotheray & Gilbert 2011); some Bombyliidae (Deyrup 1988), Empididae (Downes & Smith 1969), Muscidae (Elvers 1980), Tabanidae (Magnarelli et al. 1979) and even Ceratopogonidae (Downes 1955) have all been recorded as eating pollen. Digestion can even be external in Drosophilidae (Nicolson 1994), as has been reported for some species of butterflies (e.g.,Boggs 1987). Many species of Diptera known for feeding on vertebrate blood feed commonly on nectar (e.g., in Tabanidae, Culicidae, Simuliidae) (Downes 1958; Magnarelli & Anderson 1977; Woodcock et al. 2014).

Although flower – fly relationships have a reputation as being unspecialized there are some remarkable examples of specialization, including flowers with long-tubed corollas pollinated by flies with proboscides three times their body length (up to 33 mm) (Anderson & Johnson 2008; Goldblatt et al. 1995; Potgieter et al. 1999; Woodcock et al. 2014). Other flowers have spectacular adaptations for attracting flies, such as those sapromyophilous blossoms that mimic carrion or dung (e.g., Stensmyr et al. 2002; Woodcock et al. 2014), including the largest flowers in the world (Beaman et al. 1988); van der Niet et al. (2011) found that a carrion mimic only attracted a subset of the flies found on actual carrion. Other interesting examples include an orchid species that fools flat-footed flies (Platypezidae) into pollinating by faking fungus-infected foliage (Ren et al. 2011); a daisy pollinated by male bombyliid flies that are misled by insect-like petal ornaments to try to copulate with its flowers (Ellis & Johnson 2010); and deceptive flowers that produce no nectar (Pansarin 2008), but may produce floral fragrances that attract fungus-eating flies (Orchidaceae – Endara et al. 2010; Balanophoraceae – Goto et al. 2012). A recent paper describes a pollination relationship in which pollinating flies lay their eggs on the plants, and their larvae eat decaying male inflorescences (Goto et al. 2012). It has also been suggested that some maggots may derive nutrition from decaying flowers of some *Aristolochia* spp. (Burgess et

---

[1] From a database with 10,800 entries culled from the literature on fly visitation of flowers; available from DWI.

al. 2004).

Despite the importance and diversity of pollination by flies, this relationship has received disproportionately little attention in the literature. Earlier papers in this series have thus reviewed the taxonomic diversity of anthophilous and pollinating flies (Larson et al. 2001), and the attractants and rewards that plants produce to attract them (Woodcock et al. 2014). In this paper we review what is known about the ecology of foraging by Diptera and the pollination that results from this activity. It is important to understand the ecology of floral foraging by Diptera because their access to nutritional resources at flowers is so critical to their fitness (Magnarelli & Anderson 1977; Haslett 1989a; Gu et al. 2011;).

DIEL AND WEATHER EFFECTS

The activity level of foraging Diptera depends greatly on temperature, as few species have the ability to warm themselves. Endothermy is found in only a few fly families (e.g., Asilidae and Pantophthalmidae, but also some flower-visiting Tabanidae, Tachinidae, Syrphidae (Bartholomew & Lighton 1986; Chappell & Morgan 1987)). Thus, most anthophilous Diptera must use solar basking, sometimes in flowers (Kevan 1975) or elevated air temperatures to achieve the thoracic temperatures required for flight, and their diel patterns of flower foraging are constrained therefore by various environmental factors such as solar radiation, ambient temperature, cloud cover, humidity and wind. Despite these constraints, flies often forage under conditions when bees or butterflies do not (e.g., Levesque & Burger 1982; Morse 1981). Pollen availability as well as both the secretion and concentration of nectar also vary through the course of the day, partly because of their relation with temperature and humidity (Corbet et al. 1979). This is particularly true in open, cup-shaped flowers whose relative humidity is likely near equilibrium with the atmosphere. For these reasons, it is difficult to disentangle the confounding effects of reward availability from hygrothermal constraints when analysing daily rhythmicity of flower visitation by flies (Willmer 1983; Herrera 1990). Willmer (1983) showed that the foraging patterns of flies on *Tilia* (Tiliaceae) and *Heracleum sphondylium* L. (Apiaceae) were less dependent on the availability of nectar rewards than on avoidance of overheating. Other studies have corroborated this evidence (Herrera 1990), indicating that dipteran activity does not simply reflect daily patterns of reward availability. In contrast to foraging Hymenoptera and Lepidoptera, the crystallization of nectars during the warmest part of the day is not problematic to flies because many can re-dissolve sugars by "spitting" on them (Corbet 1978).

The size, thermal reflectance and behaviour of ectothermic Diptera determine their heat budget and hence, their ability to withstand extremes of heat and cold. Diptera foraging at flowers during the warmest part of the day exhibit one or more of three traits that are less common in those foraging early and late in the day: they are generally smaller, more reflective (either metallic or light-coloured) and more pilose, or have a stronger cuticula (Maier & Waldbauer 1979a; Willmer 1983; Gilbert 1985). These trends result in smaller temperature excesses (difference between body and ambient temperature) and higher cooling rates, so that the flies can forage during the midday temperature peak without overheating or losing excessive water (Willmer & Unwin 1981; Willmer 1983); however visitation rates are typically lower in mid-day when many species reduce their activity (Ssymank 1989; Ssymank 1991; Ssymank 2001).

Large, dark Diptera usually reach and maintain body temperatures conducive to flight more easily than do small ones, so they are able to fly in the early morning and evening (Willmer & Unwin 1981). They can also visit flowers earlier on warm mornings than on cool ones, as shown for milesiine syrphids in Illinois (Maier & Waldbauer 1979a). During the middle of the day, large flies can be endangered by direct insolation and high temperatures, which lead to overheating and possibly dehydration, so they forage mainly in the shade (Maier & Waldbauer 1979a; Willmer & Unwin 1981). In Britain, *Sarcophaga* species (Sarcophagidae) present an anomaly, because they are relatively large and dark, yet forage in the middle of the day. However, their cuticles are highly reflective (cuticular reflectance = 6 - 8.5%) and they are able to thermoregulate by shunting blood from their thorax into their abdomen, which acts as a radiator (Willmer 1982b). This contrasts with *Calliphora* (Calliphoridae), *Tachina* (Tachinidae), and *Musca* (Muscidae) species, which are relatively inactive during warm periods; even though *Calliphora* are metallic they cannot cool as easily as *Sarcophaga*.

Some smaller, more reflective anthophilous Diptera are less active when irradiance is low, but as the temperature rises they begin to forage. In the forest understory, they may stay warm by foraging in sun flecks (Rotheray & Gilbert 2011). In contrast to large flies, their lower temperature excesses and higher cooling rates also permit them to take advantage of local shade to cool, which allows them to forage during the warmest part of the day (Maier & Waldbauer 1979a; Willmer & Unwin 1981). If it is sunny it is physiologically stressful for even small flies, if they are darkly coloured, to visit flowers. Some medium-sized Diptera are also able to forage early in the day, possibly by endothermic thermoregulation, as shown for basking and shivering *Syrphus* (Syrphidae) (Heinrich & Pantle 1975) and suggested for *Mesograpta marginata* Say (Syrphidae) (Mesler 1977) and some tabanids (Inouye & Pyke 1988).

These physiological constraints on foraging Diptera help to explain observed temporal patterns of foraging activity. For example, in large and/or relatively non-reflective species, suitable temperatures for foraging may occur both in the morning and afternoon, with only mid-day too warm for foraging. This is reflected by a bimodal daily pattern of foraging, with morning and afternoon peaks, as shown for Syrphidae, Tachinidae and Calliphoridae on *Lavandula latifolia* Vill. (Lamiaceae) in Spain (Herrera 1990); Syrphidae, Muscidae, Anthomyiidae, *Lucilia* (Calliphoridae) and *Sarcophaga* on *Heracleum sphondylium* (Apiaceae) in Britain (Willmer 1983); various Empididae, *Notiphila brunnipes* R.-D. (Ephydridae) and *Hydromyza livens* Fabricius (Scathophagidae) on water-lily leaves and flowers

in Britain (Willmer 1982a); and *Chrysomya* species and *Cochliomya macellaria* Fabricius (Calliphoridae) on *Sterculia chicha* St. Hil. (Sterculiaceae) in Brazil (Taroda & Gibbs 1982). On cool days, bimodal patterns may be replaced by unimodal visitation (e.g., Willmer 1982a). Careful observation can reveal more complicated patterns of visitation; Ssymank (2001) found evidence for seven different species-specific patterns, of which the bi-modal was only represented by a small number of species.

Even within the Syrphidae there can be significant differences in responses to temperature and light, which can result in spatial partitioning. Birtele and Hardersen (2012) compared captures from Malaise traps suspended in forest canopy and on the ground and found that the 53 syrphid species they collected differed significantly between the two habitats. The vertical stratification was correlated with height of the Malaise traps and estimated age of dominant trees, and it seems likely that the differences in temperature (on average 1.3°C higher in the canopy) and humidity (on average 11% lower in the canopy) may have been largely responsible for the differences in fly distribution.

By arriving early in the morning, flies may ensure access to the rich nectar and pollen rewards that are present before other foragers arrive (Faegri & van der Pijl 1979). Typically *Platycheirus* and *Melanostoma* species are "early birds" before sunrise, provided that the grass flowers from which they collect pollen are dry or at least partially dry (Ssymank 2001்.) The depletion of nectar and pollen over the course of the day may explain those instances when only the morning peak is well-defined, such as in the milesiine Syrphidae studied by Maier and Waldbauer (1979a), and the Syrphidae (especially *E. tenax*) on *Rosa setigera* Michx. (Rosaceae) in Ontario, Canada (Kevan et al. 1990). This may also produce separate peaks for nectar and pollen foragers, such as for foragers on *Crataegus monogyna* Jacq. (Rosaceae) and a species of *Tilia* in England (Corbet et al. 1979). As another example, Dötterl et al. (2012) detected differential visitation by flies (in the morning) and bees (in the afternoon) that in part reflected the diel changes in floral fragrance produced by flowers of *Silene otitis*. Alternatively, there may be only a single activity peak because smaller or more reflective species forage only around midday when other species are absent because of the heat (e.g, *Systoechus* sp. (Bombyliidae) on *Lavandula* (Herrera 1990), Stratiomyidae on *Heracleum* (Willmer 1983), and Dolichopodidae on water-lily (Willmer 1982a)). In open habitats, even smaller reflective species may overheat if insolation is high (i.e., greater than 600 WM2 (Willmer 1983)). Careful study of foraging by flies may also reveal differences between males and females, as Hövemeyer (1995) found for *Cheilosia fasciata*; males flew at lower temperatures and the times of females' foraging for pollen was linked to their oviposition.

Although most anthophilous Diptera are diurnal, there are many exceptions. In various environments, night-time and crepuscular temperatures may be warm enough for Diptera to forage. Among Syrphidae, *Melanostoma mellinum* L. (Syrphidae) has been found foraging on the flowers of *Rosa carolina* L. (Rosaceae) before sunrise

(Morse 1981) and *Volucella vesicularia* Curran (Syrphidae) has been collected in large numbers feeding at *Cephalanthus occidentalis* L. (Rubiaceae) during crepuscular hours in Indiana (Waldbauer 1963). The *Volucella* began to arrive about 40 minutes before sunset, and their numbers peaked during a period extending from 20 minutes before sunset to 20 minutes after, when they departed. Many biting Nematocera are markedly crepuscular. Sandholm and Price (1962) found that both sexes of the culicid genera *Aedes, Culex, Culiseta* and *Mansonia* feed on the nectar of various flowers, with peak activity during the first hour or so after dark, and Grimstad and DeFoliart (1974) found similar results for *Aedes, Anopheles, Coquillettidia, Culex,* and *Culiseta*. In the tropics, phorids that visit *Herrania* (Sterculiaceae) species, cecidomyiids that visit cacao (*Theobroma cacao* L. (Sterculiaceae)) flowers, and ceratopogonids reported to pollinate rubber trees (*Hevea brasiliensis* Muell.) are crepuscular (Warmke 1952; Young 1984; Young 1985). Crane flies (Tipulidae) in montane New Zealand are often active flower visitors at night (Primack 1983), as has also been observed in the Colorado Rocky Mountains (Inouye, pers. obs). Many Mediterranean Syrphidae such as *Mallota, Eumerus* and *Merodon*-species during the hot summer months are crepuscular (Ssymank, unpublished).

Many anthophilous Diptera are hampered by cloudiness, wind and rain. Rain and wet fog generally lead to a cessation of flower-visiting by flies (e.g., Winder 1977; Levesque & Burger 1982). Inouye and Pyke (1988) have shown that visitation rate (in the fly-dominated pollinator community of the Australian alpine) was positively affected by temperature and light levels, but negatively affected by wind speed. This may reflect the fact that moderate wind speeds can increase rates of cooling (Willmer & Unwin 1981). McCall and Primack (1992) found similar results for a tundra site in New Hampshire, where flies were the most common pollinators; visits were least common early in the day and when light levels were low, winds moderate, and temperatures lowest (Willmer & Unwin 1981). Many flies become inactive during cloudy periods, but crepuscular and shade-loving species may become active at these times (Kevan & Baker 1983). Christensen (1992) suggested that scent release by tropical orchids is positively correlated with relative humidity, and that the small pollinating Diptera that visit them are thus active during cloudy and rainy periods and early in the day.

Although Chironomidae are not noteworthy as flower visitors there are several Arctic species that imbibe floral nectar (Kevan 1970). *Smittia velutina*, a parthenogenetic species basks in flowers while imbibing nectar, and as the sun tracks 360o during the continual sunshine of an Arctic sunny day, so these flies circumnavigate cushions of *Saxifraga oppositifolia* to stay in insolated flowers. In cloudy weather, they seem not to move from flower to flower, but in rainy weather exit the flowers to hide beneath the petals (Kevan 2007).

Syrphids are sun-lovers, and they rarely visit flowers during cloudy periods (Maier & Waldbauer 1979a; Levesque & Burger 1982). However, Maier and Waldbauer (1979a)

noted that they are active during intermittently cloudy periods on warm days and on overcast days following several rainy days. Minimum activity temperature for Syrphidae in Europe typically changes over the year; in March it is lowest, then climbing up in summer with highest minimum activity temperatures in the warmest months, July and August, and decreasing again in autumn (Grosser & Klapperstück 1977; Ssymank 2001). Muscoids are generally less sensitive to cloudy, adverse conditions. Darkly-coloured *Thricops* species (Muscidae) foraging on Mount Washington were more sensitive to a combination of high wind and complete cloud cover than to high wind (> 40 km/h) and low temperature (5°C) (Levesque & Burger 1982). During cold and cloudy conditions in New Zealand, the tachinid *Protohystricia* was the predominant visitor to manuka flowers (*Leptospermum scoparium* Forst. (Myrtaceae) (Primack 1978); tachinids can perhaps forage under these conditions because of their hairiness (Primack 1983). Jiron and Hedstrom (1985), on the other hand, recorded a decrease in muscoid activity at mango in Costa Rica during cloudy and windy periods (e.g., Winder 1977; Levesque & Burger 1982).

The changing climate also has the potential to influence seasonal and temporal patterns of foraging activity by flies. Iler et al. (2013) studied a high-altitude population of Syrphidae in the Colorado Rocky Mountains, and found that snowmelt was the best predictor of syrphid emergence, while temperature and precipitation best predicted the end of their flight season. Flowering phenology tracked the earlier snowmelt more closely than syrphid emergence did, which resulted in more days of overlap between the flower and syrphid communities in years of early snowmelt, because of longer flowering (which also responds to snowmelt date) and fly activity periods during these years. In contrast to the situation for some other pollinator groups at this site (e.g., bumble bees – Thomson 2010), phenological asynchrony seems unlikely to be a significant problem, at least for the foreseeable future.

FORAGING PATTERNS

Anthophilous Diptera do not gain proximally from the pollination event *per se*; rather, they forage for access to the primary attractants that the plant provides. Foraging can be very expensive metabolically, and optimal foraging models predict that anthophiles should ensure that their foraging decisions lead to a net energy gain (Pyke 1978a). There are likely alternative foraging strategies that can provide a net energy gain, and the wide range of relationships between flowers and foraging Diptera support this view. In some cases, selection has favoured a "mess and soil" relationship, wherein relatively unspecialized Diptera visit numerous species of choripetalous, actinomorphic flowers for their rewards, and haphazardly carry pollen grains among them, occasionally causing pollination (Faegri & van der Pijl 1979). This may be energetically efficient for the fly, because it does not have to spend time and energy learning how to search for, or forage from, a particular type of flower. At the other extreme, highly interdependent, coevolved mutualisms may develop, which ensure that the needs of both the plant

and the fly are regularly met. In general, the foraging behaviour of Diptera is likely to have many similarities to that of Hymenoptera and other pollinators, with some specialization (flower constancy) likely within foraging bouts, and differences among individuals and populations depending on their prior experience.

The rewards offered by specialized flowers are typically greater than those of generalized flowers, presumably as an offset to the cost of pollinator learning time and/or the more expensive foraging costs of specialized visitors (Chittka & Thomson 2005), such as bee flies (Bombyliidae), tanglewing flies (Nemestrinidae), horse flies (Tabanidae) and small headed flies (Acroceridae) (e.g., Goldblatt et al. 1995). However, at least one orchid species practices deceptive pollination on a nemestrinid fly with a proboscis 57 mm long, four times its body length (Johnson & Steiner 1997)! Rewards must meet the energetic demands of the fly, but they must also be offered at a rate that necessitates continued visitation of other conspecific blossoms (Kevan & Baker 1983). From the point of view of the fly, it is most efficient to revisit flowers that have been rewarding, and they are more likely to do so if the flowers are easy to find and easy to handle.

Foraging patterns may be considered at various scales, ranging from constancy to a given species of flower, through inter-floral movement patterns, to behaviour at individual flowers. Each of these influences the effectiveness of pollen transfer and hence plant fitness (Campbell 1985b; Campbell & Motten 1985). Floral constancy is exhibited when an anthophile restricts its visits to one type of flower because of either an innate preference (monotropy) or a periodic predilection (fidelity) (see Faegri & van der Pijl 1979). These two types of constancy may be difficult to differentiate in the field, so they are often lumped. If a fly has experienced the rewards and recognizes the attractants of a given flower, it may be conditioned to repeated visits to this flower, despite the availability of alternative blossoms. If this represents fidelity, it typically varies both temporally and spatially. For example, an anthophile may show fidelity for a different species on successive foraging bouts, or its visits may shift to different species as their blossoming periods succeed one another (Kevan 1970; Kevan 1972; Waldbauer 1984). It is possible that some plants have evolved to capitalize on the latter tendency; McGuire and Armbruster (1991) have suggested that *Saxifraga tricuspidata* Rottb. (Saxifragaceae) in Alaska, by flowering later, is taking advantage of the familiarity of syrphid pollinators with the morphologically similar, early-flowering species *S. reflexa* Hook., although flies in this family visit a wide range of flowers so learning may not play an important role. In Arctic and alpine communities there are typically few flowers in bloom at a given time, and this may constrain flower-visiting Diptera to show fidelity (Kevan 1970; Kevan 1972; Hippa et al. 1981; Levesque & Burger 1982; Pont 1993).

Ssymank (2003) suggests that floral constancy in Syrphidae is quite high due to a combination of preferences for flower height, flower colour, and flower type preference in combination with local flowering phenology. By filtering

flower choice with all of these variables the result can lead to rather narrow choices, promoting floral constancy.

Flowers of the South African iris *Lapeirousia oreogena* produce nectar guides to which its sole pollinator, a long-proboscid nemestrinid fly, responds (Hansen et al. 2012). Removal of the guides had little effect on the approaches by flies to flowers from a distance, but dramatically reduced the likelihood of proboscis insertion. The value of the guides to reproductive fitness was demonstrated by experiments showing that removal of guides reduced export of pollen dye analogue (an estimate of male fitness) to almost zero, and fruit set (a measure of female fitness) was also significantly reduced.

The historic literature downplays the constancy of Diptera (but for syrphids, see Kugler 1950), especially when contrasted with that of higher Hymenoptera. However, recent studies have shown that under certain conditions the members of some families may exhibit constancy equivalent to that of bees. For example, *Eurimyia lineata* Fabr., *Neoascia tenur* Harris (Syrphidae), and *Asindulum nigrum* Latreille (Mycetophilidae) were prevalent visitors and pollinators of *Saxifraga hirculus* L. (Saxifragaceae) in Denmark, and analysis of the amount of pollen within their alimentary tracts showed that individuals often had only 1-2 "major" constituents (> 25% of pollen) and a few "minors" (5-25% of pollen) (Olesen & Warncke 1989b), which is comparable to what has been documented for bumblebees (Heinrich 1976). Syrphid flies can have significant differences among individuals in their gut pollen contents, with some being more selective than others (Haslett 1989b); some of these differences are related to whether the flies are females, needing protein for egg production (Haslett 1989a; Hickman et al. 1995). Tabanidae from Louisiana were found to have differences in their gut pollen contents depending on the habitat (alluvial vs. salt marsh) where they were collected (Wilson & Lieux 1972). Shaw and Taylor (1986) compared pollen loads on four bumblebees and eight syrphid species, and found that bee corbiculae contained pollen from an average of 3.3 plant species compared to 4.3 for flies' bodies. Goulson and Wright (1998) found that two species of Syrphidae exhibited marked floral constancy when foraging in a mixed-plant community. On a pavement plain in southern California, 80-85% of the pollen load carried by syrphid and bombyliid flies consisted of one main type of pollen (O'Brien 1980) that was conspecific with the flowers they were visiting.

Other studies have also shown that individual flies collect pollen or have pollen loads from predominantly one species (Beattie 1972; Lindsey 1984; Grimaldi 1988; Zietsman 1990; Kearns 1992; Johnson & Midgley 1997;), even if the entire fly population in a given area visits a wider range of flowers. Campbell and Motten (1985), on the other hand, found that 45% of visits by *Bombylius major* L. (Bombyliidae) to *Stellaria pubera* Michx. (Caryophyllaceae) were preceded by one to another species. Anthophiles are usually more strongly bound to pollen than nectar sources (Faegri & van der Pijl 1979; Pont 1993), so their constancy partly depends on which reward they are seeking. But even in nectarless species of plants there can be significant constancy.

Li et al. (2012) found that two sympatric co-flowering species of *Cypripedium* orchids were pollinated by different groups of flies (dung flies and fruit flies) yet did not hybridize despite their cross-compatibility.

Syrphids are generally selective of the floral resources that they utilize, but some species are more specialized than others, and males are more selective than females (Gilbert 1981; Shaw & Taylor 1986; Haslett 1989b; Cowgill et al. 1993). Large, hairy flower flies such as *Eristalis tenax* L. and *Lasiopticus* [*Scaeva*] *pyrastri* L. often contain pollen of numerous plant species in their crops (Schneider 1958; Schneider 1969; Holloway 1976), so they appear to exhibit little flower constancy, although their migratory behaviour could be responsible for some of this diversity. On the other hand, studies have shown that the smaller, sparsely hairy Syrphidae species (especially of the genera *Melanostoma* and *Platycheirus*) that visit reputedly anemophilous plants are relatively constant to at most two families of plants (Goot & Grabandt 1970; Holloway 1976; Leereveld 1982). There are several species of these "anemophilous" plants that are visited by Syrphidae that probably serve as pollinators (Leereveld et al. 1976; Stelleman & Meeuse 1976; Leereveld et al. 1981; Stelleman 1984; Leereveld et al. 1991). In order to clarify this dichotomy, Holloway (1976) compared the pollen-foraging behaviour of *Eristalis tenax* with *Melanostoma fasciatum* Macq.. She found that the former species has palynophilic hairs that trap pollen indirectly while it forages for nectar, whereas the latter has only a simple vestiture and eats pollen directly. *Platycheirus* males also comb or squeeze pollen out of anthers with their broadened front tarsi (Ssymank, unpublished). The concomitant collection of pollen and nectar, and a morphology and feeding behaviour convergent with the honey bee (Holloway 1976; Levesque & Burger 1982; Srinivasan & Guy 1990) indicate that *Eristalis* is an efficient forager (Holloway 1976; Levesque & Burger 1982; Srinivasan & Guy 1990).

Given that a foraging fly is relatively constant, the next tier of behaviours relates to patterns of movement between patches, plants within a patch, flowers on a plant, and within flowers, all of which are probably governed largely by energetic considerations (Kevan & Baker 1983). Optimal foraging theory predicts that the length of time in a patch (or on a flower) should be positively correlated with its productivity and the distance between patches (flowers) and inversely correlated with the profitability of the environment as a whole (Charnov 1976). There has been little testing of these predictions for foraging Diptera.

When floral resources are scattered and have little reward, pollinators sometimes return repeatedly to inflorescences along a trap-line, in order to decrease foraging uncertainty (e.g., Janzen 1971 for Euglossine bees). There have been observations of Diptera that repeatedly visit individual flowers in this manner (Maier & Waldbauer 1979b; Nilsson et al. 1985), and while in most cases it is not known whether these behaviours represent trap-lining and/or territoriality, for some Syrphidae it seems to represent territoriality (Fitzpatrick & Wellington 1983; Ssymank, unpublished). Collett and Land (1975) found that

Eristalis species remember their positions in space relative to visual landmarks in their surroundings and may use that capability to guide them to foraging sites. Territoriality on flowers or flower patches has been observed in Bombyliidae (Evenhuis 1983) and Syrphidae (Wellington & Fitzpatrick 1981; Fitzpatrick & Wellington 1983; Rotheray & Gilbert 2011).

Within a rewarding patch, an anthophile should tend to move shorter distances between flowers and exhibit more turning than a forager in a less rewarding patch (Pyke 1978b). This pattern has generally been verified for higher Hymenoptera, but it may be less applicable to foraging Diptera if revisitation is less detrimental for them because they remove less of the available pollen and/or nectar during initial visits. For example, Olesen and Warncke (1989a) found that 30% of the flights by the aforementioned *Asindulum nigrum* Latreille (Mycetophilidae) were back to the *Saxifraga hirculus* (Saxifragaceae) flower they had just left, compared to < 5% for syrphid visitors (which may remove more rewards during an initial visit). They also showed that the direction that Diptera departed flowers was chosen randomly.

Flight distance has often been used to evaluate pollen flow, but pollen carryover must also be considered (Herrera 1987). In addition, the rare, long-distance foragers, rather than the average individuals, may contribute most significantly to plant outcrossing. For example, *Eurimyia lineata* (Syrphidae) is the most significant pollinator of *Saxifraga hirculus* (Saxifragaceae) in the short-term; but moths make many more long, cross-population flights than the syrphid, so they may be more important for pollen flow (Olesen & Warncke 1989c). There have been few studies of the flight distances flown by pollinating Diptera, but interplant flight distances are usually short and distributed leptokurtically (skewed towards more short flights than expected) (Beattie 1976; Herrera 1987; Olesen & Warncke 1989c; Zietsman 1990). Distances flown may depend on plant density; for example, Schmitt (1983) showed that the flight distances flown by *Bombylius* foraging on *Linanthus bicolor* (Nutt.) Greene (Polemoniaceae) increased as the density of flowering plants declined through the season. In potted arrays of *Stellaria pubera* (Caryophyllaceae), there was a 69% probability that a foraging *Bombylius major* would leave a plant for a nearest neighbour. Although the flies flew shorter distances between plants than did *Nomada* species (Hymenoptera: Anthophoridae), their flights were more directional and they carried more pollen, and hence moved pollen further overall (Campbell 1985a).

Data on long-distance dispersal are more difficult to obtain, but a few studies directly or indirectly support the hypothesis that Diptera can be long-distance pollinators. Using radioisotopes, Decazy et al. (1980) found that cecidomyiid midges may travel up to 35 metres between cocoa plants, and further distances are possible if air currents are favourable (Entwistle 1972). Dempster et al. (1995) used chloride salts applied to host plants to label tephritid flies, which are at least flower visitors if not pollinators of some plants; they commonly recovered flies two kilometres from where they were marked. Bänziger (1991) has proposed

that Calliphoridae, which are energetic, nomadic flyers, may be essential long-distance pollinators of *Rafflesia* plants (Rafflesiaceae), which are typically rare and widely dispersed. Fly-pollinated neotropical *Sterculia* (Sterculiaceae) trees typically exist as widely isolated individuals that set fruit despite a self-incompatibility mechanism, suggesting that the Diptera are effective long-distance pollen vectors for this genus (Taroda & Gibbs 1982). An extreme demonstration of long-distance movements by Syrphidae is the report of individuals caught and marked in alpine passes in Switzerland that were later recovered in passes over 160 km away (Aubert & Goeldlin de Tiefenau 1981). The migratory behaviour of the syrphid fly *Episyrphus balteatus* has been studied using microsatellites, isotopic signatures, and morphological techniques, and although this behaviour may be important from a demographic and genetic perspective, its impact on pollination is not clear (Raymond et al. 2013; Raymond et al. 2014). Migration by Syrphidae is also reviewed by Gatter and Schmid (1990).

To evaluate the potential for pollination, movement between and within the flowers on a plant must also be considered (de Jong et al. 1993). There are relatively few data on such movements for flies, probably because of the difficulty of following small, fast-flying insects that may frequently move long distances. Pollinators that do not revisit flowers save themselves energy and reduce geitonogamy (pollination among flowers on the same plant), but if they obtain enough resources for satiation during one floral visit (e.g., mosquitoes visiting *Silene otites* (Caryophyllaceae; Brantjes 1976), the opportunities for cross-pollination are minimal. Visitation of clustered flowers saves energy for foraging flies, as does walking between flowers because hovering and flying are more expensive (Kevan & Baker 1983). *Viola rostrata* Pursh. (Violaceae) is one of the few eastern North American violets with many, clustered flowers open at one time, and Beattie (1974; 1976) concluded that this was an adaptation for attraction of its major pollinators, bee flies, whose hovering flight is energetically expensive. Diptera foraging on racemes of *Ceratonia siliqua* (Leguminosae) showed "a very marked tendency to visit the flowers situated closest to the apex of the raceme first", which had consequences for the pattern of fruit development (Arista et al. 1999). The visitation rate by the tachinid *Protohystricia huttoni* (Malloch) to *Myosotis colensoi* (Kirk) Macbride (Boraginaceae) in New Zealand increased linearly with display size, but the number of flowers visited on a plant concomitantly declined (Robertson 1992; Robertson & Macnair 1995). The upshot was that the proportion of available flowers that was visited declined too, so that flowers received visits at about the same rate (and pollen removal, deposition and seed set remained constant) regardless of display size.

Flower colour appears to make some difference to foraging flies (Woodcock et al. 2014). Flies can learn to discriminate flowers based on flower colour (Lunau 1993b) and learn to discriminate rewarding and unrewarding flowers based on colour, for example in cases where flower colour changes with age, and indicates a change in reward (Casper & La Pine 1984; Roy 1994). Sutherland (1999) found that *Eristalis* (Syrphidae) seem to prefer yellow, and Schneider

(1958) was successful in attracting syrphids to yellow artificial flowers. In *Eristalis*, naïve freshly emerged flies prefer yellow, and a spontaneous reflex response of the proboscis remains for yellow pollen or stigmas (Lunau 1993a; Lunau 1993b; Lunau & Wacht 1994; Lunau 2000; Lunau et al. 2005), while older flies may visit red or violet-coloured thistles much more than yellow flowers (Ssymank, unpublished).

Yellow and white crucifer flowers were found attractive to flies and small bees in Israel (Dukas & Shmida 1989), and yellow flowers were preferred by syrphid flies in Michigan (Lee & Snow 1998), but syrphid flies in California preferred pink flowers of *Raphanus sativus* over yellow or white (in constrast to honey bees, which preferred white or yellow) (Stanton 1987). The attraction of flies to pseudoflowers (which do offer a reward) could be facilitated by their yellow colour (Roy 1994). More detailed discussion of this topic is provided by Woodcock et al. (2014).

Flies also have potential for experimental studies, which would shed more light on their foraging behaviour. For example, they will visit model flowers (Johnson & Dafni 1998; Sutherland et al. 1999). This might be one way to study the potential effects of electrostatics in fly pollination (McGonigle & Jackson 2002). Schneider (1958) used 15-cm flat yellow paper flowers, with a mixture of peppermint, thyme, and anise oil applied to them along with a sugar solution. He laid these lures out in meadows in groups of 15-25, and found that they attracted large numbers of syrphid, muscid, tachinid, sepsid, and helomyzid flies. The sex ratio was biased toward females for some syrphids, and for males for a few others. He also investigated the effects of temperature and clouds on foraging activity, and looked at the gut contents to identify species of pollen being collected by the flies. Ilse (1949) used flower models made from coloured paper to test colour discrimination in droneflies (*Eristalis tenax*). Johnson and Dafni (1998) used model flowers for choice experiments with model flowers to determine the responses to visual cues, such as shape, size, colour and pattern. Sutherland et al. (1999) used artificial flowers to study foraging of the syrphid *Episyrphus balteatus*, and found evidence for a preference for smaller flowers and yellow flowers, and for nectar as a reward more than pollen.

THE EFFECTS OF COMPETITION AND PREDATION ON FORAGING

The competitive interactions affecting anthophilous Diptera have scarcely been investigated, and research to date has been highly syrphid-biased. Intraspecific effects are almost unknown, other than territoriality by male syrphids (Fitzpatrick & Wellington 1983; Wellington & Fitzpatrick 1981), but the interspecific effects between sympatric Diptera, and between flies and bees, have been studied in a few instances. Inter- and intraspecific exploitation competition is likely common, because all anthophiles indirectly compete for the declining stores of nectar and pollen each day. It is therefore competitively advantageous for an anthophile to match its foraging activity to the daily rhythm of reward production of the flowers it visits (Faegri

& van der Pijl 1979, but see 'Diel effects' above). Male syrphids exhibit interference competition in their aggressive defense of territories for mating (Maier & Waldbauer 1979b; Primack 1978; Wellington & Fitzpatrick 1981), and some larger hoverflies may be the targets of aggressive behaviour by *Anthidium* bees (Ssymank, unpublished). These territories are not always floral, but they may still have negative effects on other foragers.

When floral resources are in short supply, both exploitation and interference competition are likely to become increasingly important. Asymmetries in such competition may result in a linear competitive hierarchy of species, whereby subordinates are restricted to less desirable flowers (Kikuchi 1962a; Kikuchi 1962b; Kikuchi 1962c; Kikuchi 1963a; Kikuchi 1963b; Kikuchi 1964; Faegri & van der Pijl 1979; Toft 1983; Toft 1984). In Kikuchi's studies, *Eristalis* was the most dominant syrphid genus of those studied, and *E. tenax* was more dominant than its congeners. The hierarchy amongst bombyliids (Homeophthalmae) studied in California does not result from interference competition, but the mechanism is unknown (Toft 1983; Toft 1984). Reader et al. (2005) reported that *Rubus* flowers that had been visited by syrphid flies were less attractive to foraging bees than unvisited flowers, and concluded that bees can respond to some scent mark left behind by foraging flies. This kind of subtle interaction is difficult to discern without making careful experiments.

Using various exclusion experiments, Morse (1981) studied the interference competition between bumblebees (*Bombus terricola* Kirby and *B. vagans* Smith) and two small Syrphidae, *Melanostoma mellinum* L. and *Toxomerus marginatus* (Say), at *Rosa carolina* in Maine. *Melanostoma* began foraging earlier in the morning than did *Toxomerus* or the bumblebees, which gave it exclusive access to floral resources. *Melanostoma* interfered with *Toxomerus'* foraging, so when the latter began to forage it chose flowers free of *Melanostoma*. When a bumblebee approached a flower, the syrphids foraging on it left. However, *Toxomerus* quickly returned to the flower when the bumblebee departed, whereas *Melanostoma* did not. Morse concluded that *Melanostoma* had a greater impact on *Toxomerus* than did the bumblebees, because it foraged at the flowers longer than did the bees, which excluded *Toxomerus* for longer time periods. Therefore, by causing *Melanostoma* to leave rose flowers, the net effect of bumblebees on *Toxomerus* was positive. In cryptically dioecious *Rosa setigera* (Rosaceae), competitive interactions with bees forced syrphids to visit the less-rewarding female flowers increasingly as the day progressed, which may have increased the efficacy of pollen transfer from male to female flowers (Kevan et al. 1990).

Amongst Syrphidae, floral resources are partitioned by spatial and temporal means, morphological character displacement (Gilbert et al. 1985), and differing floral colour preferences (Haslett 1989b). In the latter case, behavioural flexibility may allow the adoption of new floral colour preferences as a compensatory mechanism in the event of variation in resource availability or competitors. Kendall and Solomon (1973) reported 16 species of Syrphidae visiting apple flowers in an orchard. Although this is a

somewhat artificial situation, with a large abundance of flowers of a single species, the presence of so many species of a single insect family (together with 17 species from 12 other families of Diptera, 25 species of Hymenoptera and a few Coleoptera and Megaloptera), suggests that if resource partitioning is occurring it is subtle. Gilbert and Owen (1990) also suggested that there was no real community organization among the 33 most common species of Syrphidae caught during a 15-year study of flies captured in a garden with a Malaise trap.

Branquart and Hemptinne (2000) found no strong flower preferences of adults of the Syrphinae subfamily; although they tended to visit plants having large, flat inflorescences or flowers (e.g. Apiaceae, Asteraceae, Ranunculaceae and Rosaceae), they do visit flowers with a diversity of morphologies. These authors defined seven foraging guilds according to flies' dietary patterns, reflecting primarily "a sequential exploitation of flowers at different times of the year and in different habitats". Few species of this subfamily successfully colonize open and anthropogenic habitats, such as field margins and fallow areas; the majority live in forests where they form highly diversified communities. But the species that are dominant in open habitats all over western Europe are polyphagous, which may be an important behavioural characteristic for colonizing open and ephemeral habitats (Branquart & Hemptinne 2000). Many of the open anthropogenic grassland habitats have a diverse fauna of Syrphidae, including some species that have larvae that eat bulbs (genera *Merodon*, *Eumerus*) especially in dry mediterranean grasslands (Rotheray & Gilbert 2011).

From the plant perspective, patch size is potentially a way to manipulate pollinator behaviour. Large patches could be more visible and hence, or because of the greater nectar resource they represent, be more attractive. When Johnson et al. (2012) investigated the effects of patch size on pollinator visitation and seed set in the iris *Lapeirousia oreogena* by a specialist fly pollinator, however, they found that seed production per flower showed a significant negative relationship with patch size, but was not affected by flower density or distance to neighbouring patches.

Another ecological interaction that has the potential to affect pollinator foraging is predation, and although this has not been well studied in Diptera, one meta-analysis found that flower visitation rates and time spent on flowers by Diptera were not affected by presence of predators, in contrast to Lepidoptera, Hymenoptera, and Squamata (Romero et al. 2011).

Some Diptera use flowers as sites for predatory activity. Notable are some Scathophagidae and some tiger flies (*Coenosia* spp. (Muscidae)), as well as some Conopidae and Asilidae. In the Canadian High Arctic, Kevan (1970) recorded *Scathophaga apicalis* ambushing Syrphidae in flowers.

EFFECTIVENESS OF DIPTERA AS POLLINATORS

An effective pollinator must simply transfer enough pollen grains to stigmas of conspecific flowers to cause seed-

set, and its method of doing this can vary greatly. The pollinating potential of an anthophile may be evaluated in terms of both quantity and quality (Herrera 1987; Herrera 1989), which relate to the foraging patterns described above. The former concerns factors such as the abundance of the pollinator and its rate of flower visitation, whereas the latter evaluates the effectiveness of pollen transfer. Specialized pollinators generally have lower "quantity" than generalists, but their ability to transfer pollen is typically higher.

Generalized systems are often inefficient because they result in the loss of pollen and nectar rewards with no consequent pollination, and the deposition of heterospecific pollen on stigmas can decrease the fertility of conspecific pollen deposited later (Motten et al. 1981; Campbell 1985b; Campbell & Motten 1985;). However, when pollinator visits are rare or unpredictable, it may be beneficial for the plant to have a suite of opportunistic visitors. Their services, under poor conditions, may outweigh the costs of interspecific and/or geitonogamous pollen flow (Motten 1986; Patt et al. 1989; Kearns 1992). It might be thought that it is better for a plant to have any visitor than no visitor at all, but that contention is probably incorrect in cases such as Bombyliid flies reported to eat pollen directly from anthers, which are thus unlikely to serve as pollinators (Deyrup 1988).

Number of flies visiting, and visitation rates

The rate at which Diptera visit flowers is a product of their abundance and activity level. Flies are often prevalent flower visitors and have frequently been reported as the most common visitors to flowers from a variety of plant families (Tab. 1). Few studies have counted the flies in trap flowers and Araceae, but 2-6 per flower seems typical (Wolda & Sabrosky 1986; Lack & Diaz 1991; Patt et al. 1995). More than eight individuals of *Psychoda phalaenoides* L. (Psychodidae) were found in 36% of the *Arum maculatum* L. (Araceae) inflorescences studied by Lack and Diaz (1991), and only 10% captured none. The average number of *Colocasiomyia* flies (Drosophilidae) in traps of protogynous *Alocasia odora* C. Koch (Araceae) in Japan increased from 56 in the female phase to 112 in the male phase, presumably because attractive scents were released throughout the flowering period (Yafuso 1993). The record for average number of flies found in trap flowers seems to be for *Aristolochia grandiflora*, with an average of 3-400 (of multiple species) in Mexico (Burgess et al. 2004). Coombs et al. (2011) hypothesized, based on experiments with *Ceropegia*, that trapping by flowers may be an adaptation to enhance female success through pollen deposition rather than pollen export.

Visitation rate depends on both the time spent flying between flowers (flight time) and the time spent extracting the rewards from each flower visited (handling time) (see Herrera 1989). In plants visited predominantly by flies, the fly visitation rate is usually between 0.5 and 3 visits per flower per hour, but this varies widely among species, over the day, and with elevation (Motten et al. 1981; McCall & Primack 1992; Kearns & Inouye 1994), and in some cases it can be as much as an order of magnitude lower (Schmitt (1983). For example, the bee-fly *Megapalpus nitidus* Macq. visited 2.4 capitula of *Gorteria diffusa* Thunb. (Asteraceae)

TABLE I.　Examples of plant species that are visited primarily (> 50% of visits) by Diptera. The mean percentage of all visits by Diptera is given (%DV), and this is apportioned among Syrphidae (%SV), Bombyliidae (%BV) and Muscoidea (%MV) when possible. The evidence for the pollination resulting from these visits was variable.

Plant Species	Location	%DV	%SV	%BV	%MV	Reference
Adonis ramosa (Ranunculaceae)	Japan	95.7	6		9.2	Kudo 1995
Antennaria parviflora (Asteraceae)	alpine Colorado, USA	63				Bierzychudek 1987
Cardamine angustata (Brassicaceae)	North Carolina, USA	59		54.9		Motten 1986
Caulophyllum thalictroides (Berberidaceae)	Michigan, USA	78	39		39	Hannan and Prucher 1996
Cryptantha humilis (Boraginaceae)	Utah, USA	61		23		Caspar and LaPine 1984
Disa draconis (Orchidaceae)	South Africa	~100				Johnson and Steiner 1997
Disa oreophila (Orchidaceae)	South Africa	~100				Johnson and Steiner 1995
Gorteria diffusa (Geraniaceae)	South Africa	>99		>99		Johnson and Midgley 1997
Heracleum sphondylium (Apiaceae)	United Kingdom	93				Willmer 1983
Linanthus bicolor (Polemoniaceae)	California, USA	88		88		Schmitt 1983
Linum lewisii (Linaceae)	montane Colorado, USA	95				Kearns and Inouye 1993a, 1994
Leontopodium alpinum (Asteraceae)	Swiss Alps	89	1		80	Erhardt 1993
Listera cordata (Orchidaceae)	northern California, USA	99.9				Mesler *et al.* 1980
Lithophragma parviflorum (Saxifragaceae)	Washington, USA	68-88		68-88		Thompson and Pellmyr 1992
Minuartia groenlandica (Caryophyllaceae)	alpine New Hampshire, USA	97	14		84	Levesque and Burger 1982
Oritrophium limnophilum (Asteraceae)	Andean paramo, Venezuela	83.6				Smith 1975
Potentilla gracilis	montane Colorado, USA (3 different elevations)	46;73; 76	0-20		15-83	Kearns 1990
Ranunculus inamoenus (Ranunculaceae)	montane Colorado, USA	92			85	Roy 1994
*Rubus chamaemorus** (Rosaceae)	Arctic Norway	80+	61,6-10		19,80	Hippa *et al.* 1981
Saxifraga hirculus (Saxifragaceae)	Denmark;alpine Switzerland	90;77	70;35		0; 24	Olesen and Warncke 1989a,b,c; Warncke *et al.* 1993
Saxifraga reflexa ** (Saxifragaceae)	Alaska, USA	99	99			McGuire and Armbruster 1991
*Saxifraga tricuspidata** (Saxifragaceae)	Alaska, USA	55	55			McGuire and Armbruster 1991
Scoliopus bigelowii (Liliaceae)	northern California, USA	99.9				Mesler *et al.* 1980
Stellaria pubera (Caryophyllaceae)	North Carolina, USA	65; 58		65; 54		Campbell 1985; Motten 1986
Thalictrum thalictroides (Ranunculaceae)	North Carolina, USA	86.4		80.2		Motten 1986
Viola reichenbachiana (Violaceae)	United Kingdom	78	70	8		Beattie 1974
Viola rostrata (Violaceae)	United Kingdom	70	15	55		Beattie 1974
*Zizia trifoliata*** (Apiaceae)	montane North Carolina, USA	97	97			Lindsey 1984

*The first value corresponds to the Finnish Forest Lapland site and the second to the Finnish Fell Lapland site in Hippa et al. (1981). Both values are estimates and the %MV value includes Empididae.
**During "*S. tricuspidata* period"
***Grandfather Mountain site (GM) in Lindsey (1984).

TABLE 2.   Duration of fly visits to flowers of different plant species.

Plant species	Location	Fly visitor	Mean duration of flower visits (s)	Reference
Brassica napus L. (Brassicaceae)	Japan	*Eristalis cerealis* Fabricius (Syrphidae) pollen parent flowers cytoplasmic male sterile seed parents	120 50	Ohsawa and Namai (1988)
Gorteria diffusa Thunb. (Geraniaceae)	South Africa	*Megapalpus nitidus* Macq. (Bombyliidae)	7.4 (9.3 am; 1.7 pm)	Johnson and Midgley (1997)
Hedyotis caerulea (L.) Hook. (Rubiaceae)	New York, USA	*Bombylius* spp. (Bombyliidae)	7.0	Grimaldi (1988)
Lavandula latifolia Vill. (Lamiaceae)	Spain	Calliphoridae *Systoechus* sp. (Bombyliidae) Five syrphid genera *Nowichia strobeli* (Tachinidae)	77.7 4.2 7.9-18.8 15.3	Herrera (1989)
Potentilla gracilis Douglas *(Rosaceae)*	montane Colorado	Muscidae	49.6 - 200.2	Kearns (1990)
Rosa setigera (Michx.) (Rosaceae)	Ontario, Canada	*Eristalis tenax* (Syrphidae) On male flowers On female flowers	63.5 26.6	Kevan *et al.* (1990)
Saxifraga hirculus L. (Saxifragaceae)	Denmark	*Eurimyia lineata* (Fabr.) (Syrphidae) *Neoascia tenur* (Harris) (Syrphidae) *Asindulum nigrum* Latreille (Mycetophilidae)	11.7 27.4 30.7	Olesen and Warncke 1989c)
Ziziphus mucronata Willd. (Rhamnaceae)	South Africa	*Musca domestica* L. (Muscidae) *Sarcophaga* sp. (Sarcophagidae)	7 (mode = 1-2) 8 (mode = 5-6)	Zietsman (1990)

per hour in the morning, but 19.8 capitula per hour in the same patch in early afternoon, when visits were shorter in duration (Johnson & Midgley 1997). In one hour, a single *Bombylius* may visit 125 *Hedyotis caerulea* (L.) Hook. (Rubiaceae) flowers in New York populations (Grimaldi 1988) and an edelweiss (*Leontopodium alpinum* Cass. (Asteraceae)) inflorescence in the Swiss Alps may receive 30 visits (Erhardt 1993).

Diptera have a lower foraging rate than bees mainly because of their greater handling time (Herrera 1989; Kearns & Inouye 1993a), which is generally between 5 and 30 seconds per flower, and sometimes much longer (Tab. 2). Floral visits by unspecialized flies such as fungus gnats and empidids may last from 3 to 20 minutes (Mesler et al. 1980; Patt et al. 1989), and Muscidae (*Thricops, Phaonia,* and *Coenosia*) visiting edelweiss spent as long as 15 minutes on individual clones, walking between inflorescences by using the ray bracts as bridges (Erhardt 1993). *Syrphus torvus* Osten Sacken (Syrphidae) takes 5 to 10 minutes to exit the trap flowers of *Cypripedium reginae* Walter (Orchidaceae) Walter (Vogt 1990), and *Scaeva pyrastri* (Syrphidae) also took that long for visits to *Fatsia japonica* (Araliaceae) (Wang et al. 2011). Gilbert (1981) found that the handling time of composite florets by syrphids was usually less than two seconds, but that it increased with floret depth. Despite their typically lower visitation rate, flies often forage under poorer conditions than bees (Levesque & Burger 1982), and this, combined with their abundance, contributes to their significance as pollinators.

Quality

Even if a foraging fly is constant and carries a relatively pure pollen load (see constancy, above), its effectiveness as a pollinator also depends on the amount of pollen that it carries and more importantly, the number and quality of pollen grains it deposits on stigmas (Herrera 1987). The amount of pollen carried by an anthophile may correlate with the number of grains deposited, so it is often used as an estimate of the suitability of a flower visitor as a pollinator because the latter is more difficult to measure (Kearns & Inouye 1993b). Flies generally carry fewer pollen grains than bees (Kendall & Solomon 1973; O'Brien 1980; Hippa et al. 1981; Boyle & Philogène 1983; Herrera 1987; Kearns 1992; Kearns & Inouye 1993a) and may deliver many fewer pollen grains (Bischoff et al. 2013). The number of grains carried depends in part on grain size, but also on the size of the insect's body (Kearns 1992; Erhardt 1993), so pollen load can be quite variable. In general, pilosity (e.g., among syrphids, *Parasyrphus* > *Sphaerophoria*) and size (e.g., among muscids, *Phaonia* > *Thricops* or *Spilogona*) are directly correlated with pollen-carrying ability (Hippa et al. 1981; Levesque & Burger 1982; Erhardt 1993).

A small number of studies report pollen loads from Diptera collected while visiting flowers (Tab. 3). In many cases the pollen loads are large, suggesting that the flies may be effective pollinators. Two studies have examined pollen loads on insects visiting *Pyrus malus* L. (Rosaceae). The first found means of over 2,000 grains for species of Syrphidae and Conopidae, putting them in the same category as honey

TABLE 3.   Sizes of Dipteran pollen loads reported in the literature.

Plant species	Location	Fly visitor (Family)	Mean number of pollen grains	Reference
Disa oreophilia (Orchidaceae)	South Africa	*Prosoeca ganglbaueri* Lichtwardt (Nemestrinidae)	Mean = 2.8 pollinia	Johnson & Steiner 1995
Eriogonum pelinophilum (Polygonaceae)	Colorado	Bombyliidae, Milichiidae, Muscidae, Syrphidae, and Stratiomyidae	Range 1.0 – 14.6	Tepedino et al. 2011
Leontopodium alpinum (Asteraceae)	Switzerland	Muscidae	219.6	Erhardt 1993
Trollius europaeus (Ranunculaceae)	France	Anthomyiidae	2,288	Després 2003
Zizia trifoliata (Apiaceae)	2 populations	*Meliscaeva cinctlla* (Zetterstedt) (Syrphidae)	198 5,912	Lindsey 1984
Minuartia groenlandica (Caryophyllaceae)	New Hampshire	*Eristalis tenax* (Syrphidae) Muscidae, Anthomyiidae, Scathophagidae	300 3.5 - 26	Levesque & Burger 1982
Various species of bog flowers	Denmark	*Eurimyia lineata* (Syrphidae) *Neoascia tenur* (Syrphidae	1,031 137	Olesen & Warncke 1989c
Various species of montane flowers	Colorado	Muscoid flies	71	Kearns 1990
Four species of Rosaceae	England	Eristalis spp.	135 - 337	Yeboah Gyan & Woodell 1987

bees and some species of bumblebees (Kendall & Solomon 1973), while the other found 806 pollen grains of apple on syrphids in Ontario, but usually much less than one-quarter of this on other foraging Diptera (Boyle & Philogène 1983). The majority of bombyliid and syrphid flies (57.6%) carried between 100 and 1,000 pollen grains of the plant species studied by O'Brien (1980) in California. Individual *Psychoda* visiting *Arum maculatum* often carried over 150 pollen grains, which was more than enough to pollinate the plant, but fruit set was limited by pollinator availability (Lack & Diaz 1991). Hippa *et al.* (1981) found that small Sciaridae and Chironomidae, as well as "accidental" flower visitors such as Dolichopodidae, Tachinidae, Phoridae and Agromyzidae carried very few, if any, pollen grains of cloudberry, compared to the larger and/or more constant muscids, syrphids and empidids.

The number of grains deposited may also depend on their distribution on the body in relation to floral morphology. For example, the fit between the body size of the fly and the structure of the flower may determine whether a visitor is a pollinator or a thief, as has been noted by numerous authors; e.g., for calliphorids on *Sterculia* (Sterculiaceae) (Taroda & Gibbs 1982), and for orchids (Pijl & Dodson 1966). Pollen grains were most prevalent on the thorax of the four commonest Diptera visitors (*Thricops hirtulus* (Zetterstedt) (Muscidae), *Nupedia aestiva* (Meigen), *Delia platura* (Meigen) (Anthomyiidae) and *Carposcalis obscurus* (Say) (Syrphidae)) of *Minuartia groenlandica* (Caryophyllaceae) on Mount Washington, New Hampshire, with varying numbers occurring on head, legs, and abdomen (Levesque & Burger 1982), and on muscid pollinators of

edelweiss they were concentrated on the legs, but also located on most other parts of the body (Erhardt 1993). Generalized pollen distribution is expected for these, and other relatively open, unspecialized flowers (see O'Brien 1980; Kato et al. 1995) for additional examples), and contrasts with concentrations on the proboscis in flies visiting more specialized and/or tubular flowers, such as *Bombylius* on *Hedyotis caerulea* (Rubiaceae) (Grimaldi 1988), *Prosoeca* species (Nemestrinidae) on *Disa oreophila* H. Bolus (Orchidaceae) (Johnson & Steiner 1995), empidids on *Platanthera stricta* Lindley (Orchidaceae) (Patt et al. 1989), and muscoids and milichiids on stapeliads (Asclepiadaceae) (Meve & Liede 1994). Concentrations of pollen grains on or about the head and proboscis are also reported for muscoids foraging on relatively open flowers (e.g., pollinators of *Ziziphus mucronatus* Willd. (Rhamnaceae) (Zietsman 1990) and *Sterculia chicha* (Sterculiaceae) (Taroda & Gibbs 1982)).

Perhaps the most thorough investigation of the distribution of pollen grains on Diptera is the paper by Tepedino et al. (2011) that reports the mean number of grains on face, head, and lower and upper thorax and abdomen for 12 of the abundant fly species found visiting a rare buckwheat (*Eriogonum pelinophilum*: Polygonaceae). For nine of those species the distribution of grains was significantly different across the flies' bodies, with the thorax having the most in seven species and the head in the other two.

There have been few investigations of the amount of pollen deposited by flies during a single visit to a flower.

Flies generally deposited fewer grains (mean = 10.4) on stigmas of *Linum lewisii* Pursh. (Linaceae) in the Rocky Mountains than did bees (mean for all bees = 17.2), but this was mainly due to the large number deposited by bumblebees (mean = 26.6), which were very uncommon visitors (Kearns & Inouye 1994). Muscoid flies and small solitary bees were the most common visitors of *L. lewisii*, and they deposited similar amounts of pollen, but the bees deposited more heterospecific pollen. McGuire and Armbruster (1991) showed that syrphids (unidentified species) and halictid bees (*Evylaeus* and *Dialictus* species) produced similar seed set after single visits to *Saxifraga* species (Saxifragaceae) in Alaska. After visiting a *Stellaria pubera* (Caryophyllaceae) flower, a *Bombylius major* deposited about 23% of the pollen on its body in visits to subsequent flowers, which was less than the 47% of that deposited by *Nomada* bee species (Campbell 1985a). However, pollen deposition declined less rapidly in subsequent floral visits by the flies than the bees, so they transferred more pollen overall. Tachinid pollinators retain nearly 90% of the pollen on their body during visits to *Myosotis colensoi* (Boraginaceae) and this high level of carryover may reduce geitonogamy when numerous flowers on a plant are visited (Robertson 1992). In contrast, pollen carryover between sapromyophilous flowers may be minimal, especially if the flies are trapped for a long period of time (Lack & Diaz 1991).

Overall Effectiveness

Although the quantity and quality of efficient pollen transfer have been considered separately above, it is important to realize that they are, in fact, complementary. The only true measure of the effectiveness of a visitor in terms of pollination is the number and fitness of seeds resulting from its visits, and this depends on both quality and quantity of pollen deposition. A plant visited frequently by flies and only occasionally by bees could still be pollinated primarily by the bees if they transfer much larger quantities of pollen per visit, but plants visited by inefficient fly pollinators could still rely more on them than on infrequent but more efficient bees (e.g., Kearns & Inouye 1994; Zheng et al. 2011). Occasionally, large numbers of only one species of fly have been seen at the flowers of a species of plant, and it has been concluded that they may have a considerable role in pollination even if their individual contributions are small (Burgett 1980; Levesque & Burger 1982). However, when weighing the quality of various visitors, one cannot assume that frequency of visitation alone results in regular pollen transfer. For example, Diptera were prevalent visitors of *Listera ovata* (L.) R. Br. (Orchidaceae) in Sweden, but they only rarely carried pollinia (Nilsson 1981), and there are numerous such examples in the literature. Researchers in arctic and alpine regions have noted that flies often remain in individual flowers for long periods of time, possibly for warmth (Kevan 1970; Kearns & Inouye 1993a; Kudo 1993). Whether this behaviour causes much intra-floral self-pollination, which could decrease the number and quality of seeds produced, is not well known.

It is rare for researchers to differentiate between male and female flies in studies of pollinator effectiveness, but one study that did found that fewer seeds were produced by a single visit from a male *Chiastocheta* fly to its *Trollius* host plant (5.4% of total seed production) than a visit from a female (12%) (Després 2003). This difference seems to be the consequence of females spending more time inside the flower than males, given that the number of ovules fertilized is significantly correlated with the time insects spent inside the closed corolla. However, the lower efficiency of ovule fertilization per visit by males is compensated for by the higher rate of flower visitation by males; flowers receive about twice as many visits from males as from females.

It is generally assumed that flies are ineffective pollinators (Faegri & van der Pijl 1979). However, few researchers have considered both quality and quantity of pollination for the fly fauna visiting a particular plant species, and those that have rarely quantify both measurements. For example, Kevan (1970; 1972) noted the abundance of anthophilous flies in the Arctic and their ability to carry pollen grains, and was able to infer pollinating ability based on their manner of foraging. He noted that various species of flies assumed different stances that would enhance pollen movement and interfloral transfer. Flies of Empididae and Anthomyidae assumed any of four stances on the open bowl-shaped flowers (especially *Dryas integrifolia*) they visited. Sometimes they would forage for nectar by standing on the petals with their dorsal aspects touching the anthers. Others stood on the stamens and foraged by dipping so that their dorsal aspects touch the stigmas while their ventral aspects became dusted with pollen. Others stood on the pistils and foraged by dipping so that their dorsal aspects rubbed the anthers while any pollen on their venters could be off-loaded to the stigmas.

Mesler *et al.* (1980) have shown that fungus gnats are the major pollinators of *Listera cordata* (L.) R. Br. (Orchidaceae) and *Scoliopus bigelovii* Torr. (Liliaceae) in California redwood forests. The probability of pollen transfer by an individual gnat is low, but their large numbers and foraging behaviour ensure that pollinations do occur (about 50% xenogamously), resulting in a high fruit set (61-99%) relative to other orchids pollinated by flies (e.g., 15.5% in *Epipactis consimilis* Don (Ivri & Dafni 1977); 14% in *Platanthera obtusata* (Banks ex Pursh) Lindley (Thien & Utech 1970)). Nonetheless, additional data on pollinia transfer probabilities during visits by individual gnats are required to determine their effectiveness relative to other insects.

Studies by Motten *et al.* (1981), Campbell (1985a), Campbell and Motten (1985), and Motten (1986) have elucidated many of the intricacies of *Bombylius major* foraging on eastern North American spring wildflowers. Motten (1986) found that *Bombylius* was the most common visitor for the 10 plant species he studied (38% of all visits) and that it was as effective a pollinator of *Claytonia virginica* L. (Portulacaceae) as the oligolectic andrenid bee *Andrena erigeniae* Robertson (Andrenidae) (Motten et al. 1981). However, it was the least discriminating forager of those he studied, and would often visit flowers of four plant genera in a square-meter plot.

Muscoid flies and small bees are the major visitors of *Linum lewisii* (Linaceae) in the Rocky Mountains of

Colorado, and Kearns and Inouye (1993a; 1994) investigated their relative effectiveness as pollinators. The small bees deposited slightly more pollen grains on a flax flower's stigma in a single visit than did muscoid flies (see above). However, at higher elevations the flies had a greater relative visitation rate, so their total pollen deposition was over an order of magnitude greater than that of the bees. A similar story is reported for a comparison of bumble bee and calliphorid fly pollination of *Cypripedium flavum* orchids in China (Zheng et al. 2011); flies are less efficient per visit, but make more visits so overall they are the more important pollinators.

As is true for any kind of pollinator, insufficient pollen deposition by flies can lead to pollen limitation of seed set. An experimental study of the tundra species *Parrya nudicaulis* (Brassicaceae) demonstrated that syrphid and muscid flies were the major pollinators, but hand pollination increased seed production five-fold, indicating significant pollen limitation (perhaps due to overproduction of ovules as part of a bet-hedging strategy) (Fulkerson et al. 2012). Pollen limitation has also been documented in other species of plants pollinated primarily (Johnson & Steiner 1997) or in part (Patt et al. 1989) by Diptera.

CROP POLLINATION BY DIPTERA

Diptera have been used for pollination in breeding experiments and for crops since at least the 1930s (Free 1970), and their effectiveness as pollinators of crops has been recognized in a growing number of studies (Ssymank et al. 2008; Ssymank et al. 2009). In temperate areas they have been used for onions, parsnips, brassica crops, carrots, celery, and other plants with small flowers that are difficult for hand pollination (Free 1970). In tropical areas flies are the primary pollinators of cacao (Winder 1978), and they also pollinate mango (Jiron & Hedstrom 1985), cashew (Heard et al. 1990) and tea (Wickramaratne & Vitarana 1985), while in temperate regions they have been studied as pollinators of onion (Kumar et al. 1985), strawberry (Nye & Anderson 1974), *Brassica* (Langridge & Goodman 1975; Smith & Mee 1984; Jauker & Wolters 2008), sweet pepper (Jarlan et al. 1997), and apples (Boyle & Philogène 1983; de Oliveira et al. 1984). Rader et al. (2009) found that *Eristalis tenax* were as efficient as the honeybee and as effective (in terms of rate of flower visitation) for *Brassica* pollination, so it and other unmanaged pollinators were important for this mass-flowering crop (Rader et al. 2012). Roubik (1995) lists pollinators of 785 species of cultivated plants in the tropics, and 26-31 of these are apparently pollinated only by flies, 32-33 by flies as the primarily pollinators, and 87-101 more by flies as secondary pollinators. Wickramaratne and Vitarana (1985) reported that Diptera were the most numerous visitors to flowers in a tea seed garden; at least seven families were represented, with individual flies carrying up to 500 pollen grains. Diptera may be of use in glasshouse or other controlled pollination studies: syrphid flies were used successfully in recent trials of glasshouse cultivation of sweet peppers, and muscids were used by Green (1973) for caged onions in plant breeding studies. Syrphids have also been used for controlled pollination of *Allium* for crop

genetic resources (unpublished report of the ECP/GR *Allium* Working Group, European Cooperative Programme for Crop Genetic Resources Networks) and *Eristalis tenax* mass-rearing was used for a variety of wild plants to maintain the stock of the German plant genebank in Gatersleben (Gladis 1994). The calliphorid fly *Lucilia sericata* is now sold commercially for use in pollination of a variety of crops with small flowers (http://www.koppert.com/products/pollination/products-pollination/detail/natufly/).

CONCLUSIONS

Our survey of the literature on Diptera indicates that they share many similarities with other, better studied, pollinators in terms of environmental effects on their foraging, their foraging behaviour, their responses to competitors, and their effectiveness as pollinators. This conclusion is based on study of a very small percentage of the flower-visiting Diptera. The following numbers give some indication of how much remains to be learned. In tropical areas of the world the diversity of Diptera (in families recorded as flower visitors) can rival or exceed that of Hymenoptera. For example, 4,856 species of Diptera are recorded from Australasia from flower-visiting families, compared with approximately 2,570 bees (superfamily Apoidea), while for the Neotropics the estimates are >2,940 species for Diptera and 5,630 species for bees (Roubik 1995). The relatively recent discovery that Diptera can be a very important component of temperate pollinator communities too, especially at high altitudes, also points to the potential for additional work. The significance of Diptera as pollinators should engender the same concern about their conservation that has been raised for pollinators in general (Kearns 2001; Kearns & Inouye 1997; Kearns et al. 1998) and for pollinators of crops in particular (Allen-Wardell et al. 1998).

ACKNOWLEDGEMENTS

REFERENCES

Allen-Wardell G et al. (1998) The potential consequences of pollinator declines on the conservation of biodiversity and stability of food crop yields. Conservation Biology 12:8-17.

Anderson B, Johnson SD (2008) The geographical mosaic of coevolution in a plant-pollinator mutualism. Evolution 62:220-225.

Arista M, Ortiz PL, Talavera S (1999) Apical pattern of fruit production in the racemes of *Ceratonia siliqua* (Leguminosae: Caesalpinioideae): Role of pollinators. American Journal of Botany 86:1708-1716.

Aubert J, Goeldlin de Tiefenau P (1981) Observations sur les migrations de Syrphides (Dipt.) dans les Alpes de Suisse occidentale. Bulletin Société entomologique Suisse 54:377-388.

Bänziger H (1991) Stench and fragrance: Unique pollination lure of Thailand's largest flower, *Rafflesia kerrii* Meijer. Natural History Bulletin of the Siam Society 39:19-52.

Bartholomew GA, Lighton JRB (1986) Endothermy and energy metabolism of a giant tropical fly, *Pantophthalmus tabaninius* Thunberg. Journal of Comparative Physiology B 156:461-467.

Beaman RS, Decker PJ, Beaman JH (1988) Pollination of *Rafflesia* (Rafflesiaceae). American Journal of Botany 75:1148-1162.

Beattie AJ (1972) The pollination ecology of *Viola*. 2. Pollen loads of insect-visitors. Watsonia 9:13-25.

Beattie AJ (1974) Floral evolution in *Viola*. Annals of the Missouri Botanical Garden 61:781-793.

Beattie AJ (1976) Plant dispersion, pollination and gene flow in *Viola*. Oecologia 25:291-300.

Birtele D, Hardersen S (2012) Analysis of vertical stratification of Syrphidae (Diptera) in an oak-hornbeam forest in northern Italy. Ecological Research 27:755-763.

Bischoff M, Campbell DR, Lord JM, Robertson AW (2013) The relative importance of solitary bees and syrphid flies as pollinators of two outcrossing plant species in the New Zealand alpine. Austral Ecology 38:169-176.

Boggs CL (1987) Ecology of nectar and pollen feeding in Lepidoptera. In: Slansky FJ, Rodreguez JG (eds) Nutritional ecology of insects, mites and spiders. John Wiley & Sons, New York, New York, pp 369-391.

Boyle RMD, Philogène BJR (1983) The native pollinators of an apple orchard: variations and significance. Journal of Horticultural Science 58:355-363.

Branquart E, Hemptinne JL (2000) Selectivity in the exploitation of floral resources by hoverflies (Diptera : Syrphinae). Ecography 23:732-742.

Brantjes NJB (1976) Riddles around the pollination of *Melandrium album* (Mill.) Garcke (Caryophyllaceae) during the oviposition by *Hadena bicruris* Hufn. (Noctuidae: Lepidoptera). II. Proceedings Koninklijle Nederlandse Akademie Van Wetnschappen Series C Biological and Medical Science 79:127-141.

Burgess KS, Singfield J, Melendez V, Kevan PG (2004) Pollination biology of *Aristolochia grandiflora* (Aristolochiaceae) in Veracruz, Mexico. Annals of the Missouri Botanical Garden 91:346-356.

Burgett M (1980) Pollination of parsley (*Petroselinum crispum*) grown for seed. Journal of Apicultural Research 19:79-82.

Campbell DR (1985a) Pollen and gene dispersal: the influences of competition for pollination. Evolution 39:418-431.

Campbell DR (1985b) Pollinator sharing and seed set of *Stellaria pubera*: competition for pollination. Ecology 66:544-553.

Campbell DR, Motten AF (1985) The mechanism of competition for pollination between two forest herbs. Ecology 66:554-563.

Casper BB, La Pine TR (1984) Changes in corolla color and other floral characteristics in *Cryptantha humilis* (Boraginaceae): cues to discourage pollinators? Evolution 38:128-141.

Chappell MA, Morgan KR (1987) Temperature regulation, endothermy, resting metabolism, and adult energetics of tachinid flies (Nowickia sp.). Physiological Zoology 60:550-559.

Charnov EL (1976) Optimal foraging: The marginal value theorem. Theoretical Population Biology 9:129-136.

Chittka L, Thomson JD (eds) (2005) Cognitive Ecology of Pollination. Cambridge University Press, Cambridge.

Christensen DE (1992) Notes on the reproductive biology of *Stelis argentata* Lindl. (Orchidaceae: Pleurothallidinae) in eastern Ecuador. Lindleyana 7:28-33.

Collett TS, Land MF (1975) Visual spatial memory in a hoverfly. Journal of Comparative Physiology 100:59-84.

Coombs G, Dold A, Peter C (2011) Generalized fly-pollination in *Ceropegia ampliata* (Apocynaceae–Asclepiadoideae): the role of trapping hairs in pollen export and receipt. Plant Systematics and Evolution 296:137-148.

Corbet SA (1978) Bee visits and the nectar of *Echium vulgare* L. and *Sinapis alba* L. Ecological Entomology 3:25-37.

Corbet SA, Unwin DM, Prys-Jones OE (1979) Humidity, nectar and insect visits to flowers, with special reference to *Crataegus*, *Tilia* and *Echium*. Ecological Entomology 4:9-22.

Cowgill SE, Wratten SD, Sotherton NW (1993) The selective use of floral resources by the hoverfly *Episyrphus balteatus* (Diptera, Syrphidae) on farmland. Annals of Applied Biology 122:223-231.

de Jong TJ, Waser NM, Klinkhamer PGL (1993) Geitonogamy: the neglected side of selfing. Trends in Ecology and Evolution 8:321-325.

de Oliveira D, Pion S, Paradis RO (1984) La pollinisation et la production de pommes. In: Vincent C, Bostanian NJ (eds) La phytoprotection des vergers de pommiers au Québec. Agriculture Canada, Saint-Jean, Quebec, pp 203-220?.

Decazy B, Massaux F, Tchiendju C, Misse C (1980) Use of radioisotopes (32P) in the study of pollinating agents of the cacao tree in the ecological conditions of South Cameroon.

Dempster JP, Atkinson DA, French MC (1995) The spatial population dynamics of insects exploiting a patch food resource. II. Movements between patches. Oecologia 104:354-362.

Després L (2003) Sex and pollen: the role of males in stabilising a plant-seed eater pollinating mutualism. Oecologia 135:60-66.

Deyrup MA (1988) Pollen-feeding in *Poecilognathus punctipennis* (Diptera: Bombyliidae). The Florida Entomologist 71:597-605.

Downes JA (1955) The food habits and distribution of *Atrichopogon pollinivorous* sp. n. (Diptera: Ceratopogonidae). Transactions of the Royal Entomological Society, London 106:439-453.

Downes JA (1958) The feeding habits of biting flies and their significance in classification. Annual Review of Entomology 3:249-266.

Downes JA, Smith SM (1969) New or little known feeding habits in Empididae (Diptera). Canadian Entomologist 101:404-408.

Dukas R, Shmida A (1989) Correlation between the color, size and shape of Israeli crucifer flowers and relationships to pollinators. Oikos 54:281-286.

Dötterl S, Jahreiß K, Jhumur US, Jürgens A (2012) Temporal variation of flower scent in *Silene otites* (Caryophyllaceae): a species with a mixed pollination system. Botanical Journal of the Linnean Society 169:447-460.

Ellis Allan G, Johnson Steven D (2010) Floral mimicry enhances pollen export: The evolution of pollination by sexual deceit outside of the Orchidaceae. The American Naturalist 176:E143-E151.

Elvers I (1980) Pollen eating *Thricops* flies (Diptera, Muscidae) on *Arrhenatherum pubescens* and some other grasses. Botaniska Notiser 133:49-52.

Endara L, Grimaldi DA, Roy BA (2010) Lord of the flies: Pollination of *Dracula* orchids. Lankesteriana 10:1-11.

Entwistle PF (1972) Pests of Cocoa. Longman, London.

Erhardt A (1993) Pollination of the edelweiss, *Leontopodium alpinum*. Botanical Journal of the Linnean Society 111:229-240.

Evenhuis NL (1983) Observations on the territoriality of *Oligodranes mitis* Cresson (Diptera: Bombyliidae) on flowers of

Erigeron neomexicanus (Asteraceae). Entomological News 94:25-28.

Faegri K, van der Pijl L (1979) The Principles of Pollination Ecology, 3rd edn. Pergamon Press, Oxford.

Fitzpatrick SM, Wellington WG (1983) Insect territoriality. Canadian Journal of Zoology 61:471-486.

Free JB (1970) Insect Pollination of Crops. Academic Press, New York.

Fulkerson JR, Whittall JB, Carlson ML (2012) Reproductive ecology and severe pollen limitation in the polychromic tundra plant, *Parrya nudicaulis* (Brassicaceae). PLoS ONE 7:e32790.

Gatter W, Schmid U (1990) Die Wanderungen der Schwebfliegen (Diptera, Syrphidae) am Randecker Maar. Spixiana supplement 15:1-100.

Gilbert F, Owen J (1990) Size, shape, competition, and community structure in hoverflies (Diptera: Syrphidae). Journal of Animal Ecology 59:21-39.

Gilbert FS (1981) Foraging ecology of hoverflies: morphology of the mouthparts in relation to feeding on nectar and pollen in some common urban species. Ecological Entomology 6:245-262.

Gilbert FS (1985) Diurnal activity patterns in hoverflies (Diptera: Syrphidae). Ecological Entomology 10:385-392.

Gilbert FS, Harding EF, Line JM, Perry I (1985) Morphological approaches to community structure in hoverflies (Diptera, Syrphidae). Proceedings of the Royal Society. London. B 224:115-130.

Gladis T (1994) Aufbau und Nutzung einer Massenzucht von *Eristalis tenax* (Diptera, Syrphidae) in der Genbank Gatersleben. [Establishment and utilization of a mass rearing of *Eristalis tenax* (Diptera, Syrphidae) in the Gatersleben genebank] Insecta, Berlin 1:287-294.

Goldblatt P, Manning JC, Bernhardt P (1995) Pollination biology of *Lapeirousia* subgenus *Lapeirousia* (Iridaceae) in Southern Africa; floral divergence and adaptation for long-tongued fly pollination. Annals of the Missouri Botanical Garden 82:517-534.

Goot VSvd, Grabandt RAJ (1970) Some species of the genera *Melanostoma*, *Platycheirus* and *Pyrophaena* (Diptera: Syrphidae) and their relation to flowers. Entomologische Berichten 30:135-143.

Goto R, Yamakoshi GEN, Matsuzawa T (2012) A novel brood-site pollination mutualism?: the root holoparasite *Thonningia sanguinea* (Balanophoraceae) and an inflorescence-feeding fly in the tropical rainforests of West Africa. Plant Species Biology 27:164-169.

Goulson D, Wright NP (1998) Flower constancy in the hoverflies *Episyrphus balteatus* (Degeer) and *Syrphus ribesii* (L.) (Syrphidae). Behavioral Ecology 9:213-219.

Green JH (1973) Note on the use of flies for onion pollination under arid conditions in Nigeria. Tropical Agriculture 50:165-167.

Grimaldi D (1988) Bee flies and bluets: *Bombylius* (Diptera: Bombyliidae) flower-constant on the distylous species *Hedyotis caerulea* (Rubiaceae), and the manner of foraging. Journal of Natural History 22:1-10.

Grimstad PR, DeFoliart GR (1974) Mosquito nectar feeding in Wisconsin in relation to twilight and microclimate. Journal of Medical Entomology 11:691-698.

Grosser N, Klapperstück J (1977) Ökologische Untersuchungen an Syrphiden zweier Agrobiozönosen. Hercynia 14:124-144.

Gu W, Müller G, Schlein Y, Novak RJ, Beier JC (2011) Natural plant sugar sources of *Anopheles* mosquitoes strongly impact malaria transmission potential. PLoS ONE 6:e15996.

Hansen DM, Van der Niet T, Johnson SD (2012) Floral signposts: testing the significance of visual 'nectar guides' for pollinator behaviour and plant fitness. Proceedings of the Royal Society B: Biological Sciences 279:634-639.

Haslett JR (1989a) Adult feeding by holometabolous insects: pollen and nectar as complementary nutrient sources for *Rhingia campestris* (Diptera: Syrphidae). Oecologia 81:361-363.

Haslett JR (1989b) Interpreting patterns of resource utilization: randomness and selectivity in pollen feeding by adult hoverflies. Oecologia 78:433-442.

Heard TA, Vithanage V, Chacko EK (1990) Pollination biology of cashew in the Northern Territory of Australia. Australian Journal of Agricultural Research 41:1101-1114.

Heinrich B (1976) Foraging specializations of individual bumblebees. Ecological Monographs 46:105-128.

Heinrich B, Pantle C (1975) Thermoregulation in small flies (*Syrphus* sp.): basking and shivering. Journal of Experimental Biology 62:599-610.

Herrera CM (1987) Components of pollinator "quality": comparative analysis of a diverse insect assemblage. Oikos 50:79-90.

Herrera CM (1989) Pollinator abundance, morphology, and flower visitation rate: analysis of the "quantity" component in a plant-pollinator system. Oecologia 80:241-248.

Herrera CM (1990) Daily patterns of pollinator activity, differential pollinating effectiveness, and floral resource availability, in a summer-flowering Mediterranean shrub. Oikos 58:277-278.

Hickman JM, Lovei GL, Wratten SD (1995) Pollen feeding by adults of the hoverfly *Melanostoma fasciatum* (Diptera: Syrphidae). New Zealand Journal of Zoology 22:387-392.

Hippa H, Koponen S, Osmonen O (1981) Pollen transport and pollinating efficiency of flower visitors to the cloudberry (*Rubus chamaemorus* L.) in northern Fennoscandia. Reports from the Kevo Subactic Research Station 17:58-66.

Holloway BA (1976) Pollen-feeding in hover-flies (Diptera: Syrphidae). New Zealand Journal of Zoology 3:339-350.

Hövemeyer K (1995) Seasonal and diurnal activity patterns in the hoverfly species *Cheilosia fasciata* (Diptera: Syrphidae). Entomologia Generalis 20:87-102.

Iler AM, Inouye DW, Hoye TT, Miller-Rushing AJ, Burkle LA, Johnston EB (2013) Maintenance of temporal synchrony between syrphid flies and floral resources despite differential phenological responses to climate. Global Change Biology 19:2348-2359.

Ilse D (1949) Colour discrimination in the dronefly, *Eristalis tenax*. Nature 163:255-256.

Inouye DW, Pyke GH (1988) Pollination biology in the Snowy Mts. of Australia, with comparisons with montane Colorado, U. S. A. Australian Journal of Ecology 13:191-210.

Irvin NA, Wratten SD, Frampton CM, Bowie MH, Evans AM, Moar NT (1999) The phenology and pollen feeding of three hover fly (Diptera: Syrphidae) species in Canterbury, New Zealand. New Zealand Journal of Zoology 26:105-115.

Ivri Y, Dafni A (1977) The pollination ecology of *Epipactis consimilis* Don (Orchidaceae) in Israel. New Phytologist 79:173-177.

Janzen DH (1971) Euglossine bees as long-distance pollinators of tropical plants. Science 171:203-205.

Jarlan A, de Oliveira D, Gingras J (1997) Pollination by *Eristalis tenax* (Diptera: Syrphidae) and seed set of greenhouse sweet pepper. Journal of Economic Entomology 90:1646-.

Jauker F, Wolters V (2008) Hover flies are efficient pollinators of oilseed rape. Oecologia 156:819-823.

Jiron LF, Hedstrom (1985) Pollination ecology of mango (*Mangifera indica* L.) (Anacardiaceae) in the Neotropic region. Turrialba 35:269-277.

Johnson SD, Dafni A (1998) Response of bee-flies to the shape and pattern of model flowers: implications for floral evolution in a Mediterranean herb. Functional Ecology 12:289-297.

Johnson SD, Hollens H, Kuhlmann M (2012) Competition versus facilitation: conspecific effects on pollinator visitation and seed set in the iris *Lapeirousia oreogena*. Oikos 121:545-550.

Johnson SD, Midgley JJ (1997) Fly pollination of *Gorteria diffusa* (Asteraceae), and a possible mimetic function for dark spots on the capitulum. American Journal of Botany 84:429-436.

Johnson SD, Steiner KE (1995) Long-proboscid fly pollination of two orchids in the Cape Drakensberg mountains, South Africa. Plant Systematics and Evolution 195:169-175.

Johnson SD, Steiner KE (1997) Long-tongued fly pollination and evolution of floral spur length in the *Disa draconis* complex (Orchidaceae). Evolution 51:45-53.

Karkkainen K, Savolainen O, Koski V (1999) Why do plants abort so many developing seeds: bad offspring or bad maternal genotypes? Evolutionary Ecology 13:305-317.

Kato M, Inoue T, Nagamitsu T (1995) Pollination biology of *Gnetum* (Gnetaceae) in a lowland mixed dipterocarp forest in Sarawak. American Journal of Botany 82:862-868.

Kearns CA (1992) Anthophilous fly distribution across an elevation gradient. American Midland Naturalist 127:172-182.

Kearns CA (2001) North American dipteran pollinators: Assessing their value and conservation status. Conservation Ecology 5:5. [online].

Kearns CA, Inouye DW (1993a) Pistil-packing flies. Natural History 102:30-37.

Kearns CA, Inouye DW (1993b) Techniques for Pollination Biologists. University Press of Colorado, Niwot, CO.

Kearns CA, Inouye DW (1994) Fly pollination of *Linum lewisii* (Linaceae). American Journal of Botany 81:1091-1095.

Kearns CA, Inouye DW (1997) Pollinators, flowering plants, and conservation biology. BioScience 47:297-307.

Kearns CA, Inouye DW, Waser NM (1998) Endangered mutualisms: the conservation of plant-pollinator interactions. Annual Review of Ecology and Systematics 29:83-112.

Kendall DA, Solomon ME (1973) Quantities of pollen on the bodies of insects visiting apple blossom. Journal of Applied Ecology 10:627-634.

Kevan PG (1970) High arctic insect-flower relations: the inter-relationships of arthropods and flowers at Lake Hazen, Ellesmere Island, Northwest Territories, Canada. Dissertation, University of Alberta, Edmonton, Alberta, Canada.

Kevan PG (1972) Insect pollination of High Arctic flowers. Journal of Ecology 60:831-847.

Kevan PG (1975) Sun-tracking solar furnaces in high arctic flowers: significance for pollination and insects. Science 189:723-726.

Kevan PG (2007) Diaheliotaxis and ombrophobia in an anthophilous High Arctic midge, *Smittia velutina* (Lundbeck, 1898) (Chironomidae). Chironomus - Newsletter on Chironmidae Research 20:29-31.

Kevan PG, Baker HG (1983) Insects as flower visitors and pollinators. Annual Review of Entomology 28:407-453.

Kevan PG, Eisikowitch D, Ambrose JD, Kemp JR (1990) Cryptic dioecy and insect pollination in *Rosa setigera* Michx. (Rosaceae), a rare plant of Carolinian Canada. Biological Journal of the Linnean Society 40:229-243.

Kikuchi T (1962a) Studies on the coaction among insects on flowers. III. Dominance relationship among flower-visiting flies, bees and butterflies. Science Reports of Tohoku University Series IV (Biology) 29:1-8.

Kikuchi T (1962b) Studies on the coaction among insects visiting flowers. II. Dominance relationships in the so-called drone fly group. Scientific Reports of the Tohoku University, Section 4, Biology 28:47-51.

Kikuchi T (1962c) Studies on the coaction among insects visiting flowers. I. Ecological groups in insects visiting chrysanthemum flower, *Chrysanthemum leucanthemum*. Science Reports of Tohoku University Series IV (Biology) 28:17-22.

Kikuchi T (1963a) Studies on the coaction among insects visiting flowers. IV. Preferring behaviour of some syrphid flies, *Eristolomyia tenax*, *Eristalis cerealis*, and *Sphaerophoria cylindrica*, in relation to the age of the chrysanthemum flower, *Chrysanthemum leucanthemum*. Science Reports of Tohoku University Series IV (Biology) 29:9-14

Kikuchi T (1963b) Studies on the coaction among insects visiting flowers. V. Effects of the dominant insects on the density of the subordinate ones. Science Reports of Tohoku University Series IV (Biology) 29:107-115.

Kikuchi T (1964) Studies on the coaction among insects visiting flowers. VI. The distribution of the subordinate insects in one flower garden. Science Reports of Tohoku University Series IV (Biology) 30:143-149.

Kudo G (1993) Relationship between flowering time and fruit set of the entomophilous alpine shrub, *Rhododendron aureum* (Ericaceae), inhabiting snow patches. American Journal of Botany 80:1300-1304.

Kugler H (1950) Der Blütenbesuch der Schlammfliege (*Eristalomyia tenax*). Zeitschrift für vergleichende Physiologie 32:328-347.

Kumar J, Mishra RC, Gupta JK (1985) The effect of mode of pollination on *Allium* species with observation on insects as pollinators. Journal of Apicultural Research 24:62-66.

Lack AJ, Diaz A (1991) The pollination of *Arum maculatum* L. - a historical review and new observations. Watsonia 18:333-342.

Langridge DF, Goodman RD (1975) A study on pollination of oilseed rape (*Brassica campestris*). Australian Journal of Experimental Animal Husbandry 15:285-288.

Larson BMH, Kevan PG, Inouye DW (2001) Flies and flowers: taxonomic diversity of anthophiles and pollinators. Canadian Entomologist 133:439-465.

Lee TN, Snow AA (1998) Pollinator preferences and the persistence of crop genes in wild radish populations (*Raphanus raphanistrum*, Brassicaceae). American Journal of Botany 85:333-339.

Leereveld H (1982) Anthecological relations between reputedly anemophilous flowers and syrphid flies. III. Worldwide survey of crop and intestine contents of certain anthophilous syrphid flies. Tijdschrift voor Entomologie 125:25-35.

Leereveld H, Meeuse ADJ, Stelleman P (1976) Anthecological relations between reputedly anemophilous flowers and syrphid flies. II. *Plantago media* L. Acta Botanica Neerlandica 25:205-211.

Leereveld H, Meeuse ADJ, Stelleman P (1981) Anthecological relations between reputedly anemophilous flowers and syrphid flies. IV. A note on the anthecology of *Scirpus maritimus* L. Acta Botanica Neerlandica 30:465-473.

Leereveld H, Meeuse ADJ, Stelleman P (1991) Some cases of visiting of anemophiles by syrphid flies in Madagascar. Israel Journal of Botany 40:219-223.

Levesque CM, Burger JF (1982) Insects (Diptera, Hymenoptera) associated with *Minuartia groenlandica* (Caryophyllaceae) on Mount Washington, New Hampshire, U.S.A. and their possible role as pollinators. Arctic and Alpine Research 14:117-124.

Li P, Pemberton R, Zheng G, Luo Y (2012) Fly pollination in *Cypripedium*: a case study of sympatric *C. sichuanense* and *C. micranthum*. Botanical Journal of the Linnean Society 170:50-58.

Lindsey AH (1984) Reproductive biology of Apiaceae. I. Floral visitors to *Thaspium* and *Zizia* and their importance in pollination. American Journal of Botany 71:375-387.

Lunau K (1993a) Angeborne und erlernte Blütenerkennung bei Insekten. Ein entdecktes Geheimnis der Natur. Biologie in unserer Zeit 23:48-54.

Lunau K (1993b) Interspecific diversity and uniformity of flower colour patterns as cues for learned discrimination and innate detection of flowers. Experientia 49:1002-1010.

Lunau K (2000) The ecology and evolution of visual pollen signals. Plant Systematics and Evolution 222:89-111.

Lunau K, Hofmann N, Valentin S (2005) Response of the hoverfly species *Eristalis tenax* towards floral dot guides with colour transition from red to yellow (Diptera: Syrphidae). Entomologia Generalis 27:249-256.

Lunau K, Wacht S (1994) Optical releasers of the innate proboscis extension in the hoverfly *Eristalis tenax* L. (Syrphidae, Diptera). Journal of Comparative Physiology A 174:575-579.

Magnarelli LA, Anderson JF (1977) Follicular development in salt marsh Tabanidae (Diptera) and incidence of nectar feeding with relation to gonotrophic activity. Annals of the Entomological Society of America 70:529-533.

Magnarelli LA, Anderson JF, Thorne JH (1979) Diurnal nectar-feeding of salt marsh Tabanidae (Diptera). Environmental Entomology 8:544-548.

Maier CT, Waldbauer GP (1979a) Diurnal activity patterns of flower flies (Diptera: Syrphidae) in an Illinois sand area. Annals of the Entomological Society of America 72:237-245.

Maier CT, Waldbauer GP (1979b) Dual mate-seeking strategies in male syrphid flies (Diptera: Syrphidae). Annals of the Entomological Society of America 72:54-61.

McCall C, Primack RB (1992) Influence of flower characteristics, weather, time of day, and season on insect visitation rates in three plant communities. American Journal of Botany 79:434-442.

McGonigle DF, Jackson CW (2002) Effect of surface material on electrostatic charging of houseflies (*Musca domestica* L.). Pest Management Science 58:374-380.

McGuire AD, Armbruster WS (1991) An experimental test for reproductive interactions between two sequentially blooming *Saxifraga* species (Saxifragaceae). American Journal of Botany 78:214-219.

Mesler M, Ackerman JD, Lu KL (1980) The effectiveness of fungus gnats as pollinators. American Journal of Botany 67:564-567.

Mesler MR (1977) Notes on the floral biology of *Plantago* in Michigan. Michigan Botanist 16:73-82.

Meve U, Liede S (1994) Floral biology and pollination in stapeliads - New results and a literature review. Plant Systematics and Evolution 192:99-116.

Morse DH (1981) Interactions among syrphid flies and bumblebees on flowers. Ecology 62:81-88.

Motten AF (1986) Pollination ecology of the spring wildflower community of a temperate deciduous forest. Ecological Monographs 56:21-42.

Motten AF, Campbell DR, Alexander DE, Miller HL (1981) Pollination effectiveness of specialist and generalist visitors to a North Carolina population of *Claytonia virginica*. Ecology 62:1278-1287.

Nicolson SW (1994) Pollen feeding in the eucalypt nectar fly, *Drosophila flavohirta*. Physiological Entomology 19:58-60.

Nilsson LA (1981) The pollination ecology of *Listera ovata* (Orchidaceae). Nordic Journal of Botany 1:461-480.

Nilsson LA, Jonsson L, Rason L, Randrianjohany E (1985) Pollination of *Plectranthus vestitus* (Lamiaceae) by trap-lining hovering bees in Madagascar. Plant Systematics and Evolution 150:223-236.

Nye WP, Anderson JL (1974) Insect pollinators frequenting strawberry blossoms and the effect of honey bees on yield and fruit quality. Journal of the American Society of Horticultural Science 99:40-44.

O'Brien MH (1980) The pollination biology of a pavement plain: Pollinator visitation patterns. Oecologia 47:213-218.

Olesen JM, Warncke E (1989a) Flowering and seasonal changes in flower sex ratio and frequency of flower visitors in a population of *Saxifraga hirculus*. Holarctic Ecology 12:21-30.

Olesen JM, Warncke E (1989b) Predation and potential transfer of pollen in a population of *Saxifraga hirculus*. Holarctic Ecology 12:87-95.

Olesen JM, Warncke E (1989c) Temporal changes in pollen flow and neighbourhood structure in a population of *Saxifraga hirculus* L. Oecologia 79:205-211.

Pansarin ER (2008) Reproductive biology and pollination of *Govenia utriculata*: A syrphid fly orchid pollinated through a pollen-deceptive mechanism. Plant Species Biology 23:90-96.

Patt JM, French JC, Schal C, Lech J, Hartman TG (1995) The pollination biology of Tuckahoe, *Peltandra virginica* (Araceae). American Journal of Botany 82:1230-1240.

Patt JM, Merchant MW, Williams DRE, Meeuse BJD (1989) Pollination biology of *Platanthera stricta* (Orchidaceae) in Olympic National Park, Washington. American Journal of Botany 76:1097-1106.

Pijl L, van der, Dodson CH (1966) Orchid flowers: their pollination and evolution. University of Miami Press, Coral Gables.

Pont AC (1993) Observations on anthophilous Muscidae and other Diptera (Insecta) in Abisko National Park, Sweden. Journal of Natural History 27:631-643.

Potgieter CJ, Edwards TJ, Miller RM, van Staden J (1999) Pollination of seven *Plectranthus* spp. (Lamiaceae) in southern Natal, South Africa. Plant Systematics and Evolution 218:99-112.

Primack RB (1978) Variability in New Zealand montane and alpine pollinator assemblages. New Zealand Journal of Ecology 1:66-73.

Primack RB (1983) Insect pollination in the New Zealand mountain flora. New Zealand Journal of Botany 21:317-333.

Pyke GH (1978a) Are animals efficient harvesters? Animal Behaviour 26:241-250.

Pyke GH (1978b) Optimal foraging: movement patterns of bumblebees between inflorescences. Theoretical Population Biology 13:72-98.

Rader R, Howlett BG, Cunningham SA, Westcott DA, Edwards W (2012) Spatial and temporal variation in pollinator effectiveness: do unmanaged insects provide consistent pollination services to mass flowering crops? Journal of Applied Ecology 49:126-134.

Rader R et al. (2009) Alternative pollinator taxa are equally efficient but not as effective as the honeybee in a mass flowering crop. Journal of Applied Ecology 46:1080-1087.

Raymond L, Plantegenest M, Vialatte A (2013) Migration and dispersal may drive to high genetic variation and significant genetic mixing: the case of two agriculturally important, continental hoverflies (*Episyrphus balteatus* and *Sphaerophoria scripta*). Molecular Ecology 22:5329-5339.

Raymond L, Vialatte A, Plantegenest M (2014) Combination of morphometric and isotopic tools for studying spring migration dynamics in *Episyrphus balteatus*. Ecosphere 5:art88.

Reader T, MacLeod I, Elliott PT, Robinson OJ, Manica A (2005) Inter-order interactions between flower-visiting insects: Foraging bees avoid flowers previously visited by hoverflies. Journal of Insect Behavior 18:51-57.

Ren Z-X, Li D-Z, Bernhardt P, Wang H (2011) Flowers of *Cypripedium fargesii* (Orchidaceae) fool flat-footed flies (Platypezidae) by faking fungus-infected foliage. Proceedings of the National Academy of Sciences 108(18): 7478–7480.

Robertson AW (1992) The relationship between floral display size, pollen carryover and geitonogamy in *Myosotis colensoi* (Kirk) Macbride (Boraginaceae). Biological Journal of the Linnean Society 46:333-349.

Robertson AW, Macnair MR (1995) The effects of floral display size on pollinator service to individual flowers of *Myosotis* and *Mimulus*. Oikos 72:106-114.

Romero GQ, Antiqueira PAP, Koricheva J (2011) A meta-analysis of predation risk effects on pollinator behaviour. PLoS ONE 6:e20689.

Rotheray GE, Gilbert F (2011) The Natural History of Hoverflies. Forrest Text, Ceredigion, UK.

Roubik DW (ed) (1995) Pollination of cultivated plants in the tropics. Food and Agriculture Organization of the United Nations, Rome.

Roy BA (1994) The effects of pathogen-induced pseudoflowers and buttercups on each other's insect visitation. Ecology 75:352-358.

Sandholm HA, Price RD (1962) Field observations on the nectar-feeding habits of some Minnesota mosquitoes. Mosquito News 22:346-349.

Schmitt J (1983) Density-dependent pollinator foraging, flowering phenology, and temporal pollen dispersal patterns in *Linanthus bicolor*. Evolution 37:1247-1257.

Schneider F (1958) Künstliche Blumen zum Nachweis von Winterquartieren, Futterpflanzen und Tageswanderungen von *Lasiopticus pyrastri* (L.) und anderen Schwebfliegen (Syrphidae Dipt.). Mitteilungen der Schweizerischen entomologischen Gesellschaft 31:1-24.

Schneider F (1969) Bionomics and physiology of aphidophagous Syrphidae. Annual Review of Entomology 14:103-124.

Shaw DC, Taylor RJ (1986) Pollination ecology of an alpine fell-field community in the North Cascades. Northwest Science 60:21-31.

Smith BM, Mee C (1984) Seed multiplication of brussels sprout inbred lines. Zeitschrift für Pflanzenzüchtung 92:259-262.

Srinivasan MV, Guy RG (1990) Spectral properties of movement perception in the dronefly *Eristalis*. Journal of Comparative Physiology A 166:287-295.

Ssymank A (1989) Das Vegetationsmosaik eines Waldgebietes der Schwarzwaldvorbergzone und seine funktionale Bedeutung für blütenbesuchende Insekten - unter besonderer Berücksichtigung der Syrphidae (Diptera) [Dissertation], Universität Freiburg, Freiburg (Breisgau).

Ssymank A (1991) Die funktionale Bedeutung des Vegetationsmosaiks eines Waldgebietes der Schwarzwaldvorbergzone für blütenbesuchende Insekten - untersucht am Beispiel der Schwebfliegen (Diptera, Syrphidae). Phytocoenologia 19:307-390.

Ssymank A (2001) Vegetation und blütenbesuchende Insekten in der Kulturlandschaft. – Pflanzengesellschaften, Blühphänologie, Biotopbindung und Raumnutzung von Schwebfliegen (Diptera, Syrphidae) im Drachenfelser Ländchen sowie Methodenoptimierung und Landschaftsbewertung. - Tierwelt in der Zivilisationslandschaft, Teil V Schriftenreihe für Landschaftspflege und Naturschutz, vol. 5, pp 1-513.

Ssymank A (2003) Habitatnutzung blütenbesuchender Schwebfliegen (Diptera, Syrphidae) in Wald-Offenland-Vegetationsmosaiken. Berichte der Reinhold-Tüxen-Gesellschaft 15:215-228.

Ssymank A, Hamm A, Vischer-Leopold M (2009) Caring for Pollinators. Safeguarding agro-biodiversity and wild plant diversity. - Results of a workshop and research project commissioned by the German Federal Agency for Nature Conservation BfN-Skripten, vol. 250. Bundesamt für Naturschutz, Bonn, pp 1-191.

Ssymank A, Kearns CA, Pape T, Thompson FC (2008) Pollinating flies (Diptera): A major contribution to plant diversity and agricultural production. Biodiversity Issues 9:86-89.

Stanton ML (1987) Reproductive biology of petal color variants in wild populations of *Raphanus sativus*: I. Pollinator response to color morphs. American Journal of Botany 74:178-187.

Stelleman P (1984) Reflections on the transition from wind pollination to ambophily. Acta Botanica Neerlandica 33:497-508.

Stelleman P, Meeuse ADJ (1976) Anthecological relationships between reputedly anemophilous flowers and syrphid flies I. The possible role of syrphid flies as pollinators of *Plantago*. Tijdschrift voor Entomologie 119:15-31.

Stensmyr MC, Urru I, Collu I, Celander M, Hansson BS, Angioy A-M (2002) Rotting smell of dead-horse arum florets. Nature 420:625-626.

Sutherland JP, Sullivan MS, Poppy GM (1999) The influence of floral character on the foraging behaviour of the hoverfly, *Episyrphus balteatus*. Entomologia Experimentalis et Applicata 93:157-164.

Taroda N, Gibbs PE (1982) Floral biology and breeding system of *Sterculia chicha* St. Hil. (Sterculiaceae). New Phytologist 90:735-743.

Thien LB, Utech F (1970) The mode of pollination in *Habenaria obtusata* (Orchidaceae). American Journal of Botany 57:1031-1035.

Thomson JD (2010) Flowering phenology, fruiting success and progressive deterioration of pollination in an early-flowering geophyte. Philosophical Transactions of the Royal Society B: Biological Sciences 365:3187-3199.

Toft CA (1983) Community patterns of nectivorous adult parasitoids (Diptera, Bombyliidae) on their resources. Oecologia 57:200-215.

Toft CA (1984) Resource shifts in bee flies (Bombyliidae): interactions among species determine choice of resources. Oikos 43:104-112.

van der Niet T, Hansen DM, Johnson SD (2011) Carrion mimicry in a South African orchid: flowers attract a narrow subset of the fly assemblage on animal carcasses. Ann Bot 107:981-992.

Vogt CA (1990) Pollination in *Cypripedium reginae* (Orchidaceae). Lindleyana 5:145-150.

Waldbauer GP (1963) Crepuscular flower visits of adult *Volucella vesicularia* Curran (Diptera, Syrphidae). Entomological News 74:135-137.

Waldbauer GP (1984) Mating behavior at blossoms and the flower associations of mimetic *Temnostoma* spp. (Diptera: Syrphidae) in northern Michigan. Proceedings of the Entomological Society of Washington 96:295-304.

Wang J, Ma Y-X, Cui D-L, Wang R-X, Lu Y-Y, Qin J (2011) An observation on pollinating insects and their flower-visiting behavior on *Fatsia japonica*. Chinese Journal of Applied Entomology 2011-03.

Warmke HE (1952) Studies on natural pollination of *Hevea brasiliensis* in Brazil. Science 116:474-475.

Warncke E, Terndrup U, Michelsen V, Erhardt A (1993) Flower visitors to *Saxifraga hirculus* in Switzerland and Denmark, a comparative study. Botanica Helvetica 103:141-147.

Wellington WG, Fitzpatrick SM (1981) Territoriality in the drone fly, *Eristalis tenax* (Diptera: Syrphidae). Canadian Entomologist 113:695-704.

Wickramaratne MRT, Vitarana SI (1985) Insect pollination of tea (*Camellia sinensis* L.) in Sri Lanka. Tropical Agriculture 62:243-247.

Willmer PG (1982a) Hygrothermal determinants of insect activity patterns: the Diptera of water-lily leaves. Ecological Entomology 7:221-231.

Willmer PG (1982b) Thermoregulatory mechanisms in *Sarcophaga*. Oecologia 53:382-385.

Willmer PG (1983) Thermal constraints on activity patterns in nectar-feeding insects. Ecological Entomology 8:455-469.

Willmer PG, Unwin DM (1981) Field analyses of insect heat budgets: reflectance, size and heating rates. Oecologia 50:250-255.

Wilson BH, Lieux M (1972) Pollen grains in the guts of field collected tabanids in Louisiana. Annals of the Entomological Society of America 65:1264-1266.

Winder JA (1977) Field observations on Ceratopogonidae and other Diptera: Nematocera associated with cocoa flowers in Brazil. Bulletin of Entomological Research 67:57-63.

Winder JA (1978) Cocoa flower Diptera; their identity, pollinating ability and breeding sites. Pans [International Journal of Pest Management] 24:5-18.

Wirth L et al. (2011) Effects of floral neighborhood on seed set and degree of outbreeding in a high-alpine cushion plant. Oecologia 167:427-434.

Wolda H, Sabrosky CW (1986) Insect visitors to two forms of *Aristolochia pilosa* in Las Cumbres, Panama. Biotropica 18:295-299.

Woodcock TS, Larson BMH, Kevan PG, Inouye DW, Lunau K (2014) Flies and flowers II: Floral rewards and attractants. Journal of Pollination Ecology 12:63-94.

Yafuso M (1993) Thermogenesis of *Alocasia odora* (Araceae) and the role of *Colocasiomyia* Flies (Diptera, Drosophilidae) as cross-pollinators. Environmental Entomology 22:601-606.

Young AM (1984) Mechanism of pollination by Phoridae (Diptera) in some *Herrania* species (Sterculiaceae) in Costa Rica. Proceedings of the Entomological Society of Washington 86:503-518.

Young AM (1985) Studies of cecidomyiid midges (Diptera: Cecidomyiidae) as cocoa pollinators (*Theobroma cacao*) in Central America. Proceedings of the Entomological Society of Washington 87:49-79.

Zheng G, Li P, Pemberton R, Luo Y (2011) Mixed bumblebee and blowfly pollination of *Cypripedium flavum* (Orchidaceae) in Sichuan, China. Ecological Research 26:453-459.

Zietsman PC (1990) Pollination of *Ziziphus mucronata* subsp. *mucronata* (Rhamnaceae). Journal of South African Botany 56:350-355.