

## FLIES AND FLOWERS II: FLORAL ATTRACTANTS AND REWARDS

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*Abstract*—This paper comprises Part II of a review of flower visitation and pollination by Diptera (myiophily or myophily). While Part I examined taxonomic diversity of anthophilous flies, here we consider the rewards and attractants used by flowers to procure visits by flies, and their importance in the lives of flies. Food rewards such as pollen and nectar are the primary reasons for flower visits, but there is also a diversity of non-nutritive rewards such as brood sites, shelter, and places of congregation. Floral attractants are the visual and chemical cues used by Diptera to locate flowers and the rewards that they offer, and we show how they act to increase the probability of floral visitation. Lastly, we discuss the various ways in which flowers manipulate the behaviour of flies, deceiving them to visit flowers that do not provide the advertised reward, and how some flies illegitimately remove floral rewards without causing pollination. Our review demonstrates that myiophily is a syndrome corresponding to elements of anatomical, behavioural and physiological adaptations of flower-visiting Diptera. The bewildering diversity of anthophilous Diptera and of the floral attractants and rewards to which they respond allows for only broad generalizations on myiophily and points to the need for more investigation. Ecological relationships between flies and flowers are critical to the survival of each group in many habitats. We require greater understanding of the significance of flies in pollination, especially in the face of recent pollinator declines.

*Keywords:* Diptera, fly pollination, flower visit, mutualism, ecological interaction, alternative pollinators

### INTRODUCTION

Pollination by insects, including flies, is commonly a mutualistic interaction, in which both the plant and the insect benefit. The plant receives self or outcross pollen on receptive stigmas and/or exports pollen to a conspecific plant's stigmas, and the insect gains a nutritional or other reward. The most often sought visitor rewards are nectar, which fuels flight and may contain a variety of compounds in addition to sugars, and to a lesser extent pollen, an important protein resource, but there are also various non-nutritive rewards. Flowers are able to signal their presence at both long and short distances, and to guide the movements of visitors, using a variety of attractants. Over evolutionary time, animal and flower interactions have produced plants with visual, chemical, and other traits that entice pollinators to visit conspecific flowers. Conversely, animal visitors, such as flies, have behavioural, physiological, and morphological traits that facilitate their interactions with flowers. And, as with any mutualistic interaction, there are plenty of opportunities for deception and cheating on both sides.

Despite the frequency with which Diptera are recorded as flower visitors, relatively little is known about fly pollination (myophily or myiophily) compared to other groups of pollinators such as bees, birds, and bats. We do know that numerous families of Diptera include flower

visitors, with examples of the most common including Mycetophilidae, Bibionidae, and Culicidae (Nematocera); Syrphidae, Bombyliidae, Conopidae, Stratiomyidae, and Nemestrinidae (lower Brachycera); and among the higher Brachycera (Cyclorrhapha), the Muscidae, Anthomyiidae, Tachinidae, Calliphoridae, and others (Kastinger & Weber 2001; Larson et al. 2001; Rotheray & Gilbert 2011). Floral visitation by small Diptera, including acalyptrates, has often been discounted as unimportant in pollination, and in many cases empirical confirmation of successful pollination is lacking (Larson et al. 2001; Willmer 2011). However, Diptera can be highly important pollinators in some systems (e.g. Ssymank et al. 2008; Barraclough & Slotow 2010), and may also be important in the reproduction of certain threatened and endangered plants (e.g., Wiesenborn 2003; Murugan et al. 2006; Humeau et al. 2011). We have previously reviewed the importance of Diptera as pollinators (Larson et al. 2001), and in this paper we turn to reviewing what is known about the attractants and rewards that entice Diptera to visit flowers. We have separated floral rewards (“primary attractants” of Faegri & van der Pijl (1979)) from advertisements (“secondary attractants” of Faegri & van der Pijl (1979) or simply “attractants” of many anthecologists), and discuss them in that order. Rewards are the main attractants for flower visiting insects and include pollen and nectar, whereas advertisements are visual, chemical, or structural cues that provide information to potential pollinators about location of and access to floral rewards. The final section of the paper will discuss the numerous types and examples of cheating by both sides in the fly-flower relationship, in which flies obtain rewards without

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effecting pollination and flowers may attract visitors by advertising rewards that do not exist.

### REWARDS FOR FORAGING FLIES

The Diptera are among the most ancient pollinators of flowering plants (Gottsberger 1974; Crepet 1979; Bernhardt & Thien 1987; Kato & Inoue 1994; Labandeira 1998), primarily visiting flowers to procure highly nutritious nectar or pollen (Faegri & van der Pijl 1979; Simpson & Neff 1981; Larson et al. 2001). As the onset of diversification in Diptera predates angiosperm diversification (Grimaldi 1999), it is likely that adaptation to flower visitation evolved independently in different lines of Diptera. Pollen grains (or microspores) are essential to terrestrial plant reproduction and probably were an original reward and attractant for spore-vectoring and pollinating insects (Kevan et al. 1975; Kevan & Baker 1983; Willemstein 1987). Nevertheless, pollination droplets of sugary liquids, such as those from the sexual structures of various ancient plants, may have been consumed by insects prior to the evolution of the Angiospermae (Taylor 1981; Wetschnig & Depisch 1999; Ren et al. 2009). Diptera and Hymenoptera, with mouthparts appropriate to imbibing liquids, are known from the fossil record during this period, and may have sought those sugary liquids (Labandeira 1997; Krenn et al. 2005). Regardless of the reproductive importance of nectar in ancient plants, production of floral nectar throughout the angiosperms is indicative of its value and it is now the foremost reward for many pollinators (Kevan & Baker 1983, 1999), including a diverse array of Diptera (Larson et al. 2001). In addition to pollen and nectar rewards, flowers attract Diptera of both sexes and so may be mating sites, or they may function as sites for predatory flies to await prey. Flowers may also give protection from predators and inclement weather, or provide brood places for larvae. The warmth generated or concentrated by some flowers may act as a secondary attractant, but may be more important for its physiological effects on anthophiles, so we consider it a reward.

#### *Primary floral rewards - Nectar*

Nectar is the most commonly sought reward by flower-visiting flies (Tab. I). It is predominately a source of carbohydrates, most commonly containing the disaccharide sucrose and the hexose sugars glucose and fructose. Nectar can also contain other sugars, various amino acids, proteins, lipids and vitamins (Baker & Baker 1973a, b, 1983a). Nectar constituents and concentrations are often adapted to the desired group of pollinators. Nectars with a preponderance of sucrose, for example, are taken mostly by long-tongued Diptera (e.g., Goldblatt et al. 1997). The nectar used by most flies (short-tongued or lapping) is characteristically hexose-rich and of relatively high (but variable) sugar concentration (Percival 1965; Baker & Baker 1983b; Kevan & Baker 1999). The sugars in nectar may crystallize, but many generalist flies are able to re-liquify the nectar with saliva and then imbibe it (Elton 1966; Baker & Baker 1983a; Willmer 2011), as is also reported for Diptera feeding on honeydew (Downes & Dahlem 1987).

Both sexes of most flies use the carbohydrates in nectar for short-term energy needs (Hocking 1953; Downes 1955; Downes & Smith 1969), especially during periods of peak activity such as swarming, mating and oviposition, dispersal, and migration (Kevan 1973; Haslett 1989a, Service 1997; Branquart & Hemptinne 2000; Willmer 2011). In female mosquitoes, at least, nectar feeding and blood feeding are antagonistic and mutually exclusive, but little is known about how such insects choose which resource to pursue (Foster 1995). Vrzal et al. (2010) found that female mosquitoes can acquire appreciable quantities of amino acids from nectar, increasing longevity and possibly decreasing the need for a blood meal. Rather than consuming nectar, David et al. (2011) reported *Drosophila suma* scarifying the floral tissues of *Ipomoea* and *Crinum* with spiny fore tarsi adapted to the purpose and consuming the forthcoming liquid.

It is surprising that there is little information on the importance of micro-nutrients in the physiology of Diptera; even economically important Diptera have not been rigorously studied. Numerous authors have indicated that nectars can contain amino acids (Baker & Baker 1973a, b, 1983a, b, 1986; Kevan & Baker 1983, 1999; Potter & Bertin 1988; Rathman et al. 1990; Gardener & Gillman 2002; Vrzal et al. 2010), but experimental evidence for an adaptive role of amino acids in the attraction and nutrition of pollinators is sparse. Nectar availability can increase insects' life spans (Nayar & Sauerman 1971; Grimstad & DeFoliart 1974; Kevan & Baker 1983; Vrzal et al. 2010), presumably due to the presence of minor nutrients (Haslett 1989a). *Stomoxys calcitrans* (L.) (Muscidae) fed dilute honey lived longer than those fed sugar syrup (Jones et al. 1992). Rathman et al. (1990) found that *Sarcophaga bullata* Parker (Sarcophagidae) chose an amino acid-containing nectar over a sucrose-only nectar only when protein deprived and previously without access to protein or amino acid sources. This suggests a nutritional role for the amino acids in nectar, especially for reproductive females and when other protein rich foods are scarce (Vrzal et al. 2010). Foraging flies that have nectar as their primary source of protein-building amino acids feed from flowers with higher concentrations of amino acids than do those that have alternative protein sources (e.g., pollen) (Baker & Baker 1983a, 1986).

The possible benefits to Diptera of other nectar constituents, such as lipids, antioxidants and proteins, are also not well understood. Lipids are common in the nectar of flowers visited by flies, which presumably have digestive lipases or esterases to break them down (Dadd 1973; Chapman 1998; Kevan & Baker 1999). Dethier's classic book (1976) makes little mention of lipids in the diets of flies. Lipids likely provide energy as polyunsaturated fatty acids, or have a role in hormonal biosynthesis as sterols (Downer 1978). Reports on Diptera feeding on lipid-rich floral tissues invoke special floral structures (Dafni & Werker 1982; Aronne et al. 1993). Antioxidants such as organic "reducing" acids (ascorbic acid) are often found in lipidic nectars, where they may help to delay rancidity (Baker & Baker 1983a). Nectar may also contain small quantities of vitamins and minerals (Baker & Baker 1983a) and these too may play roles in dipteran nutrition. Various salts have phagostimulative effects and may be available as a reward in

TABLE I. Selected records of fly consumption of edible rewards offered by the reproductive organs of selected angiosperms.

Plant Family	Plant Taxon	Reward(s)*				Fly Taxon**	Reference
		FN	PO	EX	MS		
Acanthaceae	<i>Justicia americana</i> (L.)	-	+	-	-	Syrphidae, Bombyliidae, Conopidae	Robertson 1928
Aceraceae	<i>Acer</i> spp.	-	+	-	-	<i>Eristalis tenax</i> (L.), <i>Orthonevra nitida</i> Wd. (Syrphidae)	Haslett 1989b
Alismaceae	<i>Sagittaria latifolia</i> (Willd.)	-	+	-	-	various	Robertson 1928
Amaryllidaceae	<i>Sternbergia clusiana</i> (Ker-Gawler) Spreng.	-	-	+	-	various (PC)	Dafni & Werker 1982
Anacardiaceae	<i>Rhus glabra</i> L.	-	+	-	-	<i>Anthrax sinuosa</i> Wd. (Bombyliidae)	Robertson 1928
Apiaceae	<i>Angelica sylvestris</i> L.	-	+	-	-	<i>Episyrphus balteatus</i> (De Geer) (Syrphidae)	Haslett 1989b
Apocynaceae	<i>Apocynum androsaemifolium</i> L.	+	-	-	-	<i>Aedes vexans</i> (Meigen) (Culicidae)	Sandholm & Price 1962
Araceae	<i>Amorphophallus</i> spp.	-	-	+	-	Drosophilidae, Muscidae, Calliphoridae	Punekar & Kumaran 2010
Araliaceae	<i>Fatsia japonica</i> (Thunb.) Dcne. et Planch	+	+	-	-	<i>Scaeva pyrastris</i> (L.) (Syrphidae), <i>Chrysomya megacephala</i> (Fabricius) (Calliphoridae)	Wang et al. 2011
Aristolochiaceae	<i>Aristolochia inflata</i> Kunth	+	-	-	-	<i>Megaselia sakaiae</i> Disney (Phoridae)	Sakai 2002a,b
Asclepiadaceae	<i>Asclepias syriaca</i> L.	+	-	-	-	<i>Aedes dorsalis</i> (Meigen) (Culicidae)	Sandholm & Price 1962
Asteraceae	<i>Achillea millefolium</i> L.	-	+	-	-	<i>Anthomyia sulciventris</i> Ztt. (Anthomyiidae)	Willis & Burkhill 1895
Brassicaceae	<i>Lobularia maritima</i> (L.) Desv.	-	+	-	-	<i>Eupeodes corolla</i> F. (Syrphidae)	Pérez-Bañón et al. 2003
Campanulaceae	<i>Campanula rotundifolia</i> L.	+	+	-	-	<i>Thricops cunctans</i> Meigen (Muscidae)	Pont 1993
	<i>Wahlenbergia albomarginata</i> Hook.	-	+	-	-	<i>Allograpta</i> sp. (Syrphidae) (PC)	Bischoff et al. 2013
Caprifoliaceae	<i>Lonicera periclymenum</i> L.	-	+	-	-	<i>Episyrphus balteatus</i> (De Geer) (Syrphidae)	Haslett 1989b
Caryophyllaceae	<i>Silene dioica</i> L. (Clairville)	-	+	-	-	<i>Rhingia campestris</i> Meigen (Syrphidae)	Haslett 1989b
Chenopodiaceae	<i>Chenopodium album</i> L.	-	+	-	-	<i>Melanostoma fasciatum</i> (Macquart) (Syrphidae)	Hickman et al. 1995
Cistaceae	<i>Helianthemum nummularium</i> (L.) Mill.	-	+	-	-	<i>Anthomyia radicum</i> L. (Anthomyiidae)	Willis & Burkhill 1895
Commelinaceae	<i>Cuthbertia rosea</i> Ventnat	-	+	-	-	<i>Poecilognathus punctipennis</i> Walker (Bombyliidae)	Deyrup 1988
Convolvulaceae	<i>Convolvulus arvensis</i> L.	-	+	-	-	<i>Melanostoma mellinum</i> L. (Syrphidae)	van der Goot & Grabandt 1970
Cornaceae	<i>Cornus stolonifera</i> Michx.	+	-	-	-	<i>Aedes cinereus</i> (Meigen) (Culicidae)	Sandholm & Price 1962
Corylaceae	<i>Corylus</i> sp.	-	+	-	-	<i>Melangyna quadrimaculata</i> Verrall (Syrphidae)	Stubbs & Chandler 1978
Crassulaceae	<i>Sedum</i> sp.	-	+	-	-	<i>Melanostoma novaezelandae</i> Macquart (Syrphidae)	Irvin et al. 1999
Cyperaceae	<i>Scirpus maritimus</i> (L.) Lye	-	+	-	-	<i>Melanostoma mellinum</i> L. (Syrphidae)	Leereveld 1984
Dilleniaceae	<i>Hibbertia scandens</i> (Willd.) Dryand.	-	+	-	-	<i>Melangyna viridiceps</i> Macquart (Syrphidae)	Armstrong 1979
Dipsacaceae	<i>Scabiosa succisa</i> L.	+	+	-	-	<i>Calliphora erythrocephala</i> Mg. (Calliphoridae)	Willis & Burkhill 1895
Droseraceae	<i>Drosera</i> c.f. <i>binata</i>	-	+	-	-	<i>Paragus</i> sp. (Syrphidae)	Holloway 1976
Ebenaceae	<i>Diospyros virginiana</i> L.	-	+	-	-	<i>Allograpta obliqua</i> Say (Syrphidae)	Robertson 1928

TABLE I. continued

Plant Family	Plant Taxon	Reward(s)*				Fly Taxon**	Reference
		FN	PO	EX	MS		
Elaeagnaceae	<i>Hippophae rhamnoides</i> L.	-	+	-	-	<i>Melangyna lasiophthalma</i> Zetterstedt (Syrphidae)	Ssymank & Gilbert 1993
Ericaceae	<i>Calluna vulgaris</i> (L.)	-	+	-	-	<i>Eriozona syrphoides</i> (Fall.) (Syrphidae)	Haslett & Entwistle 1980
Escalloniaceae	<i>Quintinia</i> sp.	-	+	-	-	<i>Eristalis tenax</i> (Linnaeus) (Syrphidae)	Holloway 1976
Euphorbiaceae	<i>Euphorbia amygdaloides</i> L.	-	+	-	-	<i>Empis tessellata</i> F. (Empididae)	Hobby & Smith 1961
Fabaceae	<i>Lathyrus pratensis</i> L.	-	+	-	-	<i>Episyrphus balteatus</i> (De Geer) (Syrphidae)	Haslett 1989b
Fagaceae	<i>Fagus sylvatica</i> L.	-	+	-	-	<i>Melangyna quadrimaculata</i> Verrall (Syrphidae)	Ssymank & Gilbert 1993
Gentianaceae	<i>Sebaea</i> sp.	-	+	-	-	<i>Paragus</i> sp. (Syrphidae)	Holloway 1976
Geraniaceae	<i>Geranium robertianum</i> L.	+	-	-	-	<i>Eulonchus sapphirinus</i> Osten Sacken (Acroceridae) (PC)	Borkent & Schlinger 2008
Hydrophyllaceae	<i>Pelargonium stipulaceum</i> (L.f.) Willd.	+	-	-	-	<i>Philoliche gulosa</i> Wiedemann (Tabanidae) (PC)	Combs & Pauw 2009
	<i>Ellisia nyctelea</i> (L.)	-	+	-	-	<i>Mesogramma geminate</i> Say (Syrphidae)	Robertson 1928
Hypericaceae	<i>Hypericum perforatum</i> L.	-	+	-	-	<i>Anthomyia radicum</i> L. (Anthomyiidae)	Willis & Burkhill 1895
Iridaceae	<i>Babiana</i> spp.	+	-	-	-	<i>Prosoeca</i> (Nemestrinidae) (PC)	Goldblatt & Manning 2007a
	<i>Gladiolus</i> spp.	+	-	-	-	<i>Philoliche</i> (Tabanidae), <i>Psilodera</i> (Acroceridae), Nemestrinidae (PC)	Goldblatt et al. 1997, 2001
	<i>Melasphaerula ramosa</i> (Burm. f.) N.E. Br	+	-	-	-	<i>Bibio longirostris</i> Rondani (Bibionidae) (PC)	Goldblatt et al. 2005
	<i>Romulea syringodeoflora</i> M.P de Vos	+	-	-	-	<i>Prosoeca</i> (Nemestrinidae) (PC)	Goldblatt & Manning 2007b
Lamiaceae	<i>Sisyrinchium vaginatum</i> Spreng.	-	+	-	-	<i>Toxomerus watsoni</i> , <i>Toxomerus</i> sp. (Syrphidae) (PC)	Freitas & Sazima 2003
	<i>Ajuga reptans</i> L.	+	-	-	-	<i>Bombylius major</i> L. (Bombyliidae)	Knight 1967
Liliaceae	<i>Lilium superbum</i> L.	+	-	-	-	<i>Aedes vexans</i> (Meigen) (Culicidae)	Sandholm & Price 1962
Linaceae	<i>Linum lewisii</i> Pursh.	+	-	-	-	<i>Thricops septentrionalis</i> Stein (Muscidae)	Kearns & Inouye 1994
Malvaceae	<i>Sterculia foetida</i> L.	+	-	-	-	<i>Chrysomya megacephala</i> (Fab.) (Calliphoridae) (PC)	Atluri et al. 2004
Molluginaceae	<i>Mollugo verticillata</i>	+	+	-	-	<i>Mesogramma marginata</i> (Syrphidae)	Robertson 1928
Myrtaceae	<i>Eucalyptus</i> spp.	+	+	-	-	<i>Drosophila flavohirta</i> Malloch (Drosophilidae) (PC)	Nicolson 1994
Nymphaeaceae	<i>Nymphaea odorata</i> ssp. <i>tuberosa</i> (Paine) Wiersema & Hellq.	-	+	-	-	<i>Helophilus latrifons</i> Lw. (Syrphidae)	Robertson 1928
Oleaceae	<i>Ligustrum vulgare</i> L.	-	+	-	-	<i>Volucella pellucens</i> L. (Syrphidae)	Haslett 1989b
Onagraceae	<i>Epilobium hirsutum</i> L.	-	+	-	-	<i>Eristalis tenax</i> L. (Syrphidae)	Haslett 1989b
Orchidaceae	<i>Disa scullyi</i> H. Bolus	+	-	-	-	<i>Prosoeca ganglbaueri</i> Lichtwardt (Nemestrinidae) (PC)	Johnson 2006
Plantaginaceae	<i>Plantago</i> sp.	-	+	-	-	<i>Pyrophaena granditarsa</i> Forst. (Syrphidae)	van der Goot & Grabandt 1970
	<i>Ourisia glandulosa</i> Hook. f.	-	+	-	-	<i>Allograpta</i> sp. (Syrphidae) (PC)	Bischoff et al. 2013
Plumbaginaceae	<i>Plumbago auriculata</i> (Lam.)	+	-	-	-	<i>Philoliche aethiopica</i> (Thunberg) (Tabanidae) (PC)	Ferrero et al. 2009
Poaceae	<i>Secale</i> sp.	-	+	-	-	<i>Platycheirus scambus</i> Staeger (Syrphidae)	Leereveld 1982

TABLE I. continued

Plant Family	Plant Taxon	Reward(s)*				Fly Taxon**	Reference
		FN	PO	EX	MS		
Polemoniaceae	<i>Phlox paniculata</i> L.	+	-	-	-	<i>Aedes dorsalis</i> (Meigen) (Culicidae)	Sandholm & Price 1962
Polygonaceae	<i>Polygonum</i> spp.	-	+	-	-	<i>Melanostoma novaezelandae</i> <i>Macquart</i> (Syrphidae)	Irvin et al. 1999
Portulacaceae	<i>Claytonia virginica</i> L.	+	+	-	-	<i>Bombylius major</i> L. (Bombyliidae)	Motten et al. 1981
Primulaceae	<i>Primula vulgaris</i> Huds.	-	+	-	-	<i>Hylemyia</i> sp. (Anthomyiidae)	Willis & Burkill 1903
Ranunculaceae	<i>Ranunculus repens</i> L.	-	+	-	-	<i>Eristalis tenax</i> Linnaeus (Syrphidae)	Haslett 1989b
Rhizophoraceae	<i>Avicennia officinalis</i> L.	+	+	-	-	<i>Chrysomya megacephala</i> Fabricius (Calliphoridae)	Aluri 1990
Rosaceae	<i>Rubus fruticosus</i> L.	-	+	-	-	<i>Episyrphus balteatus</i> (De Geer) (Syrphidae)	Haslett 1989b
Rubiaceae	<i>Galium trifidum</i> L.	+	-	-	-	<i>Sphaerophoria cylindrica</i> Say (Syrphidae)	Robertson 1928
Salicaceae	<i>Populus tremula</i> L.	-	+	-	-	<i>Melangyna lasiophthalma</i> Zetterstedt (Syrphidae)	Ssymank & Gilbert 1993
Santalaceae	<i>Osyris alba</i> L.	-	-	+	-	various (PC)	Aronne et al. 1993
Sarraceniacae	<i>Sarracenia purpurea</i> L.	+	+	-	-	<i>Fletcherimyia fletcheri</i> (Aldrich) (Sarcophagidae) (PC)	Ne'eman et al. 2006
Saxifragiaceae	<i>Tolmiea menziesii</i> (Pursh) Torr. & Gray	+	-	-	-	<i>Gnoriste megarrhina</i> Osten Sacken (Mycetophilidae) (PC)	Goldblatt et al. 2004
Schisandraceae	<i>Kadsura longipedunculata</i> Finet & Gagnepain	-	+	-	-	<i>Megommata</i> sp. (Cecidomyiidae) (PC)	Yuan et al. 2008; Thien et al. 2009
	<i>Schisandra henryi</i> Clarke	-	+	-	-	<i>Megommata</i> sp. (Cecidomyiidae) (PC)	Yuan et al. 2007; Thien et al. 2009
	<i>Schisandra spenantha</i> Rehder & E.H.Wilson	-	+	-	-	<i>Resseliella</i> sp. (Cecidomyiidae) (PC)	Du et al. 2012
Scrophulariaceae	<i>Hebe</i> sp.	-	+	-	-	<i>Melangyna ropalus</i> (Walker) (Syrphidae)	Holloway 1976
Solanaceae	<i>Solanum nigrum</i>	-	+	-	-	<i>Melanostoma mellinum</i> L. (Syrphidae)	van der Goot & Grabandt 1970
Sparganiaceae	<i>Sparganium erectum</i> L.	-	+	-	-	<i>Syrphus ribesii</i> L. (Syrphidae)	Leereveld 1984
Staphyleaceae	<i>Staphylea trifolia</i>	+	-	-	-	<i>Eristalis flavipes</i> Wk. (Syrphidae)	Robertson 1928
Stylidiaceae	<i>Forstera</i> sp.	-	+	-	-	<i>Paragus</i> sp. (Syrphidae)	Holloway 1976
Tiliaceae	<i>Tilia</i> sp.	-	+	-	-	<i>Xylota sylvarum</i> Linnaeus (Syrphidae)	Ssymank & Gilbert 1993
Trimeniaceae	<i>Trimenia moorei</i> (Oliv.) Philipson	-	+	-	-	<i>Melangyna</i> sp., <i>Triglyphus</i> <i>fulvicornis</i> Bigot (Syrphidae)	Bernhardt et al. 2003
Typhaceae	<i>Typha latifolia</i> L.	-	+	-	-	<i>Platycheirus peltata</i> Meigen (Syrphidae)	Leereveld 1982
Urticaceae	<i>Urtica dioica</i> L.	-	+	-	-	<i>Xylota sylvarum</i> Linnaeus (Syrphidae)	Ssymank & Gilbert 1993
Verbenaceae	<i>Verbena officinalis</i> L.	+	-	-	-	<i>Platycheirus</i> sp. (Syrphidae)	Willis & Burkill 1895
Violaceae	<i>Viola lutea</i> Smith	-	+	-	-	<i>Anthomyia</i> spp. (Anthomyiidae)	Willis & Burkill 1903
Welwitschiaceae	<i>Welwitschia mirabilis</i> Hook	-	-	-	+	Calliphoridae, Sarcophagidae, Ulidiidae (PC)	Wetschnig & Depisch 1999
Winteraceae	<i>Pseudowintera colorata</i> (Raoul) Dandy	-	-	+	-	<i>Smittia</i> (Chironomidae)	Lloyd & Wells 1992
Variety of plants		+	+	-	-	<i>Atrichopogon pollenivorus</i> Downes (Ceratopogonidae)	Downes 1955; De Meillon & Wirth 1989
		+	+	-	-	<i>Anthalia</i> spp. (Empididae)	Downes & Smith 1969

\* FN = Floral nectar; EX = Exudates, stigmatic or otherwise, MS = Micropylar secretions, PO = Pollen

\*\* PC = pollination confirmed

the nectar of some flowers (Waller et al. 1972; Dethier 1976). However, high concentrations of salt in solution are rejected by *Eristalis tenax* (L.), possibly because they inhibit the water detection cells of the labial taste sensilla (Wacht et al. 2000).

### Primary floral rewards - Pollen

Pollen is another resource consumed by some fly families (Tab. 1). Larvae of some flower-brooding flies may feed directly on pollen during their development (Gao 2011). Females of most biting Culicidae, Simuliidae and Ceratopogonidae obtain protein from the bodily fluids of other animals (Downes 1955, 1958; Downes & Smith 1969), but some acquire it from pollen (Downes 1955; Downes & Smith 1969; De Meillon & Wirth 1989; Yuan et al. 2007, 2008). Young male flies may need pollen for testicular maturation and to initiate sperm production (e.g., Kevan 1970), whereas some females require pollen for both normal ovarian development (Schneider 1948; Maier 1978; Hickman et al. 1995) and yolk deposition (Haslett 1989a). Males of many Syrphidae (Haslett 1989a), Bombyliidae (Panov 2007), and some anthophilous muscoids (Kearns 1992; Pont 1993; Larson et al. 2001; Dlusskii 2002) generally consume more nectar and less pollen than do females.

Pollen contains proteins, carbohydrates and lipids, in addition to various amino acids, minerals and vitamins (Stanley & Linskens 1974; Alba et al. 1995; Bonvehi & Jorda 1997; Roulston & Cane 2000; Villanueva et al. 2001). To obtain the nutrients within the indigestible exine, some Diptera consume entire grains, whereas others puncture them and suck out the protoplasm. In the former case, the nutrients presumably diffuse out through germination pores in the exine during digestion or the exine is destroyed by osmotic shock (Haslett 1983; Kevan & Baker 1983; Roulston & Cane 2000). Some syrphids soak pollen in saliva exuded by their proboscis, then imbibe the slurry (Proctor & Yeo 1973). They may ingest so much pollen that their abdomens appear bloated and yellow, and digested pollen is observed easily in their feces. The mouthparts of many Bombyliidae are poorly suited to pollen collection directly from anthers, but a few species can harvest pollen using specialized structures on the tarsi that rake the anthers and convey material to the mouth (Neff et al. 2003).

Pollen contains numerous amino acids that may have other nutritional benefits (Kevan & Baker 1983, 1999; Roulston & Cane 2000), though proline is the most significant of them; plants usually need it in large amounts (e.g., 2% of dry weight) to support pollen tube growth (Linskens & Schrauwen 1969). The proline in the pollen of anemophilous flowers (Stanley & Linskens 1974) can be used by insects to power their flight (Gilbert 1985a; Candy et al. 1997). The importance of proline in fly nutrition was confirmed by Wacht et al. (2000) who found that it is the only amino acid of 20 they tested that can be perceived in the sub-millimolar range by the salt receptor of the labellar chemosensory hairs of *Eristalis tenax*. In the Syrphidae, adults obtain protein solely from pollen and nectar (Oldroyd 1964), with the relative intake determined by their immediate needs (Haslett 1989a) and the constraints of

proboscis structure (Gilbert 1981, 1985b). In general, as the length of the proboscis increases, the apparent importance of pollen in the diet decreases as the flies concentrate on flowers with longer corolla tubes and greater nectar rewards (Gilbert 1981).

Some syrphids, such as members of the genera *Melanostoma* and *Platycheirus* in Europe, feed almost exclusively on the pollen of various anemophilous plants that offer no nectar reward (Goot & Grabandt 1970; Leereveld et al. 1976, 1991; Gilbert 1981; Leereveld 1982, 1984; Sharma et al. 1993; Ssymank & Gilbert 1993). The pollen of anemophilous plants tends to be smoother and has less of a *pollenkitt* (sticky or oily material on the outside of pollen grains) than that of entomophilous plants (Ackerman 2000, Pacini & Hesse 2005), so syrphids may not contribute significantly to pollination. However, intraspecific variation in pollen characteristics of some plants corresponds to the environments in which the plants grow, suggesting that syrphids may sometimes be significant pollinators of anemophilous plants. For example, pollen from *Plantago lanceolata* L. (Plantaginaceae) growing in forested areas in Luxembourg, where wind is minimal and biotic pollen vectors are most adaptive, has a higher adhesive capacity than pollen from conspecifics in exposed coastal Netherlands (Stelleman 1980, 1984).

### Secondary floral rewards - Location of mates and prey

Because the females of many species of flies must visit flowers to obtain nectar and pollen, flowers could be excellent places for males to locate mates (Tab. 2). Maier (1978, 1982), Maier & Waldbauer (1979) and Waldbauer (1984) have shown that males of *Temnostoma* and *Mallota* species, *Somula decora* Macquart, and *Spilomyia hamifera* Loew (Syrphidae) patrol flowers in the morning, and oviposition sites in the afternoon, and so locate mates (Waldbauer & Ghent 1984). In some cases, they establish a patrol route territory or "trap-line", containing ten to twenty prime flowers, which they over-fly repeatedly (Maier & Waldbauer 1979). They feed periodically at various flowers along the route and thereby may act as pollinators. According to Speight (1978), various syrphids commonly hold floral territories where they await females. Certain bombyliid flies also use flowers as mating rendezvous sites, possibly defending territories for this purpose (Evenhuis 1983, Johnson & Dafni 1998). As a final example, Nagasaki (2007) reported numerous individuals of *Notiphila maritima* Krivosheina (Ephydriidae) mating and ovipositing on flowers of *Nuphar subintegerrima* (Casp.) Makino and carrying pollen. The larvae were not found to feed in the flowers, but presumably in submerged sediments near the water lily roots, which they may have tapped for oxygen as described by Larson & Foote (1997) for *Notiphila* associated with the yellow water lily, *Nuphar luteum*.

Anthophilous predators are well known among the ambush bugs (Reduviidae), crab spiders (Thomisidae), other spiders (e.g., Theridiidae) (Greco & Kevan 1994; Kevan & Greco 2001), and mantids (Mantodea) (Kevan & Baker 1999), but there are few records of predatory Diptera using flowers. Kevan (1973) reports that empidid flies and dung

TABLE 2. Fly exploitation of selected flowers as mating/prey/brood sites

Plant Family	Plant Taxon*	Fly Taxon	Floral Function**	Reference
Araceae	<i>Alocasia</i> spp.	<i>Colocasiomyia</i> spp. (Drosophilidae)	BS, PC	Miyake & Yafuso 2003, 2005; Toda & Lakim 2011; Takano et al. 2012
	<i>Alocasia macrorrhiza</i> (L.) G. Don	<i>Neurochaeta inversa</i> McAlpine (Diptera: Neurochaetidae)	BS, MS?	Shaw et al. 1982
	<i>Alocasia pubera</i> Schott. (S)	<i>Atherigona</i> spp. (Anthomyiidae)	BS, PC	van der Pijl 1953; Simpson & Neff 1981
	<i>Peltandra virginica</i> Kunth	<i>Elachiptera formosa</i> Loew (Chloropidae)	BS, PC	Patt et al. 1995
Aristolochiaceae	<i>Aristolochia</i> spp. (some S)	Phoridae, Drosophilidae	BS, PC	Disney & Sakai 2001; Sakai 2002a,b
Asteraceae	<i>Erigeron neomexicanus</i> Gray	<i>Oligodranes mitis</i> Cresson (Bombyliidae)	MS, PC	Evenhuis 1983
Balanophoraceae	<i>Thonningia sanguinea</i> Vahl	<i>Morellia</i> sp. (Muscidae)	BS, PC	Goto et al. 2012
Balsaminaceae	<i>Impatiens uniflora</i> Hayata, <i>I. tayemonii</i> Hayata	<i>Hirtodrosophila actinia</i> (Okada), <i>H. yapingi</i> Gao (Drosophilidae)	BS, MS?	Gao 2011
Campanulaceae	<i>Centropogon solanifolius</i> Benth.	<i>Zygothrica neolinea</i> (Drosophilidae)	BS	Weiss 1996
Linaceae	<i>Linum pubescens</i> Banks & Solander	<i>Usia bicolor</i> Macq. (Bombyliidae)	MS, PC	Johnson and Dafni 1998
Monimiaceae	<i>Siparuna</i> spp.	Cecidomyiidae	BS, PC	Feil 1992
Moraceae	<i>Artocarpus integer</i> (Thunb.) Merr. (S)	<i>Contarinia</i> spp. (Cecidomyiidae) <i>Dettopsomyia</i> spp. (Drosophilidae)	BS, PC BS, PC	Sakai et al. 2000, 2002a van der Pijl 1953, Simpson & Neff 1981
Myrtaceae	<i>Eucalyptus</i> spp.	<i>Drosophila flavohirta</i> Malloch (Drosophilidae)	BS, PC	du Toit 1987; Tribe 1991; Nicolson 1994a,b
Nymphaeaceae	<i>Nuphar subintegerrima</i> (Casp.) Makino Various	<i>Notiphila maritima</i> Krivosheina (Ephydriidae) <i>Notiphila brunnipes</i> (Ephydriidae)	MS, BS BS	Nagasaki 2007 van der Velde et al. 1978
Orchidaceae	<i>Pleurothallis</i> spp.	<i>Tricimba</i> spp. (Chloropidae) <i>Megaselia</i> spp. (Phoridae)	BS, PC	Borba & Semir 2001
Ranunculaceae	<i>Trollius europaeus</i> L. (S)	<i>Chiastochaeta</i> spp. (Anthomyiidae)	MS, BS, PC	Pellmyr 1989, Despres & Jaeger 1999, Ferdy et al. 2002, Despres 2003, Despres et al. 2007
Saxifragaceae	<i>Saxifraga oppositifolia</i> L.	<i>Scathophaga apicalis</i> (Curtis in Ross) (Scathophagidae)	PH, PC	Kevan 1973

\*(S) indicates that the brood develops in senescent floral tissue

\*\*BS = Brood Site, MS = Mating Site, PH = Prey-hunting site; PC = pollination confirmed

flies (Scathophagidae) in the Arctic sometimes take flower-foraging prey at flowers. It is possible that other predaceous families such as Asilidae also visit flowers to locate their prey (e.g., O'Neill & Kemp 1991), and *Coenosia* spp. (Muscidae) capture prey from flowers in southern Ontario (S. Marshall, personal communication). Conopid and phorid parasitoids wait near flowers to inject eggs into their hymenopteran hosts (Freeman 1966; Otterstatter et al. 2002; Willmer 2011). The pollination value of any of these mating or predation behaviours is unclear, but if predator populations

are high enough they may interfere with the pollinating activities of the prey (Morse 1986; Morse & Fritz 1989).

#### Secondary floral rewards - Brood places

Several families of Diptera use flowers as brood places, but their effectiveness at pollen transfer during these activities is unknown (van der Velde et al. 1978; Inouye & Taylor 1979; Larson et al. 2001; Sakai 2002a). However, there are several records of brood places used

by Diptera involved in pollination (Pellmyr 1989; Feil 1992; Patt et al. 1995; Despres & Jaeger 1999; Sakai et al. 2000; Ferdy et al. 2002; Despres et al. 2002, 2007; Despres 2003; Luo et al. 2010; Gao 2011) (Tab. 2). For example, the pitcher plant, *Sarracenia purpurea* L., provides larval habitat in its phytotelmata, rather than flowers, to *Fletcherimyia fletcheri* (Aldrich) (Sarcophagidae), adults of which visit the flowers for nectar and pollen (Ne'eman et al. 2006). Ovipositing females may be effective pollinators, while their larvae later develop in the senescent floral tissue (van der Pijl 1953; Disney & Sakai 2001; Sakai 2002a, b; Quilichini et al. 2010).

Pollen movement may occur as individual flies visit multiple flowers during multiple mating or oviposition events, and may occur in concert with the breeding system of the plant. For instance, in the pollination of protogynous *Peltandra virginica* Kunth (Araceae) by *Elachiptera formosa* Loew (Chloropidae), the flies oviposit mainly in female-phase inflorescences (differentiated by floral odour), and their larvae feed on the copious pollen released during the male phase. Pollen transfer is frequent and occurs as the ovipositing flies move between female-phase inflorescences, where they mate and oviposit, and male-phase inflorescences, where they consume nutritional pollen (Patt et al. 1995).

Similar to the mutualisms between *Yucca* (Agavaceae), *Ficus* (Moraceae), *Elaeis* (Arecaceae) and their non-Diptera pollinators, larval flies may be provisioned with resources, such as pollen or seeds, in exchange for pollination service. Mostly, insects that use flowers as brood places are destructive, but the relationship will persist if there is a net benefit to the plant in terms of propagules produced (Pettersson 1992; Brody 1992; Zimmerman & Brody 1998; Brody & Morita 2000; Despres et al. 2002; Gao 2011). However, larvae may consume floral resources to the extent that the reproductive success of the plant may be lower due to reduced rewards to pollinators (du Toit 1987; Tribe 1991; Nicolson 1994a, b; Weiss 1996).

### *Secondary floral rewards - Warmth, protection and shelter*

Although some bees are known to sleep in flowers (Dafni et al. 1981; Willis & Kevan 1995), similar behaviours have been reported rarely among other flower-visiting insects (Tab. 3). In the Arctic, Hocking & Sharplin (1965) and Hocking (1968) noted *Aedes* spp. (Culicidae) basking at the foci of the parabolic corollas of heliotropic *Dryas integrifolia* and *Papaver radicum* Rottb., where the temperature was often 6°C above that of the ambient air. Basking flies were observed disproportionately often on flowers aligned with the sun, so heliotropism and the sun-focussing shape of the flowers provide heat rewards that increase the probability of pollinator visitation (Kevan 1989; Stanton & Galen 1989; Kudo 1995; Krannitz 1996; Totland 1996; Luzar & Gottsberger 2001; Yuan et al. 2008). Heliotropism is recorded in numerous plant families, most notably in the Asteraceae, Papaveraceae, Ranunculaceae and Rosaceae (Kevan 1972a; Stanton & Galen 1989; Totland 1996; Luzar & Gottsberger 2001; Orueta 2002), and seems relatively common in arctic and alpine regions where heat rewards

could be sought by foraging Diptera. In two species of tropical Convolvulaceae (*Ipomoea pes-capri* and *Merremia borneensis*), Patiño et al. (2002) noted that seasonal heliotropism and floral orientation combine to regulate internal temperatures for both seed fertilization and development, and that insects preferentially visit the sunlit flowers. If the insects are reluctant to leave the heat, basking behaviour may not be conducive to cross-pollination. Extra warmth may benefit the plant by optimizing temperature for pollen germination and fertilization (Orueta 2002).

Kevan (1970) has suggested that Diptera that bask in the diaheliotropic and parabolic corollas of arctic flowers such as *Dryas integrifolia* M. Vahl. (Rosaceae) are able, from such vantage points, to detect the shadows of potential predators. Some Diptera bask in flowers and the increased warmth may speed metabolism and ovarian maturation, and preheat flight muscles (Knutson 1974, 1979; Kevan 1975, 1989; Yafuso 1993). Tatler et al. (2000) have shown that extra warmth results in accelerated optical neuronal processing in insects (e.g., *Calliphora vicina*, Calliphoridae). Certain parabolic, campanulate, and funnel-shaped flowers may be used by flies for physical protection from adverse weather conditions (Drabble & Drabble 1927; Parmenter 1958; Kevan 1973, 2007). The capacity for heat production, particularly in basal angiosperm lineages and in Araceae (Lamarck 1777; Thien et al. 2009), may have several functions, including acceleration of floral growth and development, improved volatilization of pollinator attracting molecules, and shelter and warmth for the entrapped pollinators (Meeuse 1966; Knutson 1974, 1979; Moodie 1976; Thien et al. 2000; Patiño et al. 2002; Quilichini et al. 2010; Willmer 2011). Luo et al. (2010) demonstrated that heat generated by floral tissues was not necessary for seed or fruit development in *Illicium* spp. (Schisandraceae), but that larvae of cecidomyiid pollinators developing in the flowers would die without the added warmth.

### FLORAL ADVERTISEMENTS TO FORAGING FLIES

The visual and olfactory advertisements used by flies to locate flowers operate over different distances. Distinctive floral advertisements and guides benefit the plant because they increase the likelihood that the pollinator can learn their "search image" and thus more easily revisit other plants of the same species. This constancy greatly improves the effectiveness of visiting insects as pollen vectors (Waser 1983, 1986; Fenster et al. 2004), but has not been well studied in Diptera. Goulson & Wright (1998), for example, noted that the hover flies *Episyrphus balteatus* (De Geer) and *Syrphus ribesii* (L.) (Syrphidae) can be remarkably constant to the flowers they visit, although reasons for this constancy and the floral features involved are undocumented. Other visual and chemical cues operate at closer range, guiding the flies' behaviour on the flower. The whole suite of floral advertisements probably operates to attract anthophiles through both innate and learned responses.

TABLE 3. Fly exploitation of selected flowers for warmth or shelter.

Plant Family	Plant Taxon	Fly Taxon	Benefit*	Reference
Araceae	<i>Alocasia odora</i> C. Koch	<i>Colocasiomyia alocasiae</i> (Okada), <i>C. xenalocasiae</i> (Okada) (Drosophilidae)	MT	Yafuso 1993, Miyake & Yafuso 2003
Aristolochiaceae	<i>Aristolochia</i> spp.	various	MT	Disney & Sakai 2001; Sakai 2002a
Asteraceae	<i>Oritrophium limnophilum</i> (Sch. Bip.) Cuatr.	various	PS	Stanton and Galen 1989
	<i>Calendula arvensis</i> L.	<i>Usia aurata</i> Fabr. (Bombyliidae)	SH	Orueta 2002
Campanulaceae	<i>Campanula rotundifolia</i> L.	many	PS	Drabble & Drabble 1927, Parmenter 1958
Convolvulaceae	<i>Convolvulus</i> spp.	many	PS	Drabble & Drabble 1927, Parmenter 1958
Geraniaceae	<i>Pelargonium tricolor</i> Curt.	<i>Megapalpus capensis</i> Wiedemann (Bombyliidae)	SH	McDonald & van der Walt 1992
Illiciaceae	<i>Illicium floridanum</i> Ellis	many	MT	Thien et al. 2009
	<i>Illicium</i> spp.	<i>Clinodiplosis</i> sp. nov. (Cecidomyiidae)	MT	Luo et al. 2010
Nymphaeaceae	Various	<i>Notiphila brunripes</i> (Ephydriidae)	PS	van der Velde et al. 1978
Ranunculaceae	<i>Adonis ramosa</i> Franch.	Agromyzidae	PS	Kudo 1995
	<i>Ranunculus adoneus</i> Gray	various	PS	Smith 1975
Rosaceae	<i>Dryas integrifolia</i> M. Vahl.	<i>Aedes</i> spp. (Culicidae)	SH	Hocking & Sharplin 1965; Hocking 1968; Kevan 1975
		<i>Rhamphomyia</i> spp. (Empididae)	SH	Kevan 1975
		<i>Carposcalis carinata</i> (Curran) (Syrphidae)	SH	Kevan 1975
		<i>Boreellus atriceps</i> (Zetterstedt) (Calliphoridae)	SH	Kevan 1975
Saxifragaceae	<i>Saxifraga oppositifolia</i> L.	<i>Smittia velutina</i> (Lundbeck) (Chironomidae)	PS	Kevan 1973, 2007
Scrophulariaceae	<i>Digitalis</i> spp	many	PS	Drabble & Drabble 1927, Parmenter 1958

\*MT = metabolic thermogenesis, SH = solar heat, PS = physical shelter

### Background on fly vision

As in other diurnal pollinators, most flower-visiting flies use floral colour as their primary cue to recognize preferred flowers (Tab. 4). Due to interactions between different visual cues in the orientation process, it is difficult to separate the elements of the suite of cues presented by flowers, and much of what is known about insect vision and the implications of floral colours for anthecology comes from studies of bees (e.g. Menzel & Shmida 1993; Kevan & Backhaus 1998; Chittka & Menzel 1992; Vorobyev & Brandt 1997; Kelber et al. 2003). Weiss (2001) has pointed out that vision and learning in various lesser understood groups of pollinators, including Diptera, is a fertile ground for research. It has been shown in behavioural experiments that *Lucilia cuprina* (Calliphoridae), *Bombylius fuliginosus* (Bombyliidae) and *Eristalis tenax* (Syrphidae) possess colour vision (Ilse 1949; Kugler 1950; Lunau & Wacht 1994; Kelber et al. 2003 for review), and thus discriminate colour

shades due to their chromaticity and independent of their brightness.

The insect eye is less able to resolve shape and details of pattern than is the human eye (Land 1997, Dafni et al. 1997), but insects have remarkable abilities to perceive and resolve rapid motion. Because insects are fast flyers and lack the ability to move the eyes, their orientation is supported by effective motion resolution of more than 200 pictures per second (Ruck 1961). Thus, flies can perceive the forms of flowers even when in rapid flight (Kevan & Baker 1983; Dafni et al. 1997; O'Carroll et al. 1996). It is noteworthy that the motion-sensitive neurons in the eyes of hovering insects (e.g., Bombyliidae) are tuned to detection of lower rates of motion than are non-hovering insects (O'Carroll et al. 1996). The Diptera preference toward characteristically "open" flowers is probably not related to visual advertisements, but caused by their limited abilities to manipulate flowers.

TABLE 4. Floral colour preference(s) of selected flower-visiting flies. Colours are defined by reflected wavelengths, and not by the perception of the viewer.

Fly Taxon	Wavelength									Reference	
	R	O	Y	G	B	P	OB	OW	UV		
Bombyliidae											
<i>Bombylius</i> sp.					+	+					Knoll 1921
Calliphoridae											
<i>Lucilia</i> sp.			+								Kugler (1951, 1956)
Muscidae											
<i>Pyrellia cyanicolor</i> Zetterstedt			+								Cameron & Troilo 1982
Syrphidae											
<i>Cheilosia albitarsus</i> (Meigen)			+								Haslett 1989b
<i>Eristalis pertinax</i> (Scopoli)			++					+			Haslett 1989b
<i>Eristalis tenax</i> (L.)			++	+	+				+		Ilse 1949; Kugler 1950; Haslett 1989b; Lunau & Wacht 1994; Lunau & Maier 1995; Lunau 1996
<i>Rhingia campestris</i> Meigen					+	+					Haslett 1989b
<i>Volucella pellucens</i> (L.)								+			Haslett 1989b

\*R = red, O = orange, Y = yellow, G = Green, B = blue, P = shades of purple and violet, OB = optic black, OW = optic white, UV = ultra violet patterns

In contrast to other insects, flies have two morphologically and physiologically separated visual subsystems. The apposition subsystem consists of two receptor cell tandems, only one of which is present in each ommatidium. Providing the eye with a set of four retinula cells that differ in their spectral sensitivities enables tetrachromatic colour vision, but with less sensitivity and less acuity than the neural superposition subsystem (Hardie 1979; Pichaud et al. 1999). The neuronal superposition subsystem is monovariant and thus colourblind but highly sensitive, collecting visual input from six retinula cells of six neighbouring ommatidia (Anderson & Laughlin 2000). This system enables flies to orient visually in dim light conditions without loss of spatial information, unlike optical superposition eyes of nocturnal Lepidoptera. Together, the two subsystems allow for a parallel processing of motion perception and colour vision (Kelber et al. 2003).

#### Visual advertisements - Colour

Most flies have tetrachromatic colour vision with sensitivity from ultraviolet (UV) over blue and green to yellow wavelengths (Menzel & Backhaus 1991; Troje 1993; Kelber et al. 2003). According to the colour vision model of Troje (1993), flies exhibit categorical colour vision such that they discriminate colours in only four categories. These categories are determined by the superior excitation of one of the two photoreceptor cells in each tandem and can be regarded as fly-blue, UV, fly-green and fly purple (Arnold et al. 2009).

Many Diptera are observed either on yellow or white flowers, although some species prefer blue or red (Weems 1953; Sandholm & Price 1962; Kevan & Baker 1983; de Buck 1990; Campbell et al. 2010; Willmer 2011). These

responses are plastic to some degree. It is also unknown whether the flower visits were determined by an underlying innate colour preference, by a limited variety of alternatively coloured flowers, or by experience of individual flies. Interestingly, the categorical colour vision model of Troje (1993) predicts that flies have a limited ability to discriminate between yellow and white flowers, if both absorb ultraviolet light. In wild radish (*Raphanus raphanistrum* L. (Brassicaceae)), the yellow flower morphs are preferentially visited by flies and have a UV-reflective target pattern that the white morph lacks (Kay 1976, 1978). Innate colour preferences of naive flies have not yet been studied systematically; the hoverflies *Eristalis tenax* and *Episyrphus balteatus* exhibit preferences for yellow colours (Lunau & Maier 1995, Sutherland et al. 1999).

Some studies provide information about colour preferences in distinct species (Ssymank 2001, Laubertie et al. 2006). The notion that in regions where Diptera predominate as floral visitors, flowers are more often white and yellow than elsewhere (Inouye & Pyke 1988 for Australian alpine; Kevan 1972b, 1973 for Canadian Arctic; Kevan (unpubl. data) for Rocky Mountain alpine; Primack (1978, 1983) for New Zealand) has been questioned by Arnold et al. (2009), who found no significant change of flower colour with altitude in an alpine region of Norway.

Evidence from behavioural experiments shows that flies can be trained to colours that initially were less attractive to them. Kelber (2001) trained syrphid flies, which were initially attracted to yellow flowers, to visit flowers of other colours. After a period of training on blue flowers, the flies had no preference for yellow flowers when given a choice of blue or yellow. Haslett (1989b) studied the pollen foraging of six species of Syrphidae in the wild and at experimental

arrays of artificial flowers of different colours, and showed that these species had colour preferences ranging from white and yellow to blue and violet. The preference for yellow colours in *Eristalis tenax* is innate, wavelength-specific and varies with proximity to the flower (Lunau & Wacht 1994; Lunau & Maier 1995; Lunau 1996). Once the flies land, however, only deep yellow colours with strong absorption in the ultraviolet waveband release proboscis extension behaviour in inexperienced flies. This innate response is fine-tuned to the spectral reflection properties of pollen that reflects green and yellow wavelengths > 510 nm. Ultraviolet and blue wavelengths < 510 nm, which are typically absorbed by yellow pollen, strongly inhibit the proboscis reaction (Lunau 2000, 2007). Wacht et al. (1996) noted that both optical and chemical stimuli control pollen feeding in *Eristalis tenax* and other syrphid flies. The fixed innate search images for pollen signals constrains the evolution of flowers' signalling devices and leads to the standardisation of floral signalling components, for example the colour signals of pollen, anthers, and pollen- and anther-mimicking floral guides (Lunau 2004, 2007).

Red flowers are normally associated with specialist pollinators, such as birds and those insects (butterflies, some beetles) that have red-sensitive vision (Kevan & Backhaus 1998; Kevan et al. 2001; Bernhardt 2000). In this context it has been shown that red bird-pollinated flowers are less attractive to potentially nectar thieving bees and thus provide a private niche for their pollinators (Lunau et al. 2011). Most flies are unable to perceive red, but flowers with reddish hues are also found within the mimetic complex of sapromyophilous blooms and this may relate to the sensitivity of the eyes of some Diptera to red (Autrum & Stumpf 1953). The colours of sapromyophilous blossoms tend to be dark and mimic the substrate associated with their odours (carrion, dung, etc.), but little is known of the linkage between the visual systems of the pollinators and orientation and attraction cues from the plants involved. There are assemblages of flies that are frequent visitors to blue-violet, pink or red flowers, but these often have tubular corollas and hidden nectar, thus only flies with elongate, specialized mouthparts can forage from them (Knuth 1906-1909; Robertson 1928; de Buck 1990; Proctor et al. 1996; Goldblatt et al. 2001; Kasting & Weber 2001; Goldblatt & Manning 2007a, b; Willmer 2011). In numerous South African flowers visited predominately by long-tongued flies, a high incidence of scentless red, pink, or blue-violet flowers, which would usually suggest pollination by birds, has been recorded (Rebelo & Siegfried 1985; Goldblatt et al. 2001; Goldblatt & Manning 2007a, b). In addition to Bombyliidae, Nemestrinidae and Tabanidae, long-tongued Syrphidae, Conopidae, Empididae and Tachinidae are able to feed from these deep-tubed flowers, as well as from shallow, unspecialized ones. Observations by numerous investigators have shown the predilection of bombyliids for bluish flowers, which are often pollinated by bees (Knuth 1906-1909; Knoll 1921; Scott 1953; Kevan & Baker 1999; Kasting & Weber 2001).

Despite the generalizations above, floral colour preferences vary both spatially and temporally, depending on the availability of flowers, floral rewards, competitors, and

those factors in combination. Fruit flies react differently to the colours and scents of natural and artificial (trap) fruits depending on age and sex (Owens & Prokopy 1986; Duan & Prokopy 1994). Physiologically-induced changes (Brown 1993) and sexual differences in flies' reactions to flowers may be especially important in some of the mutualistic relations. In some flowers, corolla colour changes over time, and the colour phase of the rewarding flowers is often more attractive to naive visitors than the colour of spent flowers (Kugler 1950; Cameron & Troilo 1982; Gori 1983; Casper & La Pine 1984; Cruzan et al. 1988; Zietsman 1990; Robertson & Lloyd 1993; Weiss 1991; Lunau 1996).

### Visual advertisements - Size and form

There is a positive correlation between the size of flowers, inflorescences or patches of bloom, and attractiveness to insects, and small, inconspicuous flowers are often aggregated into large inflorescences to attract pollinators more effectively (Faegri & van der Pijl 1979; Kevan & Baker 1983; Dafni et al. 1997). However, this relationship has been investigated in detail for only a few fly-visited flowers. Andersson (1991) showed that ray and inflorescence size of *Achillea ptarmica* L. (Asteraceae) have additive effects on the attraction of Syrphidae (*Eristalis*, *Syrphus*, *Volucella*). Abbott & Irwin (1988) found that ligulate inflorescences were visited much more frequently by Syrphidae than were the smaller non-ligulate ones in polymorphic populations of *Senecio vulgaris* L. (Asteraceae). The visitation rate by the tachinid *Protohystricia huttoni* (Malloch) to *Myosotis colensoi* (Kirk) Macbride (Boraginaceae) in New Zealand increased linearly with display size, but because the number of flowers visited on a plant concomitantly decreased, visitation rate to individual flowers remained more or less constant, regardless of display size (Robertson 1992; Robertson & Macnair 1995). The number of insect visits per unit time to clones of Edelweiss (*Leontopodium alpinum* Cass. (Asteraceae)) remained constant across all clone sizes, decreasing the chance of a given flower being visited in larger clones, but enhancing out-crossing (Erhardt 1993). Golding et al. (1999) noted that visits by *Episyrphus balteatus* (Degeer) (Syrphidae) to variously manipulated flowers of *Brassica rapae oleifera* (Brassicaceae) were more strongly related to the number of anthers present than with the size of corolla display.

Moller (2000) indicated that floral symmetry is perceived by pollinators, and that symmetrical (radial or bilateral) flowers are preferentially visited and pollinated over flowers that deviate from symmetry. He suggests that deviations represent developmental instability and reflect reduced Darwinian fitness, and thus may be correlated with minor floral rewards. Nevertheless, asymmetries in flowers are more common than are generally recognized (Dafni & Kevan 1996) and can result from physical corolla damage or natural variation even in populations of plants bearing flowers that are described as symmetrical. However, the nature of the optical boundary between a flower and its background (i.e., edge effect) may also be important in attracting foraging flies. Consideration of edge effects also apply to flowers with broken outlines and appendages that may further stimulate the eyes of foraging flies (Faegri & van

der Pijl 1979), but the data are equivocal. Kugler (1950) detected no innate preference of *Eristalis* for star-shaped over circular models of flowers of the same size, although they were able to discriminate between them. Others have found preference for flowers with dissected outlines over those with simple outlines (e.g., Kugler 1956; Johnson & Dafni 1998). Despite the findings noted above, the generally held view that flowers with broken outline lengths are more visible to foraging anthophiles requires further critical examination and empirical testing.

#### Visual advertisements - Guides, staminodes and motion

Many flowers have visual guides that direct the foragers to hidden rewards, and ensure contact with the stigma, stamens or both (Sprenkel 1793; Dafni & Giurfa 1999; Lunau 2006) (Tab. 5). These guides also affect the foraging efficiency of the visitor and have a positive effect on pollinator attraction and successful interaction with the flowers (Kevan & Baker 1983; Dafni et al. 1997; Hansen et al. 2012). Johnson & Dafni (1998), for example, showed that landing and orientation of *Usia bicolor* Macquart (Bombyliidae) to the centres of models were encouraged by converging lines. Dinkel & Lunau (2001) used circular dummy flowers to show that inexperienced *Eristalis tenax* were quicker to find a potential food source in the centre if black line markings were present than if not. In contrast to the yellow, UV-absorbing central dot used as a potential food source, the black line markings were never touched with the proboscis.

A row of yellow dots instead of black lines increased the handling time of *Eristalis tenax* flies, because the yellow dots are probed with the proboscis. On natural flowers the probing of a number of floral guides may intensify the movements of the flies and thus increase the chance of touching anthers and stigma. Vertically-oriented staminodia are often important structures that act as landing platforms, and may act as a physical guide to nectaries at the base of the flower (Brew 1987; Pellmyr 1992) or themselves exude nectar (Anderson & Hill 2002), and their reflectance patterns may play a role in attraction of Diptera (Kugler 1951; Percival 1965; Young et al. 1987a). Sparkling or glistening surfaces may attract some flies (Kugler 1951; Percival 1965; Patt et al. 1989; Bänziger 1996). Nectar guides often offer contrast in the UV (Kugler 1963; Lunau 2000; Kevan et al. 2001), to which insects are sensitive (Bishop 1974; Kevan & Backhaus 1998).

Some flowers take advantage of the aggregation instinct of insects (Elvers 1980; Morse 1981) and trick foragers into believing that there are already insects feeding at the flower. Dark spots or florets may give the illusion of small, crawling insects being present and attract certain floral visitors (Dodson 1962; Weismann 1962; Faegri & van der Pijl 1979; Eisikowitch 1980; McDonald & van der Walt 1992; Westmoreland & Muntan 1996; Johnson & Midgley 1997; Johnson & Dafni 1998; Lamborn & Ollerton 2000). However, the dark central florets of the wild carrot *Daucus carota* L. have been shown to repel egg-laying females of the

TABLE 5. Fly attraction to two dimensional (pigment pattern) and three-dimensional guides in selected flowers.

	Plant Taxon	ES	PP V	PU V	St	VA	Fly Taxon	Reference
Araceae	<i>Arisaema</i> sp.	+	-	-	-	-	Mycetophilidae Sciaridae	Vogel & Martens 2000
Asclepiadaceae	<i>Ceropegia</i> sp.	-	-	-	-	+		Percival 1965
Asteraceae	<i>Gorteria diffusa</i> Thunb.	-	+	-	-	-	<i>Megapalpus nitidus</i> Macq., <i>M. capensis</i> Wiedemann (Bombyliidae)	Johnson & Midgley 1997; Ellis & Johnson 2010; Duncan & Ellis 2011 Kay 1976, 1978
Brassicaceae	<i>Raphanus raphanistrum</i> L.	-	-	+	-	-		
Geraniaceae	<i>Pelargonium tricolor</i> Curtis	-	+	-	-	-		McDonald & van der Walt 1992
Iridaceae	<i>Lapeirousia oreogena</i> Schltr. ex Goldblatt	-	+	-	-	-	<i>Prosoeca</i> sp. (Nemestrinidae)	Hansen et al. 2012
Linaceae	<i>Linum pubescens</i> Banks & Solander	-	+	-	-	-		Johnson & Dafni 1998
Malvaceae	<i>Herrania</i> spp.	-	-	+	+	+		Young 1984; Young et al. 1987b
	<i>Theobroma</i> spp.	-	-	+	+	-		Young 1984; Young et al. 1987b
Orchidaceae	<i>Cypripedium reginae</i> Walter	-	-	-	+	-	Syrphidae	Vogt 1990
	<i>Paphiopedilum villosum</i> (Lindley)	-	-	-	+	-	Syrphidae	Bänziger 1996
	<i>Platanthera stricta</i> Lindley	+	-	-	-	-	Empididae	Patt et al. 1989

\* ES = epidermal sculptures on petals/sepals (includes cilia, hairs and raised cells) PPV = pigmentation pattern visible to human eyes, PUV = Ultraviolet pigmentation pattern, St = staminodes, VA = vibrating appendage

gall midge *Kiefferia pericarpicola* by mimicking galls, and thus play a role for reducing infestation (Polte & Reinhold 2013). Physical vibration of flowers or flower parts as they move in the wind may also serve as an attractant, and some flowers accentuate their movement with motile appendages (Tab. 5) and may attract flower-visiting Diptera (Percival 1965; van der Pijl & Dodson 1966; Kevan 1970; Kevan & Baker 1983; Young 1984; Young et al. 1987a).

### Chemical advertisements

Flies perceive chemical stimuli in a way that is unique among insects. In contrast to bees and other insects, many flies have no flagelliform antennae with which to touch floral surfaces. Flies have taste sensilla on the labellum, the tarsi of the forelegs and the ovipositor. Fly taste sensilla have four receptor cells: a water receptor, a salt receptor, a sugar receptor and an anion receptor. Taste sensilla have an additional mechanoreceptor providing those flies with the combined gustatory and tactile information of potential food touched with the tarsi or with the extended proboscis (Hansen 1978; Hanson 1987). Using an electrophysiological tip-recording technique for single labellar chemosensory hairs of *Eristalis tenax*, Wacht et al. (2000) showed that pollen extract and the amino acid proline stimulate the salt receptor, but in contrast to salt stimuli, do not inhibit the water receptor at the same time. Thus, the across-fibres pattern of excitation of taste receptors is responsible for the perception of phagostimulants in pollen.

Odours are often liberated from flowers, either to attract pollinators from a distance or to direct them to certain portions of the flower (Dobson 1994; Dobson & Bergström 2000; Knudsen et al. 2006; Willmer 2011). However, Diptera are usually attracted to flowers by a combination of visual and olfactory stimuli (e.g., Beaman et al. 1988). Generally it is thought that long-range attraction is visual (but see Giurfa et al. 1996; Kevan & Backhaus 1998) and that odour acts nearer the flower (Kugler 1951, 1970), at least in diurnally active flowers. However, Liebermann (1925) showed that numerous species of muscoid flies approached covered plants of *Cicuta* (Apiaceae) only when they passed downwind of them. Others have observed the attraction of nocturnal mosquitoes to flowers or floral extracts, and their downwind approach in the absence of visual stimuli suggests airborne attractants (Brantjes & Leemans 1976; Jepson & Healy 1988; Healy & Jepson 1988). Although difficult to see in the field, zig-zag flights from flower to flower are indicative of olfactory orientation, whereas direct flights, regardless of wind direction, signify visual orientation. At close range, odour can act similarly to visual nectar guides, by directing the visitor to the resources, and position them appropriately to contact sexual structures and effect pollination (Brantjes 1981; Young 1984, 1985; Young et al. 1984, 1987a, b; Patt et al. 1989). Strength of attractiveness of the odour is apparently proportional to hunger (i.e. time since previous feeding; Jhumur et al. 2006).

Flower-visiting Diptera can be attracted by odours that are either pleasant or unpleasant to human beings (Tab. 6),

but the latter are often accented in the literature in connection with deceitful attraction and the syndrome of sapromyophily. There is a preference among many Diptera for “unpleasant” odours (Galen & Kevan 1980; Galen 1983, 1985; Galen & Newport 1988; Bänziger 1996; Pombal & Morellato 2000; Goldblatt et al. 2009). Nonetheless, numerous fly-visited flowers have a sweet, musty, or yeasty scent that is devoid of amine components (e.g., indole and scatole) associated with unpleasant smells (Erhardt 1993; Meve & Liede 1994; Johnson & Steiner 1995; Patt et al. 1995; Pombal & Morellato 2000; Goodrich et al. 2006; Hansson et al. 2010). Roy & Raguso (1997) did not find a strong attraction of some flies to indole, further indicating that flies respond differently to floral odours.

Certain Diptera do not find mates at flowers, but obtain rewards from flowers in the form of chemical precursors to sexual attractants. The gathering of floral scents is known among the Euglossinae (Apoidea), in which it is used by the males to attract mates (Eltz et al. 1999). In the Diptera, possibly the best studied is the collection of the scent components methyl eugenol, zingerone, and related phenylpropanoids, for use in pheromone synthesis by some male *Bactrocera* (Tephritidae) (Nishida et al. 1997, 2004; Shelly 2001; Tan et al. 2002, 2006, 2011; Tan & Nishida 2007, 2012). Some *Bactrocera* also collect raspberry ketone, another phenylpropanoid, as a defensive compound against predators (Tan & Nishida 2005).

### Tactile advertisements and guides

Although texture has been invoked as a sensory cue by which pollinators can orient on flowers, and distinguish between flowers of different species (Kevan & Lane 1985), the sense of touch in Diptera is hardly studied. The fly *Exorista japonica* Townsend (Diptera: Tachinidae) may use, through tarsal examination, the texture and curvature of substrates in oviposition behaviour (Tanaka et al. 1999). Vogel & Martens (2000) noted that tactile cues characteristic of fungi may be important in attracting Mycetophilidae and Sciaridae to spathes of *Arisaema* spp. (Araceae), and Kevan (1970) observed mosquitoes using grooves in the corollae of *Pedicularis* (Scrophulariaceae) flowers to guide their mouthparts to the nectar. Pollen texture and exine ornamentation may play a role in feeding by anthophiles, as in *Eristalis tenax* (Wacht et al. 2000).

### FLORAL ATTRACTION OF FLIES BY DECEIT

The classification of deceptive attraction for purposes of pollination used below generally follows that presented in the review by Dafni (1984). Many mutualisms are open to “cheating” by one partner or the other, and plant-pollinator interactions are no exception (Dafni 1984; Addicott 1998; Schiestl et al. 1999; Paxton and Tengö 2001; Willmer 2011). In many instances flowers mimic the cues used by flies to locate other flowers or substrates that they normally visit for sustenance or oviposition, activating the innate or learned searching behaviour of prospective visitors to search for a nonexistent reward. Pollen or nectar rewards may be available to the visitor, but the advertised reward is not.

TABLE 6. Olfactory attractants in selected fly-pollinated flowers.

Plant Family	Plant Taxon	Dominant Components*	Odour Description**	Fly Taxon	Reference
Annonaceae	<i>Monodora tenuifolia</i> Benth.	U	F	Various	Gottsberger et al. 2011
	<i>Uvariopsis congolana</i> (De Wild.) R.E. Fr.	U	F	Various	Gottsberger et al. 2011
Apocynaceae	<i>Huernia hystrix</i> N.E.Br.	B, Ph	F	Calliphoridae, Sarcophagidae, Muscidae	Johnson & Jurgens 2010
	<i>Orbea variegata</i> Haw.	AD, Su	F	Calliphoridae, Sarcophagidae, Muscidae	Johnson & Jurgens 2010
	<i>Orbea verrucosa</i> (Masson) L.C.Leach	M	F	Calliphoridae, Sarcophagidae, Muscidae	Johnson & Jurgens 2010
	<i>Stapelia gigantea</i> N.E.Br.	M, Su	F	Calliphoridae, Sarcophagidae, Muscidae	Johnson & Jurgens 2010
	<i>Stapelia leendertziae</i> N.E.Br.	Su	F	Calliphoridae, Sarcophagidae, Muscidae	Johnson & Jurgens 2010
Araceae	<i>Alocasia</i> spp.	B, T	N	<i>Colocasiomyia</i> spp. (Drosophilidae)	Miyake & Yafuso 2005
	<i>Arum italicum</i> Mill.	AL, AP	F	Psychodidae, Sciaridae, Chironomidae	Diaz & Kite 2002; Albre et al. 2003
	<i>Arum maculatum</i> L.	AD, AL, AP	F	<i>Psychoda phalaenoides</i> L. (Psychodidae), <i>Smittia pratorum</i> Goetghebuer (Chironomidae)	Diaz & Kite 2002; Albre et al. 2003
	<i>Arum cyrenaicum</i> Hruby, <i>Arum concinatum</i> Schott	AL, AP	F	Various	Urru et al. 2010
	<i>Colocasia esculenta</i> (L.) Schott	Ph	N	<i>Bactrocera dorsalis</i> (Hendel) (Tephritidae)	Tan & Nishida 2012
	<i>Spathiphyllum cannaefolium</i> (Dryand. ex Sims) Schott	Ph	N	<i>Bactrocera</i> spp. (Tephritidae)	Tan & Nishida 2012
	<i>Symplocarpus foetidus</i> (L.) Nutt.		P, F	Various	Kevan 1989b
	Aristolochiaceae	<i>Aristolochia cymbifera</i> Mart. & Zucc.		F	Calliphoridae, Sarcophagidae, Muscidae
<i>Aristolochia gigantea</i> Mart. & Zucc.		AL	P	<i>Megaselia</i> spp., others (Phoridae)	Hipolito et al. 2012
<i>Aristolochia grandiflora</i> Vahl			F	Calliphoridae, others	Burgess et al. 2004
<i>Aristolochia littoralis</i> Parodi			F	Phoridae	Hall & Brown 1993
Asteraceae	<i>Achillea millefolium</i> L.	M		Culicidae	Healy & Jepson 1988; Jepson & Healy 1988
	<i>Leucanthemum vulgare</i> Lam.	M		Culicidae	Healy & Jepson 1988; Jepson & Healy 1988
	<i>Cirsium arvense</i> (L.) Scop	B, M		<i>Episyrphus balteatus</i> De Geer (Syrphidae)	Primante & Dotterl 2010
Austrobaileyaceae	<i>Austrobaileya scandens</i> C.T. White		F	Drosophilidae	Endress 2001; Thien et al. 2009
Caryophyllaceae	<i>Silene otites</i> (L.)	B, M	P	Culicidae	Brantjes & Leemans 1976, Jhumur et al. 2006, 2008
Euphorbiaceae	<i>Antidesma montanum</i> Blume		P	<i>Chrysomya</i> sp. (Calliphoridae), <i>Drino</i> sp. (Tachinidae), <i>Spilogona</i> sp., <i>Mitroplatia</i> sp. (Muscidae)	Li & Zhang 2007
Fabaceae	<i>Acacia cyclops</i> A. Cunn. ex G. Don	AP, T		<i>Dasineura dielsi</i> Rübsaamen (Cecidomyiidae)	Kotze et al. 2010

TABLE 6 continued

Plant Family	Plant Taxon	Dominant Components*	Odour Description**	Fly Taxon	Reference
Hyacinthaceae	<i>Eucomis humilis</i> Baker, <i>Eucomis bicolor</i> Baker	Su	F		Shuttleworth & Johnson 2010
Iridaceae	<i>Ferraria</i> spp.	AL, Ph	P, F	<i>Calliphora</i> , <i>Lucilia</i> (Calliphoridae), <i>Scathophaga</i> (Sarcophagidae), Muscidae, Tachinidae	Goldblatt et al. 2009, Johnson & Jurgens 2010
Liliaceae	<i>Scoliopus bigelovii</i> Torr.	U	F	Mycetophilidae	Mesler et al. 1980
Loganiaceae	<i>Fagraea berteriana</i> A. Gray	Ph, AL		<i>Bactrocera dorsalis</i> (Hendel) (Tephritidae)	Nishida et al. 1997; Shelly 2001; Tan & Nishida 2012
Orchidaceae	<i>Bulbophyllum</i> spp.	Ph, AL	P	<i>Bactrocera</i> spp. (Tephritidae)	Tan et al. 2002, 2006, 2011; Nishida et al. 2004; Tan & Nishida 2005, 2007, 2012
	<i>Epipactis palustris</i> (L.) Crantz			<i>Syrphididae</i> <i>Syrphididae</i>	Brantjes 1981
	<i>Listera cordata</i> (L.) R. Br.		F	Mycetophilidae	Ackerman & Mesler 1979
	<i>Paphiopedilum villosum</i> Lindley		F	Syrphidae	Bänziger 1996
	<i>Phalaenopsis bellina</i> (Rchb.f.) Christenson	Ph	N	<i>Bactrocera</i> spp. (Tephritidae)	Tan & Nishida 2012
	<i>Phalaenopsis violacea</i> H. Witte	Ph	N	<i>Bactrocera</i> spp. (Tephritidae)	Tan & Nishida 2012
	<i>Platanthera stricta</i> Lindley			Empididae	Patt et al. 1989
	<i>Satyrium pumilum</i> Thunb.	Su, B	F	Sarcophagidae	van der Niet et al. 2011
	<i>Schizochilus angustifolius</i> Rolfe.	B		<i>Orthellia</i> sp. (Muscidae)	van der Niet et al. 2010
	<i>Schizochilus bulbinella</i> Rchb.f.	B		Tephritidae, Chloropidae, <i>Allotrichoma pluvialis</i> Giordani Soika (Ephydriidae)	van der Niet et al. 2010
	<i>Schizochilus zeyheri</i> Sond.	B		<i>Linnaemya</i> sp. (Tachinidae), <i>Orthellia</i> sp. (Muscidae)	van der Niet et al. 2010
Polemoniaceae	<i>Polemonium viscosum</i> Nutt.		F		
Rafflesiaceae	<i>Rafflesia kerrii</i> spp.	AD	F	Calliphoridae	Beaman et al. 1988; Bänziger 1991; Meve & Liede 1994
Ranunculaceae	<i>Trollius europaeus</i> L.	ST, others		<i>Chiastochaeta</i> spp. (Anthomyiidae)	Ibanez et al. 2010
Rutaceae	<i>Metrodorea nigra</i> A. St.-Hil.		F	<i>Pseudoptiloleps nigripoda</i> (Muscidae) <i>Fannia</i> sp. (Fanniidae)	Pombal & Morellato 2000
	<i>Metrodorea stipularis</i> Mart.		P	<i>Phaenicia eximia</i> (Calliphoridae); <i>Palpada</i> sp., <i>Ornidia obesa</i> (Syrphidae)	Pombal & Morellato 2000
Schisandraceae	<i>Kadsura longipedunculata</i> Finet & Gagnepain	AP	N	<i>Megommata</i> sp. (Cecidomyiidae)	Yuan et al. 2008; Thien et al. 2009

\* AD = amine derivatives, AL = Alcohols, AP = aliphatics, B = benzenoids, M = monoterpenoids, Ph = phenylpropanoids, ST = sesquiterpenoids, Su = sulfur compounds, T = terpenes, U = unidentified.

\*\* P = pleasant-agreeable, F = foul, N = neutral

is not. Because it is often difficult to determine whether or not a reward is present in a deceptive flower, we consider flowers that initially mislead a visitor as deceitful even if a reward is later offered (Ackerman & Mesler 1979; Mesler et al. 1980). For example, *Rafflesia* spp. (Rafflesiaceae) are usually considered deceptive (Beaman et al. 1988), but *Rafflesia kerrii* Meijer apparently delivers substantial rewards to its calliphorid pollinators (Bänziger 1991; see also Meve & Liede 1994). The flowers attract pollinators by their form and "cadaveric stench of rotting snakes", so acting as a sensory trap upon flies searching for food or a brood site when neither of these are present. In addition, a fruity scent arising from the center of the flower (not previously reported because it was hidden by the stench) may deter the flies from laying doomed eggs. The anthers of male flowers exude a nutritious pollen mush that is likely consumed by the flies, and flowers of both sexes secrete a potentially rewarding slime. Some mimetic trap flowers do provide an apparent reward for visitors, but it may not be used, such as nectar in *Arum maculatum* L. (Lack & Diaz 1991). In trap flowers such as aroids, stigmatic exudates and nectaries may function to increase the lifespan of the visitor by maintaining the relative humidity of the chamber (Daumann 1971; Wolda & Sabrosky 1986).

#### Foul-smelling flowers

Flowers that emit odours of carrion and dung deceptively attract a particular guild of Diptera and Coleoptera that seek decaying organic matter for food and oviposition (Bernhardt 2000; Johnson & Jurgens 2010). Typical Diptera attracted include saprophilous families such as Calliphoridae, Sarcophagidae, Sphaeroceridae, Mycetophilidae, and Drosophilidae (Agnew 1976; Faegri & van der Pijl 1979; Wolda & Sabrosky 1986; Proctor et al. 1996; Burgess et al. 2004; Johnson & Jurgens 2010; Stoekl et al. 2010; Gottsberger et al. 2011) (Tab. 6, 7). By convergently mimicking the odour, appearance, and sometimes elevated temperature of these substrates, members of the Asclepiadaceae (*Stapelia* spp. and relatives), Aristolochiaceae (Burgess et al. 2004), Rafflesiaceae, Araceae (Lack & Diaz 1991; Yafuso 1993; Albre et al. 2003; Chouteau et al. 2008; Urru et al. 2010), Malvaceae (van der Pijl 1953), Hydnoraceae, Taccaceae, Burmanniaceae, Orchidaceae (Dressler 1981; Pemberton 2010) and Splachnaceae (a family of Bryophyta, see Koponen 1990) successfully attract these pollen (or spore) vectors, and mostly provide no reward (Faegri & van der Pijl 1979).

In such blooms, the unpleasant odours are often considered the long-distance lure, and in dense forests where some species are found, flowers may be visually inconspicuous (Percival 1965; Bänziger 1991, 1996). On the other hand, Faegri & van der Pijl (1979) suggested that the carrion flies patrol large areas on the wing and are likely to see the flowers. Certainly, some such blooms are huge and visually conspicuous (e.g., *Amorphophallus* (Araceae), *Rafflesia*, and some *Aristolochia* spp.), and also emit large quantities of volatiles. Many aroids (Araceae) volatilize the amines by rapid respiration and the concomitant release of heat and carbon dioxide also simulate a substrate for oviposition (Dormer 1960; Meeuse 1966, 1978; Moodie

1976; Albre et al. 2003; Seymour et al. 2003; Quilichini et al. 2010; van der Niet et al. 2011 but see Uemura et al. 1993). Many orchids in the huge genus *Bulbophyllum* (c.2000 species) smell of carrion, sometimes of rather specific varieties, and attract appropriate fly species as pollinators (Pemberton 2010).

The nectar of sapromyophilous flowers offering it tends to be rich in amino acids, by an order of magnitude higher than in other flowers. These high levels of amino acid may reward female flies lured from their normal oviposition substrates (Baker & Baker 1983a, b) with fuel for flight and nutrients for ovarian maturation. Nectar may also be a means of correctly orienting the visitors to reproductive structures (Johnson & Jurgens 2010).

Visual attraction of carrion flies to sapromyophilous flowers is presumably enhanced by their brown, red and purplish, and often blotchy, flowers, which further the mimicry of breeding and feeding venues for the flies (Proctor & Yeo 1973; Pemberton 2010). Wrinkled surfaces, filamentous appendages, and blotches (perhaps resembling hordes of indulgent flies) are also common and may serve as attractants, and windows (transparent areas) direct the movements at close range of positively phototactic visitors (Faegri & van der Pijl 1979; Seymour et al. 2003). The blotches also produce patterns that are more attractive than monotone surfaces to landing Diptera (Steiner 1948). Ultraviolet reflectance may be important for the attraction of sapromyophilic Muscidae (e.g., Moring 1978; Agee & Patterson 1983), but has not been investigated. Although most flies are thought unable to perceive red, certain carrion flies can detect red reflections (Autrum & Stumpf 1953), but it is not known if those are involved in colour perception (see Kevan et al. 2001). In a series of experiments, Kugler (1951, 1956) showed that greenbottle flies (*Lucilia* sp.), blow flies (*Calliphora* sp.) and flesh flies (*Sarcophaga* sp.) favour yellow and white coloured models over brown and purple ones in the presence of a sweet scent, but the opposite in the presence of a carrion scent. Unscented models were ignored.

It follows that the suite of characters, common to deceitful flowers such as *Ceropegia*, *Aristolochia*, *Rafflesia* and *Stapelia*, act synergistically to mislead anthophiles. Overall, it appears that olfaction and vision (including colour vision) are important, but that each sensory modality may take precedence at different distances depending on plant species and floral stage, pollinator species and physiological state, and environmental conditions.

#### Other host mimicry

Some flowers mimic odours and substrates that are attractive to guilds of Diptera other than the carrion flies mentioned above (Tab. 7). Best known in this regard are the flowers that mimic Basidiomycetes and entice fungus gnats (Mycetophilidae, Sciaridae) to oviposit. Plants of this type occur in various genera, such as *Arisarum* and *Arisaema* spp. (Araceae), *Aristolochia*, *Asarum* and *Heterotropa* spp. (Aristolochiaceae), *Corybas*, *Dracula*, *Masdevallia* spp. and *Cypripedium* spp. (Orchidaceae) (Vogel 1973, 1978; Dressler 1981; Sugawara 1988; Mesler & Lu 1993; Vogel &

TABLE 7. Modes of pollination-by-deceit in selected fly-pollinated plants.

Plant Family	Plant Taxon	Mode of Deceit*	Fly Taxon	Reference
Apiaceae	<i>Daucus carota</i> L.	AM	Muscidae	Eisikowitch 1980; Westmoreland & Muntan 1996
Apocynaceae	<i>Ceropegia dolichophylla</i> Schltr.	FM	<i>Desmometopa sordida</i> (Fallen) (Milichiidae)	Heiduk et al. 2010
Araceae	<i>Arum conophalloides</i> Kotschy ex Schott.	FM	Ceratopogonidae	Knoll 1926
	<i>Arum italicum</i> Mill.	BSM	Psychodidae, Sciaridae, Chironomidae	Diaz & Kite 2002; Albre et al. 2003; Chartier et al. 2011
	<i>Arum maculatum</i> L.	BSM	<i>Psychoda phalaenoides</i> L. (Psychodidae), <i>Smittia pratorum</i> Goetghebuer (Chironomidae)	Proctor & Yeo 1973; Lack & Diaz 1991; Diaz & Kite 2002; Albre et al. 2003; Chartier et al. 2011
	<i>Arum palaestinum</i> Boiss.	BSM, FM	<i>Drosophila</i> spp., <i>Zaprionus</i> spp. (Drosophilidae)	Stoekl et al. 2010
	<i>Arum pictum</i> L.	BSM	Sphaeroceridae	Quilichini et al. 2010
	<i>Arisaema</i> spp.	BSM		Vogel & Martens 2000
	<i>Arisaema triphyllum</i> (L.)	BSM	Mycetophilidae, Sciaridae, others	Barriault et al. 2010
	<i>Arisarum</i> spp.	BSM		
	<i>Helicodiceros muscivorus</i> (Schott ex. K. Koch)	BSM	<i>Calliphora</i> spp., <i>Lucilia</i> spp. (Calliphoridae), <i>Fannia</i> sp. (Fanniidae)	Stensmyr et al. 2002; Seymour et al. 2003
	Aristolochiaceae	<i>Aristolochia baenzigeri</i> B.Hansen & Phuph.	BSM?	Phoridae
	<i>Aristolochia grandiflora</i>	BSM	Calliphoridae, others	Burgess et al. 2004
	<i>Aristolochia littoralis</i> Parodi	BSM, DF?	Phoridae	Hall & Brown 1993
	<i>Aristolochia pilosa</i> H. B. & K.	BSM	Chloropidae, Milichiidae	Wolda & Sabrosky 1986
	<i>Aristolochia watsonii</i> (Wooton & Standley)	FM	Ceratopogonidae	Crosswhite & Crosswhite 1984
	<i>Asarum hartwegii</i> S. Wats.	BSM	<i>Suillia thompsoni</i> Gill (Heleomyzidae) <i>Hylemya fugax</i> (Meigen) (Anthomyiidae), <i>Scaptomyza pallida</i> Zetterstedt (Drosophilidae) <i>Docosia</i> spp. (Mycetophilidae)	Mesler & Lu 1993
	<i>Heterotropa</i> spp.	BSM		Sugawara 1988
Asteraceae	<i>Gorteria diffusa</i> Thunb.	DF	<i>Megapalpus nitidus</i> Macq., <i>M. capensis</i> Wiedemann (Bombyliidae)	Johnson & Midgley 1997; Ellis & Johnson 2010
	<i>Dimorphotheca pluvialis</i> (L.) Moench	DF?	<i>Megapalpus</i> spp., <i>Usia bicolor</i> Macq. (Bombyliidae)	Johnson & Midgley 1997
Geraniaceae	<i>Pelargonium tricolor</i> Curt.	NM, DF?	<i>Megapalpus</i> spp., <i>Usia bicolor</i> Macq. (Bombyliidae)	McDonald & van der Walt 1992; Johnson & Midgley 1997
Gnetaceae	<i>Gnetum cuspidatum</i> Blume	BSM	<i>Homoneura</i> (Lauxaniidae), <i>Anopheles</i> (Culicidae), others	Kato et al. 1995
Linaceae	<i>Linum pubescens</i> Banks & Solander	DF?	<i>Usia bicolor</i> Macq.	Johnson & Midgley 1997
Orchidaceae	<i>Brownleea galpinii</i> (Bolus) H.P. Linder	FM	<i>Prosoeca</i> spp. (Nemestrinidae), <i>Philoliche andrenoides</i> Usher (Tabanidae)	Johnson et al. 2003
	<i>Bulbophyllum variegatum</i> Thouars		Platystomatidae	Humeau et al. 2011

TABLE 7 continued

Plant Family	Plant Taxon	Mode of Deceit*	Fly Taxon	Reference
	<i>Corybas</i> spp.	BSM		Dressler 1981
	<i>Cypripedium debile</i> Reichb.	BSM		Dressler 1981
	<i>Cypripedium fargesii</i> Franch.	FM	<i>Agathomyia</i> sp. (Platyezidae)	Ren et al. 2011
	<i>Cypripedium reginae</i> Walter	PM	<i>Syrphus torvus</i> Osten-Sacken (Syrphidae)	Vogt 1990
	<i>Disa cephalotes</i> Rchb.f.	FM	<i>Prosoeca</i> spp. (Nemestrinidae), <i>Philoliche andrenoides</i> Usher (Tabanidae)	Johnson et al. 2003
	<i>Disa draconis</i> (L.f.) Sw.	FM	<i>Moegistorhynchus longirostris</i> Wiedemann (Nemestrinidae)	Johnson & Steiner 1997
	<i>Disa harveiana</i> Lindl.	FM	<i>Philoliche rostrata</i> Linnaeus (Tabanidae)	Johnson & Steiner 1997
	<i>Disa karoovica</i> Johnson & Linder	FM	<i>Philoliche gulosa</i> Wiedemann (Tabanidae)	Combs & Pauw 2009
	<i>Disa nervosa</i> Lindl.	FM	<i>Philoliche aethiopica</i> (Thunberg) (Tabanidae)	Johnson & Morita 2006
	<i>Disa nivea</i> H.P. Linder	FM	<i>Prosoeca ganglbaueri</i> Lichtwardt (Nemestrinidae)	Anderson et al. 2005
	<i>Disa pulchra</i> Sond.	FM	<i>Philoliche aethiopica</i> (Thunberg) (Tabanidae)	Johnson 2000; Jersakova & Johnson 2006
	<i>Dracula</i> spp.	BSM	<i>Zygothrica</i> , <i>Hirtodrosophila</i> (Drosophilidae)	Dressler 1981; Endara et al. 2010
	<i>Epipactis consimilis</i> Don.	BSM	<i>Sphaerophoria ruepellii</i> Wiedemann, <i>S. scripta</i> L. (Syrphidae)	Ivri & Dafni 1977
	<i>Epipactis veratrifolia</i> Don.	BSM	<i>Ischiodon aegyptus</i> Wiedemann, <i>Eupeodes corollae</i> (F.), <i>Episyrphus balteatus</i> De Geer (Syrphidae)	Stoekl et al. 2011
	<i>Govenia utriculata</i> (Sw.) Lindl. Dressler	FM	<i>Salpingogaster</i> spp. (Syrphidae)	Pansarin 2008
	<i>Lepanthes</i> spp.	DF	<i>Bradysia</i> sp. (Sciaridae)	Blanco & Barboza 2005
	<i>Masdevallia</i> spp.	BSM		Dressler 1981
	<i>Paphiopedilum villosum</i> (Lindl.) Stein	NM	Various	Bänziger 1996
	<i>Phragmipedium pearcei</i> (Rchb.f.) Rauh & Senghas	BSM	<i>Ocyrtamus antiphates</i> (Walker) (Syrphidae)	Pembererton 2011
	<i>Satyrium pumilum</i> Thunb.	BSM	Sarcophagidae	van der Niet et al. 2011
	<i>Thelymitra antennifera</i> Hook.	PM	Syrphidae	Dafni & Calder 1987
Rafflesiaceae	<i>Rafflesia kerrii</i> spp.	BSM	Calliphoridae	Bänziger 1991; Meve & Liede 1994
Rosaceae	<i>Rubus chamaemorus</i> L.	CD	Syrphidae	Agren et al. 1986; Bierzychudek 1987
Santalaceae	<i>Osyris alba</i> L.	CD	Muscidae, Mycetophilidae	Aronne et al. 1993
Saxifragaceae	<i>Parnassia palustris</i> L.	NM	Calliphoridae, Syrphidae	Kugler 1956

\* AM = insect aggregation mimic, BSM = brood site mimic, CD = cryptically dioecious, DF = dummy female (pseudocopulatory mimic), FM = food mimic (incl. mimics of rewarding flowers), HM = oviposition host mimic, NM = nectar/nectary mimic, PM = pollen mimic.

Martens 2000; Dentinger & Roy 2010; Endara et al. 2010; Ren et al. 2011). In Malaysia, lianas of *Gnetum cuspidatum* Blume (Gnetaceae) have cauline strobili near the forest floor that attract *Homoneura* (Lauxaniidae), *Anopheles* (Culicidae), and other Diptera with their fungus-like odour and nectar reward (Kato et al. 1995). Typically, fungus-mimetic flowers pollinated by fungus gnats are dark purplish brown and borne close to the ground, and they often exude a strong fungus-like odour, which is the main attractant (Vogel 1973). Although other mimetic characters such as visual and tactile cues are presumably important attractants, odours have the most important role, at least in *Arisaema* (Vogel & Martens 2000; Barriault et al. 2010) and in *Dracula* (Dentinger & Roy 2010; Endara et al. 2010). High humidity caused by intense local transpiration further intensifies the mushroom guise. In *Artocarpus integer* (Thunb.) Merr., female gall midges pick up pollen while ovipositing and feeding on fungus that infect the male flowers; female flowers do not contain fungus, but mimic the scent of infected male flowers to attract the pollen-bearing flies (Sakai et al. 2000).

Tactile cues may play a role in short-range attraction and guidance of the exploring flies once they alight on the flower. Fungoid lamellae and pores are found on parts of the blossom in bolete-mimics, and the deception is so complete that the flies oviposit, and in the process pick up pollen grains in their hairs (Sugawara 1988). On *Asarum hartwegii* in northern California, Mesler & Lu (1993) found eggs of several fly species (see Tab. 7). The fungivorous larvae usually die upon eating the toxic tissue of these plants. Monoecious Araceae are protogynous, luring pollen-bearing flies and trapping them in contact with the female flowers, then releasing pollen and allowing the flies to escape (Albre et al. 2003). Sciaridae and Mycetophilidae attracted to the kettle trap blossoms of dioecious *Arisaema* escape through exit holes of male spathes, but die in female spathes after potential pollination (Vogel & Martens 2000; Barriault et al. 2010). In fungus-mimetic flowers pollinated by mycophagous Diptera such as Muscidae and Phoridae, there may be severe reduction of reproductive success of females ovipositing into the flowers. These factors may result in a coevolutionary arms race between fungus gnats (the search image for brood substrate) and plants with fungus-mimicking flowers (deceptive stimuli).

Other flowers imitate the odours and, in some cases, morphologies of prey or host animals (Knoll 1926; Vogel 1973, 1978; Crosswhite & Crosswhite 1984). Certain female simuliid flies are strongly visually attracted to distinct body parts of their hosts, and *Wilhelmia equina* L. (Simuliidae) is preferably attracted to the "ears" of horse dummies (Wenk & Schlörer 1963). Coloured swellings on the labellum of some orchids resemble aphids (and may emit an aphid-honeydew-like odour) and induce aphidophagous syrphids (subfamily Syrphinae) to visit the flowers, oviposit and perhaps pollinate (Ivri & Dafni 1977; Pemberton 2010). *Epipactis veratrifolia* Don. (Orchidaceae) accomplishes the same effect with scent by mimicking aphid alarm pheromone (Stoekl et al. 2011). While nectar may be offered to the ovipositing syrphids, if the larvae are unable to find real

aphids to eat they will die (Pemberton 2010; Stoekl et al. 2011). Many milichiid flies are kleptoparasites, taking nourishment from seeping wounds of insects captured by spiders, and *Ceropegia dolichophylla* Schltr. (Apocynaceae) mimics the odour of insect hemolymph to lure milichiid pollinators (Heiduk et al. 2010).

### *Pseudonectar and pseudopollen*

Pseudonectaries (organs resembling nectaries but not producing nectar) take the form of glistening, shiny, or refractile structures or areas on the blossom, and may distract pollinators from true nectaries, if they exist (Faegri & van der Pijl 1979; Chase & Peacor 1987; McDonald & van der Walt 1992; Vogel 1993; Bänziger 1996; Pemberton 2010). The exact role of the pseudonectaries in reproduction is unclear in many cases (Tab. 7). Glistening structures, such as the "mesmerizing wart" of *Paphiopedilum villosum* (Lindl.) Stein (Orchidaceae) may lure visitors into a trap where they contact the pollen (Bänziger 1996), or possibly distract less desirable visitors from rewards intended for pollinators, as in *Parnassia palustris* L. (Saxifragaceae) (Kugler 1956). Many flowering plants have a corolla bearing yellow, UV-absorbing spots that imitate the colour of pollen and anthers (Lunau 2000; Pansarin 2008). Visitors attempting to collect pollen from these spots may be maneuvered into contact with the real pollen, and thus serve as a form of floral guide although no reward is given (Dafni & Calder 1987; Vogt 1990). The petals of some *Saxifraga* flowers (Saxifragaceae) display a particular type of floral guide consisting of an array of small spots on the petals that are apically red and basally yellow and combined with red or white pollen and anthers. Using artificial flowers that simulated this colour pattern, naive *Eristalis tenax* L. (Syrphidae) were selectively directed by the transition of colour from red over orange to yellow and moved towards the yellow coloured dots more often than towards the red coloured dots (Lunau et al. 2005). In actual flowers, attraction to the yellow spots acts to bring the pollen-foraging fly into contact with the actual pollen, which has less visibility or contrast, without it being eaten. Some plants have floral staminodes that produce pseudopollen (Tab. 7). The material may be used to provision brood by bees (Apoidea), but actual feeding by Diptera on pseudopollen has not been reported.

### *Mimicry of rewarding flowers by non-rewarding flowers*

In "mistake pollination" male and female unisexual flowers differ in the reward that they offer, and potential pollinators would be less likely to visit the poorer-rewarding flowers if they were distinguishable, adversely affecting cross-pollination (Baker 1976). The most common example is the lack of pollen in female flowers, which then mimic the appearance of male flowers (e.g., have sexually functionless anthers), and attract visitors seeking the missing reward (Agren et al. 1986; Bierzychudek 1987; Aronne et al. 1993; Charlesworth 1993; Yuan et al. 2007, 2008). *Eristalis tenax* and other Syrphidae visit the rewarding flowers of male plants of "cryptically dioecious" *Rosa setigera* Michx. (Rosaceae) in southern Ontario, Canada, early in the morning, but seem to be displaced to the female plants by bees later in the day. The malformed and inviable "pollen"

from the female plants probably provides some nutrition. This strategy provides systematic pollen transfer from males to females over the course of the day, but the relative importance of the native anthophiles to the flowers of this plant for pollination could not be assessed given the preponderance of European honey bees (Kevan et al. 1990).

There are also examples of heterospecific non-rewarding flowers that are pollinated via their mimicry of rewarding flowers (Tab. 7). At a community level, nectarless plants may ensure visitation if their flowers are similar to those of rewarding species, in a form of Batesian mimicry. There are numerous examples, particularly among the tubular flowers visited by long-tongued Nemestrinidae, Bombyliidae, and Tabanidae in southern Africa, of plant species that offer no nectar reward (e.g., Schiestl 2005; Pemberton 2010; see Tab. 7). These plants often co-occur with a suite of plants that have similar, but nectariferous flowers, and it has been proposed that floral mimicry alone ensures visitation to the nectarless species. This system encourages out-crossing in the mimic and acts as an evolutionary selective force in maintaining populations of both model and mimic.

### Sexual deception

Some flowers mimic the appearance of female insects or emit scents that mimic sex pheromones to attract males, sometimes at concentrations much greater than the female insects themselves (Schiestl 2005) (Tab. 7). The best known example is pseudocopulation by male bees and wasps with flowers that mimic females (e.g., *Ophrys* orchids; Faegri & van der Pijl 1979). Pseudocopulation is less widely documented in the Diptera, but is a possible mechanism in *Microdon* hoverfly pollination of some *Ophrys* orchids (Paulus 2005), and confirmed in sciarid pollination of several *Lepanthes* species (Blanco & Barbosa 2005; Pemberton 2010). There is also evidence that spots in certain Asteraceae, Geraniaceae, and Linaceae are reflective mimics of female bombyliids that may be attractive to males seeking mates (Johnson & Midgley 1997; Ellis & Johnson 2010).

### Floral larcenists

Some insects are ill-adapted for the pollination of flowers they visit (Faegri & van der Pijl 1979; Inouye 1980), and may become nectar (or pollen) robbers or thieves (see Inouye 1980 for the terminology of floral larceny). Robbers bite holes at the bases of corollas in order to reach hidden rewards. Because they do not interact with the reproductive structures of the flower in obtaining the reward, they do not cross-pollinate the flower. Although it is unlikely that many Diptera are nectar robbers due to lack of suitable mouthparts, many small Diptera are probably secondary robbers that utilize the holes created by primary robbers. For example, Kevan (unpubl.) often noted mosquitoes feeding through holes made by bumble bees (*Bombus* spp.) in the bases of the tubular flower of *Mertensia ciliata* (Torr.) G. Don (Boraginaceae) in the subalpine zone of Colorado. Other nectar (or pollen) thieves may enter flowers to obtain nectar without damaging the flower, but also without contacting anthers or stigmas.

Any fly species that commonly visits a plant for its rewards, but seldom pollinates it, is a thief. For example, flies were the most common visitors of *Listera ovata* (L.) R. Br. (Orchidaceae) in Sweden, but they were considered unimportant as pollinators (Nilsson 1981). Pont (1993) lists some Muscidae that commonly visit flowers for nectar, but avoid contact with the anthers. *Delia flavifrons* Zetterstedt abuses the system even further: These flies feed, mate and lay their eggs on flowers of *Silene vulgaris* (Moench) Garcke (Caryophyllaceae), but do not pollinate them (Pettersson 1992). Given the small size of many Nematocera and Acalyptratae, it is likely that they are often nectar and pollen thieves, but the importance of this behaviour to either the thieves or the flowers has been little-studied. Zhang et al. (2013) found that flies of the genus *Scatopse* (Scatopsidae) were nectar thieves of *Corydalis ambigua* (Papaveraceae) flowers, and that their presence deterred the pollinating bumble bees (Apidae: *Bombus* sp.).

### CONCLUSIONS

The taxonomic, ecological and behavioural diversity of Diptera as anthophiles is probably greater than for any other insect order, including Hymenoptera. Myiophily is a major component of pollination, and the floral features reflect fly biology. Nectar is the most sought reward by flies, many of whom depend on the energy it provides for flight, and often has other nutrition benefits such as amino acid content. Pollenophagy is widespread in Diptera, but not as universal as in Apoidea, which primarily collect pollen for larval provisioning. Pollen is highly variable in its chemical and nutritional characteristics, and even pollen form sometimes reflects the importance of pollination by Diptera. Flies also seek mates, prey, protection, and brood sites in flowers. They find and forage at flowers by visual and olfactory cues that present a complex array of attractants of differing relative importance depending on the types of flies, their sexes, their immediate nutritional needs, and innate and learned behaviours. Sensory capabilities of flies are outstanding among insects and are highly varied from colour vision to shape, size, and motion perception and contact chemoreception to olfactory discrimination.

Our synthesis illustrates the complexity of myiophily in terms of rewards and attractants, but elucidates some general and unifying principles. Overall, it is difficult to separate attractants and rewards, and even more difficult to tease apart the relative importance of the different sensory modalities of floral attraction to Diptera, or even for particular taxa within the order. Moreover, the complexity of myiophily, from neurophysiology to community ecology, begs for imaginative and synthetic research. There is need for metabolic and physiological studies on pollen and nectar consumption and neurophysiological studies on the perception of floral colour and odour stimuli for a better understanding of fly visitation and activity in pollination. It becomes evident that myiophily is not a clear-cut phenomenon but rather multifaceted, integrating over groups of Diptera with different physiological capabilities and different motivations to visit flowers. Especially, competition with bees has not been adequately studied, though many

flowering plants achieve reproductive success through both bee and fly pollinators (e.g., Kearns & Inouye 1994). The trade-offs for flowering plants that either specialise in fly pollination or compromise by attracting and nourishing bees as well as flies and use both as pollen vectors, are not well understood, even though “generalist” pollination by diverse arrays of pollinators has excited recent scientific interest (Waser et al. 1996; Herrera 1996; Ollerton 1996; Johnson & Steiner 2000).

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