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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. 1). 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 1. Selected records of fly consumption of edible rewards offered by the reproductive organs of selected angiosperms.

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

TABLE 1. continued

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

TABLE 1. continued

Plant Family	Plant Taxon	Reward(s)* FN	PO	EX	MS	Fly Taxon**	Reference
Polemoniaceae	*Phlox paniculata* L.	+	-	-	-	*Aedes dorsalis* (Meigen) (Culicidae)	Sandholm & Price 1962
Polygonaceae	*Polygonum* spp.	-	+	-	-	*Melanostoma novaezelandae* Macquart (Syrphidae)	Irvin et al. 1999
Portulacaceae	*Claytonia virginica* L.	+	+	-	-	*Bombylius major* L. (Bombyliidae)	Motten et al. 1981
Primulaceae	*Primula vulgaris* Huds.	-	+	-	-	*Hylemyia* sp. (Anthomyiidae)	Willis & Burkill 1903
Ranunculaceae	*Ranunculus repens* L.	-	+	-	-	*Eristalis tenax* Linnaeus (Syrphidae)	Haslett 1989b
Rhizophoraceae	*Avicennia officinalis* L.	+	+	-	-	*Chrysomya megacephala* Fabricius (Calliphoridae)	Aluri 1990
Rosaceae	*Rubus fruticosus* L.	-	+	-	-	*Episyrphus balteatus* (De Geer) (Syrphidae)	Haslett 1989b
Rubiaceae	*Galium trifidum* L.	+	-	-	-	*Sphaerophoria cylindrica* Say (Syrphidae)	Robertson 1928
Salicaceae	*Populus tremula* L.	-	+	-	-	*Melangyna lasiophthalma* Zetterstedt (Syrphidae)	Ssymank & Gilbert 1993
Santalaceae	*Osyris alba* L.	-	-	+	-	various (PC)	Aronne et al. 1993
Sarraceniaceae	*Sarracenia purpurea* L.	+	+	-	-	*Fletcherimyia fletcheri* (Aldrich) (Sarcophagidae) (PC)	Ne'eman et al. 2006
Saxifragiaceae	*Tolmiea menziesii* (Pursh) Torr. & Gray	+	-	-	-	*Gnoriste megarrhina* Osten Sacken (Mycetophilidae) (PC)	Goldblatt et al. 2004
Schisandraceae	*Kadsura longipedunculata* Finet & Gagnepain	-	+	-	-	*Megommata* sp. (Cecidomyiidae) (PC)	Yuan et al. 2008; Thien et al. 2009
	Schisandra henryi Clarke	-	+	-	-	*Megommata* sp. (Cecidomyiidae) (PC)	Yuan et al. 2007; Thien et al. 2009
	Schisandra spenanthera Rehder & E.H.Wilson	-	+	-	-	*Resseliella* sp. (Cecidomyiidae) (PC)	Du et al. 2012
Scrophulariaceae	*Hebe* sp.	-	+	-	-	*Melangyna ropalus* (Walker) (Syrphidae)	Holloway 1976
Solanaceae	*Solanum nigrum*	-	+	-	-	*Melanostoma mellinum* L. (Syrphidae)	van der Goot & Grabandt 1970
Sparganiaceae	*Sparganium erectrum* L.	-	+	-	-	*Syrphus ribesii* L. (Syrphidae)	Leereveld 1984
Staphyleaceae	*Staphylea trifolia*	+	-	-	-	*Eristalis flavipes* Wk. (Syrphidae)	Robertson 1928
Stylidiaceae	*Forstera* sp.	-	+	-	-	*Paragus* sp. (Syrphidae)	Holloway 1976
Tiliaceae	*Tilia* sp.	-	+	-	-	*Xylota sylvarum* Linnaeus (Syrphidae)	Ssymank & Gilbert 1993
Trimeniaceae	*Trimenia moorei* (Oliv.) Philipson	-	+	-	-	*Melangyna* sp., *Triglyphus fulvicornis* Bigot (Syrphidae)	Bernhardt et al. 2003
Typhaceae	*Typha latifolia* L.	-	+	-	-	*Platycheirus peltata* Meigen (Syrphidae)	Leereveld 1982
Urticaceae	*Urtica dioica* L.	-	+	-	-	*Xylota sylvarum* Linneaus (Syrphidae)	Ssymank & Gilbert 1993
Verbenaceae	*Verbena officinalis* L.	+	-	-	-	*Platycheirus* sp. (Syrphidae)	Willis & Burkhill 1895
Violaceae	*Viola lutea* Smith	-	+	-	-	*Anthomyia* spp. (Anthomyiidae)	Willis & Burkill 1903
Welwitschiaceae	*Welwitschia mirabilis* Hook	-	-	-	+	Calliphoridae, Sarcophagidae, Ulidiidae (PC)	Wetschnig & Depisch 1999
Winteraceae	*Pseudowintera colorata* (Raoul) Dandy	-	-	+	-	*Smittia* (Chironomidae)	Lloyd & Wells 1992
Variety of plants		+	+	-	-	*Atrichopogon pollenivorus* Downes (Ceratopogonidae)	Downes 1955; De Meillon & Wirth 1989
		+	+	-	-	*Anthalia* 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 (Ephydridae) 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	*Alocasia* spp.	*Colocasiomyia* spp. (Drosophilidae)	BS, PC	Miyake & Yafuso 2003, 2005; Toda & Lakim 2011; Takano et al. 2012
	Alocasia macrorrhiza (L.) G. Don	*Neurochaeta inversa* McAlpine (Diptera: Neurochaetidae)	BS, MS?	Shaw et al. 1982
	Alocasia pubera Schott. (S)	*Atherigona* spp. (Anthomyiidae)	BS, PC	van der Pijl 1953; Simpson & Neff 1981
	Peltandra virginica Kunth	*Elachiptera formosa* Loew (Chloropidae)	BS, PC	Patt et al. 1995
Aristolochiaceae	*Aristolochia* spp. (some S)	Phoridae, Drosophilidae	BS, PC	Disney & Sakai 2001; Sakai 2002a,b
Asteraceae	*Erigeron neomexicanus* Gray	*Oligodranes mitis* Cresson (Bombyliidae)	MS, PC	Evenhuis 1983
Balanophoraceae	*Thonningia sanguinea* Vahl	*Morellia* sp. (Muscidae)	BS, PC	Goto et al. 2012
Balsaminaceae	*Impatiens uniflora* Hayata, *I. tayemonii* Hayata	*Hirtodrosophila actinia* (Okada), *H. yapingi* Gao (Drosophilidae)	BS, MS?	Gao 2011
Campanulaceae	*Centropogon solanifolius* Benth.	*Zygothrica neolinea* (Drosophilidae)	BS	Weiss 1996
Linaceae	*Linum pubescens* Banks & Solander	*Usia bicolor* Macq. (Bombyliidae)	MS, PC	Johnson and Dafni 1998
Monimiaceae	*Siparuna* spp.	Cecidomyiidae	BS, PC	Feil 1992
Moraceae	*Artocarpus integer* (Thunb.) Merr. (S)	*Contarinia* spp. (Cecidomyiidae)	BS, PC	Sakai et al. 2000, 2002a
		Dettopsomyia spp. (Drosophilidae)	BS, PC	van der Pijl 1953, Simpson & Neff 1981
Myrtaceae	*Eucalyptus* spp.	*Drosophila flavohirta* Malloch (Drosphilidae)	BS, PC	du Toit 1987; Tribe 1991; Nicolson 1994a,b
Nymphaeaceae	*Nuphar subintegerrima* (Casp.) Makino	*Notiphila maritima* Krivosheina (Ephydridae)	MS, BS	Nagasaki 2007
	Various	*Notiphila brunnipes* (Ephydridae)	BS	van der Velde et al. 1978
Orchidaceae	*Pleurothallis* spp.	*Tricimba* spp. (Chloropidae) *Megaselia* spp. (Phoridae)	BS, PC	Borba & Semir 2001
Ranunculaceae	*Trollius europaeus* L. (S)	*Chiastochaeta* spp. (Anthomyiidae)	MS, BS, PC	Pellmyr 1989, Despres & Jaeger 1999, Ferdy et al. 2002, Despres 2003, Despres et al. 2007
Saxifragaceae	*Saxifraga oppositifolia* L.	*Scathophaga apicalis* (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 radicatum* 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	*Alocasia odora* C. Koch	*Colocasiomyia alocasiae* (Okada), *C. xenalocasiae* (Okada) (Drosophilidae)	MT	Yafuso 1993, Miyake & Yafuso 2003
Aristolochiaceae	*Aristolochia* spp.	various	MT	Disney & Sakai 2001; Sakai 2002a
Asteraceae	*Oritrophium limnophilum* (Sch. Bip.) Cuatr.	various	PS	Stanton and Galen 1989
	Calendula arvensis L.	*Usia aurata* Fabr. (Bombyliidae)	SH	Orueta 2002
Campanulaceae	*Campanula rotundifolia* L.	many	PS	Drabble & Drabble 1927, Parmenter 1958
Convolvulaceae	*Convolvulus* spp.	many	PS	Drabble & Drabble 1927, Parmenter 1958
Geraniaceae	*Pelargonium tricolor* Curt.	*Megapalpus capensis* Wiedemann (Bombyliidae)	SH	McDonald & van der Walt 1992
Illiciaceae	*Illicium floridanum* Ellis	many	MT	Thien et al. 2009
	Illicium spp.	*Clinodiplosis* sp. nov. (Cecidomyiidae)	MT	Luo et al. 2010
Nymphaeaceae	Various	*Notiphila brunnipes* (Ephydridae)	PS	van der Velde et al. 1978
Ranunculaceae	*Adonis ramosa* Franch.	Agromyzidae	PS	Kudo 1995
	Ranunculus adoneus Gray	various	PS	Smith 1975
Rosaceae	*Dryas integrifolia* M. Vahl.	*Aedes* spp. (Culicidae)	SH	Hocking & Sharplin 1965; Hocking 1968; Kevan 1975
		Rhamphomyia spp. (Empididae)	SH	Kevan 1975
		Carposcalis carinata (Curran) (Syrphidae)	SH	Kevan 1975
		Boreellus atriceps (Zetterstedt) (Calliphoridae)	SH	Kevan 1975
Saxifragaceae	*Saxifraga oppositifolia* L.	*Smittia velutina* (Lundbeck) (Chironomidae)	PS	Kevan 1973, 2007
Scrophulariaceae	*Digitalis* 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 R	O	Y	G	B	P	OB	OW	UV	Reference
Bombyliidae										
Bombylius sp.					+	+				Knoll 1921
Calliphoridae										
Lucilia sp.			+							Kugler (1951, 1956)
Muscidae										
Pyrellia cyanicolor Zetterstedt			+							Cameron & Troilo 1982
Syrphidae										
Cheilosia albitarsus (Meigen)			+							Haslett 1989b
Eristalis pertinax (Scopoli)			++					+		Haslett 1989b
Eristalis tenax (L.)			++	+	+				+	Ilse 1949; Kugler 1950; Haslett 1989b; Lunau & Wacht 1994; Lunau & Maier 1995; Lunau 1996
Rhingia campestris Meigen					+	+				Haslett 1989b
Volucella pellucens (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 proboscidial 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 potentionally 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; Kastinger & 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; Kastinger & 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 (Browne 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. (Astercaeae)) 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 (Sprengel 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	PPV	PUV	St	VA	Fly Taxon	Reference
Araceae	*Arisaema* sp.	+	-	-	-	-	Mycetophilidae Sciaridae	Vogel & Martens 2000
Asclepiadaceae	*Ceropegia* sp.	-	-	-	-	+		Percival 1965
Asteraceae	*Gorteria diffusa* Thunb.	-	+	-	-	-	*Megapalpus nitidus* Macq., *M. capensis* Wiedemann (Bombyliidae)	Johnson & Midgley 1997; Ellis & Johnson 2010; Duncan & Ellis 2011
Brassicaceae	*Raphanus raphanistrum* L.	-	-	+	-	-		Kay 1976, 1978
Geraniaceae	*Pelargonium tricolor* Curtis	-	+	-	-	-		McDonald & van der Walt 1992
Iridaceae	*Lapeirousia oreogena* Schltr. ex Goldblatt	-	+	-	-	-	*Prosoeca* sp. (Nemestrinidae)	Hansen et al. 2012
Linaceae	*Linum pubsecens* Banks & Solander	-	+	-	-	-		Johnson & Dafni 1998
Malvaceae	*Herrania* spp.	-	-	+	+	+		Young 1984; Young et al. 1987b
	Theobroma spp.	-	-	+	+	-		Young 1984; Young et al. 1987b
Orchidaceae	*Cypripedium reginae* Walter	-	-	-	+	-	Syrphidae	Vogt 1990
	Paphiopedilum villosum (Lindley)	-	-	-	+	-	Syrphidae	Bänziger 1996
	Platanthera stricta 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 pericarpiicola* 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 sapromyiophily. 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	*Monodora tenuifolia* Benth.	U	F	Various	Gottsberger et al. 2011
	Uvariopsis congolana (De Wild.) R.E. Fr.	U	F	Various	Gottsberger et al. 2011
Apocynaceae	*Huernia hystrix* N.E.Br.	B, Ph	F	Calliphoridae, Sarcophagidae, Muscidae	Johnson & Jurgens 2010
	Orbea variegata Haw.	AD, Su	F	Calliphoridae, Sarcophagidae, Muscidae	Johnson & Jurgens 2010
	Orbea verrucosa (Masson) L.C.Leach	M	F	Calliphoridae, Sarcophagidae, Muscidae	Johnson & Jurgens 2010
	Stapelia gigantea N.E.Br.	M, Su	F	Calliphoridae, Sarcophagidae, Muscidae	Johnson & Jurgens 2010
	Stapelia leendertziae N.E.Br.	Su	F	Calliphoridae, Sarcophagidae, Muscidae	Johnson & Jurgens 2010
Araceae	*Alocasia* spp.	B, T	N	*Colocasiomyia* spp. (Drosophilidae)	Miyake & Yafuso 2005
	Arum italicum Mill.	AL, AP	F	Psychodidae, Sciaridae, Chironomidae	Diaz & Kite 2002; Albre et al. 2003
	Arum maculatum L.	AD, AL, AP	F	*Psychoda phalaenoides* L. (Psychodidae), *Smittia pratorum* Goetghebuer (Chironomidae)	Diaz & Kite 2002; Albre et al. 2003
	Arum cyrenaicum Hruby, *Arum concinnatum* Schott	AL, AP	F	Various	Urru et al. 2010
	Colocasia esculenta (L.) Schott	Ph	N	*Bactrocera dorsalis* (Hendel) (Tephritidae)	Tan & Nishida 2012
	Spathiphyllum cannaefolium (Dryand. ex Sims) Schott	Ph	N	*Bactrocera* spp. (Tephritidae)	Tan & Nishida 2012
	Symplocarpus foetidus (L.) Nutt.		P, F	Various	Kevan 1989b
Aristolochiaceae	*Aristolochia cymbifera* Mart. & Zucc.		F	Calliphoridae, Sarcophagidae, Muscidae	Johnson & Jurgens 2010
	Aristolochia gigantea Mart. & Zucc.	AL	P	*Megaselia* spp., others (Phoridae)	Hipolito et al. 2012
	Aristolochia grandiflora Vahl		F	Calliphoridae, others	Burgess et al. 2004
	Aristolochia littoralis Parodi		F	Phoridae	Hall & Brown 1993
Asteraceae	*Achillea millefolium* L.	M		Culicidae	Healy & Jepson 1988; Jepson & Healy 1988
	Leucanthemum vulgare Lam.	M		Culicidae	Healy & Jepson 1988; Jepson & Healy 1988
	Cirsium arvense (L.) Scop	B, M		*Episyrphus balteatus* De Geer (Syrphidae)	Primante & Dotterl 2010
Austrobaileyaceae	*Austrobaileya scandens* C.T. White		F	Drosophilidae	Endress 2001; Thien et al. 2009
Caryophyllaceae	*Silene otites* (L.)	B, M	P	Culicidae	Brantjes & Leemans 1976, Jhumur et al. 2006, 2008
Euphorbiaceae	*Antidesma montanum* Blume		P	*Chrysomya* sp. (Calliphoridae), *Drino* sp. (Tachinidae), *Spilogona* sp., *Mitroplatia* sp. (Muscidae)	Li & Zhang 2007
Fabaceae	*Acacia cyclops* A. Cunn. ex G. Don	AP, T		*Dasineura dielsi* Rübsaamen (Cecidomyiidae)	Kotze et al. 2010

TABLE 6 continued

Plant Family	Plant Taxon	Dominant Components*	Odour Description**	Fly Taxon	Reference
Hyacinthaceae	*Eucomis humilis* Baker, *Eucomis bicolor* Baker	Su	F		Shuttleworth & Johnson 2010
Iridaceae	*Ferraria* spp.	AL, Ph	P, F	*Calliphora, Lucilia* (Calliphoridae), *Scathophaga* (Sarcophagidae), Muscidae, Tachinidae	Goldblatt et al. 2009, Johnson & Jurgens 2010
Liliaceae	*Scoliopus bigelovii* Torr.	U	F	Mycetophilidae	Mesler et al. 1980
Loganiaceae	*Fagraea berteriana* A. Gray	Ph, AL		*Bactrocera dorsalis* (Hendel) (Tephritidae)	Nishida et al. 1997; Shelly 2001; Tan & Nishida 2012
Orchidaceae	*Bulbophyllum* spp.	Ph, AL	P	*Bactrocera* spp. (Tephritidae)	Tan et al. 2002, 2006, 2011; Nishida et al. 2004; Tan & Nishida 2005, 2007, 2012
	Epipactis palustris (L.) Crantz			*Syritta pipiens* L. (Syrphidae)	Brantjes 1981
	Listera cordata (L.) R. Br.		F	Mycetophilidae	Ackerman & Mesler 1979
	Paphiopedilum villosum Lindley		F	Syrphidae	Bänziger 1996
	Phalaenopsis bellina (Rchb.f.) Christenson	Ph	N	*Bactrocera* spp. (Tephritidae)	Tan & Nishida 2012
	Phalaenopsis violacea H. Witte	Ph	N	*Bactrocera* spp. (Tephritidae)	Tan & Nishida 2012
	Platanthera stricta Lindley			Empididae	Patt et al. 1989
	Satyrium pumilum Thunb.	Su, B	F	Sarcophagidae	van der Niet et al. 2011
	Schizochilus angustifolius Rolfe.	B		*Orthellia* sp. (Muscidae)	van der Niet et al. 2010
	Schizochilus bulbinella Rchb.f.	B		Tephritidae, Chloropidae, *Allotrichoma pluvialis* Giordani Soika (Ephydridae)	van der Niet et al. 2010
	Schizochilus zeyheri Sond.	B		*Linnaemya* sp. (Tachinidae), *Orthellia* sp. (Muscidae)	van der Niet et al. 2010
Polemoniaceae	*Polemonium viscosum* Nutt.		F		
Rafflesiaceae	*Rafflesia kerrii* spp.	AD	F	Calliphoridae	Beaman et al. 1988; Bänziger 1991; Meve & Liede 1994
Ranunculaceae	*Trollius europaeus* L.	ST, others		*Chiastochaeta* spp. (Anthomyiidae)	Ibanez et al. 2010
Rutaceae	*Metrodorea nigra* A. St.-Hil.		F	*Pseudoptiloleps nigripoda* (Muscidae) *Fannia* sp. (Fanniidae)	Pombal & Morellato 2000
	Metrodorea stipularis Mart.		P	*Phaenicia eximia* (Calliphoridae); *Palpada* sp., *Ornidia obesa* (Syrphidae)	Pombal & Morellato 2000
Schisandraceae	*Kadsura longipedunculata* Finet & Gagnepain	AP	N	*Megommata* 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	*Daucus carota* L.	AM	Muscidae	Eisikowitch 1980; Westmoreland & Muntan 1996
Apocynaceae	*Ceropegia dolichophylla* Schltr.	FM	*Desmometopa sordida* (Fallen) (Milichiidae)	Heiduk et al. 2010
Araceae	*Arum conophalloides* Kotschy ex Schott.	FM	Ceratopogonidae	Knoll 1926
	Arum italicum Mill.	BSM	Psychodidae, Sciaridae, Chironomidae	Diaz & Kite 2002; Albre et al. 2003; Chartier et al. 2011
	Arum maculatum L.	BSM	*Psychoda phalaenoides* L. (Psychodidae), *Smittia pratorum* Goetghebuer (Chironomidae)	Proctor & Yeo 1973; Lack & Diaz 1991; Diaz & Kite 2002; Albre et al. 2003; Chartier et al. 2011
	Arum palaestinum Boiss.	BSM, FM	*Drosophila* spp., *Zaprionus* spp. (Drosophilidae)	Stoekl et al. 2010
	Arum pictum L.	BSM	Sphaeroceridae	Quilichini et al. 2010
	Arisaema spp.	BSM		Vogel & Martens 2000
	Arisaema triphyllum (L.)	BSM	Mycetophilidae, Sciaridae, others	Barriault et al. 2010
	Arisarum spp.	BSM		
	Helicodiceros muscivorus (Schott ex. K. Koch)	BSM	*Calliphora* spp., *Lucilia* spp. (Calliphoridae), *Fannia* sp. (Fannidae)	Stensmyr et al. 2002; Seymour et al. 2003
Aristolochiaceae	*Aristolochia baenzigeri* B.Hansen & Phuph.	BSM?	Phoridae	Disney & Bänziger 2009
	Aristolochia grandiflora	BSM	Calliphoridae, others	Burgess et al. 2004
	Aristolochia littoralis Parodi	BSM, DF?	Phoridae	Hall & Brown 1993
	Aristolochia pilosa H. B. & K.	BSM	Chloropidae, Milichiidae	Wolda & Sabrosky 1986
	Aristolochia watsonii (Wooton & Standley)	FM	Ceratopogonidae	Crosswhite & Crosswhite 1984
	Asarum hartwegii S. Wats.	BSM	*Suillia thompsoni* Gill (Heleomyzidae) *Hylemya fugax* (Meigen) (Anthomyiidae), *Scaptomyza pallida* Zetterstedt (Drosophilidae) *Docosia* spp. (Mycetophilidae)	Mesler & Lu 1993
	Heterotropa spp.	BSM		Sugawara 1988
Asteraceae	*Gorteria diffusa* Thunb.	DF	*Megapalpus nitidus* Macq., *M. capensis* Wiedemann (Bombyliidae)	Johnson & Midgley 1997; Ellis & Johnson 2010
	Dimorphotheca pluvialis (L.) Moench	DF?	*Megapalpus spp., Usia bicolor*Macq. (Bombyliidae)	Johnson & Midgley 1997
Geraniaceae	*Pelargonium tricolor* Curt.	NM, DF?	*Megapalpus spp., Usia bicolor*Macq. (Bombyliidae)	McDonald & van der Walt 1992; Johnson & Midgley 1997
Gnetaceae	*Gnetum cuspidatum* Blume	BSM	*Homoneura* (Lauxaniidae), *Anopheles* (Culicidae), others	Kato et al. 1995
Linaceae	*Linum pubescens* Banks & Solander	DF?	*Usia bicolor* Macq.	Johnson & Midgley 1997
Orchidaceae	*Brownleea galpinii* (Bolus) H.P. Linder	FM	*Prosoeca* spp. (Nemestrinidae), *Philoliche andrenoides* Usher (Tabanidae)	Johnson et al. 2003
	Bulbophyllum variegatum Thouars		Platystomatidae	Humeau et al. 2011

TABLE 7 continued

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

Abbott RJ, Irwin JA (1988) Pollinator movements and the polymorphism for outcrossing rate at the ray floret locus in groundsel, *Senecio vulgaris* L. Heredity 60: 295-298.

Ackerman JD (2000) Abiotic pollen and pollination: ecological, functional, and evolutionary perspectives. Plant Systematics and Evolution 222: 167-185.

Ackerman JD, Mesler MR (1979) Pollination biology of *Listera cordata* (Orchidaceae). American Journal of Botany 66: 820-824.

Addicott JF (1998) Regulation of mutualism between yuccas and yucca moths: Population level processes. Oikos 81: 119-129

Agee HR, Patterson RS (1983) Spectral sensitivity of stable, face, and horn flies and behavioral responses of stable flies to visual traps (Diptera: Muscidae). Environmental Entomology 12: 1823-1828.

Agnew JD (1976) A case of myophily involving Drosophilidae (Diptera). Journal of South African Botany 42: 85-95.

Agren J, Elmqvist T, Tunlid A (1986) Pollination by deceit, floral sex ratios and seed set in dioecious *Rubus chamaemorus* L.. Oecologia 70: 332-338.

Alba F, Romero L, Diaz De La Guardia D, Valle F (1995) Analysis of micronutrients in olive pollen. Journal of Plant Nutrition 18: 2247-2259.

Albre J, Quilichini A, Gibernau M (2003) Pollination ecology of *Arum italicum* (Araceae). Botanical Journal of the Linnean Society 141:205-214.

Aluri RJS (1990) Observations on the floral biology of certain mangroves. Proc. Indian Natn. Sci. Acad. B B56:367-374.

Anderson GJ, Hill JD (2002) Many to flower, few to fruit: the reproductive biology of *Hamamelis virginiana* (Hamamelidaceae). American Journal of Botany 89:67-78.

Anderson J, Laughlin SB (2000) Photoreceptor performance and the co-ordination of achromatic and chromatic inputs in the fly visual system. Vision Research 40: 13-31.

Anderson B, Johnson SD, Carbutt C (2005) Exploitation of a specialized mutualism by a deceptive orchid. American Journal of Botany 92:1342-1349.

Andersson S (1991) Floral display and pollination success in *Achillea ptarmica*. Holarctic Ecology 14: 186-191.

Armstrong JA (1979) Biotic pollination mechanisms in the Australian flora - a review. New Zealand Journal of Botany 17:467-508.

Arnold SEJ, Savolainen V, Chittka L (2009) Flower colours along an alpine altitude gradient, seen through the eyes of fly and bee pollinators. Arthropod-Plant Interactions 3:27-43.

Aronne G, Wilcock CC, Pizzolongo P (1993) Pollination biology and sexual differentiation of *Osyris alba* (Santalaceae) in the Mediterranean region. Plant Systematics and Evolution 188: 1-16.

Arroyo MTK, Primack R, Armesto J (1982) Community studies in pollination ecology in the high temperate Andes of central Chile. I. Pollination mechanisms and altitudinal variation. American Journal of Botany 69: 82-97.

Atluri JB, Ramana SPVR, Subba C (2004) Sexual system and pollination of *Sterculia foetida* Linn. Beitraege zur Biologie der Pflanzen 73:223-242.

Autrum H, Stumpf H (1953) Elektrophysiologische Untersuchungen über das Farbensehen von *Calliphora*. Zeitschrift für Vergleichende Physiologie 35:71-104.

Baker HG (1976) "Mistake" pollination as a reproductive system with special reference to the Caricaceae. In: Burley J, Styles BT (eds) Tropical trees: Variation, breeding and conservation. Academic Press, London, pp 161-69.

Baker HG, Baker I (1973a) Amino acids in nectar and their evolutionary significance. Nature 241:543-545.

Baker HG, Baker I (1973b) Some anthecological aspects of the evolution of nectar-producing flowers, particularly amino acid production in nectar. In: Heywood, VH (ed) Taxonomy and ecology. Academic Press, New York, pp 243-264.

Baker HG, Baker I (1983a) A brief historical review of the chemistry of floral nectar. In: Bentley B, Elias T (eds) The biology of nectaries. Columbia University Press, New York, pp 126-152.

Baker HG, Baker I (1983b) Floral nectar sugar constituents in relation to pollinator type. In: Jones CE, Little RJ (eds) Handbook of experimental pollination biology. Van Nostrand Reinhold, New York, pp. 117-41.

Baker HG, Baker I (1986) The occurrence and significance of amino acids in floral nectar. Plant Systematics and Evolution 151:175-186.

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

Bänziger H (1996) The mesmerizing wart: the pollination strategy of an epiphytic lady slipper orchid *Paphiopedilum villosum* (Lindl.) Stein (Orchidaceae). Botanical Journal of the Linnean Society 121:59-90.

Barraclough D, Slotow R (2010) The South African keystone pollinator *Moegistorhynchus longirostris* (Wiedemann, 1819) (Diptera: Nemestrinidae): notes on biology, biogeography, and proboscis length variation. African Invertebrates 51:397-403.

Barriault I, Barabe D, Cloutier L, Gibernau, M (2010) Pollination ecology and reproductive success in Jack-in-the-pulpit *(Arisaema triphyllum*) in Quebec (Canada). Plant Biology 12:161-171.

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

Bernhardt P (2000) Convergent evolution and adaptive radiation of beetle-pollinated angiosperms. Plant Systematics and Evolution 222:293-320

Bernhardt P, Thien LB (1987) Self-isolation and insect pollination in the primitive angiosperms: new evaluations of older hypotheses. Plant Systematics and Evolution 156:159-176.

Bernhardt P, Sage T, Weston P, Azuma H, Lam M, Thien LB, Bruhl J (2003) The pollination of *Trimenia moorei* (Trimeniaceae): Floral volatiles, insect/wind pollen vectors and stigmatic self-incompatibility in a basal angiosperm. Annals of Botany 92:445-458.

Bierzychudek P (1987) Pollinators increase the cost of sex by avoiding female flowers. Ecology 68:444-447.

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

Bishop LG (1974) An ultraviolet photoreceptor in a dipteran compound eye. Journal of Comparative Physiology A 91:267-275.

Blanco MA, Barboza G (2005) Pseudocopulatory pollination in *Lepanthes* (Orchidaceae: Pleurothallidinae) by fungus gnats. Annals of Botany 95:763-772.

Bonvehi JS, Jorda RE (1997) Nutrient composition and microbiological quality of honeybee-collected pollen in Spain. Journal of Agricultural and Food Chemistry 45:725-732.

Borba EL, Semir J (2001) Pollinator specificity and convergence in fly-pollinated *Pleurothallis* (Orchidaceae) species: a multiple population approach. Annals of Botany 88:75-88.

Borkent CJ, Schlinger EI (2008) Flower-visiting and mating behaviour of *Eulonchus sapphirinus* (Diptera: Acroceridae). Canadian Entomologist 140:250-256.

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

Brantjes NBM (1981) Ant, bee and fly pollination in *Epipactis palustris* (L.) Crantz (Orchidaceae). Acta Botanica Neerlandica 30:59-68.

Brantjes NBM, Leemans JAAM (1976) *Silene otites* (Caryophyllaceae) pollinated by nocturnal Lepidoptera and mosquitoes. Acta Botanica Neerlandica 25:281-295.

Brew AH (1987) The effect of colours and specific features of floral parts on the pollination of cocoa by ceratopogonid midges in Ghana. In: Proceedings of the 10th International Cocoa Research Conference. Santo Domingo, Dominican Republic, Cocoa Producers Alliance, Lagos, Nigeria. pp 307-310.

Briscoe AD, Chittka L (2001) The evolution of color vision in insects. Annual Review of Entomology 46:471-510.

Brody AK (1992) Oviposition choices by a pre-dispersal seed predator (*Hylemya* sp.). II A psotive association between female choice and fruit set. Oecologia 19:63-67.

Brody AK, Morita SI (2000) A positive association between oviposition and fruit set: female choice or manipulation? Oecologia 124:418-425.

Browne LB (1993) Physiologically induced chnages in resoure-oriented behavior. Annual Review of Entomology 38:1-25.

de Buck N (1990) Bloembezoek en bestuivingsecologie van zweefvliegen (Diptera, Syrphidae) in het bijzonder voor België. Studiedocumenten van het K.B.I.N. 167 pp.

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

Cameron RG, Troilo D (1982) Fly-mediated spore disperal in *Splachnum ampullaceum* (Musci). Michigan Botanist 21:59-65.

Campbell DR, Bischoff, Lord JM, Robertson AW (2010) Flower color influences insect visitation in alpine New Zealand. Ecology 91:2638-2649.

Candy, DJ, Becker A, Wegener G (1997) Coordination and integration of metabolism in insect flight. Comparative Biochemistry and Physiology B 117:497-512.

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

Charlesworth D (1993) Why are unisexual flowers associated with wind pollination and unspecialized pollinators? American Naturalist 141:481-490.

Chapman RF (1998) The Insects: Structure and Function (4th edition). Cambridge University Press, Cambridge, UK.

Chartier M, Pelozuelo L, Giberneau M (2011) Do floral odor profiles geographically vary with the degree of specificity for pollinators? Investigation in two sapromyophilous *Arum* species (Araceae). Annales de la Société Entomologique de France 47:71-77.

Chase MW, Peacor DR (1987) Crystals of calcium oxalate on the perianth of *Stelis* Sw. Lindleyana 2:91-94.

Chittka L, Menzel R (1992) The evolutionary adaptation of flower colours and insect pollinators' colour vision. Journal of Comparative Physiology A 171:171-181.

Chouteau M, Gibernau M, Barabe D (2008) Relationships between floral characters, pollination mechanisms, life forms, and habitats in Araceae. Botanical Journal of the Linnean Society 156:29-42.

Combs JK, Pauw A (2009) Preliminary evidence that the long-proboscid fly, *Philoliche gulosa*, pollinates *Disa karooica* and its proposed Batesian model *Pelargonium stipulaceum*. South African Journal of Botany 75:757-761.

Cooley JR (1995) Floral heat rewards and direct benefits to insect pollinators. Annals of the Entomological Society of America 88:576-579.

Corbet, PS (1972) The microclimate of Arctic plants and animals, on land and in fresh water. Acta Arctica 18:1-43.

Crepet WL (1979) Insect pollination: a palaeontological perspective. BioScience 29: 102-108.

Crosswhite FS, Crosswhite CD (1984) The southwestern pipevine (*Aristolochia watsonii*) in relation to snakeroot oil, swallowtail butterflies, and ceratopogonid flies. Desert Plants 6: 203-207.

Cruzan MB, Neal PR, Willson MF (1988) Floral display in *Phyla incisa*: consequences for male and female reproductive success. Evolution 42:505-515.

Dadd RH (1973) Insect nutrition: current developments and metabolic implications. Annual Review of Entomology 18:381-420

Dafni A (1984) Mimicry and deception in pollination. Annual Review of Ecology and Systematics 15: 259-278.

Dafni A, Calder DM (1987) Pollination by deceit and floral mimesis in *Thelymitra antennifera* (Orchidaceae). Plant Systematics and Evolution 158:11-22.

Dafni A, Giurfa M (1999) The functional ecology of floral guides in relation to insects behaviour and vision. In: Wasser SP (ed) Evolutionary theory and processes: Papers in honour of Eviatar Nevo. Kluwer Academic Publishers, Dordrecht, Netherlands, pp 1-22.

Dafni A, Kevan P (1996) Floral symmetry and nectar guides: ontogenetic constraints from floral development, colour pattern rules and functional significance. Botanical Journal of the Linnean Society 120:371-377.

Dafni A, Werker E (1982) Pollination ecology of *Sternbergia clusiana* (Ker-Gawler) Spreng. (Amaryllidaceae). New Phytologist 91:571-577.

Dafni A, Ivri Y, Brantjes NBM (1981) Pollination of *Serapias vomeracea* Briq. (Orchidaceae) by imitation of holes for sleeping solitary male bees (Hymenoptera). Acta Botanica Neerlandica 30:69-73.

Dafni A, Lehrer M, Kevan PG (1997) Spatial flower parameters and insect spatial vision. Biological Reviews 72: 239-282.

Daumann E (1971) Zur Bestäubungsökologie von *Aristolochia clematitis* L. Preslia 43:105-11.

David JR, Yassin A, Rasamizafi LA, Ravaomanarivo LHR, Debat V (2011) Scratching for food: an original feeding behavior in an African flower breeding *Drosophila*. Fly 5:285-290.

Dentinger BTM, Roy BA (2010) A mushroom by any other name would smell as sweet: *Dracula* orchids. McIlvainea 19:1-13.

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

Despres L, Jaeger N (1999) Evolution of oviposition strategies and speciation in the globe-flower flies *Chiastocheta* spp. (Anthomyiidae). Journal of Evolutionary Biology 12:822-831.

Despres L, Pettex E, Plaisance V, Pompanon F (2002) Speciation in the globeflower fly *Chiastocheta* spp. (Diptera: Anthomyiidae) in relation to host plant species, biogeography, and morphology. Molecular Phylogenetics and Evolution 22:258-268.

Despres L, Ibanez S, Hemborg AM, Godelle B (2007) Geographical and within-population variation in the globeflower-globeflower fly interaction: the costs and benefits of rearing pollinator's larvae. Oecologia 153:69-79.

Dethier VG (1976) The Hungry Fly: A physiological study of the behavior associated with feeding. Harvard University Press, Cambridge MA.

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

Diaz A, Kite GC (2002) A comparison of the pollination ecology of *Arum maculatum* and *A. italicum* in England. Watsonia 24:171-181.

Dinkel T, Lunau K (2001) How drone flies (*Eristalis tenax* L, Syrphidae, Diptera) use floral guides to locate food sources. Journal of Insect Physiology 47:1111-1118.

Disney RHL, Bänziger H (2009) Further records of scuttle flies (Diptera: Phoridae) imprisoned by *Aristolochia baenzigeri* (Aristolochiaceae) in Thailand. *Mitteilungen der Schweizerischen Entomologischen Gesellschaft* 82:233-251.

Disney RHL, Sakai S (2001) Scuttle flies (Diptera: Phoridae) whose larvae develop in flowers of *Aristolochia* (Aristolochiaceae) in Panama. European Journal of Entomology 98:367-373.

Dlusskii GM (2002) Diet of imago in some antophylous Muscidae (Diptera). Zoologichesky Zhurnal 81:825-832.

Dobson HEM (1994) Floral volatiles in insect biology. In: Bernays EA (ed) Insect-plant interactions. Vol V. CRC Press, Boca Raton FL, pp47-81.

Dobson HEM, Bergström G (2000) The ecology and evolution of pollen odors. Plant Systematics and Evolution 222:63-87.

Dodson CH (1962) The importance of pollination in the evolution of the orchids of tropical America. American Orchid Society Bulletin 31:641-735.

Dormer KJ (1960) The truth about pollination in *Arum*. New Phytologist 59:298-301.

Downer RGH (1978) Functional role of lipids in insects. In: Rockstein M (ed) Biochemistry of Insects. Academic Press, New York, pp 58-92.

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

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

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

Downes WL, Dahlem GA (1987) Keys to the evolution of Diptera: role of Homoptera. Environmental Entomology 16:847-854.

Drabble E, Drabble H (1927) Some flowers and their dipteran visitors. New Phytologist 26: 115-123.

Dressler RL (1981) The Orchids: Natural History and Classification. Harvard University Press, Cambridge MA.

Du W, Huang LJ, Wang XF (2012) Deceit pollination and the effect of deforestation on reproduction in dioecious *Schisandra sphenanthera* (Schisandraceae) in central China. Journal of Systematics and Evolution 50:36-44.

Duan JJ, Prokopy RJ (1994) Apple maggot fly response to red spheres in relation to fly age and experience. Entomologia Experimentalis et Applicata 73:279-287.

Duncan G, Ellis AG (2011) *Gorteria diffusa* Compositae. Curtis's Botanical Magazine 28:341-348.

Eberling H, Oleson JM (1999) The structure of a high latitude plant-flower visitor system: the dominace of flies. *Ecography* 22:314-323.

Eisikowitch D (1980) The role of dark flowers in the pollination of certain Umbelliferae. Journal of Natural History 14:737-742.

Ellis AG, Johnson SD (2010) Floral mimicry enhances pollen export: the evolution of pollination by sexual deceit outside of the Orchidaceae. The American Naturalist 176:143-151.

Elton C (1966) The Pattern of Animal Communities. Methuen & Co., London UK.

Eltz T, WhittenWM, Roubik DW, Linsenmair KE (1999) Fragrance collection, storage, and accumulation by individual male orchid bees. Journal of Chemical Ecology 25:157-176.

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

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

Endress PK (2001) The flowers in extant basal angiosperms and inferences on ancestral flowers. International Journal of Plant Sciences 162:1111-1140.

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

Evenhuis NL (1983) Observations on territorality of *Oligodranes mitis* Cresson (Diptera: Bombyliidae) on flowers of *Erigeron neomexicanus* (Asteraceae). Entomological News 94:25-28.

Faegri K, van der Pijl L (1979) The principles of pollination ecology (3rd edition). Pergamon Press, New York NY.

Feil JP (1992) Reproductive ecology of dioecious *Siparuna* (Monimiaceae) in Ecuador-a case of gall midge pollination. Botanical Journal of the Linnean Society 110:171-203.

Fenster CB, Armbruster WS, Wilson P, Dudash MR, Thomson JD (2004) Pollination syndromes and floral specialization. Annual Review of Ecology, Evolution and Systematics 35:375-403,

Ferdy J, Despres L, Godele B (2002) Evolution of mutualism between globeflowers and their pollinating flies. Journal of Theoretical Biology 217:219-234.

Ferrero V, de Vega C, Stafford GI, van Staden J, Johnson SD (2009) Heterostyly and pollinators in *Plumbago auriculata* (Plumbaginaceae). South African Journal of Botany 75:778-784.

Foster WA (1995) Mosquito nectar feeding and reproductive energetics. Annual Review of Entomology 40:443-474.

Free JB (1993) Insect pollination of crops (2nd edition). Academic Press, London UK.

Freeman BA (1966) Notes on conopid flies including insect host, plant and phoretic relationships (Diptera: Conopidae). Journal of the Kansas Entomological Society 39:123-131.

Freitas L, Sazima M (2003) Daily blooming pattern and pollination by syrphids in *Sisyrinchium vaginatum* (Iridaceae) in southeastern Brazil. Journal of the Torrey Botanical Society 130:55-61.

Galen C (1983) The ecology of floral scent variation in *Polemonium viscosum* Nutt. (Polemoniaceae). Ph. D. Dissertation., University of Texas, Austin.

Galen C (1985) Regulation of seed-set in *Polemonium viscosum*: floral scents, pollination, and resources. Ecology 66:792-797.

Galen C, Kevan PG (1980) Scent and colour, floral polymorphisms and pollination biology in *Polemonium viscosum* Nutt. American Midland Naturalist 104:281-289.

Galen C, Newport ME (1988) Pollination quality, seed set, and flower traits in *Polemonium viscosum*: complementary effects of variation in flower scent and size. American Journal of Botany 75:900-905.

Gao JJ (2011) Description of a new species of the *Hirtodrosophila limbicostata* species complex (Diptera, Drosophilidae) breeding on *Impatiens* L. flowers. Acta Zootaxonomica Sinica 36:74-79.

Gardener MC, Gillman MP (2002) The taste of nectar-a neglected area of pollination ecology. Oikos 98:552-557.

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

Gilbert FS (1985a) Diurnal activity patterns in hover flies (Diptera: Syrphidae). Ecological Entomology 10:385-92.

Gilbert FS (1985b) Ecomorphological relationships in hover flies (Diptera: Syrphidae). Proceedings of the Royal Society of London B 224:92-105.

Giurfa M, Vorobyev M, Kevan PG, Menzel R (1996) Detection of colored stimuli by honey bees: minimum visual angles and receptor specific contrasts. Journal of Comparative Physiology A 178:699-709.

Goldblatt P, Manning JC (2000) The long-proboscid fly pollinastion system in southern Africa. Annals of the Missouri Botanical Garden 87:146-170.

Goldblatt P, Manning JC (2007a) Floral biology of *Babiana* (Iridaceae: Crocoideae): Adaptive floral radiation and pollination. Annals of the Missouri Botanical Garden 94:709-733.

Goldblatt P, Manning JC (2007b) Pollination of *Romulea syringodeoflora* (Iridaceae: Crocoideae) by a long-proboscid fly, *Prosoeca* sp (Diptera : Nemestrinidae). South African Journal of Botany 73:56-59.

Goldblatt P, Manning JC, Bernhardt P (1997) Notes on the pollination of *Gladiolus brevifolius* (Iridaceae) by bees (Anthophoridae) and bee mimicking flies (*Psilodera*: Acroceridae). Journal of the Kansas Entomological Society 70:297-304.

Goldblatt P, Manning JC, Bernhardt, P (2001) Radiation of pollination systems in *Gladiolus* (Iridaceae : Crocoideae) in southern Africa. Annals of the Missouri Botanical Garden 88:713-734.

Goldblatt P., Bernhardt P, Vogan P, Manning JC (2004) Pollination by fungus gnats (Diptera: Mycetophilidae) and self-recognition sites in *Tolmiea menziesii* (Saxifragaceae). Plant Systematics and Evolution 244:55-67.

Goldblatt P, Manning JC, Bernhardt P (2005) Observations on the floral biology of *Melasphaerula* (Iridaceae: Crocoideae): is this monotypic genus pollinated by march flies (Diptera: Bibionidae)? Annals of the Missouri Botanical Garden 92:268-274.

Goldblatt P, Bernhardt P, Manning JC (2009) Adaptive radiation of the putrid perianth: *Ferraria* (Iridaceae: Irideae) and its unusual pollinators. Plant Systematics and Evolution 278:53-65.

Golding, YC, Sullivan MS, Sutherland JP (1999) Visits to manipulated flowers by *Episyrphus balteatus* (Diptera: Syrphidae): partitioning the signals of petals and anthers. Journal of Insect Behavior 12:39-46.

Goodrich KR, Zjhra ML, Ley CA, Raguso RA (2006) When flowers smell fermented: the chemistry and ontogeny of yeasty floral scent in pawpaw (*Asimina triloba*: Annonaceae). International Journal of Plant Sciences 167:33-46.

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

Gori DF (1983) Post-pollination phenomena and adaptive floral changes. In: Jones CE, Little RJ (eds) Handbook of experimental pollination biology. Van Nostrand Reinhold, New York NY, pp31-49.

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

Gottsberger G (1974) The structure and function of the primitive angiosperm flower-a discussion. Acta Botanica Neerlandica 23:461-471.

Gottsberger G, Meinke S, Porembski S (2011) First records of flower biology and pollination in African Annonaceae: *Isolona, Piptostigma, Uvariodendron, Monodora* and *Uvariopsis*. Flora 206:498-510.

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

Greco C, Kevan PG (1994) Contrasting patch choosing by anthophilous ambush predators: vegetation and floral cues for decisions by a crab spider (*Misumena vatia*) and males and females of an ambush bug (*Phymata americana*). Canadian Journal of Zoology 72:1583-1588.

Grimaldi D (1999) The co-radiations of pollinating insects and angiosperms in the cretaceous. Annals of the Missouri Botanical Garden 86:373-406.

Grimstad PR, DeFoliart GR (1974) Nectar sources of Wisconsin mosquitoes. Journal of Medical Entomology 11:331-341.

Hall DW, Brown BV (1993) Pollination of *Aristolochia littoralis* (Aristolochiales: Aristolochiaceae) by males of *Megaselia* spp. (Diptera: Phoridae). Annals of the Entomological Society of America 86:609-613.

Hansen K (1978) Insect chemoreception. In: Hazelbauer GL (ed) Taxis and behavior. J. Wiley, New York NY, pp 233-292.

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

Hanson FE (1987) Chemoreception in the fly. In Chapman RF, Bernays EA, Stoffolano JG (eds) Perspectives in Chemoreception and Behaviour. Springer Verlag, Berlin, Heidelberg, New York. pp99-122.

Hansson BS, Knaden M, Sachse S, Stensmyr MC, Wicher D (2010) Towards plant-odor-related olfactory neuroethology in *Drosophila*. Chemoecology 20:51-61.

Hardie RC (1979) Electrophysiological analysis of fly retina. I: Comparative properties of R 1-6 and R7 and 8. Journal of Comparative Physiology 129:19-33.

Haslett JR (1983) A photographic account of pollen digestion by adult hover flies. Physiological Entomology 8:67-171.

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

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

Haslett JR, Entwistle PF (1980) Further notes on *Eriozona syrphoides* (Fall.) (Diptera, Syrphidae) in Hafren Forest, mid-Wales. Entomologist's Monthly Magazine 116:36.

Healy TP, Jepson PC (1988) The location of floral nectar sources by mosquitoes: the long-range responses of *Anopheles arabiensis* Patton (Diptera: Culicidae) to *Achillea millefolium* flowers and isolated floral odour. Bulletin of Entomological Research 78:651-657.

Heiduk A, Brake I, Tolasch T, Frank J, Jurgens A, Meve U, Dotterl S (2010) Scent chemistry and pollinator attraction in the deceptive trap flowers of *Ceropegia dolichophylla*. South African Journal of Botany 76:762-769.

Herrera CM (1996) Floral traits and plant adaptation to insect pollinators: a devil's advocate approach. In: Lloyd DG, Barrett SCH (eds) Floral biology: Studies on floral evolution in animal-pollinated plants. Chapman & Hall, New York NY, pp 65-87.

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

Hipolito J, Viana BF, Selbach-Schnadelbach A, Galetto L, Kevan PG (2012) Pollination biology and genetic variability of a giant perfumed flower (*Aristolochia gigantea* Mart. & Zucc.- Aristolochiaceae) visited mainly by small Diptera. Botany 90:815-829.

Hobby BM, Smith KGV (1961) The bionomics of *Empis tessellata* F. (Diptera: Empididae). Entomologist's Monthly Magazine 97:2-10.

Hocking B (1953) The intrinsic range and flight speed of insects. Transactions of the Royal Entomological Society of London 104:223-345.

Hocking B (1968) Insect-flower associations in the High Arctic with special reference to nectar. Oikos 19:359-88.

Hocking B, Sharplin CD (1965) Flower basking by Arctic insects. Nature 206:15.

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

Humeau L, Micheneau C, Jacquemyn H, Gauvin-Bialecki A, Fournel J, Pailler T (2011) Sapromyiophily in the native orchid, *Bulbophyllum variegatum*, on Reunion (Mascarene Archipelago, Indian Ocean). Journal of Tropical Ecology 27:591-599.

Ibanez S, Doetterl S, Anstett MC, Baudino S, Caissard JC, Gallet C, Despres L (2010) The role of volatile organic compounds, morphology and pigments of globeflowers in the attraction of their specific pollinating flies. New Phytologist 188:451-463.

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

Inouye DW (1980) The terminology of floral larceny. Ecology 61:1251-1253.

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

Inouye DW, Taylor OR (1979) A temperate region plant-ant-seed predation system: consequences of extrafloral nectar secretion by *Helianthella quinquenervis*. Ecology 60:1-7.

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

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

Jepson PC, Healy TP (1988) The location of floral nectar sources by mosquitoes: an advanced bioassay for volatile plant odours and initial studies with *Aedes aegypti* (L.) (Diptera: Culicidae). Bulletin of Entomological Research 78:641-650.

Jersakova J, Johnson SD (2006) Lack of floral nectar reduces self-pollination in a fly-pollinated orchid. Oecologia 147:60-68.

Jhumur US, Dotterl S, Jurgens A (2006) Naive and conditioned responses of *Culex pipiens pipiens* biotype *molestus* (Diptera: Culicidae) to flower odors. Journal of Medical Entomology 43:1164-1170.

Jhumur US, Dotterl S, Jurgens A (2008) Floral odors of *Silene otites*: Their variability and attractiveness to mosquitoes. Journal of Chemical Ecology 34:14-25.

Johnson SD (2000) Batesian mimicry in the non-rewarding orchid *Disa pulchra*, and its consequences for pollinator behaviour. Biological Journal of the Linnean Society 71:119-132.

Johnson SD (2006) Pollination by long-proboscid flies in the endangered African orchid *Disa scullyi*. South African Journal of Botany 72:24-27.

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

Johnson SD, Jurgens A (2010) Convergent evolution of carrion and faecal scent mimicry in fly-pollinated angiosperm flowers and a stinkhorn fungus. South African Journal of Botany 76:796-807.

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

Johnson SD, Morita S (2006) Lying to Pinocchio: floral deception in an orchid pollinated by long-proboscid flies. Botanical Journal of the Linnean Society 152:271-278.

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

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

Johnson SD, Steiner K (2000) Generalization versus specialization in plant pollination systems. Trends in Ecology and Evolution 15:140-143.

Johnson SD, Alexandersson R, Linder HP (2003) Experimental and phylogenetic evidence for floral mimicry in a guild of fly-pollinated plants. Biological Journal of the Linnean Society 80:289-304.

Jones, CJ, Milne DE, Patterson RS, Schreiber ET, Milio JA (1992) Nectar feeding by *Stomoxys calcitrans* (Diptera: Muscidae):

effects of reproduction and survival. Environmental Entomology 21:141-147.

Kastinger C, Weber A (2001) Bee-flies (*Bombylius* spp., Bombyliidae, Diptera) and the pollination of flowers. Flora 196:3-25.

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

Kato M, Inoue T (1994) Origin of insect pollination. Nature 368:195.

Kay QON (1976) Preferential pollination of yellow-flowered morphs of *Raphanus raphanistrum* by *Pieris* and *Eristalis* spp. Nature (London) 261:230-232.

Kay QON (1978) The role of preferential and assortative pollination in the maintenance of flower colour polymorphisms. In: Richards AJ (ed) The pollination of flowers by insects. Symposium of the Linnean Society of London No. 6. Academic Press, New York NY, pp 175-190.

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

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

Kelber A (2001) Receptor based models for spontaneous colour choices in flies and butterflies. Entomologia Experimentalis et Applicata 99:231-244.

Kelber A, Vorobyev M, Osorio D (2003) Animal colour vision-behavioural tests and physiological concepts. Biological Reviews 78:81-118.

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

Kevan PG (1972a) Heliotropism in some Arctic flowers. Canadian Field-Naturalist 86:41-44.

Kevan PG (1972b) Insect pollination of High Arctic flowers. Journal of Ecology 60:831-867.

Kevan PG (1973) Flowers, insects and pollination ecology in the Canadian high arctic. Polar Record 16:667-674.

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

Kevan PG (1989) Thermoregulation in arctic insects and flowers: adaptation and co-adaptation in behaviour, anatomy, and physiology. *In*: Mercer JB (ed) Thermal physiology: Proceedings of the international symposium on thermal physiology, Tromso, Norway, 16-21 July, 1989. Excerpta Medica, New York NY, pp 747-753.

Kevan PG (2007) Diaheliotaxis and ombrophobia in an anthophilous high arctic midge, *Smittia velutina* (Lundbeck, 1898) (Chironomidae). Chironomus 20:29-31.

Kevan PG, Backhaus WGK (1998) Color vision: ecology and evolution in making the best of the photic environment. In: Backhaus WGK, Kleigl R, Werner JS (eds) Color vision: Perspectives from different disciplines. W. de Gruyter, New York NY, pp163-183.

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

Kevan PG, Baker HG (1999) Insects on flowers: pollination and floral visitations. In: Huffaker CB Gutierrez A (eds) Ecological entomology. J. Wiley & Sons, New York NY, pp 553-584.

Kevan PG, Greco CF (2001) Contrasting patch choice between immature ambush predators, a spider (*Misumena vatia*) and an insect (*Phymata americana*). Ecological Entomology 26:148-153.

Kevan PG, Lane MA (1985) Flower petal microtexture is a tactile cue for bees. Proceedings of the National Academy of Sciences U SA 82:4750-4752.

Kevan, PG, Chaloner WG, Savile DBO (1975) Interrelationships of early terrestrial arthropods and plants. Palaeontology 18 (Part 2):391-417.

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

Kevan PG, Chittka L, Dyer AG (2001) Limits to the salience of ultraviolet: lessons from colour vision in bees and birds. Journal of Experimental Biology 204:2581-2587.

Knight GH (1967) Observations on the behaviour of *Bombylius major* L. and *B. discolor* Mik. (Dipt., Bombyliidae) in the midlands. Entomologist's Monthly Magazine 103:177-181.

Knoll F (1921) *Bombylius fuliginosus* und die Farbe der Blumen (Insekten und Blumen I). Abhandlungen der Zoologisch-Botanischen Gesellschaft in Wien 12:17-119.

Knoll F (1926) Die *Arum*-Blütenstände und ihre Besucher. Abhandlungen der Zoologisch-Botanischen Gesellschaft in Wien 12:379-481.

Knudsen JT, Eriksson R, Gershenzon J, Stahl B (2006) Diversity and distribution of floral scent. The Botanical Review 72:1-120.

Knuth P. (1906-1909) Handbook of flower pollination. 3 Vol. (Transl. by J. R. Ainsworth Davis). Oxford University Press, Oxford UK.

Knutson RM (1974) Heat production and temperature regulation in eastern Skunk Cabbage. Science 186:746-747.

Knutson RM (1979) Plants in heat. Natural History 88:42-47.

Koponen A (1990) Entomophily in the Splachnaceae. Botanical Journal of the Linnean Society 104:115-127.

Kotze MJ, Jurgens A, Johnson SD, Hoffmann JH (2010) Volatiles associated with different flower stages and leaves of *Acacia cyclops* and their potential role as host attractants for *Dasineura dielsi* (Diptera. Cecidomyiidae). South African Journal of Botany 76:701-709.

Krannitz PG (1996) Reproductive biology of *Dryas integrifolia* in the high arctic semi-desert. Canadian Journal of Botany 74:1451-1460.

Krenn HW, Plant JD, Szucsich NU (2005) Mouthparts of flower-visiting insects. Arthropod Structure and Development 34:1-40.

Kudo G (1995) Ecological significance of flower heliotropism in the spring ephemeral *Adonis ramosa* (Ranunculaceae). Oikos 72:14-20.

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

Kugler H (1951) Blütenökologische Untersuchungen mit Goldfliegen (Lucilien). Berichte der Deutschen Botanischen Gesellschaft 64:327-341.

Kugler H (1956) Über die optische Wirkung von Fliegenblumen auf Fliegen. *Berichte* der Deutschen Botanischen Gesellschaft 69:387-398.

Kugler H (1963) UV-Musterungen auf Blüten und ihre Zustandekommen. Planta 59:296-329.

Kugler H (1970) Blütenökologie. G. Fischer Verlag, Stuttgart, Germany.

Labandeira CC (1997) Insect mouthparts: ascertaining the paleobiology of insect feeding strategies. Annual Review of Ecology and Systematics 28:153-193.

Labandeira CC (1998) How old is the flower and the fly? Science 280:57-59.

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

Lamarck JB (1777) Flore française, ou, Descriptions succinctes de toutes les plantes qui croissent naturellement en France, disposées selon une novelle méthode d'analyse, et précédées par un exposé des principes élémentaires de la botanique. Desray, Paris, France.

Lamborn E, Ollerton J (2000) Experimental assessment of the functional morphology of infloresceneces of *Daucus carota* (Apaiaceae): testing the 'fly catcher effect'. Functional Ecology 14:445-454.

Land MF (1997) Visual acuity in insects. Annual Review of Entomology 42:147-177.

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

Larson L, Foote BA (1997) Biology of four species of *Notiphila* Fallén (Diptera: Ephydridae) associated with the yellow water lily, *Nuphar luteum* (Nymphaeaceae). Proceedings of the Entomological Society of Washington 99:541-559.

Laubertie EA, Wratten SD, Sedcole JR (2006) The role of odour and visual cues in the pan-trap catching of hoverflies (Diptera: Syrphidae). Annals of Applied Biology 148: 173-178.

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

Leereveld H (1984) Anthecological relations between reputedly anemophilous flowers and syrphid flies. VI. Aspects of the anthecology of Cyperaceae and *Sparganium erectum* L. Acta Botanica Neerlandica 33:475-482.

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

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

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

Li YQ, Zhang DX (2007) Fly pollination of *Antidesma montanum* (Euphorbiaceae) in Hainan, China. Acta Phytotaxonomica Sinica 45:217-226.

Liebermann A (1925) Korrelation zwischen den antennalen Geruchsorganen und der Biologie der Musciden. Zeitschrift für Morphologie und Ökologie der Tiere 5:1-97.

Linskens HF, Schrauwen J (1969) The release of free amino acids from germinating pollen. Acta Botanica Neerlandica 18:605-614.

Lunau K (1996) Unidirectionality of floral colour changes. Plant Systematics and Evolution 200:125-140.

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

Lunau K (2004) Adaptive radiation and coevolution – pollination biology case studies. Organisms, Diversity and Evolution 4:207-224.

Lunau K (2007) Stamens and mimic stamens as components of floral colour patterns. Botanische Jahrbuecher fuer Systematik Pflanzengeschichte und Pflanzengeographie 127:13-41.

Lunau K, Maier EJ (1995) Innate colour preferences of flower visitors. Journal of Comparative Physiology A 177:1-19.

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

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

Lunau K, Papiorek S, Eltz T, Sazima M (2011) Avoidance of achromatic colours by bees provides a private niche for hummingbirds. Journal of Experimental Biology 214:1607-1612.

Luo SX, Chaw SM, Zhang DX, Renner SS (2010) Flower heating following anthesis and the evolution of gall midge pollination in Schisandraceae. American Journal of Botany 97:1220-1228.

Luzar N, Gottsberger G (2001) Flower heliotropism and floral heating of five alpine plant species and the effect of flower visiting in *Ranunculus montanus* in the Austrian alps. Arctic, Antarctic and Alpine Research 33:93-99.

Maier CT (1978) The immature stages and biology of *Mallota posticata* (Fabricius) (Diptera: Syrphidae). Proceedings of the Entomological Society of Washington 80:424-440.

Maier CT (1982) Larval habitats and mate-seeking sites of flower flies (Diptera: Syrphidae, Eristalinae). Proceedings of the Entomological Society of Washington 84:603-609.

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

McDonald DJ, van der Walt JJA (1992) Observations on the pollination of *Pelargonium tricolor*, section *Campylia* (Geraniaceae). Journal of South African Botany 58:386-392.

Meeuse BJD (1966) Production of volatile amines and skatoles at anthesis in some arum lily species. Plant Physiology 41:343-347.

Meeuse BJD (1978) The physiology of some sapromyophilous flowers. In: Richards AJ (ed) The pollination of flowers by insects. Symposium of the Linnean Society of London No. 6. Academic Press, New York NY, pp 175-190.

de Meillon B, Wirth WW (1989) A new pollen feeding *Atrichopogon* midge from Madagascar, with notes on closely related subsaharan species (Diptera: Ceratopogonidae). Revue Française d'Entomologie 11:85-89.

Menzel R, Backhaus WGK (1991) Colour vision in insects. In: Gouras P (ed) Vision and visual dysfunction: The perception of colour. Macmillan Press, London UK, pp 268-288.

Menzel R, Shmida A (1993) The ecology of flower colours and the natural colour vision of insect pollinators: the Israeli flora as a case study. Biological Reviews of the Cambridge Philosophical Society 68:81-120.

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

Mesler MR, Lu KL (1993) Pollination biology of *Asarum hartwegii* (Aristolochiaceae): an evaluation of Vogel's mushroom-fly hypothesis. Madroño 40:117-125.

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

Miyake T, Yafuso M (2003) Floral scents affect reproductive success in fly-pollinated *Alocasia odora* (Araceae). American Journal of Botany 90:370-376.

Miyake T, Yafuso M (2005) Pollination of *Alocasia cucullata* (Araceae) by two *Colocasiomyia* flies known to be specific pollinators for *Alocasia odora*. Plant Species Biology 20:201-208.

Moller AP (2000) Developmental stability and pollination. Oecologia 123:149-157.

Moodie GEE (1976) Heat production and pollination in Araceae. Canadian Journal of Botany 54:545-546.

Moring J (1978) Spectral sensitivity of monopolar neurons in the eye of *Calliphora*. Journal of Comparative Physiology A 123:335-338.

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

Morse DH (1986) Predatory risk to insects foraging at flowers. Oikos 46:223-228.

Morse DH, Fritz RS (1989) Milkweed pollinia and predation risk to flower-visting insects by the crab spider *Misumena vatia*. American Midland Naturalist 121:188-193.

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

Müller H (1881) Die Alpenblumen: ihre Befruchtung durch Insekten und ihre Anpassungen an dieselben. W. Englemann, Leipzig, Germany.

Murugan R, Shivanna KR, Rao RR (2006) Pollination biology of *Aristolochia tagala*, a rare species of medicinal importance. Current Science 91:795-798.

Nagasaki O (2007) Pollination of the yellow water lily *Nuphar subintegerrima* (Nymphaeaceae) by the shore fly *Notiphila (Notiphila) maritima* (Diptera: Ephydridae). Plant Species Biology 22:227-230.

Nayar JK, Sauerman DM (1971) The effects of diet on life-span, fecundity and flight potential of *Aedes taeniorhynchus* adults. Journal of Medical Entomology 8:506-513.

Ne'eman G, Ne'eman R, Ellison AM (2006) Limits to reproductive success of *Sarracenia purpurea* (Sarraceniaceae). American Journal of Botany 93:1660-1666.

Neff JL, Simpson BB, Evenhuis NL, Dieringer G (2003) Character analysis of adaptations for tarsal pollen collection in the Bombyliidae (Insecta: Diptera): the benefits of putting your foot in your mouth. Zootaxa 157:1-14.

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

Nicolson SW (1994b) *Eucalyptus* nectar: production, availability, composition and osmotic consequences for the larva of the eucalypt nectar fly, *Drosophila flavohirta*. South African Journal of Science 90:75-79.

van der Niet T, Jurgens A, Johnson S (2010) Pollinators, floral morphology and scent chemistry in the southern African orchid genus *Schizochilus*. South African Journal of Botany 76:726-738.

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

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

Nishida R, Shelly TE, Kaneshiro KY (1997) Acquisition of female-attracting fragrance by males of oriental fruit fly from a Hawaiian lei flower, *Fragraea berteriana*. Journal of Chemical Ecology 23:2275-2286.

Nishida R, Tan KH, Wee SL, Hee AKW, Toong YC (2004) Phenylpropanoids in the fragrance of the fruit fly orchid, *Bulbophyllum cheiri*, and their relationship to the pollinator, *Bactrocera papayae*. Biochemical Systematics and Ecology 32:245-252.

O'Carroll, DC, Bidwell NJ, Laughlin SB, Warrant EJ (1996) Insect motion detectors matched to visual ecology. Nature 382:63-66.

Ollerton J (1996) Reconciling ecological processes with phylogenetic patterns: the apparent paradox of plant-pollinator systems. Journal of Ecology 84:767-769.

Orueta D (2002) Thermal relationships between *Calendula arvensis* inflorescences and *Usia aurata* bombyliid flies. Ecology 83:3073-3085.

Oldroyd H (1964) The natural history of flies. Weidenfeld and Nicolson, London UK.

O'Neill KM, Kemp WP (1991) Foraging of *Stenopogon inquinatus* (Loew) (Diptera: Asilidae) on Montana rangeland sites. Pan-Pacific Entomologist 67:177-180.

Otterstatter MC, Whidden TL, Owen RE (2002) Contrasting frequencies of parasitism and host mortality among phorid and conopid parasitoids of bumble-bees. Ecological Entomology 27:229-237.

Owens ED, Prokopy RJ (1986) Relationship between reflectance spectra of host plant surfaces and visual detection of host fruit by *Rhagoletis pomonella* flies. Physiological Entomology 11:297-308.

Panov AA (2007) Sex-related diet specificity in *Bombylius major* and some other Bombyliidae (Diptera). Entomological Review 87:812-821.

Pacini E, Hesse M (2005) Pollenkitt - its composition, forms and functions. Flora 200:399-415.

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

Parmenter L (1958) Flies (Diptera) and their relations with plants. London Naturalist 37:115-125.

Patiño S, Aalto T, Edwards AA, Grace J (2002) Is *Rafflesia* an endothermic flower? New Phytologist 154:429-437.

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

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

Paulus HF (2005) Zur Bestäubungsbiologie der Orchideen. In: Arbeitskreis Heimische Orchideen, Die Orchideen Deutschlands pp 98-140, Uhlstädt-Kirchhasel, Germany.

Paxton RJ, Tengö J (2001) Doubly duped males: the sweet and sour of the orchid's bouquet. Trends in Ecology and Evolution 16:167-169

Pellmyr O (1989) The cost of mutualism: interactions between *Trollius europaeus* and its pollinating parasites. Oecologia 78:53-59.

Pellmyr O (1992) The phylogeny of a mutualism: evolution and coadaptation between *Trollius* and its seed-parasitic pollinators. Biological Journal of the Linnean Society 47:337-365.

Pemberton RW (2010) Biotic resource needs of specialist orchid pollinators. Botanical Review 76:275-292.

Pemberton RW (2011) Flower fly (Syrphidae) pollination and mechanical self-pollination (autogamy) in *Phragmipedium* species (Cypripedioideae). Orchids 80:364-367.

Percival M (1965) Floral biology. Pergamon Press, Oxford UK.

Pérez-Bañón C, Juan A, Petanidou T, Marcos-Garcia MA, Crespo MB (2003) The reproductive ecology of *Medicago citrina* (Font Quer) Greuter (Leguminosae): a bee-pollinated plant in Mediterranean islands where bees are absent. Plant Systematics and Evolution 241:29-46.

Peter CI, Johnson SD (2008) Mimics and magnets: the importance of color and ecological facilitation in floral deception. Ecology 89:1583-1595.

Pettersson MW (1992) Taking a chance on moths: oviposition by *Delia flavifrons* (Diptera: Anthomyiidae) on the flowers of bladder campion, *Silene vulgaris* (Caryophyllaceae). Ecological Entomology 17:57-62.

Pichaud F, Briscoe A, Desplan C (1999) Evolution of color vision. Current Opinion in Neurobiology 9:622-627.

van der Pijl L (1953) On the flower biology of some plants from Java, with general remarks on fly traps (species of *Annona, Artocarpus, Typhonium, Gnetum, Arisaema*, and *Abroma*). Annales Bogoriensis 1:77-99.

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

Polte S, Reinhold K (2013) The function of the wild carrot's dark central floret: attract, guide or deter? Plant Species Biology 28:81-86.

Pombal ECP, Morellato PC (2000) Differention of floral color and odor in two fly pollinated species of *Metrodorea* (Rutaceae) from Brazil. Plant Systematics and Evolution 221:141-156.

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

Potter CF, Bertin RI (1988) Amino acids in artificial nectar: feeding preferences of the flesh fly *Sarcophaga bullata*. American Midland Naturalist 120:156-162.

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

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

Primante C, Dotterl S (2010) A syrphid fly uses olfactory cues to find a non-yellow flower. Journal of Chemical Ecology 36:1207-1210.

Proctor M, Yeo P (1973) The pollination of flowers. Collins, London UK.

Proctor M, Yeo P, Lack A (1996) The natural history of pollination. Timber Press, Portland, OR.

Punekar SA, Kumaran KPN (2010) Pollen morphology and pollination ecology of *Amorphophallus* species from North Western Ghats and Konkan region of India. Flora 205:326-336.

Quilichini A, Macquart D, Barabe D, Albre J, Gibernau, M (2010) Reproduction of the West Mediterranean endemic *Arum pictum* (Araceae) on Corsica. Plant Systematics and Evolution 287:179-187.

Rathman ES, Lanza J, Wilson J (1990) Feeding preferences of flesh flies (*Sarcophaga bullata*) for sugar-only vs. sugar-amino acid nectars. American Midland Naturalist 124:379-389.

Rebelo AG, Siegfried WR (1985) Colour and size of flowers in relation to pollination of *Erica* species. Oecologia 65:584-590.

Ren D, Labandeira CC, Santiago-Blay JA, Rasnitsyn A, Shih CK, Bashkuev A, Logan MAV, Hotton CL, Dilcher D (2009) A probable pollination mode before angiosperms: Eurasian long-proboscid scorpionflies. Science 326:840-847.

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

Robertson C (1928) Flowers and Insects. XXV. Ecology 9:505-526.

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

Robertson AW, Lloyd DG (1993) Rates of pollen deposition and removal in *Myosotis colensoi*. Functional Ecology 7:549-559.

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

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

Roulston TH, Cane JH (2000) Pollen nutritional content and digestibility for animals. Plant Systematics and Evolution 222:187-209.

Roy BA, Raguso RA (1997) Olfactory versus visual cues in a floral mimicry system. Oecologia 109:414-426.

Ruck P (1961) Photoreceptor cell response and flicker fusion frequency in the compound eye of the fly, *Lucilia sericata* (Meigen). Biological Bulletin 120:373-383.

Sakai S (2002a) A review of brood-site pollination mutualism: plans providing breeding sites for their pollinators. Journal of Plant Research 115:161-168.

Sakai S (2002b) *Aristolochia* spp. (Aristolochiaceae) pollinated by flies breeding in decomposing flowers in Panama. American Journal of Botany 89:527-534.

Sakai S, Kato M, Nagamasu H (2000) *Artocarpus* (Moraceae)-gall midge pollination mutualism mediated by a male-flower parasitic fungus. American Journal of Botany 87:440-445.

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

Schiestl FP (2005) On the success of a swindle: pollination by deception in orchids. Naturwissenschaften 92:255-264.

Schiestl FP, Ayasse M, Paulus HF (1999) Orchid pollination by sexual swindle. Nature 399:421-422.

Schneider F (1948) Beitrag zur Kenntnis der Generationsverhaltnisse und Diapause räuberischer Schwebfliegen (Syrphidae: Diptera). Mitteilungen der Schweizerischen Entomologischen Gesellschaft 21:249-288.

Scott H (1953) Discrimination of colours by *Bombylius* (Dipt., Bombyliidae). Entomologists' Monthly Magazine 89:259-260.

Service MW (1997) Mosquito (Diptera: Culicidae) dispersal – the long and the short of it. Journal of Medical Entomology 34:579-588.

Seymour RS, Gibernau M, Ito K (2003) Thermogenesis and respiration of inflorescences of the dead horse arum *Helicodiceros muscivorus*, a pseudo-thermoregulatory aroid associated with fly pollination. Functional Ecology 17:886-894.

Sharma N, Koul P, Koul AK (1993) Pollination biology of some species of genus *Plantago* L. Botanical Journal of the Linnean Society 111:129-138.

Shaw DE, Cantrell BK, Houston KJ (1982) *Neurochaeta inversa* McAlpine (Diptera: Neurochaetidae) and seed set in *Alocasia macrorrhiza* (L.) G. Don (Araceae) in southeast Queensland. Proceedings of The Linnean Society of New South Wales 106:67-82.

Shelly TH (2001) Feeding on methyl eugenol and *Fagraea berteriana* flowers increases long-range female attraction by males of the oriental fruit fly (Diptera: Tephritidae). Florida Entomologist 84:634-640.

Shuttleworth A, Johnson SD (2010) The missing stink: sulphur compounds can mediate a shift between fly and wasp pollination systems. Proceedings Of The Royal Society B 277:2811-2819.

Simpson BB, Neff JL (1981) Floral rewards: alternatives to pollen and nectar. Annals of the Missouri Botanical Garden 68: 301-322.

Smith AP (1975) Insect pollination and heliotropism in *Oritrophium limnophilum* (Compositae) of the Andean Paramo. Biotropica 7:284-286.

Speight MCD (1978) Flower-visiting flies. In: Stubbs A, Chandler P (eds) A dipterist's handbook. Amateur Entomologist's Society, University of Wisconsin-Madison, Madison WI, pp 229-236.

Sprengel CK (1793) Das entdeckte Geheimniss der Natur im Bau und in der Befruchtung der Blumen. Friedrich Vieweg dem æltern, Berlin, Germany.

Ssymank A (2001) Tierwelt in der Zivilisationslandschaft. 5. Vegetation und blütenbesuchende Insekten in der Kulturlandschaft. Münster: Landwirtschaftsverlag, 513pp.

Ssymank A, Gilbert F (1993) Anemophilous pollen in the diet of syrphid flies with special reference to the leaf feeding strategy occurring in Xylotini (Diptera: Syrphidae). Deutsche Entomologische Zeitschrift 40:245-258.

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

Stanley RG, Linskens HF (1974) Pollen: Biology, biochemistry, management. Springer, Berlin, Germany.

Stanton ML, Galen C (1989) Consequences of flower heliotropism for reproduction in an alpine buttercup (*Ranunculus adoneus*). Oecologia 78:477-485.

Steiner G (1948) Fallenversuche zur Kennzeichnung des Verhaltens von Schmeissfliegen gegenüber verschiedenen Merkmalen ihrer Umgebung. Zeitschrift für Vergleichende Physiologie 31:1-37.

Stelleman P (1980) Anthecological relations between reputedly anemophilous flowers and syrphid flies. V. Some special aspects of the visiting of *Plantago media* and *P. lanceolata* by insects. Beitraege zur Biologie der Pflanzen 55:157-167.

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

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

Stoekl J, Strutz A, Dafni A, Svatos A, Doubsky J, Knaden M, Sachse S, Hansson BS, Stensmyr MC (2010) A deceptive pollination system targeting drosophilids through olfactory mimicry of yeast. Current Biology 20:1846-1852.

Stoekl J, Brodmann J, Dafni A, Ayasse M, Hansson BS (2011) Smells like aphids: orchid flowers mimic aphid alarm pheromones to attract hoverflies for pollination. Proceedings of the Royal Society B 278:1216-1222.

Stubbs A, Chandler P (eds) (1978) A Dipterist's Handbook. The Amateur Entomologists' Society, Middlesex.

Sugawara T (1988) Floral biology of *Heterotropa tamaensis* (Aristolochiaceae) in Japan. Plant Species Biology 3:7-12.

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

Takano KT, Repin R, Mohamed MB, Toda MJ (2012) Pollination mutualism between *Alocasia macrorrhizos* (Araceae) and two taxonomically undescribed *Colocasiomyia* species (Diptera: Drosophilidae) in Sabah, Borneo. *Plant Biology* 14:555-564.

Tan KH, Nishida R (2005) Synomone or kairomone? *Bulbophyllum apertum* flower releases raspberry ketone to attract *Bactrocera* fruit flies. Journal of Chemical Ecology 31:497-507.

Tan KH, Nishida R (2007) Zingerone in the floral synomone of *Bulbophyllum baileyi* (Orchidaceae) attracts *Bactrocera* fruit flies during pollination. Biochemical Systematics and Ecology 35:334-341.

Tan KH, Nishida R (2012) Methyl eugenol: Its occurrence, distribution, and role in nature, especially in relation to insect behavior and pollination. Journal of Insect Science 12:56.

Tan KH, Nishida R, Toong YC (2002) Floral synomone of a wild orchid, *Bulbophyllum cheiri*, lures *Bactrocera* fruit flies for pollination. Journal of Chemical Ecology 28:1161-1172.

Tan KH, Tan LT, Nishida R (2006) Floral phenylpropanoid cocktail and architecture of *Bulbophyllum vinaceum* orchid in attracting fruit flies for pollination. Journal of Chemical Ecology 32:2429-2441.

Tan KH, Tokushima I, Ono H, Nishida R (2011) Comparison of phenylpropanoid volatiles in male rectal pheromone gland after methyl eugenol consumption, and molecular phylogenetic relationship of four global pest fruit fly species: *Bactrocera invadens*, *B. dorsalis*, *B. correcta* and *B. zonata*. Chemoecology 21:25-33.

Tanaka C, Kainoh Y, Honda H (1999) Physical factors in host selection of the parasitoid fly, *Exorista japonica* Townsend (Diptera: Tachinidae). Applied Entomology and Zoology 34: 91-97.

Tatler B, O'Carroll DC, Laughlin SB (2000) Temperature and temporal resolving power of fly photoreceptors. Journal of Comparative Physiology A 186:399-407.

Taylor TN (1981) Paleobotany: An introduction to fossil plant biology. McGraw-Hill Book Co., New York NY.

Thien LB, Azuma H, Kawano S (2000) New perspectives on the pollination biology of basal angiosperms. International Journal of Plant Sciences 161 (Supplement): P 225-235.

Thien LB, Bernhardt P, Devall MS, Chen ZD, Luo YB, Fan JH, Yuan LC, Williams JH (2009) Pollination biology of basal angiosperms (ANITA grade). American Journal of Botany 96:166-182.

Toda MJ, Lakim MB (2011) Genus *Colocasiomyia* (Drosophilidae: Diptera) in Sabah, Bornean Malaysia: high species diversity and use of host aroid inflorescences. Entomological Science 14:262-270.

du Toit AP (1987) Nectar flies, *Drosophila flavohirta* Malloch, (Diptera: Drosophilidae) breeding in *Eucalyptus* flowers. South African Forestry Journal 143:53-54.

Totland O (1996) Flower heliotropism in an alpine population of *Ranunculus acris* (Ranunculaceae): effects of flower temperature, insect visitation, and seed production. American Journal of Botany 83:452-458.

Tribe GD (1991) *Drosophila flavohirta* Malloch, (Diptera: Drosophilidae) in *Eucalyptus* flowers: occurrence and parsites in eastern Australia and potential for biological control on *Eucalyptus grandis* in South Africa. Journal of the Australian Entomological Society 30:257-262.

Troje N (1993) Spectral categories in the learning behaviour of blowflies. Zeitschrift für Naturforschung 48C: 96-104.

Uemura S, Ohkawara K, Kudo G, Wada N, Higashi S (1993) Heat-production and cross-pollination of the Asian skunk cabbage *Symplocarpus renifolius* (Araceae). American Journal of Botany 80:635-640.

Urru I, Stoekl J, Linz J, Kruegel T, Stensmyr MC, Hansson BS (2010) Pollination strategies in Cretan *Arum* lilies. Biological Journal of the Linnean Society 101:991-1001.

van der Velde G, Brock TCM, Heine M, Peeters PM (1978) Flowers of Dutch Nymphaeaceae as a habitat for insects. Acta Botanica Neerlandica 27:429-438.

Villanueva MTO, Marquina AD, Serrano RB, Abellan GB (2001) Mineral content of commercial pollen. International Journal of Food Sciences and Nutrition 52:243-249.

Vogel S (1973) Fungus gnat flowers and fungus mimesis. In: Brantjes NBM, Linskens HF (eds) Pollination and dispersal. University of Nijmegen, Netherlands, pp 13-18.

Vogel S (1978) Pilzmückenblumen als Pilzmimeten. [Fungus-gnat flowers mimicking fungi]. Flora 167:329-398.

Vogel S (1993) Betrug bei Pflanzen: Die Täuschblumen. Akademie der Wissenschaften und der Literatur, Abhandlungen der Mathematisch-Naturwissenschaftlichen Klasse 1:5-48.

Vogel S, Martens J (2000) A survey of the function of lethal kettle traps of *Arisaema* (Araceae), with records of pollinating fungus gnats from Nepal. Botanical Journal of the Linnean Society 133:61-100.

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

Vorobyev M, Brandt R (1997) How do insects discriminate colors? Israel Journal of Plant Sciences 45:103-113

Vrzal EM, Allan SA, Hahn DA (2010) Amino acids in nectar enhance longevity of female *Culex quinquefasciatus* mosquitoes. Journal of Insect Physiology 56:1659-1664.

Wacht S, Lunau K, Hansen K (1996) Optical and chemical stimuli control pollen feeding in the hoverfly *Eristalis tenax*. Entomologia Experimentalis et Applicata 80:50-53.

Wacht S, Lunau K, Hansen K (2000) Chemosensory control of pollen ingestion in the hoverfly *Eristalis tenax* by labellar taste hairs. Journal of Comparative Physiology A 186:193-203.

Waldbauer GP (1984) Mating behavior at blossoms and the flower associations of mimetic *Temnostoma* spp. (Diptera: Syrphidae) in northern Michigan. Proceedings of the Entomological Society of Washington 86:295-304.

Waldbauer GP, Ghent AW (1984) Flower associations and mating behavior or its absence at blossoms by *Spilomyia* spp. (Diptera: Syrphidae). Great Lakes Entomologist 17:13-16.

Waller, GD, Carpenter EW, Ziehl OA (1972) Potassium in onion nectars and its probable effect on attractiveness of onion flowers to honey bees. Journal of the American Society for Horticultural Science 97:535-539.

Wang J, Ma YX, Cui DL, Wang RX, Lu YY, Qin J (2011) An observation on pollinating insects and their flower-visiting behavior on *Fatsia japonica*. Chinese Journal of Applied Entomology 48:764-768.

Waser NM (1983) The adaptive nature of floral traits: ideas and evidence. In: Real L (ed) Pollination biology. Academic Press, Orlando FL, pp 242-285.

Waser NM (1986) Flower constancy: definition, cause and measurement. American Naturalist 127:593-603.

Waser NM Chittka L, Price MV, Williams NM, Ollerton J (1996) Generalization in pollination systems, and why it matters. Ecology 77:1043-1060.

Weems HV (1953) Notes on collecting Syrphid flies (Diptera: Syrphidae). Florida Entomologist 36:91-98.

Weismann R (1962) Geruchsorientierung der Stubenfliege, *Musca domestica*. Zeitschrift für angewandte Entomologie 50:74-81

Weiss MR (1991) Floral colour changes as cues for pollinators. Nature 354:227-229.

Weiss MR (1996) Pollen-feeding fly alters floral phontypic gender in *Centropogon solanifolius* (Campanulaceae). Biotropica 28: 770-773.

Weiss MR (2001) Vison and learning in some neglected pollinators: beetles, flies, moths, and butterflies. In: Chittka L, Thomson JD (eds) Cognitive ecology of pollination: Animal behavior and floral evolution. Cambridge University Press, New York NY, pp171-190.

Wenk P., Schlörer G (1963) Wirtsorientierung und Kopulation bei blutsaugenden Simuliiden (Diptera). Zeitschrift für Tropenmedizin und Parasitologie 14:177-191

Westmoreland D, Muntan C (1996) The influence of dark central florets on insect attraction and fruit production in Queen Anne's Lace (*Daucus carota* L.). American Midland Naturalist 135:122-129.

Wetschnig W, Depisch B (1999) Pollination biology of *Welwitschia mirabilis* Hook. F. (Welwischiaceae, Gnetopsida). Phyton 39:167-183.

Wiesenborn WD (2003) Insects on *Pholisma sonorae* (Lennoaceae) flowers and their conspecific pollen loads. Madrono 50:110-114.

Willemstein SC (1987) An evolutionary basis for pollination biology. Leiden Botanical Series 10: 1-425. E.J.Brill, Leiden University Press, Leiden, The Netherlands.

Willis JC, Burkill IH (1895) Flowers and insects in Great Britain. I. Annals of Botany 9:227-273

Willis JC, Burkill IH (1903) Flowers and insects in Great Britain. III. Annals of Botany 17:539-570

Willis DS, Kevan PG (1995) Foraging dynamics of *Peponapis pruinosa* (Hymenoptera: Anthophoridae) on pumpkin (*Cucurbita pepo*) in southern Ontario. Canadian Entomologist 127:167-175.

Willmer P (2011) Pollination and floral ecology. Princeton University Press, Princeton NJ.

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

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

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

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

Young AM., Erickson EH, Strand MA, Erickson BJ (1987a) Pollination biology of *Theobroma* and *Herrania* (Sterculiaceae)-I. Floral biology. Insect Science Applications 8:151-164.

Young AM, Erickson BJ, Erickson EH (1987b) Steam-distilled floral oils of *Theobroma* species (Sterculiaceae) as attractants to flying insects during dry and wet seasons in a Costa Rican cocoa plantation. In: Proceedings of the 10th International Cocoa Research Conference, Santo Domingo, Dominican Republic, Cocoa Producers Alliance, Lagos, Nigeria, pp 303-306.

Young AM, Schaller M., Strand M (1984) Floral nectaries and trichomes in relation to pollination in some species of *Theobroma* and *Herrania* (Sterculiaceae). American Journal of Botany 71:466-480.

Yuan LC, Luo YB, Thien LB, Fan JH, Xu HL, Chen ZD (2007) Pollination of *Schisandra henryi* (Schisandraceae) by female, pollen-eating *Megommata* species (Cecidomyiidae, Diptera) in south-central China. Annals of Botany 99:451-460.

Yuan LC, Luo YB, Thien LB, Fan JH, Xu HL, Yukawa J, Chen ZD (2008) Pollination of *Kadsura longipedunculata* (Schisandraceae), a monoecious basal angiosperm, by female, pollen-eating *Megommata* sp (Cecidomyiidae: Diptera) in China. Biological Journal of the Linnean Society 93:523-536.

Zhang YW, Zhao JM, Inouye DW (2013) Nectar thieves influence reproductive fitness by altering behavior of nectar robbers and legitimate pollinators in *Corydalis ambigua* (Fumariaceae). Journal of Ecology, in press.

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

Zimmerman M, Brody AK (1998) Choices and consequences of oviposition by *Hylemya* (*Delia*) sp. (Diptera: Anthomyiidae). Journal of Insect Behavior 11:371-381.