TOPIC 5. **Plant-pollinator interactions**

Sílvia Castro, Marta Barberis, Marta Galloni

Pollinator behavior

- Flower visitors and pollinators
- Pollination efficiency and pollinator effectiveness
- Flower constancy
- Pollinator behavior mediated by nectar rewards (Marta Barberis)

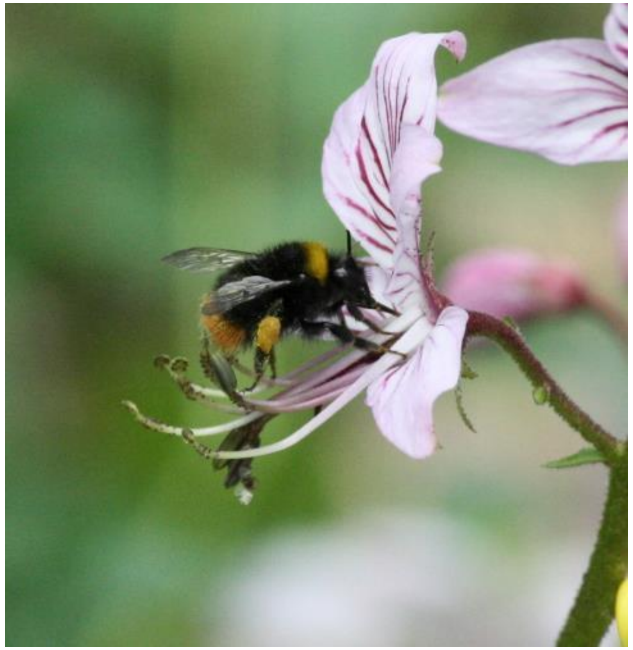
Pollinators or floral visitors?

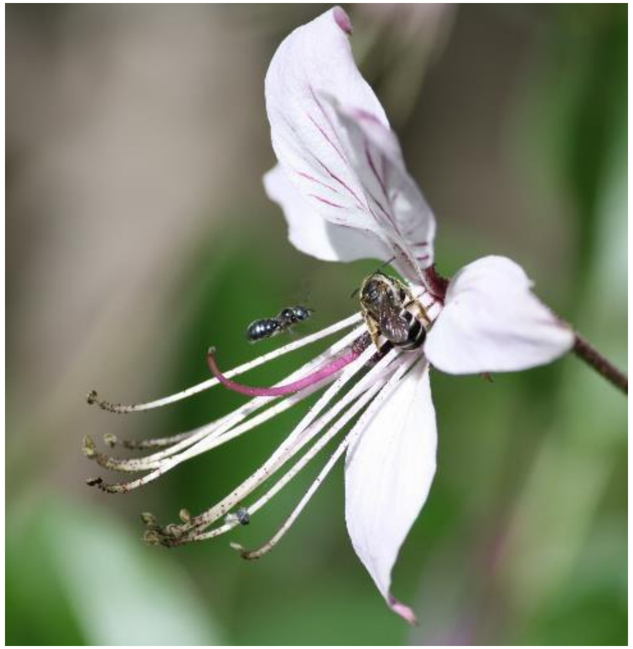
What makes an animal a pollinator?

Set the ground to define a pollinator – this is done with field data and we have to fulfil the 'Cox-Knox postulates' (Cox and Knox 1988):

1. Transfer of pollen onto a vector
2. Transport of pollen by that vector
3. Transfer of pollen from the vector to the stigma of a flower
4. The deposited pollen effecting fertilization of ovules

Who can see floral visitors missing one or several of these steps?

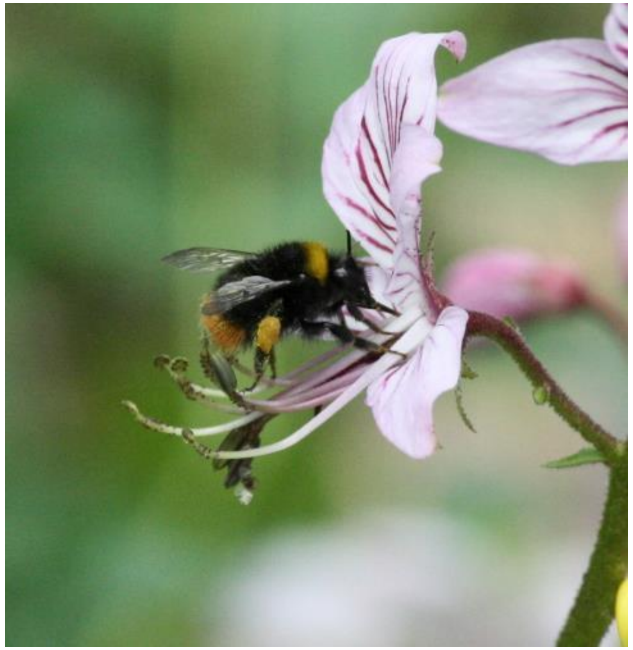


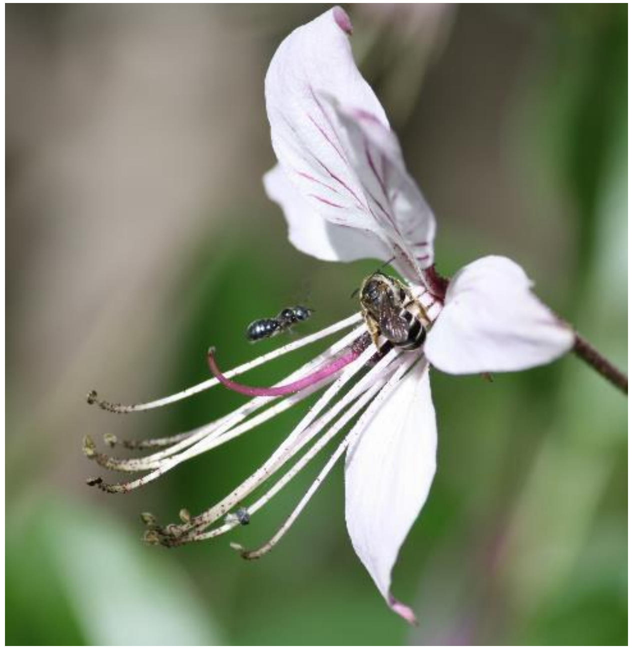


Pollinators or floral visitors?

Many of the floral visitors seen in the flowers do not pollinate them or do so poorly

We should be critical when referring to floral visitors and pollinators?





Pollinators or floral visitors?

Behavioral components of floral visitors: Dafni et al. 2005

Approach – the floral visitor is attracted by a set of cues, comes close to the flower to make a decision; visitors often inspect flowers to assess the age or reward status before rejecting it (or decide to visit)

Visit – any touch or alignment on the flower

Visit duration – the time the floral visitor stays on the flower

Pollen collection – active harvesting of pollen from the anthers may be observed (e.g. buzz pollination), but is could be passively transferred from anthers to visitor's body; information where the pollen adheres to the floral visitor is informative

Grooming behavior – floral visitors (especially insects) may groom or comb pollen to specific parts of the body (or off their bodies)

Reward collection – (usually) nectar uptake may be observed directly as floral visitors insert their proboscis, beak or tongue; may include the collection of other rewards; note the feeding behavior (Inouye 1980)

Stigma touch – a contact between the stigma and any part of the floral visitor's body; it is useful to record the part of the body to compare with the relative position above

Move to – (usually) flight to the next flower, which can be a flower of the same plant or a different plant, near or farer way

(sequence of components can be different)

Pollinators or floral visitors?

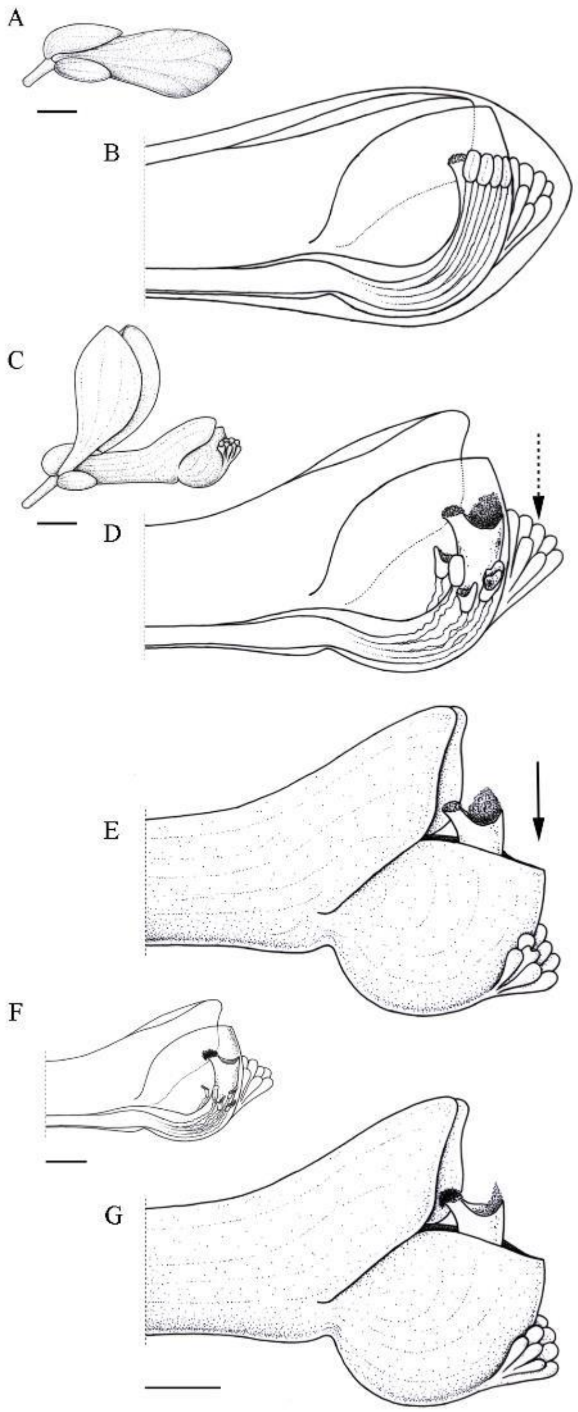
Classification of floral visitors Inouye 1980

- (Primary) Nectar robbing
- Secondary nectar robbing
- Nectar thieving
- Pollen robbing
- Pollen thieving

Different behaviours impact differently (directly and indirectly) plant fitness

TABLE 1. Definitions and usage of terms relating to methods of collecting pollen and nectar.

The behavior is called:	Which implies that:
Nectar robbing	
Primary nectar robbing	A hole is made and used to obtain nectar, bypassing the opening used by pollinators.
Secondary nectar robbing	The hole made by a primary nectar robber is used to obtain nectar, bypassing the opening used by pollinators.
Nectar thieving or nectar theft	No hole is made in the flower; the thief is using the opening used by pollinators but a mismatch of morphologies precludes pollination.
Base working	No hole is made, but the opening used by pollinators is not used either; the technique is generally restricted to flowers with polypetalous corollas.
Pollen robbing	The flower visitor is collecting pollen in a manner that precludes pollination and damages floral tissues.
Pollen thieving or pollen theft	The flower visitor is collecting pollen in a manner that precludes the possibility of pollination, but is not damaging floral tissue.



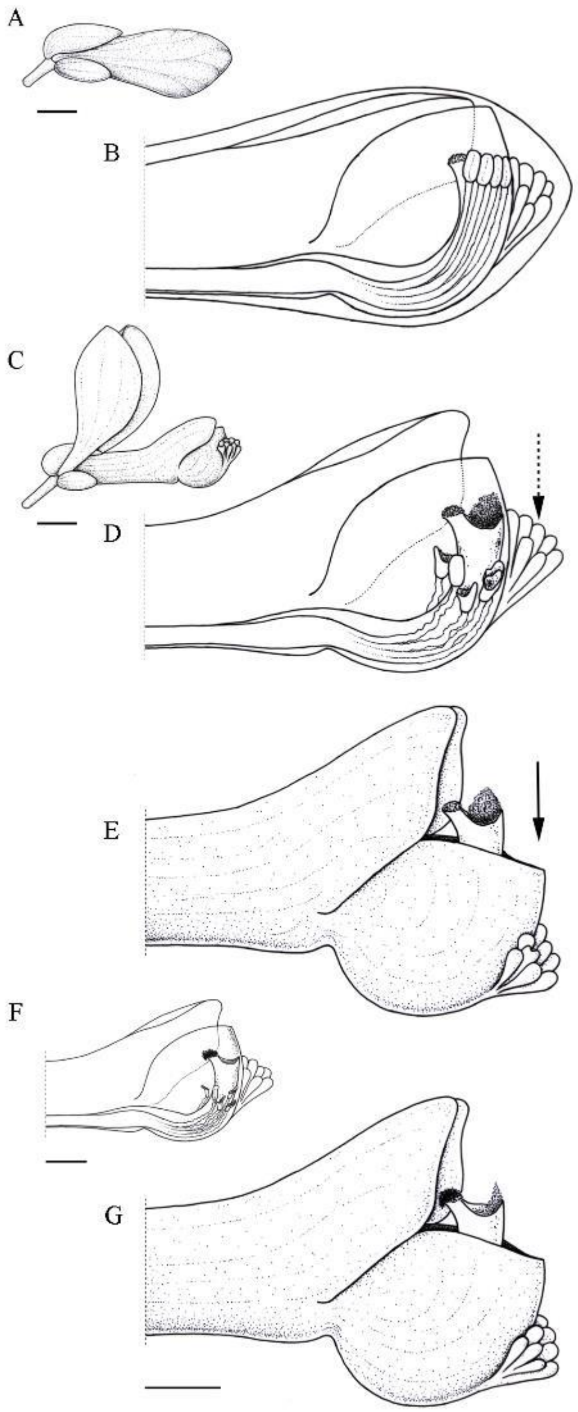
Example of *Polygala vayredae*

Floral visitors assemblage and foraging behaviour

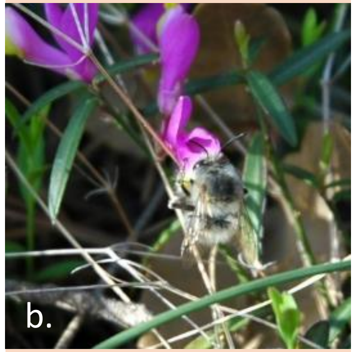
Visitor species	Type of visit	Proboscis size (mm)	Length of insect body (mm)	Visitation rate	No. flowers visited per cluster	Handling time (sec)	Deposited pollen	Distances within a cluster (cm)	Distances between clusters (cm)
Order Hymenoptera									
Anthophora sp.	L	10.4 ± 2.09	15.6 ± 1.18	**0.884**	12 ± 11.5	2.6 ± 2.25	86 ± 65.3	19.2 ± 19.51	246 ± 97.8
Bombus terrestris	R	5.8 ± 0.34	17.3 ± 1.64	**12.140**	36 ± 34.0	3.3 ± 3.20	0	17.6 ± 20.47	550 ± 169.6
Bombus pascuorum	L	8.9 ± 0.81	16.8 ± 0.91	**3.172**	22 ± 20.7	3.0 ± 2.19	122 ± 80.3	14.2 ± 15.88	595 ± 230.3
Bombus lucorum	L	5.9	17.1	0.093	36 ± 22.9	3.1 ± 4.27	111 ± 18.4	16.6 ± 13.87	>>
Bombus pratorum	R	5.7 ± 0.78	10.6 ±1.91	0.280	16 ± 16.0	3.2 ± 2.54	0	27.3 ± 21.63	>>
Bombus lapidarius	R	3.2 ± 0.64	16.9 ± 0.04	0.005		3.9 ± 4.79	0		
Bombus hortorum	R			0.016			0		
Psithyrus sp.	R	1.9	12.5	0.003			0		
Apis mellifera	T	3.1 ± 0.35	12.3 ± 0.35	0.238	12 ± 15.1	4.3 ± 3.27	0	23.2 ± 18.43	217 ± 54.7
Eucera longicornis	L	4.6	11.8	0.025	7 ± 4.9	8.8 ± 6.22	97 ± 45.8	28.9 ± 20.72	>>
Halictus sp.	L	0.9	7.6	0.081	5 ± 3.3	7.3 ± 7.42		27.4 ± 20.31	>>
Osmia rufa	T	4.7	13.8	0.054	8 ± 3.5	3.4 ± 2.25	0	19.4 ± 19.85	>>
Xylocopa violacea	R			0.005		3.2	0		
Formicidae	SR	-	<0.7	0.158	3 ± 3.8		0	-	-
Order Diptera									
Bombylius sp.	L_i	6.2 ± 0.71	8.8 ± 1.42	0.079	3 ± 1.8	1.9 ± 1.47	0	47.9 ± 18.74	>>
Order Lepidoptera									
Macroglossum stellatarum	L_i	26.0 ± 1.44	29.6 ± 1.64	**0.989**	13 ± 12.4	1.9 ± 2.68	0	24.4 ± 23.18	254 ± 107.6
Hemaris fuciformis	L_i	14.6 ± 1.32	29.5 ± 0.96	0.416	25 ± 39.5	2.2 ± 2.18	0	24.0 ± 22.03	249 ± 89.7
Gonepteryx rhamni	L_i	19.6 ± 1.04	22.4 ± 1.31	0.142	5 ± 5.7	13.9 ± 11.76	0	61.1 ± 32.84	>700
G. cleopatra	L_i			0.029	3 ± 1.8	17.0 ± 10.91	0		
Leptidea sinapis	T	<10.0	14.8 ± 0.35	0.004	2 ± 1.2		0		>>
Papilio machaon	T	13.5	24.5	0.017	10 ± 5.7	5.7 ± 5.07	0		>>
Pyronia sp.	T	<10.0	16.5	0.022	3 ± 2.0	10.1	0		
Aglais urticae	L_i			0.001			0		
Vanessa atalanta	L_i			0.008	2 ± 1.3		0	40.3 ± 21.71	>>
V. cardui	L_i			0.033	5 ± 3.1	8.9 ± 6.87	0		

Castro et al. 2013

Example of *Polygala vayredae*

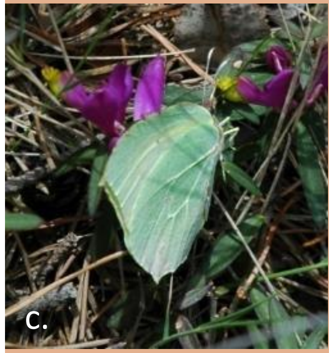


Floral visitors assemblage and foraging behaviour



a. *Bombus pascuorum*
b. *Anthophora* sp.

Legitimate pollinators



c. *Gonepterix rhamni*
d. *Macroglossum stellatarum*

Legitimate inefficient visitors

e. *Bombus terrestris*
f. *Bombus pratorum*

Nectar robbers

g. *Papilio machaon*
h. *Osmia rufa*

Nectar thieves

i. *Formica gagates*

Secondary nectar robbers

Terminology following Inouye (1980)

Castro et al. 2013

Pollinators or floral visitors?

Nectar robbers as pollinators

e.g., Navarro 2000 (*Anthyllis vulneraria*)

Pollination efficiency and pollinator effectiveness

Pollinator behaviour impacts its **efficiency in pollen transfer**, and consequently, in **plant fitness**

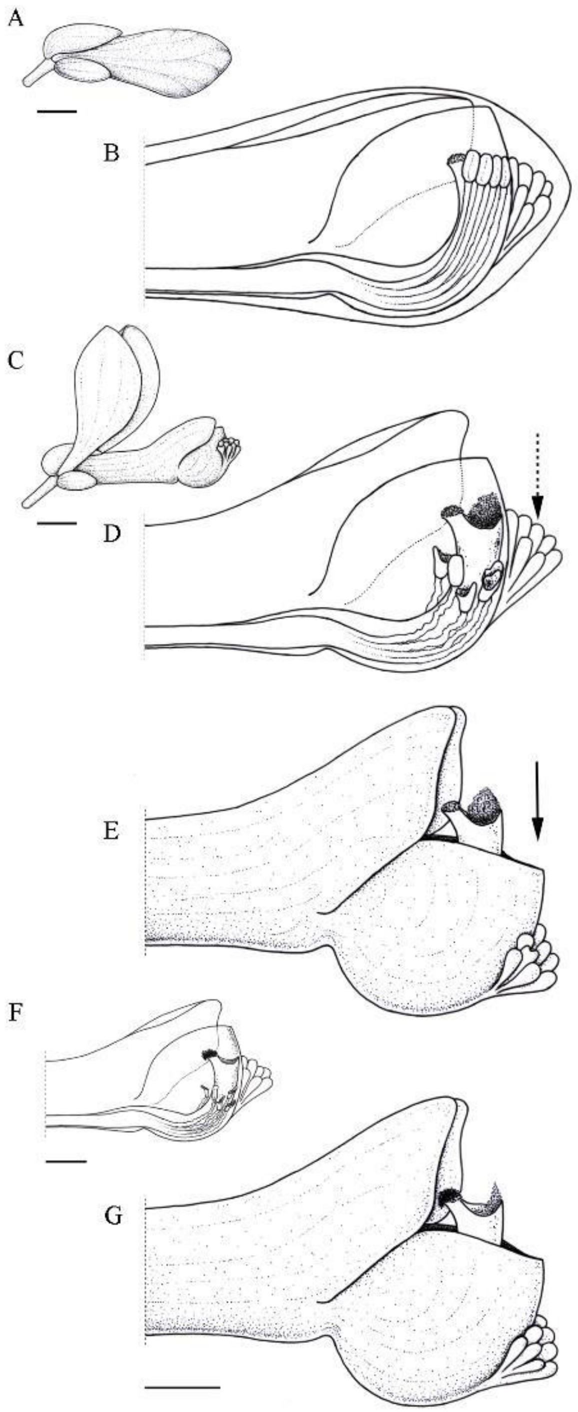
- **Pollination efficiency** – measurement of benefits (or costs) to the plant from a single visit by an animal to a flower or floral unit

  e.g., seed set, pollen removal or nectar, pollen and ovule consumption, heterospecific pollen deposition, clogged stigmas or damage to flowers

- **Pollinator effectiveness** – outcomes of a single visit by an animal and is usually used to rank the importance of different species of floral visitors

  e.g., number of pollen grains deposited, pollen removed, seeds or fruits set, percentage of flowers pollinated

Not all visitors are pollinators, and not all pollinators are equally effective in their pollination activities



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Castro et al. 2013

Example of introduced pollinators

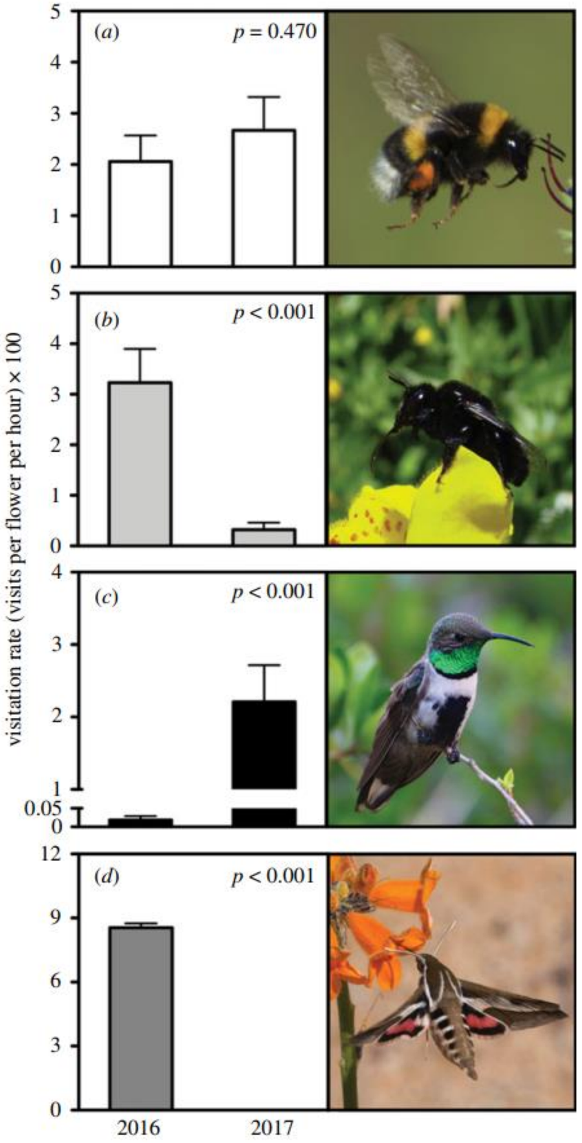

Figure 1. Mean visitation rate (s.e.) of (*a*) *Bombus terrestris*, (*b*) *Centris nigerrima*, (*c*) *Oreotrochilus leucopleurus* and (*d*) *Hyles annei* on the Andean monkeyflower, *Erythranthe lutea*, during the flowering seasons of 2016 (104 h of observation) and 2017 (138 h of observation). Credit for photograph of *H. annei*: J. P. de la Harpe.

The most effective pollinator principle applies to new invasive pollinators

species	visitation rate (V_r, visits per flower per hour) × 100		pollen deposition effectiveness: per single visit (D_v)		pollen deposition effectiveness: per unit time ($= D_v \times V_r \times r$)		
	2016	2017	2016	2017	2016	2017	mean
Hymenoptera							
Bombus dahlbomii	0.18 ± 1.05	0	345.8 ± 404.7 (8)	—	0.64 (4.2%)	—	0.64 (4.3%)
Bombus terrestris	2.06 ± 5.46	2.67 ± 7.31	158.1 ± 260.2 (126)	191.3 ± 292.7 (39)	3.26 (21.4%)	5.10 (37.0%)	4.18 (27.9%)
Centris chilensis	0.85 ± 3.12	0.42 ± 1.67	103.2 ± 207.1 (32)	315.6 ± 658.2 (13)	0.88 (5.8%)	1.32 (9.6%)	1.1 (7.4%)
Centris nigerrima	3.23 ± 7.16	0.32 ± 1.54	201.1 ± 334.8 (101)	—	6.49 (42.6%)	0.64* (4.6%)	3.57 (23.9%)
Corynura chloris	0	0.01 ± 0.07	—	—	—	—	—
Hypodynerus sp.	0.004 ± 0.04	0.02 ± 0.10	—	—	—	—	—
Megachile saulcyi	1.33 ± 3.61	0.03 ± 0.13	112.4 ± 246.6 (52)	—	1.50 (9.8%)	0.03* (0.2%)	0.77 (5.2%)
Megachile semirufa	0.06 ± 0.53	0.04 ± 0.25	—	37.0 ± 25.0 (3)	2.22* (14.6%)	1.48 (10.7%)	1.85 (12.4%)
Svastrides melanura	0.01 ± 0.11	0	38.4 ± 33.4 (7)	—	0.01 (0.1%)	—	0.01 (0.1%)
Lepidoptera							
Hyles annei	8.55 ± 22.12	0	1.3 ± 6.2 (44)	—	0.11 (0.7%)	—	0.11 (0.7%)
Pseudolucia sp.	0	0.004 ± 0.03	—	—	—	—	—
Tatochila sp.	0.02 ± 0.17	0.03 ± 0.17	—	—	—	—	—
Vanessa carye	0.01 ± 0.09	0.01 ± 0.04	0 (1)	0 (1)	0	0	0
Diptera							
Scaeva melanostoma	0.01 ± 0.05	0.01 ± 0.12	—	—	—	—	—
Bombylidae	0.02 ± 0.23	0	4 (1)	—	0.08 (0.5%)	—	0.08 (0.5%)
Apodiformes							
Oreotrochilus leucopleurus	0.02 ± 0.11	2.21 ± 6.03	—	236.5 ± 433.1 (48)	0.05* (0.3%)	5.23 (37.9%)	2.64 (17.6%)

Medel et al. 2018

Flower constancy

- **Feature of an individual flower visitor** – usually refers to behaviour within a single trip, but can also refer to successive trips or trips on successive days
- **Tendency to visit the same flower type as the one last visited**
- Requires some degree of learning based on recognition of features
- Still, many flower-foraging animals regularly check other flower species to explore and 'weight' other rewarding sources
- Flower constancy **is not a rigid behavioural choice** and can be influenced by several factors extrinsic to the floral visitor

Bee Pollen Load Compositions (Relative Frequency)

Genus	*% pure loads*	
Andrena	44–68	
Halictus	75–84	
Megachile	65–75	
Anthophora	20	
Bombus	49–69	
B. lucorum	66	Free 1970b
B. muscorum	37	Free 1970b
Apis	62–94	Multiple sources
Trigona	88	White et al. 2001

Source: Data modified from sources in Grant (1950) except where shown.

Willmer 2011

Negative frequency-dependent selection in the rewardless orchid *Dactylorhiza sambucina* Gigord et al. 2001

Pollinator behavior mediated by nectar rewards

Marta Berberis & Marta Galloni

Questions

Pause