OCEANIC ISLAND BATS AS FLOWER VISITORS AND POLLINATORS

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Abstract—Oceanic islands are relatively poor in insects compared to mainland areas. Therefore, insect-eating island birds and lizards may include other food sources into their diet, e.g. nectar and pollen. Here, we explore if insect-eating island bats face a similar problem and accordingly join the birds and lizards and incorporate plant resources into their diet. Thus, a priory, we assume flower visitation by bats to be more common on oceanic islands than elsewhere. To test this, we reviewed the literature to obtain information on the geographic distribution and diet of all 1,399 species of bats in the world and found that 49%, 21%, and 31% of species have a mainland, mixed mainland-island, and island distribution, respectively. Diets are known for only 65% (905 species) of the bats in the world, and 70%, 22%, and 8% of these, respectively, rely on insects, fruit, and floral resources as their major diet component. Twenty-seven species are even obligate flower visitors. This study confirms that flower-visiting bats, especially Pteropodidae, are significantly more frequent on oceanic islands, while insect eaters are more frequent on mainland and continental islands. Consequently, we argue that flower visitation and pollination by insect-eating island bats require more attention in future island ecology studies. For a start, we list known examples in the literature and report a case study from the Canary Islands. In the latter, we examined the foreheads of 34 museum specimens of the seven Canarian bat species. Half of them carried pollen from ≥ 9 taxa, but only three bat species had larger amounts. Pollen was not identified, but many Canarian and exotic plant species are candidates. Thus, flower visitation by bats may be an oceanic island phenomenon, but requires more focused research, especially night-time flower observations and examination of bats for pollen.

Keywords—Canary Islands, Chiroptera, diet, nectar, Phyllostomidae, Pteropodidae

INTRODUCTION

Globally, most Passerine birds and Squamata lizards live on a staple diet of invertebrates, especially insects (Wilman et al. 2014; Meiri 2018; Nyffeler et al. 2018; Uetz et al. 2023). Obviously, this is problematic in regions and during seasons that are poor in insects, e.g. on oceanic islands and high mountains, and during lean seasons (Allan et al. 1973; Janzen 1973; Spears 1987; Olesen & Valido 2003a; Olesen et al. 2010). Here, we define an insect-eater or insectivore as an animal that eats arthropods, which includes ticks, spiders, millipedes, etc., in addition to insects (*sensu* Lopes et al. 2016).

Thus, when food is limited, e.g. on oceanic islands, "classic" insectivorous birds and lizards may broaden or change their diet, and they do so by including other, perhaps sub-optimal, resources such as nectar, pollen, and pulp from fleshy fruit (Blanco et al. 2013; Abrahamczyk 2019; Valido & Olesen 2019). This opportunistic exploitation of resources of sugars, water, vitamins, and minerals, being easy to harvest, does not prevent a simultaneous intake of lipids and proteins from, for example, invertebrate prey (McKey 1975). Moreover, these birds and lizards may also function as legitimate pollinators and seed dispersers (Olesen & Valido 2003a,b; Rodríguez-Rodríguez et al. 2013; Abrahamczyk 2019; Valido & Olesen 2019). Nectar and pollen

should also be more plentiful when flower-visiting insects, like other island insects, are scarce. This fascinating niche widening, where more and new interactions get established, is termed interaction release, and seems to be a global oceanic island phenomenon (Cox & Ricklefs 1977; Olesen & Valido 2003a; *sensu* Traveset et al. 2015). However, the ability of island species to engage in interaction release depends on habitat context and the tendency of species to perform and act with high unpredictability, i.e. their foraging strategy (Morse 1971; Stewart & Dudash 2018; Olesen 2022). Interaction release reminds us ecologists not to rely too strongly on categorical thinking when we score island ecological information, and also shows us the remarkable and often surprising opportunistic capability of island nature and its biodiversity for change.

INSECT-EATING BATS ON ISLANDS–THE CONUNDRUM

If small, insectivorous island birds turn to floral resources and fleshy fruits, and if small, insectivorous island lizards do the same, then why not other small, insectivorous island animals? For example, island bats, rodents, or predatory insects must face the same food shortage problem. At present, the question cannot be answered adequately, mainly because most reports are anecdotal and we lack systematic observation, but to us, the idea certainly makes "eco-logical" sense and is worth a closer look.

Here, we focus on bats, but in the discussion, we also add a note about island rodents. Our aims are (1) to summarize what is known about the distributions and diets of the bats of the world, focusing upon flower visiting and pollinating bats on oceanic islands, and (2) to offer new, albeit preliminary, data about flower visitation by Canary Island bats.

MATERIALS AND METHODS

DATA FROM LITERATURE

Information about native geographic distribution and diet of all 1,399 bat species in the world was extracted from Wilson & Mittermeyer (2019) and González-Gutiérrez et al. (2022). All species were sorted into different distributional and dietary categories (Tables 1 and 2; see also Supp. Mat. 1 and 2). For some species, the decision about scoring a specific diet component as being

major or minor was subjective, but it was always based on the detailed diet description in Wilson & Mittermeyer (2019). Diet data were based on faecal sample analysis and field observations of species in their native range. When the diet of a species was deduced from bat morphology alone, based on the diet of congenerics, described by 'supposedly', 'quite likely' etc., or solely from experiments in captivity, the species was placed in the category 'No diet data available' (Table 2).

DATA FROM CASE STUDY

In addition, 34 specimens of the seven Canarian bat species in the collections at the Museo de Ciencias Naturales de Tenerife, MUNA (*TFMC-VM*) and the Departamento de Biología Animal, Edafología y Geología, Universidad de La Laguna (*DZUL*) were inspected for pollen by swabbing throat, nose, and forehead with a ~3 mm^3 cube of glycerin jelly, stained in red dye. Each cube was placed on a microscope slide and melted by a weak heat source, after which the sample was covered by a slip. Slides were sealed with nail polish and inspected microscopically for pollen grains. The bat specimens originated from all seven main Canarian Islands, except Lanzarote and Gran Canaria. In a study like this, there is always a risk of pollen contamination between specimens stored together. However, in our study, we see this as a minor issue because the specimens originated from two physically separated collections. Besides, at *TFMC-VM*, all specimens were stored individually, and at *DZUL*, specimens kept in the same drawer turned out to carry different pollen grain types.

RESULTS AND DISCUSSION

GEOGRAPHICAL DISTRIBUTION OF BATS

The present global bat species count is 1,399, and all these species were sorted into three major distributional categories (Table 1). This was done in two ways: continental island species were either pooled together with (1) oceanic island species (Table 1B) or (2) mainland species (Table 1C). We analysed the data both ways because, in some instances, animals may perceive and respond to continental islands as they do on oceanic islands, while in other instances, they may perceive and respond to continental islands as they do on the mainland. Almost half, 682 (48.7%) of all bats turn out to be mainland species, and 430 (30.7%) are

Table 1. Number of bat species in distributional categories (total 1,399 species) based on Wilson & Mittermeyer (2019). (A) All bats: Comparison between all categories (B) All bats: Mainland-island comparison (continental islands analysed as 'islands') (C) All bats: Oceanic island comparison (continental islands analysed as 'mainland')

	Distributional category		No. species	Pct.
(A)	Mainland only	M	682	48.70
	Continental island only	C	185	13.20
	Oceanic island only	O	165	11.80
	Mainland and continental island	MC	193	13.80
	Mainland and oceanic island	MO	9	0.60
	Continental island and oceanic island	CO	80	5.70
	Mainland, continental island, and oceanic island	MCO	85	6.10
	Total no. species	S	1399	100.00
(B)	Mainland	M	682	48.70
	Mainland and island	MC+MO+MCO	287	20.50
	Island	C+O+CO	430	30.70
	Total no. species	S	1399	100.00
(C)	Oceanic island only	O	165	11.80
	Oceanic island and others	MO+CO+MCO	174	12.40
	Mainland and /or continental island	M+C+MC	1060	75.80
	Total no. species	S	1399	100.00

island species. 165 (11.8%) of all species are also endemic to some oceanic archipelagos.

Compared to other bat families, Phyllostomidae and Pteropodidae stand out. The first is mostly found on the mainland (74.2% of the family), whereas the latter is common on oceanic islands (47.1% of the family) (Suppl. Mat. 1A).

Thus, about half, or 51.3% of all bat species in the world are members of island ecosystems, suggesting a stronger future research focus upon their ecology within an island framework.

DIET OF BATS

It is known that most bats are notorious insectivores, but they may also consume other invertebrates, vertebrates, nectar, pollen, fruit, seed, foliage, or even blood, but unfortunately, we only know the diet of 905 species, i.e. 64.7% of all bats (Table 2). Below we briefly describe the diet diversity.

All bats (except the three vampire bat species: *Desmodus rotundus*, *Diphylla ecaudata*, and *Diaemus youngi*; Phyllostomidae) can be sorted into one of three main categories, according to the major component of their diet (Table 2):

I: *Insect food.*- 630 bats (69.6% of the 905 bats with a known diet; row G in Table 2) have insects as a major diet component. 580 (92% of 630; row A) of these bats may also supplement their insect diet with minor amounts of other invertebrates, such as spiders, scorpions, crabs, or shrimps. Insect-consuming bats may also add minor amounts of vertebrates, fruit, or floral resources (50 species; rows *B–F*). In addition, 57 fruit- and floral resource-consuming bats have insects as a minor diet component (rows I, K, N, P, and R).

II: *Fruit food.*- 196 bats (21.7% of 905; row L) have fruit and seeds as major diet components, exclusively (105 species; row H) or together with minor amounts of insects or floral resources (91 species; rows I-K). In addition, 58 bats have fruit as a minor diet component (rows C, D, F, O, P, and R). All 254 fruit-eating species except six belong to Pteropodidae (131 spp.) and Phyllostomidae (117 spp.). These six are two *Mystacina* spp. (Mystacinidae), *Noctilio albiventris* (Noctilionidae), *Molossus sinaloae* (Molossidae), and *Antrozous pallidus*, and *Lasiurus pfeifferi* (Vespertilionidae).

III: *Floral food.*- 71 bats (7.8% of 905; row Q) have nectar, pollen, and other floral parts as major diet

Table 2. Number of bat species in dietary categories (total 905 species) based on the diet description in Wilson & Mittermeyer (2019). 'Fruit' includes pulp and/or seeds. Foliage as a diet component is ignored. The choice between 'flower (major)–fruit (minor)' and 'fruit (major)–flower (minor)' may, for some species, be arbitrary, e.g. for some *Epomorphorus* and *Pteropus* species.

Dietary category Major diet component	Minor diet components	No. species	Pct.
A. Insects	none or other invertebrates	580	
B. Insects	vertebrates	29	
C. Insects	vertebrates and fruit	4	
D. Insects	fruit	9	
E. Insects	flower	3	
F. Insects	fruit and flower	5	
G. Insects as a major diet component		630	69.6
H. Fruit	none	105	
I. Fruit	insects	10	
J. Fruit	flower	61	
K. Fruit	insects and flower	20	
L: Fruit as a major diet component		196	21.7
M. Flower	none	27	
N. Flower	insects	9	
O. Flower	fruit	22	
P. Flower	insects and fruit	13	
Q. Floral resources as a major diet component		71	7.8
R. Generalist diet: Insects, vertebrates, fruit, and flower		5	0.6
S. Blood as a major diet component		3	0.3
Total no. species with diet data available		905	100
No. species with no diet data available		494	

components, exclusively (27 species; row M) or more often together with minor amounts of insects or fruit (44 species; rows N-P). In addition, 94 species have floral resources as a minor diet component (rows E, F, J, K, and R). All 165 flower-visiting species except six belong to Pteropodidae (75 spp.) and Phyllostomidae (84 spp.) (Suppl. Mat. 1B, C). These six are the two *Mystacina* spp. (Mystacinidae), *Noctilio albiventris* (Noctilionidae), and *Antrozous pallidus* and two *Lasiurus* spp. (Vespertilionidae). These six species are interesting in the context here, because they show that bats outside Pteropodidae and Phyllostomidae also visit flowers. In the latter two families, nectarivory is concentrated in a few subfamilies (Suppl. Mat. 1B).

Vertebrate food is an astonishing rich buffet of birds, fish, lizards, bats, frogs, and rodents–listed in decreasing order of mentioning in Wilson & Mittermeyer (2019). Vertebrate-eating bats occur across families. However, no bat is known to be an obligate vertebrate predator, i.e. if we ignore the blood-consuming vampires *Desmodus rotundus, Diaemus youngii*, and *Diphylla ecaudata* (Phyllostomidae; row S)

In conclusion, we know the diet of 2/3 or 905 (65%) of all bats in the world, and 2/3 or 580 (64%) of these 905 are exclusive invertebrate eaters. Thus, 325 species have a wider or different diet, especially the 105 and 27 bats being exclusive fruit and floral resource consumers, respectively.

However, despite this rich diet diversity among bats, it is certainly true, that most bat research still

implicitly assumes bats, outside Pteropodidae and Phyllostomidae, to be insect eaters. Many bats are just labelled 'insectivore', seemingly without any further evidence (Wilson & Mittermeyer 2019).

FLOWER-VISITING BATS AS AN ISLAND PHENOMENON

Major diet components and geographic distribution were highly significantly associated (Table 3). On mainland and continental islands, bats are more often insectivores than insular ones (72.0% – 80.2% *vs*. 55.1%, respectively; *P* < 0.01). Whereas on islands, many more bats than expected are frugivores (fruit pulp, seeds; 35.1% *vs*. 18.9%-12.8%, respectively; *P* < 0.01) and flower consumers (nectar, pollen, other floral parts; 9.4% *vs*. 8.4%-5-4%, respectively; *P* < 0.01).

Bats with unknown diets are found all over the world, but mostly in Africa and Asia. One might perhaps expect bats with unknown diets to be more common on remote, less explored islands, but that is not the case, because mainland-island distributions of species with a known and unknown diet were similar.

ARGUMENTS FOR FLOWER VISITATION AND POLLINATION BY ISLAND BATS

Based on the global literature review, we tentatively conclude that nectarivory in bats is indeed an oceanic island phenomenon too, but also that this pattern is driven by Phyllostomidae and especially the phytophagous Pteropodidae.

Phyllostomidae shows that nectar consumption can evolve in an insect-rich mainland, i.e. nectar may be chosen over insects. Pteropodidae shows, how bats get established on remote, insect-poor islands on a broad plant diet (floral resources, fruit, but also foliage). Although the diet of insectivorous bats is generally poorly studied, a few examples show that diet diversity might be richer than we previously have assumed.

1. Phyllostomidae and the flexibility of their diet

Phyllostomidae can teach us much about the evolution of nectar consumption in bats. From insect-eating ancestors, Phyllostomidae (217 spp.) evolved to become an impressive mammalian adaptive radiation with a rich diversity in feeding morphology and behaviour (Fleming et al. 2020), especially tongue morphology and hovering flight (Datzman et al. 2010; Monteiro & Nogueria 2011; Rojas et al. 2011; Wilson & Mittermeyer 2019). Nectar-drinking evolved from insectivory at least twice, and it happened evolutionary fast. More than 1/3 of all species in the family (84 species, 38.7%, Suppl. Mat. 1B), especially Glossophaginae, take nectar and pollen from hundreds of plant species (e.g. Fleming & Kress 2013).

Most often, we talk about nectar but ignore pollen, which as a protein source, may be closer to a proper insect food substitute than sweet nectar. Some studies even show pollen to be the most

Table 3. Statistical association between geographic distribution and diet of all bats (total 905 species). See also tables 1 and 2 for details.

Major distributional category	Major diet component				No species (%)
	Insects	Fruit	Floral resources	Other categories*	Species no.**
A. Mainland-island comparison					
Mainland M	301 (72.0)	79 (18.9)	35 (8.4)	3 (0.7)	418
Mainland and island MC+MO+MCO	194 (80.2)	31 (12.8)	13 (5.4)	4 (1.7)	242
Island C+O+CO	135 (55.1)	86 (35.1)	23 (9.4)	1 (0.4)	245
B. Oceanic island comparisons					
Oceanic island only O	25 (28.1)	50 (56.2)	14 (15.7)	0 (0.0)	89
Oceanic island and others MO+CO+MCO	95 (69.3)	29 (21.2)	13 (9.5)	0 (0.0)	137
Mainland and/or continental island M+C+MC	510 (75.1)	117 (17.2)	44 (6.5)	8 (1.2)	679

A. χ^2-contingency table: association between distribution and diet. χ^2_4 = 45.0, *P* < 0.01.

B. χ^2-contingency table: association between distribution and diet. χ^2_4 = 88.6, *P* < 0.01.

*, (Table 1: Generalist diet and Blood) not included in χ^2-test.

**, the difference between these numbers and those in Table 1 is equal to the number of species with no diet data available.

important floral resource for some bat species. For example, the nectarless flowers of the Amazonian tree *Pseudobombax munguba* (Bombacaceae) get pollinated by the omnivorous, wide-foraging bat *Phyllostomus hastatus* (Phyllostomidae), being the sole flower visitor of this tree (Gribel & Gibbs 2002). The bat harvests its pollen, and faecal samples from netted bats include only *P. munguba* pollen. The tree seems to be self-sterile and thus completely dependent upon the bat for fruit set. Each of its large flowers (corolla diameter 10-14 cm) has 1,000-1,200 stamens, which must be a large amount of food to a bat. The flower opens after dusk and lasts only one night. *Pseudobombax munguba* is the only known nectarless plant being bat pollinated. Other *Pseudobombax* species are also bat pollinated, but they seem to produce nectar.

Therefore, even in insect-rich tropical mainland habitats, floral resources may be more attractive to foraging bats than to insects if available in large amounts.

2. Resource-rich islands may lead to obligate flower visitation and vice versa, resource-poor islands to diet widening

Globally, 27 bat species feed solely on floral resources, and seven of these are restricted to oceanic islands. Six of them are Pteropodidae from the Moluccas, Bismarcks, Solomons, Vanuatu Islands, and Fijis (Wilson & Mittermeyer 2019). An extinct Pteropodidae species, *Pteropus subniger*, from the Mascarenes, is the smallest known in the family. It was also a flower visitor because analysis of head and fur of nine specimens in the British Natural History Museum revealed pollen from several plant species, e.g. *Hibiscus* (Malvaceae, the archipelago has several endemic *Hibiscus* spp., *unpublished*)

Preliminary data suggest that flower-visiting oceanic island Pteropodidae as a group are characterized by a set of traits (*unpublished*): They are on average twice as heavy as mainland species, and heavy species consume both floral resources and fruit, whereas smaller species often consume either fruit or floral resources (data from Wilson & Mittermeyer 2019). Large-bodied Pteropodidae species reached remote and perhaps resource-poor oceanic islands and here survived on a broad diet of floral resources, fruit, and foliage. If food plants are in short supply on islands, they may even consume floral resources and fruit from the same

plant species, i.e. they and their food plants establish a double mutualistic relationship (Olesen et al. 2018; Kahnt et al. 2023). Flower-fruit double mutualisms are over-represented on islands and common among Pteropodidae and their food plants (Fuster et al. 2019). First, the bats consume the floral resources and then later, the fruit from their food plant. Some plants even flower and fruit simultaneously with flowers and fruit mixed on the same branches (Olesen et al. 2010). This may promote fruit-consuming bats to include floral resources into their diet. As a buffer against local food shortage, Pteropodidae also migrate between islands.

Only one obligate , oceanic island, non-Pteropodid bat, *Monophyllus plethodon* (Phyllostomidae), is known. It lives in the Lesser Antilles, from Anguilla to St. Vincent and Barbados, but fossils are known from Puerto Rico (Wilson & Mittermeyer 2019). On these islands, it requires a continuous supply of flowering plants all year round. In Dominica, for example, it visits *Wercklea* sp. (Malvaceae) together with Green-Throated Carib hummingbird (*Eulampis holosericeus*) and a Sphingidae species (Fig. 1, JM Olesen, B Dalsgaard, A Martín Gonzalez, *pers. obs.*). This plant is also visited by *Anoura cultrata* (Phyllostomidae) (Wilson & Mittermeyer 2019). Dominica is rich in native forest and may sustain a permanent *Monophyllus* population, or the species may do seasonal migration to adjacent islands.

Thus, obligate flower-visiting bats can survive on a small island, if it has a high diversity of food plants. Although the bats may compete with other nectar consumers, such as hummingbirds and lizards, for food.

The congeneric *M. redmani* from Cuba, Hispaniola, Puerto Rico, Jamaica, Bahamas, and Caicos has a wider diet, consuming invertebrates, fruit, and floral resources, e.g. from cactus, *Mucuna, Marcgravia, Centropogon, Gesneria, Lobelia, Pseudobombax, Caesalpinia, Albizzia,* and *Acacia* (D Rojas, *pers. com.*).

3. Flower visitation outside Phyllostomidae and Pteropodidae

Our data show that flower visitation does occur outside Phyllostomidae and Pteropodidae. However, we still do not know if it is rare or understudied, and under what conditions it occurs.
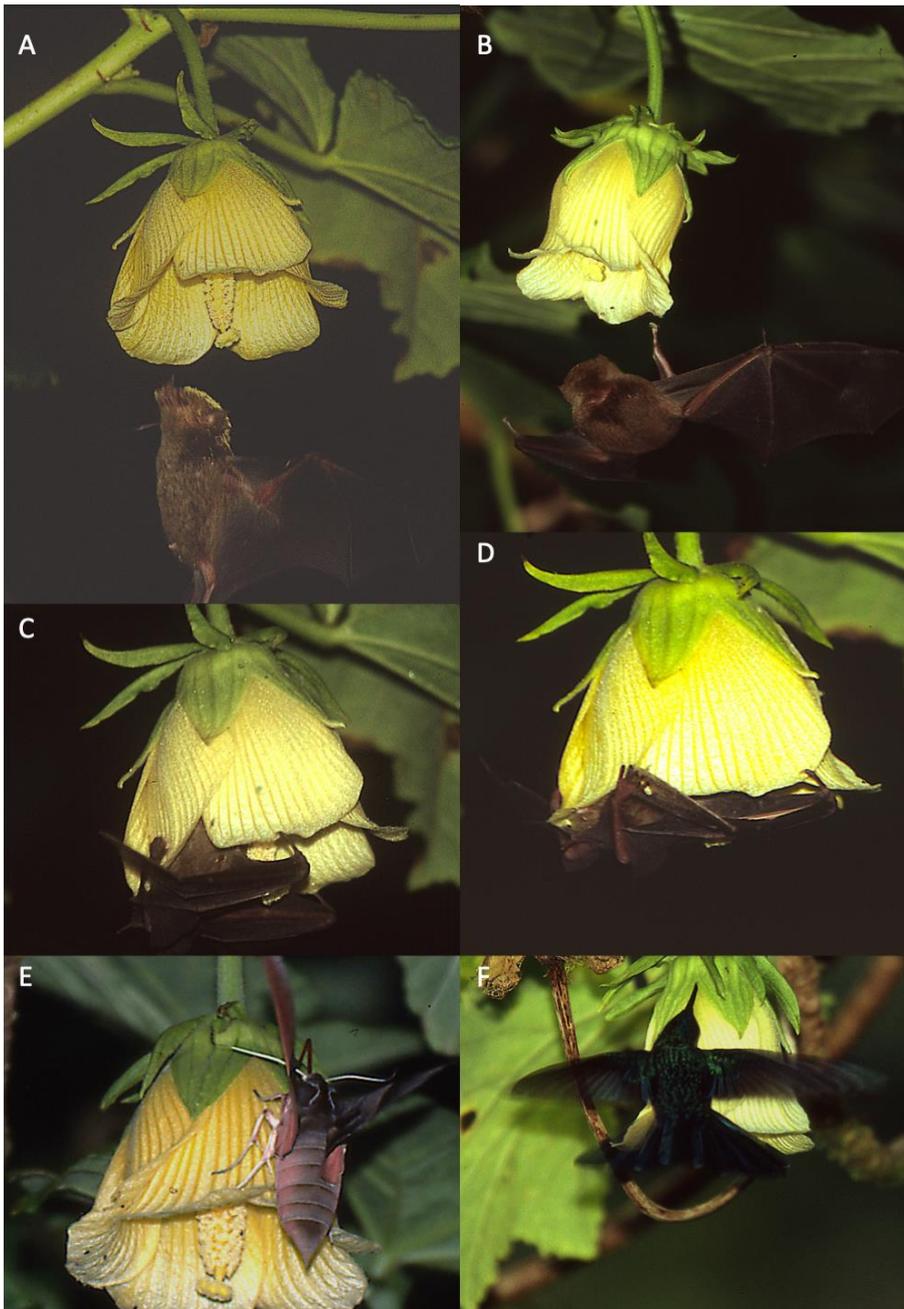
Figure 1. (A-D) The plant *Wercklea* sp. (Malvaceae) and its flower-visiting bat *Monophyllus plethodon* (Phyllostomidae), Dominica. (E-F) Green-Throated Carib hummingbird (*Eulampis holosericeus*) and *Eumorpha* cf. *vitis* (Sphingidae) also visit the flowers of the plant. The tree was 6 to 8 meters tall with 7-centimeter-long and 8-centimeter-wide, strongly and rigidly built, pendant, yellow-whitish flowers on a 9 to 10-centimeter long pedicel. Each plant has many open flowers at a time. The flower has five nectar grooves, that may be used as guides by nectar drinkers. Birds like hummingbirds and banana-quit are nectar thieves (F), inser-ting their beak between sepals and petals (B Dalsgaard, AM Martín González, JM Olesen, *pers. obs.*, made in the elfin forest, *c.* 800 m a.s.l., Morne Trois Pitons National Park, the 17th of May 2005 between 1830-1930), photo JM Olesen). Note: the hummingbird is predominantly a lowland species [Farnsworth 2020], but perhaps doing diurnal, elevational movements, e.g. to visit this highland flower after dark (B Dalsgaard, *pers. com.*)

New Zealand has an endemic bat, *Mystacina tuberculata* (Mystacinaceae). It eats invertebrates, fruit, and floral resources. Another *Mystacina* species, *M. robusta*, was last seen in 1967 (Arkins et al. 1999), but it probably also visited flowers. *M. tuberculata* lives all over New Zealand from sea level to 1,100 m a.s.l. Pollen from several flowering plants has been found in its faeces and fur, e.g. from *Dactylanthus taylorii* (Balanophoraceae), a root parasite of forest trees, but also spores from ferns and fungi are carried in the fur. The species holds the world bat record in foraging time on the ground, spending up to 40% of its time on the forest floor, filling out the "rodent" niche (but see Griffin et al. 2011). Its teeth tell it is a typical insectivore, and on the forest floor, it hunts flightless insects, such as the giant wētā crickets–being among the largest (<10 cm long) and heaviest insects in the world. Once its major food probably was flying insects, then a lack of native predators on the forest floor allowed it to forage here for ground-living insects, and as a final step, it began to include other food items on the forest floor, such as floral resources.

Recently, a parallel case was discovered in Brazil. Here, the small ground-flowering parasitic plant *Scybalium fungiforme*, also Balanophoraceae, is pollinated by the bat *Glossophaga soricina*, two species of opossum, and a tanager bird (Amorim et al. 2023). The plant offers both nectar and pollen. The bat was the most frequent visitor at two of the three study sites. However, the opossums and the bird need to remove the inflorescence bracts, before the bat can access the floral resources.

Galápagos has two insectivorous bats, *Lasiurus borealis*, and *L. villosissimus* (Vespertilionidae; the latter sometimes is included in the genus *Aeorestes*), which also may carry pollen from several plant species, e.g. cactus (Olesen et al. 2018). Both species are regarded as classic insectivorous bats.

These examples demonstrate that insectivorous, mainland or island bats may visit flowers for nectar and pollen and that no special morphology is needed, i.e. diet transitions between insects and floral resources may take place opportunistically, depending upon the local food resource and predator landscape. Our examples suggest that a shortage of insect food may be an important driver of opportunistic flower visitation. However, another study shows that this explanation perhaps is too simplistic. In the Sonora desert and on the islands in the Sea of Cortéz, the insectivorous bat, *Antrozous pallidus* (Vespertilionidae) visits cactus flowers for nectar and pollen (Frick et al. 2009; Rojas et al. 2011). This bat lacks any specialized flower-feeding traits as seen in the Phyllostomidae. The bat changes its diet opportunistically with the season. During the flowering of the cactus, it shifts to this almost cornucopian nectar resource. However, the cactus flowers may also be an important source of water and visiting insects. Diet opportunists probably switch easily to new food sources, that are adjacent to already known food, especially if the latter gets scarce. In Sonora, insect-eating birds respond in a similar way and visit cactus flowers too.

4. The bat-flower syndrome

In the Neotropics, hundreds of plant species are being pollinated by bats (e.g. Cordero-Schmidt et al. 2021; Domingos-Melo et al. 2023). Plant families with the highest numbers of bat-pollinated species are Fabaceae, Cactaceae, Malvaceae, Bromeliaceae, Campanulaceae, and Gesneriaceae, and many of their species have flowers with traits, belonging to a bat-pollination trait syndrome (chiropterophily), such as large size, robust structure, light colours, high nectar volume (even dozens of litres in a single night from a single tree), a large amount of pollen, and dusk or night flower opening (Percival 1965; Fægri & Pijl 1971; Domingos-Melo et al. 2019). However, trait-matching between bats and bat-pollinated flowers is often low (Fleming et al. 2009; Queiroz et al. 2021).

Many plant species with no or just a few bat-flower traits also get visited by bats (see references in Cordero-Schmidt et al. 2021), e.g. bee-pollinated *Jatropha mollissima*, bird-pollinated Cactaceae species, and hawkmoth-pollinated *Cereus* species, and *vice versa* bat flowers may also be visited by animals other than bats. Thus, as we all know but are inclined to forget–classic pollination syndromes are vaguely defined, but bat flowers are still rather easy to recognise (e.g. Queiroz et al. 2021). Therefore, evolutionary biology needs to tell us, how a set of linked floral traits being strongly present in a group of flowering plants can evolve in a diffuse interacting system rich in opportunists. Such a bat-flower pollination network was studied in the Brazilian caatinga (Cordero-Schmidt et al. 2021), a global hotspot for bat pollination (Queiroz et al. 2021; Domingos-Melo et al. 2023). The bats were all Phyllostomidae. An average of 2.6 pollen types were observed on each netted bat specimen. Besides plant species with bat flowers, species with non-bat flowers, especially with bee and bird flowers, were also well represented in the network, constituting ~30% of the plant community. Thus, the study network was highly generalized. In other network studies, bat-flowers and non-bat-flowers even occurred in the same network module together with their specific bat visitors (Diniz & Aguiar 2023), or network modules containing bats also include hawk-moths (Queiroz et al. 2021). In these studies, but also in several others, many classic bird- and hawkmoth-pollinated flowers are also pollinated by bats, and hence, transitions between these animal groups and their flowers seem to be one of the most common and easy shifts in pollinator guilds (Tripp & Manos 2008; Abrahamczyk et al. 2014).

In summary, widespread flower visitation and pollination by Phyllostomidae bats, even including an obligate nectar consumer (*Monophyllus*) on an

island, pollination of several New Zealand plants by 1-2 endemic, non-phyllostomid bats, a Mexican desert bat visiting cactus flowers for nectar and perhaps also insects and water, and observations of pollen in the fur of bats from the oceanic archipelago Galápagos – all together encouraged us to do a study, albeit preliminary, of more oceanic island, insectivorous bats to test, if they visit flowers. In our case, we chose the Canarian bat fauna.

A CASE STUDY: CANARIAN BATS AS FLOWER VISITORS

We tested our assumption about flower-visiting island bats on the seven bat species from the Canary Islands, none of which belong to the Phyllostomidae or Pteropodidae. The species are: *Tadarida teniotis* (Molossidae), and *Barbastella barbastellus, Hypsugo savii, Nyctalus leisleri, Pipistrellus kuhlii, P. maderensis,* and the Canarian endemic *Plecotus teneriffae* (Vespertilionidae) (Suppl. Mat. 2A, Trujillo 1991). Seventeen of the 34 bat specimens examined carried ~9 pollen taxa (Suppl. Mat. 2B and 3). The largest and most diverse pollen loads were found on specimens of *Pipistrellus maderensis, Tadarida teniotis,* and *Barbastella barbastellus.* The other species had smaller pollen loads. The three specimens from the most western island El Hierro did not have any pollen grains. Three species carried *Pinus* pollen. Although this might be air pollution or "dirt" from insect hunting, bats are known to eat *Pinus* pollen, e.g. the American phyllostomid *Choeroniscus godmani* (Wilson & Mittermeyer 2019). Thus, we conclude, that at least three Canarian bat species may be flower visitors and potential pollinators.

The pollen was not identified, but many Canarian and exotic species are likely candidates, especially some of the Canarian bird- and lizard-pollinated plant species (Valido et al. 2004; Valido & Olesen 2010; *unpublished*), e.g. *Anagyris* and *Lotus* (Fabaceae), *Echium* (Boraginaceae), *Navaea* (Malvaceae), *Isoplexis* (Plantaginaceae), *Canarina* (Campanulaceae), and *Teucrium* (Scrophulariaceae). Exotic candidates include *Agave, Aloe, Hibiscus, Kigelia, Musa, Bauhinia, Carica papaya, Crescentia, Ipomoea, Erythrina,* and some cactus and palms. In their natural habitats, many of these plants may be bat-pollinated, e.g. by Phyllostomidae and Pteropodidae.

Recently, our camera traps shot photos of unidentified flower-visiting bats visiting flowers of two Canarian species in Tenerife, confirming conclusions from our pollen study.

1, 18th of June 2023, 05.49 AM, an inflorescence of *Echium wildpretii* (Boraginaceae) – a generalized insect, bird, and lizard-pollinated plant.

2, 4th of October 2023, 07.07 AM, a flower of *Malva (Navaea) phoenicea* (Malvaceae) – a insect, bird-pollinated plant.

A PARALLEL CASE: OCEANIC ISLAND RODENTS?

In the Introduction, we mentioned that island rodents may show the same versatile feeding ecology as birds, lizards, and bats. Here, we briefly explore if oceanic island rodents also include floral resources into their diet, perhaps as a response to insect food shortage. As another, albeit non-volant, mammal group, rodents may add to our understanding of the exploitation of floral resources by bats, i.e. to the more general questions: why do some island animals visit flowers, and what drives the transition to flowers from other resources?

Thus, we extracted distributional and dietary information about all 2,470 rodent (Rodentia) species in the world from Wilson et al. (2016, 2017) (*unpublished dataset*). Geographically, Rodentia includes 74% mainland species, 8% mainland-island species, and 18% island species (calculated in the same way as the percentages for bats in Table 1B). 177 species (7% of all rodents) are true oceanic island species, mainly from oceanic Indonesia (Wallacea) (83 species, especially from the species-rich Sulawesi), and oceanic Philippines (77 spp., the continental Philippine Island Palawan is excluded here). The remaining 17 species are from a wide set of archipelagos, especially Galápagos, Andamans, oceanic Japan, Bismarcks, and Solomons.

Only 1,379 (56%) of all Rodentia species have a known diet, which most often includes seeds, green plant parts, and invertebrates. This low number was surprising to us; it means we do not know what > 25% of the world's ~6,400 mammal species are eating (1,091 rodents + 494 bats). A small group of 169 rodent species are known to visit/consume floral resources, i.e. 12% of all Rodentia with a known diet. Among rodent families, flower visitation/consumption is unevenly distributed: 36 Muridae species, i.e. 7.6%

of the 474 Muridae species with a known diet (family total is 819), and 29 Cricetidae species, i.e. 7.3% of the 399 Cricetidae species with a known diet (family total is 760), but as many as 75 Sciuridae species, i.e. 33% of the 228 Sciuridae species with a known diet (family total is here 290).

On oceanic islands, 129 Rodentia species (73% of the 177 oceanic island species) have a known diet, but only three (2%) of these consume floral resources and other floral parts.

In conclusion, 7% of all Rodentia live only on oceanic islands, mainly Wallacea and oceanic Philippines. The *in–situ* radiations on Sulawezi and the Philippines boost this frequency. Thus, few rodents have been able to colonize oceanic islands. Compared to mainland and continental island Rodentia, flower visitation/consumption by oceanic rodents is rare, 12% *vs.* 2%. The few rodents on oceanic islands seem to survive–not by a shift to floral resources–but by their capability to digest green plant parts and toxic fungi–food sources that seem inaccessible to most birds, lizards, and bats.

CONCLUSIONS

We find that the logical extension from flower visitation by island birds and lizards (Olesen & Valido 2003a; Valido et al. 2004; Valido & Olesen 2010; Traveset et al. 2015; Olesen et al. 2018; Valido & Olesen 2019; Correcher et al. 2023) to encompass island bats has some empirical support. We base this conclusion on our two approaches: the global review and the individual cases from the literature and our Canarian study case. Bat flower visitation may take place in insect-poor regions, such as oceanic islands, high mountains, and deserts. It is driven by a shortage of insect food, but perhaps also a lack of water. It may happen opportunistically when bats hunt flower-visiting insects. Bats, e.g. Phyllostomidae, visit opportunistically many kinds of flowers, certainly not just classic bat flowers. In a few cases, nectar and pollen are known to be more attractive than insects as food. Some bats, especially Pteropodidae, show interaction release, by expanding their diet to establish themselves on resource-poor islands. Whereas bats on small islands with a rich plant diversity can "afford" to become obligate floral resource consumers.

Future studies will show if bats play a significant role as flower visitors and potential pollinators on oceanic island plants. We suggest researchers test this by making night-time observations, e.g. by using camera traps, as we recently have done in Tenerife, and infrared videography, at candidate plants, and by microscoping samples for pollen from the field and museum specimens.

AUTHOR CONTRIBUTION

Concept and design, data collection, data analysis, writing, edits and approval for publication AV & JMO

DISCLOSURE STATEMENT

No potential conflict of interest was reported by the authors.

DATA AVAILABILITY STATEMENT

The data used to write this article are available in the Supplementary Material

APPENDICES

Additional supporting information may be found in the online version of this article:

Table S1A. Distribution of Phyllostomidae and Pteropodidae.

Table S1B. Frequency of floral resource use in Phyllostomidae and Pteropodidae.

Table S1C. List of floral resource consumers

Table S2A. List of Canarian bat species

Table S2B. Pollen load of Canarian bat specimens.

Appendix 3. Pollen loads on Canarian bats.

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