

# Floral scent and flower visitors of three green-flowered Costa Rican and Panamanian *Blakea* species (Melastomataceae) indicate birds rather than rodents as pollinators

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**Background and aims** – *Blakea austin-smithii*, *B. chlorantha* and *B. aff. penduliflora* from Costa Rican cloud forests share floral traits with rodent-pollinated plants, e.g. cryptic, inconspicuous, green flowers, and are known to be visited and probably pollinated by rodents. However, contrasting records indicate birds as pollen vectors for *B. chlorantha*. Previously, three Costa Rican *Blakea* species were described to have flowers lacking scent discernible to humans which is typical for bird-pollinated but not for rodent-pollinated flowers. This study aims at evaluating the role of rodents and birds as pollinators of *B. austin-smithii* and *B. chlorantha* in Costa Rica as well as the yet unstudied *B. gregii* in Panama. Therefore, additional diurnal observation data as well as data on floral traits were collected.

**Methods** – In addition to floral visitor observations during the day and measurements of nectar properties, floral colour and morphology, floral scent was analysed by means of coupled gas chromatography - mass spectrometry. Two bee-pollinated *Blakea* species were chosen as methodological standards.

**Key results** – We observed three passerine bird species, *Chlorospingus flavopectus*, *C. pileatus*, *Myioborus torquatus*, and the hummingbird *Lampornis calolaemus* visiting *B. austin-smithii* as well as the hummingbird *Panterpe insignis* visiting the similar Panamanian *B. gregii*. Whereas no scent was detected in *B. austin-smithii*, *B. chlorantha* and *B. gregii*, strong odours of *B. maurofernandeziana* (rose-like) and *B. anomala* (lemon-like) could be confirmed with the finding of > 70% phenylethyl alcohol, and monoterpenes, respectively.

**Conclusions** – The bird observations together with lacking olfactory signals point to birds as main pollinators. However, to clearly evaluate pollinator importance of the different vertebrates, further observations and proof of pollen transfer are needed.

**Key words** – Bees, birds, *Blakea*, Costa Rica, floral scent, GC-MS, Melastomataceae, Panama, pollination, rodents.

## INTRODUCTION

Pollination systems range from being generalised to specialised, according to the number of pollinator guilds involved (Fenster et al. 2004). In general, specialised systems are described by floral syndromes, a specific combination of floral traits having evolved convergently in adaptation to certain pollinator guilds (Faegri & van der Pijl 1979, Vogel 2012). The combination of floral traits can be used to predict a pollinator guild of a plant, for example bees or birds. Plant species with bee-pollinated flowers are common; they offer the bees a landing platform and a small amount of nectar with a high sugar concentration at the base of a short corolla tube. Moreover, they attract bees with conspicuous colours and

honey-like or other pleasant scent. Bird-pollinated flowers are scent-less, often red and contain large amounts of lower concentrated nectar often hidden in longer corolla tubes without offering a landing platform. Plants pollinated by rodents are very rare, especially in the New World (e.g. *Caiophora coronata* (Gillies ex Arn.) Hook. & Arn., Loasaceae; Cocucci & Sérsic 1998) and are mostly found in South Africa (Wester et al. 2009, Wiens et al. 1983). Rodent-pollinated flowers are visually inconspicuous, but emit a distinct scent being described, for example, as yeasty, cheesy or buttery, not found in plants pollinated by other pollinator groups (Rebello & Breytenbach 1987, Wester et al. 2009, Wester unpubl. data).

**Table 1 – Localities and habitat of the examined *Blakea* species.**

<i>Blakea</i> species	Locality	Habitat
<i>B. austin-smithii</i>	Cerro Dantas Wildlife Refuge, Heredia, Costa Rica, 10°05'40.8"N 84°03'32.3"W, elevation 1950 m; Zarcero, Alajuela, 10°11'14.2"N 84°20'26.7"W, elevation 2100 m	In cloud forest; exposed at windswept ridge of cloud forest patches
<i>B. chlorantha</i>	Monteverde Cloud Forest Reserve, Puntarenas, Costa Rica, 10°17'54.1"N 84°46'59.0"W, elevation 1560 m	Exposed at windswept ridge of cloud forest
<i>B. anomala</i>	Monteverde Cloud Forest Reserve, Puntarenas, Costa Rica, 10°17'58.2"N 84°47'23.4"W, elevation 1600 m	In cloud forest
<i>B. maurofernandeziana</i>	Tropical Research Station La Gamba, Puntarenas, Costa Rica, 8°42'02.5"N 83°12' 06.5"W, elevation 80 m	In lowland rainforest
<i>B. gregii</i>	Cerro Pate Macho, 8°49'36.8"N 82°23'41.4"W, elevation 2120 m; Cerro Horqueta, 8°50'5.4"N 82°25'25.5"W, elevation 1850 m both Chiriquí, Panama	Exposed at windswept ridges of cloud forest

However, plants can be visited by more than one group of animals that are (a) either all pollinators, (b) not similarly effective in pollen transfer, or (c) even nectar or pollen thieves not contributing to pollination (Hargreaves et al. 2012). Furthermore, not all of the above-mentioned traits need to be displayed, resulting in less typical representatives of a classical floral syndrome (Vogel 2012), thus making predictions about the pollinator guild more difficult.

The genus *Blakea* P.Browne (incl. *Topobea* Aubl., Melastomataceae) contains nearly 200 woody plant species in the Neotropics (Penneys & Judd 2013a, 2013b) that are pollinated by different pollinator guilds. Most *Blakea* species have nectarless flowers pollinated by pollen-collecting bees (Renner 1989, Lumer 2000). Thereby, the bees contract their indirect flight muscles in rapid succession with decoupled wings, causing flowers – including their poricidal anthers – to vibrate and thus eject pollen grains (Buchmann & Hurlley 1978, Burkart et al. 2011). However, a few *Blakea* species use vertebrates as pollen vectors, their flowers also release pollen explosively through poricidal anthers when slight pressure is applied by touching the petals or stamens (Lumer & Schoer 1986, Almeda 1989, 2000, Langtimm & Unnasch 2000, Lumer 2011). Their flowers have traits, such as pendant flowers with long pedicels, reddish colour and large nectar volumes, interpreted as adaptations to pollinating birds (Faegri & van der Pijl 1979). Some *Blakea* species have been assigned to be pollinated by rodents as they share traits with other plants pollinated by those animals such as cryptic, inconspicuous, dull flowers, large amount of easily accessible nectar and nocturnal anthesis (Lumer & Schoer 1986, Wester et al. 2009). Three Costa Rican *Blakea* species with greenish flowers have been observed to be visited by different species of rodent. Five nocturnal rodent species have been documented at *B. austin-smithii* Standl. flowers and pollination has been inferred from pollen detection on the animals' snouts (Lumer & Schoer 1986). During the day, flowers were visited only by pollen-stealing wasps, not or only accidentally affecting pollination (Lumer & Schoer 1986). At *B. chlorantha* Almeda flowers, three rodent species have frequently been recorded at night, and infrequently two hummingbird species (rarely touching the stigma) as well as a species of bumblebee (most likely not or seldom pollinating) during the day (Lumer 1980, 2000). By contrast, Langtimm & Unnasch (2000) found no evidence of pollen

transfer by nocturnal mice, but by hummingbirds and passerine birds in *B. chlorantha*. Only on two occasions, Lumer & Schoer (1986) observed rodents visiting flowers of *B. aff. penduliflora* Almeda (unknown taxon after R. Kriebel, University of Wisconsin, USA, pers. comm.).

This study aims at evaluating the role of rodents and birds as pollinators of three green-flowered *Blakea* species, *B. austin-smithii* and *B. chlorantha* in Costa Rica as well as the yet unstudied *B. gregii* Almeda in Panama. We use existing data and add our own diurnal observation data as well as an analysis of floral scent by means of coupled gas chromatography - mass spectrometry. As it is difficult to communicate potential negative results (e.g. lacking scent), *B. anomala* Donn.Sm. and *B. maurofernandeziana* (Cogn.) Penneys & Almeda, known to have conspicuous, fragrant flowers visited and most probably pollinated by pollen-collecting bees (Lumer 2000, R. Kriebel pers. comm.), were chosen as methodological standards. In addition, the matching of floral traits with known traits of floral syndromes of rodent-pollinated and bird-pollinated flowers is taken into account.

## MATERIALS AND METHODS

During February and March 2014, *Blakea austin-smithii* was studied in the Cerro Dantas Wildlife Refuge (Heredia) and near Zarcero (Alajuela), *B. chlorantha* and *B. anomala* in the Monteverde Cloud Forest Reserve (Puntarenas), *B. maurofernandeziana* in the Tropical Research Station La Gamba (Puntarenas), all Costa Rica, and *B. gregii* at Cerro Pate Macho and Cerro Horqueta in Chiriquí, Panama (table 1). *B. aff. penduliflora* could not be investigated due to the lack of locality information. Vouchers are deposited at INB (Instituto Nacional de Biodiversidad), UCH (Universidad Autónoma de Chiriquí) and B (Botanischer Garten und Botanisches Museum Berlin-Dahlem, Freie Universität Berlin). Observations for daytime flower visitors of *B. austin-smithii* took place at Cerro Dantas for about 10 h (06h00–18h30, 21–23 Feb. 2014) and of *B. gregii* at Cerro Pate Macho for about 5.5 h (10h00–15h00, 11 and 13 Feb. 2014). Floral scent was qualitatively (olfactorically) checked and additionally collected from flowers using dynamic headspace extraction (*B. gregii* (N = 5) and *B. chlorantha* (N = 5): 19h00–02h00, *B. austin-smithii* (N = 11) additionally 11h00–15h00, *B. anomala* (N = 3) 15h00–17h00 and *B. maurofernandeziana* (N = 3) 15h00–17h00).

**Table 2 – Bird species and their foraging behaviour visiting flowers of *Blakea gregii* (Cerro Pate Macho, Panama) and *B. austin-smithii* (Cerro Dantas, Costa Rica).**

H = hovering, P = perching on twig.

Floral visitors	Foraging behaviour (number of visits)	Time (date)
<i>Blakea gregii</i>		
<i>Panterpe insignis</i> Cabanis & Heine, 1860 (Fiery-throated hummingbird, Trochilidae)	H (1) P (2)	noon (11 Feb. 2014) noon, early afternoon (13 Feb. 2014)
<i>Blakea austin-smithii</i>		
<i>Lampornis calolaemus</i> (Salvin, 1865) (Purple-throated mountaingem, Trochilidae)	H (2)	early morning (23 Feb. 2014)
<i>Chlorospingus pileatus</i> Salvin, 1865 (Sooty-capped bush tanager, Emberizidae)	P (2)	early and mid-morning (22–23 Feb. 2014)
<i>Chlorospingus flavopectus</i> (Lafresnaye, 1840) (Common bush tanager, Emberizidae)	P (1)	early morning (22 Feb. 2014)
<i>Myioborus torquatus</i> (S.F.Baird, 1865) (Collared whitestart, Parulidae)	P (4)	early and mid-morning (21–22 Feb. 2014)

*ziana* (N = 6) additionally 09h00–11h00) and analysed by coupled gas chromatography - mass spectrometry (GC-MS, appendix). Floral nectar was measured as standing crop at different times between the morning till the late afternoon, or at Cerro Dantas till the early evening, using microcapillary tubes (Brand, Wertheim, Germany) for volume (minimum N = 6 per species) and hand held refractometers (Eclipse 45-81 and 45-82: 0–50% and 45–80% sucrose w/w, Bellingham & Stanley, Kent, UK) for sugar concentration (minimum N = 9 per species). Colour values of outer petal surfaces follow the CMYK colour space (Küppers 1999). To evaluate flower accessibility and strength of pedicels, length and width of pedicels was measured. To assess nectar accessibility and potential pollen transfer to the animals or the stigma, corolla tube length, diameter of flower entrance and length of stamen and style was measured. All floral measurements (to the nearest 0.5 mm; minimum N = 14 per species and trait) were taken as straight-line distance.

## RESULTS

*Blakea gregii* flowers were visited by *Panterpe insignis* Cabanis & Heine, 1860 hovering below the flowers and perching or hanging on a twig. *Blakea austin-smithii* flowers were visited by a hovering *Lampornis calolaemus* (Salvin, 1865) and three species of perching passerine bird (table 2, fig. 1A–C, electronic appendices 1–5). No other flower visitors were noticed during the time observed and numerous hours spent near the plants (additional 6 h at Cerro Dantas, 4 h at Cerro Pate Macho).

With the human nose and GC-MS analysis no scent could be detected for flowers of *B. austin-smithii*, *B. chlorantha* and *B. gregii*. In contrast, strong odours of *B. maurofernandeziana* and *B. anomala* flowers could be confirmed by GC-MS (altogether 25 and 18 compounds, respectively; appendix). Whereas the rose-like scent of *B. maurofernandeziana* is dominated by phenylethyl alcohol (= rose-oil; > 70%), the lemon-like odour of *B. anomala* is mainly composed of several (mostly lemon-scented) monoterpenes. When examined during daytime and early evening, the open flowers (fig. 1D–G)

of *B. austin-smithii*, *B. chlorantha* and *B. gregii* had pollen that was released explosively when stamens were touched (fig. 1H & I). Nectar was found mainly in large amounts and mostly weakly concentrated (table 3). In contrast to the conspicuous flowers of *B. maurofernandeziana* and *B. anomala* (fig. 1J & K, electronic appendix 6), in general, the flowers of *B. gregii*, *B. chlorantha* and *B. austin-smithii* are inconspicuous, mostly hardly distinguishable from other green plant parts or background. The corolla is mostly green, sometimes greenish-ochre or dirty purple-brownish. Due to their pale colour (light green to almost whitish in *B. gregii*) or red calyces (often bright red in *B. gregii*, occasionally reddish in *B. chlorantha* and *B. austin-smithii*), sometimes the flowers are more or less conspicuous (fig. 1A & D–I, electronic appendix 6). The flowers of *B. gregii*, *B. chlorantha* and *B. austin-smithii* are tubular-campanulate with about 1.5 cm corolla tube length and about 1 cm tube diameter at the entrance (fig. 1D–G, table 4). The length of stamens and styles are about 1–2 cm. The stigma is level with the flower entrance in *B. gregii*, but in *B. chlorantha* and *B. austin-smithii* the stigma is exposed by several millimetres (fig. 1D–G). Flowers of *B. gregii*, *B. chlorantha* and *B. austin-smithii* are pendant with short (about 1 cm in length) and strong (diameter about 2–2.5 mm; table 4) pedicels (fig. 1A & D–G). Because of its compact growth at the windswept habitats, some flowers of *B. gregii*, *B. chlorantha* and *B. austin-smithii* are located within the bush and, thus, are cryptic.

## DISCUSSION

The observed birds most probably visit the flowers for nectar and are pollinators of *B. gregii* and *B. austin-smithii*. The passerine birds' position at the flower (fig. 1B & C) and their dimensions compared to the flowers' dimensions (bill length shorter than style length; this study, Curson et al. 1994, Sánchez-González et al. 2007, Chavarría-Pizarro et al. 2010) makes pollen transfer to the birds (head and bill) as well as to the stigma very likely. Whereas no records at flowers seem to exist for *M. torquatus*, described as being insectivorous (Curson et al. 1994), the two *Chlorospingus* spe-

cies have also been observed visiting *B. chlorantha* flowers (Langtimm & Unnasch 2000) with similar floral dimensions. The authors also observed two hummingbird species visiting flowers of *B. chlorantha*, and three of these bird species

carried *Blakea* pollen on their throats and conducted transfer of fluorescent dye onto *Blakea* stigmas. Due to the explosive pollen release from the radially arranged poricidal anthers, birds with longer bills (and tongues), such as hummingbirds,



**Figure 1** – Birds visiting *Blakea* flowers (A–C, still images from video footage): A, *Panterpe insignis* retracting its bill out of a *B. gregii* flower; B, *Chlorospingus pileatus*; C, *Myioborus torquatus* visiting flowers of *B. austin-smithii*. Flowers (D–K) of D, *Blakea gregii*; E–F, *B. austin-smithii*; G–I, *B. chlorantha* (H: before and I: after touching stamens causing explosive pollen release out of poricidal anthers); as well as J, *B. maurofernandeziana* and K, *B. anomala*. D–G, lateral view; H–J, front view. Scale bars = 0.5 cm (D–G, and H–I same size, respectively).

**Table 3** – Nectar properties of *Blakea gregii*, *B. chlorantha* and *B. austin-smithii* flowers.

Mean, SD, range, sample size.

<i>Blakea</i> species (and locality)	Volume ( $\mu$ l)	Concentration (%)
<i>B. gregii</i>	85.9 $\pm$ 71.7 (15.0–177.0), 9	9.0 $\pm$ 3.1 (5.0–13.5), 9
<i>B. chlorantha</i>	10.3 $\pm$ 6.9 (4.3–23.3), 6	16.2 $\pm$ 8.7 (7.0–38), 13
<i>B. austin-smithii</i> (Cerro Dantas)	56.2 $\pm$ 44.9 (3.6–126.9), 8	16.5 $\pm$ 3.6 (11.0–21.8), 10
<i>B. austin-smithii</i> (Zarcero)	20.4 $\pm$ 31.8 (1.6–122.7), 14	30.4 $\pm$ 14.4 (7.0–48), 14

**Table 4** – Corolla, stamen and style as well as pedicel dimensions of different *Blakea* species.

Mean, SD, range, sample size.

Floral traits	<i>B. gregii</i>	<i>B. chlorantha</i>	<i>B. austin-smithii</i>
Length of corolla tube (cm)	1.7 $\pm$ 0.2 (1.4–2.0), 14	1.3 $\pm$ 0.2 (1.0–1.5), 21	1.4 $\pm$ 0.1 (1.2–1.6), 29
Diameter of corolla entrance (cm)	1.4 $\pm$ 0.4 (0.9–2.0), 13	1.0 $\pm$ 0.2 (0.7–1.6), 21	1.0 $\pm$ 0.1 (0.8–1.3), 26
Length of stamen (cm)	1.2 $\pm$ 0.1 (0.9–1.4), 15	0.8 $\pm$ 0.1 (0.5–1.0), 18	0.9 $\pm$ 0.1 (0.7–1.1), 22
Length of style (cm)	1.6 $\pm$ 0.2 (1.1–1.9), 15	1.5 $\pm$ 0.2 (1.4–1.9), 10	1.7 $\pm$ 0.3 (1.0–2.5), 29
Length of pedicel (cm)	1.2 $\pm$ 0.3 (0.6–1.9), 14	0.9 $\pm$ 0.3 (0.6–1.5), 15	0.9 $\pm$ 0.2 (0.6–1.5) 17
Width of pedicel (mm)	2.6 $\pm$ 0.5 (1.5–3.5), 15	2.0 $\pm$ 0.4 (1.3–3.0), 15	2.5 $\pm$ 0.4 (1.8–3.0), 19

are also dusted with pollen (at least on the bill), and as a result of the circular pollen ejection and application, it is very likely that the birds touch the stigma causing pollen transfer. Furthermore, *L. calolaemus*, that visited *B. austin-smithii*, was also observed at *B. chlorantha* flowers with similar style length (Langtimm & Unnasch 2000). Moreover, the bill length of *P. insignis*, visiting *B. gregii* in this study, is similar or even shorter than that of the hummingbird species visiting *B. chlorantha* (Paton & Collins 1989, Langtimm & Unnasch 2000), making pollen transfer more likely. Whereas Lumer (1980) assumed no pollen transfer by hummingbirds but by rodents in *B. chlorantha*, and found pollen on rodents that visited *B. austin-smithii* (Lumer & Schoer 1986), Langtimm & Unnasch (2000) could not confirm pollination of *B. chlorantha* by rodents (lacking evidence of pollen on rodents or fluorescent dye transfer to stigmas).

Floral traits, as potential adaptations to pollinators, can favour or exclude a pollinator group. Long pendant pedicels would tend to exclude rodents, but favour hovering hummingbirds, as in *B. fuchsoides* Almeda (pedicels up to more than 11cm; Almeda 1989), *B. purpusii* (documented to be visited/pollinated by hummingbirds, Almeda 2000, Lumer 2011) and possibly *B. penduliflora* (Almeda 1980; documented to be often visited by hummingbirds, R. Kriebel pers. comm.). The remaining green-flowered *Blakea* species with short pedicels make the flowers reachable by rodents, but also by perching birds – both animal groups visit flowers hanging upside down (Lumer 1980, this study) – and do not exclude hovering birds. Blooming within the bush also would not exclude birds (especially perching ones). The tubular-campanulate flower shape would enable both rodents and birds with longer and shorter bills to reach the nectar and touch the flowers' reproductive organs.

Since for *B. austin-smithii*, *B. chlorantha* and *B. aff. penduliflora* copious nectar production has been found only at night and for *B. chlorantha* nocturnal pollen presentation has been detected, nocturnal flower visitors were expected for these species (Lumer 1980, Lumer & Schoer 1986). Nectar in *B. chlorantha* has been reported to be sucrose-rich (Lumer 1980) and since at the time nectar sugar composition had only been examined in rodent-pollinated South African Proteaceae (Wiens et al. 1983) and the nectar of flowers pollinated by nocturnal bats was known to be hexose-rich (H. Baker in Lumer 1980), rodent-pollination was inferred (Lumer 1980). However, we found pollen and nectar in large amounts also during the day. In *B. chlorantha*, we detected lower amounts of nectar than Lumer (1980), however, we measured standing crop, possibly being influenced by flower-visiting animals. The different nectar values of *B. austin-smithii* in this study are likely due to different habitats causing different evaporation (Zarcero: exposed at windswept ridge, hot day; Cerro Dantas: in the forest, moderate temperatures). The nectar properties in *B. austin-smithii*, *B. chlorantha* and *B. gregii* would not favour rodents or birds. Nectar in rodent-pollinated plants varies in amount, concentration and sugar composition and production is not restricted to the night (Wester et al. 2009). The nectar properties of these *Blakea* species partly meet characteristics of flowers adapted to generalist pollinating birds (extremely diluted, very large quantities), but also to specialised nectarivorous birds (15–25%, 10–13  $\mu$ l, sucrose-rich; Johnson & Nicolson 2008).

In contrast to the bee-pollinated *B. anomala* and *B. maurofernandeziana* (Lumer 2000, R. Kriebel pers. comm.) with conspicuous white and pink flowers, the flowers of *B. austin-smithii*, *B. chlorantha* and *B. gregii* never or hardly attract insects, being cryptic with dull green-brownish petal colours (Lumer 1980, Lumer & Schoer 1986, Langtimm & Un-

**Table 5 – Observations and floral traits favouring bird or rodent pollinators of green-flowered *Blakea* species.**

+: favouring attraction or pollination; -: not favouring attraction or pollination; A: *Blakea austin-smithii*; C: *B. chlorantha*; G: *B. gregii*; P: *B. aff. penduliflora*.

Observation or trait	Bird pollinators	Rodent pollinators
Pollen on animal	+ C (Langtimm & Unnasch 2000)	+ A (Lumer & Schoer 1986), C (Lumer 2000) - C (Langtimm & Unnasch 2000)
Pollen transfer onto floral stigma	+ C (Langtimm & Unnasch 2000)	- C (Langtimm & Unnasch 2000)
Animals observed visiting flowers	+ C (Langtimm & Unnasch 2000, Lumer 1980), G, A: this study, P (R. Kriebel pers. comm.) + G (this study),	+ A, aff. P (Lumer & Schoer 1986), C (Lumer 1980)
Floral scent	A, C (this study, Lumer & Schoer 1986), aff. P (Lumer & Schoer 1986), P (Almeda 1980)	- (see bird pollinators)
Floral colour	+/- and + (reddish calyx) A, C, G (this study), G ( <i>de Nevers &amp; McPherson</i> 6840: US, MO), P ( <i>Solano</i> 1382: INB, 1731: CR)	+ and - (reddish calyx: A, C, G, P)
Floral nectar	+ A, C, G (this study), A, C, aff. P (Lumer & Schoer 1986), P (Almeda 1980)	+ (see bird pollinators)
Flower shape	+ (Almeda 1980, 1990)	+ (see bird pollinators)
Pedicels	+ (Almeda 1980, 1990, Lumer & Schoer 1986)	+ (see bird pollinators) - P

nasch 2000, this study). This floral colour is often found in rodent-pollinated plants (Wester et al. 2009) but rare in bird-pollinated flowers (Faegri & van der Pijl 1979; e.g. green flowers in *Fuchsia excorticata* L.f., Onagraceae; *Anigozanthos flavidus* DC, Haemodoraceae; *Erica* L. spp., Ericaceae; Delph & Lively 1985, Rebelo & Siegfried 1985, Phillips et al. 2014, or ochre-brownish flowers in *Salvia africana-lutea* L., Lamiaceae; Wester & Claßen-Bockhoff 2006). Flowers of *B. austin-smithii*, *B. chlorantha* and often *B. gregii* appear relatively conspicuous, contrasting against the foliage due to lighter green to almost whitish corollas and red or pink calyces (electronic appendix 6, fig. 1A, D & G). Flowers of *B. austin-smithii*, *B. chlorantha* and *B. aff. penduliflora* were described to lack scent discernible to humans (Lumer 1980, Lumer & Schoer 1986) and Lumer (1980) already mentioned that lack of scent in plants pollinated by nocturnal rodents is unusual. Nevertheless, Lumer (1980) found rodent teeth marks in bags that covered flowers and assumed the existence of floral scent only detectable to rodents. However, curiosity about the bags could have been one reason for the inspections. Additionally, we could not detect any floral volatiles in *B. austin-smithii*, *B. chlorantha* and *B. gregii*, but could identify specific compounds confirming the citrus-like or rose-like fragrance of the bee-pollinated *B. anomala* and *B. maurofernandeziana* flowers. In other plants pollinated by hummingbirds, scent was lacking or only found in trace amounts (Lindberg et al. 2000, Varassin et al. 2001, Knudsen et al. 2004). Whereas odour plays a key role for nocturnal rodents, particularly for foraging (Vander Wall 1998), and floral scent seems to play an essential role in rodent-pollinated plants as an attractant (Wester et al. 2009, 2013, Johnson et al. 2011), it seems to be superfluous for nectarivorous birds that tend to use visual rather than olfactory cues for finding

flowers, which are said to have generally poor olfaction and retain scent information very poorly (Faegri & van der Pijl 1979, Goldsmith & Goldsmith 1982, Ioalé & Papi 1989, Byers et al. 2014).

Taking their floral characteristics into account, the green-flowered *Blakea* species are not typical representatives of a floral syndrome, making precise predictions about pollinators (birds or/and rodents) difficult. For both, bird- and rodent-pollinated plants, the flower colour seems to play a role in sensory exclusion of bees rather than selective attraction of pollinators (Lunau et al. 2011, Wester unpubl. data). However, as odour is the most important stimulus for nocturnal animals (Vander Wall 1998), lacking floral scent in combination with lacking pollen transfer by rodents (Langtimm & Unnasch 2000, table 5) indicate that rodents might have no or only minor importance for the pollination of these species and that the flowers do not seem to be adapted to rodents. Contrary, the evidence of lacking floral scent together with bird observations and experimental proof of pollen transfer (Langtimm & Unnasch 2000, this study, table 5) indicate that birds – generalist passerines and specialist hummingbirds – are important for the pollination of *B. austin-smithii*, *B. chlorantha*, *B. gregii* and most probably *B. penduliflora* with flowers on longer pedicels less accessible to rodents.

Interestingly, the green-flowered *Blakea* species mainly occur in higher altitudes, which might be a response to selective forces as pollination services by bees decline along an altitudinal gradient, and as hummingbirds show high abundances at higher altitudes (Cruden 1972, Arroyo et al. 1982), favouring a shift from bee-pollinated to vertebrate-pollinated species (Penneys & Judd 2013b). Although it is clear that the green-flowered *Blakea* species studied here lack scent as sig-

nal for potential pollinators, beside birds, rodents may also contribute to their pollination. In fact, small mammals might also act as back-up pollinators in a bird-pollinated South African *Aloe* L. species (Asphodelaceae; Payne et al. 2015, see also Symes & Nicolson 2008). At this stage, we cannot rule out the possibility of a mixed pollination system involving two vertebrate pollinator groups contributing to pollination (to a greater or lesser extent) during the day and at night. This is also known in plant species pollinated by birds and bats (Sazima et al. 1994, Muchhala 2003, 2007, Muchhala et al. 2008) or even by birds, bats and opossums (Queiroz et al. 2016).

Nevertheless, further studies including floral visitor monitoring and experimental proof of pollen transfer resulting in seed production are necessary to clearly evaluate the importance of birds and rodents as pollinators of the green-flowered *Blakea* species. In general, extensive monitoring and experimentation to address pollinator importance are advisable to test the accuracy of allocating plants to pollination syndromes.

#### SUPPLEMENTARY DATA

Supplementary data are available at *Plant Ecology and Evolution*, Supplementary Data Site (<http://www.ingentaconnect.com/content/botbel/plecevo/supp-data>), and consist of: (1–5) different bird species visiting flowers of *Blakea gregii* and *B. austin-smithii* (MP4 video files); and (6) floral colour description for corolla (and calyx if not green) of different *Blakea* species with CMYK values (pdf).

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#### Appendix – Mean relative amounts (%) of volatile compounds identified by GC-MS from headspace samples of *Blakea maurofernandeziana* (N = 6) and *B. anomala* (N = 3) flowers.

Compounds are listed in order of increasing Kovats retention index (KRI, carbowax column) within each compound class and compound identification criteria (A = comparison of MS and retention time with published data, B = comparison with authentic standard). Compounds also found in headspace of calyx, fruit or leaf material are marked with \* (in brackets when in low amounts). Mass fragments for unknowns are listed in decreasing order of abundance. For headspace collection, flowers were enclosed in polyacetate bags (Nalophan, Kalle, Wiesbaden, Germany), the air from the bags pumped through small cartridges containing Tenax® and Carbotrap™ activated charcoal at a flow rate of 100 ml/min for 2 h (including controls per species under the same conditions) from the surrounding air. For GC-MS procedure see Shuttleworth & Johnson (2009). Compounds were identified using Varian Workstation with NIST05 mass spectral library and comparisons with retention times of authentic standards, where available, as well as comparisons between calculated Kovats retention indices and literature data. The relative amount of each substance is given as a percentage of the total ion count for all substances being absent from control samples (to exclude contaminants).

Compound	KRI	Criteria	<i>B. maurofernandeziana</i>	<i>B. anomala</i>
<b>Aliphatics</b>				
<i>Ketones</i>				
Heptadecan-2-one	2253	A	0.28	-
<i>Alcohols</i>				
Hex-3-en-1-ol*	1371	AB	4.92	-
1-Octen-3-ol*	1437	A	1.66	-
<i>Esters</i>				
Methyl decanoate	1610	A	-	0.69
<b>Aromatics</b>				
<i>Alcohols</i>				
Phenylethyl alcohol (Rose oil)(*)	1896	AB	72.27	-
<i>Aldehydes</i>				
Benzaldehyde	1518	AB	4.90	-
Benzeneacetaldehyde (=Hyacinthin)	1635	A	5.81	-
<i>Esters</i>				
Methyl salicylate*	1774	AB	0.06	-
2-Phenylethyl formate	1776	A	0.32	-
Phenylethyl acetate	1807	A	0.25	-

Appendix continued on next page

**Appendix (continued) – Mean relative amounts (%) of volatile compounds identified by GC-MS from headspace samples of *Blakea maurofernandeziana* (N = 6) and *B. anomala* (N = 3) flowers.**

Compound	KRI	Criteria	<i>B. maurofernandeziana</i>	<i>B. anomala</i>
<b>Isoprenoids</b>				
<i>Monoterpenes</i>				
(E)-Linalool oxide (furanoid)*	1470	A	0.49	-
Citronellal	1486	A	-	6.82
Linalool*	1538	AB	1.41	-
6-Octenoic acid, 3,7-dimethyl-, methyl ester (=Methyl citronellate)	1571	A	-	1.04
6-Octen-1-ol, 3,7-dimethyl-, acetate (=Citronellol acetate)	1672	AB	-	5.86
Neral*	1684	A	-	4.19
2,6-Octadienoic acid, 3,7-dimethyl-, methyl ester (=Methyl geraniate)	1698	A	-	4.19
(Z)-2,6-Octadien-1-ol, 3,7-dimethyl-, acetate (=Nerol acetate)	1729	A	-	1.53
Geranial	1732	A	-	8.10
(E)-Linalool oxide (pyranoid)*	1748	A	0.32	-
Citronellol	1752	AB	-	5.20
(E)-2,6-Octadien-1-ol, 3,7-dimethyl-, acetate (=Geraniol acetate)	1760	A	-	34.92
cis-3,7-Dimethyl-2,6-octadien-1-ol (=Nerol)	1786	A	-	16.60
Geraniol	1830	AB	-	3.74
Geranyl acetone*	1859	A	0.16	-
(E)-Butanoic acid, 3,7-dimethyl-2,6-octadienyl ester (=Geranyl butyrate)	1907	A	-	0.70
Geranyl hexanoate	2104	A	-	4.52
<i>Sesquiterpenes</i>				
Nerolidol	2033	A	1.04	0.63
(E)-2,6,10-Dodecatrienal, 3,7,11-trimethyl- (=E)-Farnesal)	2216	A	0.02	-
(Z,E)-2,6,10-Dodecatrien-1-ol, 3,7,11-trimethyl- (=Z,E)-Farnesol)	2292	A	0.02	-
(E,E)-2,6,10-Dodecatrien-1-ol, 3,7,11-trimethyl- (=E,E)-Farnesol)	2329	A	0.31	-
<b>Nitrogen-containing compounds</b>				
2-Phenylacetonitrile	1911	A	2.53	-
<b>Unknowns</b>				
m/z (71,41,43,39,86,53,67)	1307		0.31	-
m/z (69,41,39,79,81,53)*	1332		1.21	-
m/z (81,41,95,69,82,123,55,43,67,68,109,83,138)	2021		-	0.82
m/z (74,87,55,43,41,73,69,143)	2035		-	0.01
m/z (69,93,41,68,43,80,99,121)	2071		-	0.45
m/z (104,105,72,103,79,51,78)	2100		0.30	-
m/z (71,43,55,41,69,31)	2173		0.09	-
m/z (104,55,71,83,103,41)	2179		0.02	-
m/z (91,103,121,43,146,65)	2234		0.05	-
m/z (91,117,90,69,41,84,89,65,135)	2259		1.29	-
Number of compounds			25	18