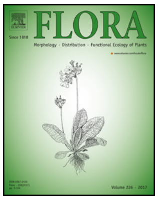
Flora 232 (2017) 22–29

Contents lists available at ScienceDirect

Flora

journal homepage: www.elsevier.com/locate/flora



Sunbird surprise: A test of the predictive power of the syndrome concept☆

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ARTICLE INFO

Article history:
Received 26 May 2016
Received in revised form 2 November 2016
Accepted 19 November 2016
Edited by Stefan Dötterl
Available online 29 November 2016

Keywords:
Convergent evolution
Floral syndrome
Pollinator prediction
Sunbird pollination
Thonningia sanguinea
Kibale forest

ABSTRACT

Floral syndromes are thought to be the product of convergent evolution, where the floral characters of unrelated species have evolved similar forms in response to shared pollinators. A contentious corollary is that floral form should be predictive of pollinators. In the forests of Uganda, we came upon the inflorescences of *Thonningia sanguinea*, a parasitic plant which previous literature suggested was part of a brood site pollination mutualism with flies (Calliphoridae and Muscidae). The general phenotype of the inflorescence suggested pollination by vertebrates, and the phenotypic similarity with several species of rodent pollinated *Protea* suggested to us that terrestrial mammals may be important pollinators. Pollinator observations and quantifications of pollen loads demonstrated that *T. sanguinea* is not visited by mammals, and that sunbirds are likely the most effective pollinators. The fact that the syndrome concept drove us to question the published literature on fly pollination demonstrates the usefulness of the concept. However, due to several phenotypic traits which did not conform to the classic sunbird pollination syndrome, sunbird visitation came as a surprise. While the syndrome concept is very useful, pollinator predictions based on syndrome traits should always be treated as working hypotheses.

1. Introduction

The enormous diversity of floral colours, shapes, scents and markings is a striking characteristic of angiosperms, but within that diversity one can discern patterns of association between pollinators and floral form: Flowers from very distantly related species often have similar phenotypic traits if they share pollinators (Vogel, 1954; Van der Pijl, 1961). A group of phenotypically similar plant species, with shared pollinators is called a pollination guild. For example, the sunbird pollinated plant guild is pollinated by sunbirds and members of this guild share many traits such as curved, tubular flowers, often red or orange in colour, copious amounts of dilute nectar, and sturdy structures for bird perching (Vogel, 1954; Rebelo et al., 1984, 1985; Johnson, 2010; Anderson et al., 2014a). This suite of shared traits is termed the sunbird pollination syndrome.

Pollination syndromes interest evolutionary biologists because they are often assumed to be the consequence of pollinator-mediated selection. That is, plants share similar phenotypes through convergence instead of common descent (as demonstrated by Anderson et al., 2014b; Newman et al., 2014). Similar floral phenotypes evolve because plants from different populations/species experience similar pollinator-mediated selective pressures. Consequently, the traits displayed by flowers can be predictive about the identity of the pollinators visiting those flowers (Johnson and Steiner, 2000). However, several studies have misused the syndrome concept to make unfounded assumptions about the driving forces of floral evolution in the absence of empirical data (e.g. Knapp, 2010; Valente et al., 2012). Consequently the use of the syndrome concept, particularly its purported predictive power has been criticized (e.g. Waser et al., 1996; Ollerton, 1998; Petanidou et al., 2008; Ollerton et al., 2009). To highlight the poor predictive power of floral traits, one global evaluation of pollination syn-

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☆ This article is part of a special feature entitled: "Patterns and mechanisms in plant-pollinator interactions" published at FLORA volume 232, 2017.

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http://dx.doi.org/10.1016/j.flora.2016.11.015
0367-2530/

dromes determined that the predictive power of floral traits was highly variable, ranging from 14% to 54% in different communities, and up to 75% for some syndromes (e.g. fly). On average they were only successful predictors of the most common visitors on 30% of occasions (Ollerton et al., 2009).

Importantly we question whether relative frequencies of pollinators as a metric (as used by Ollerton et al., 2009) should necessarily be associated with floral traits. Stebbins (1970) suggested that floral traits are adaptations to the most effective pollinators in a community; and while abundance is a component of pollinator effectiveness (sensu Stebbins, 1970), it is an incomplete measure because different pollinators differ in their efficiency of transporting pollen (pollen receipt, pollen wastage, and pollen deposition). Consequently, it is unsurprising that studies using visitation data alone (e.g. Ollerton et al., 2009) often tend to show poor support for the predictive accuracy of syndromes. However, much more accurate predictive power is found in studies that are based on data which better estimate pollinator effectiveness (e.g. Lazaro et al., 2008; Martén-Rodríguez et al., 2010; Reynolds et al., 2009; Armbruster et al., 2011; Danieli-Silva et al., 2012). In the only global analysis to use both abundance and efficiency metrics to quantify pollinator effectiveness, Rosas-Guerrero et al. (2014) found strong predictive support for pollination syndromes. Nevertheless, they did report several cases where the most efficient pollinator was not predicted by the floral traits. We suggest that some cases of nonconformity may be explained by the fact that the Stebbins (1970) hypothesis of flowers adapting to the most effective pollinator is sometimes too simplistic (Aigner, 2001, 2004). Simply put, Aigner (2001) argues that floral traits are adaptations to the additive effects of all floral visitors within pollinator communities, not just the most effective ones. Consequently, floral adaptations may even evolve for less effective pollinators if they do not have large negative effects on pollen transfer by more effective pollinators (Mayfield et al., 2001; Aigner, 2004). Thus, floral traits should predict the pollinators that played a strong role in selecting for those traits; however they may not always be predictive of the most abundant pollinators or even the most effective pollinators.

In this study, the unusual inflorescences of *Thonningia sanguinea* Vahl. (Balanophoraceae) provide a compelling example of the usefulness and shortcomings of the floral syndrome concept. The first time we encountered *T. sanguinea* was in Kibale forest, Uganda. The plant is a dioecious root parasite which infects hosts from the Euphorbiaceae, Moraceae and Apocynaceae families (Olanya and Eilu, 2009). The inflorescences can form dense clusters at ground level, among the roots of their hosts where they resemble the general form of various geoflorous species pollinated by small terrestrial mammals (*c.f.* Rourke and Wiens, 1977; Rebelo and Breytenbach, 1987). Literature suggests that they are part of a brood site mutualism with female calliphorid and muscid flies which lay their eggs on the fleshy column of inflorescences (Goto et al., 2012). They were also observed feeding from the nectar, carrying pollen, as well as laying eggs on the bracts (Goto et al., 2012). From our preliminary observations, these inflorescences did not conform to the general syndrome associated with plants which attract calliphorid and muscid flies to brood sites. Plants that attract egg laying muscid and calliphorid flies usually have a very strong, putrid stench, clearly detectable by the human nose, and the flowers are almost invariably shades of mottled brown/dark red with pale windows (e.g. Faegri and van der Pijl, 1979; Van der Niet et al., 2011). Furthermore, there is little need for these plants to produce large quantities of nectar as flies are searching for brood sites (Faegri and van der Pijl, 1979). We hypothesized that the large amounts of nectar are predictive of vertebrate pollinators such as rodents or birds. In particular, the close resemblance between *T. sanguinea* and many species of rodent pollinated Proteas (e.g. *P. humiflora* and *P. acaulos*), suggested that small mammals could be important pollinators.

2. Material and methods

2.1. Related species

Plants within the *Balanophoraceae* family may be either dioecious or monoecious and the inflorescences may be small and cryptic in the case of some *Balanophora* species (Kawakita and Kato, 2002), but bright and showy in the case of *T. sanguinea* (BA pers. obs). Possible brood site mutualisms have been suggested for some monoecious family members involving beetles for *Lophophytum mirabile* (Borchsenius and Olesen, 1990) and moths for *Balanophora kuroiwai* and *Balanophora tobiracola* (Kawakita and Kato, 2002). However the dioecious *Dactylanthus taylorii* appears to be dependent on vertebrate pollinators such as bats (Ecroyd, 1996), and may have been involved in a past pollination mutualism with kakapos, whose ranges no longer overlap with the plants (Wood et al., 2012). Introduced ship rats also appear to be attracted to the inflorescences of *D. taylorii* (Ecroyd, 1996; Holzapfel, 2001). This range of pollination systems makes the plant family especially interesting for the study of pollination syndromes.

2.2. Study system

We attempted to locate as many *T. sanguinea* plants as possible within the Kibale forest of Uganda during July 2014. Kibale forest is renowned for its long term research on primates, and the forest is crisscrossed with a closely knit network of labelled paths, which researchers and their assistants use on a daily basis to follow primates. In total, we located 10 separate clusters of *T. sanguinea* inflorescences, each associated with a different host tree. All of these clusters were unisexual, suggesting that each cluster stemmed from a single infection (i.e. single origin). Table 1 details the sex, number of open inflorescences with nectar, and distances between each infection. From here on, we refer to each infection as a plant, five of which were male and five were female. The average ± SD distance between plants was 2247 ± 1333 m and the average distance between plants of different sexes was 2111 ± 1359 m. The closest male and female plants recorded were 98 m apart.

2.3. Inflorescence characters

We attempted to compare the traits of *T. sanguinea* with the syndrome traits associated with rodent, sunbird, butterfly, ant and fly brood site pollination (sapromyophily) as found in the available literature. These syndromes were chosen either because we observed some of these animals visiting *T. sanguinea* or because Goto et al. (2012) had seen these visitors associating with *T. sanguinea*, or because we hypothesized that these visitors may associate with *T. sanguinea*. The following traits were important diagnostics for one or more of the syndromes and were consequently scored for each syndrome: Floral colour (as perceived by the human eye), nectar volume, nectar concentration, concealment of nectar (whether nectar is concealed from pollinators in long tubes), the presence of perching structures, scent (to the human nose), flowering close to ground level (geoflory), distance between potential mates, size of visual display (large or small and inconspicuous), and the robustness of tepals/sepals/bracts. We expected that rodent pollinated plants would share more traits with *T. sanguinea* than plants pollinated by any of the other pollinator groups.

We extracted standing crops of nectar from three female and two male plants (11 female and 17 male inflorescences). Nectar concentration was measured with a Bellingham and Stanley 0–50%

Table 1
Sex and number of open inflorescences with nectar for all 10 *T. sanguinea* plants found. For plant 9, the number of open inflorescences was not counted. Numbers in the lower left part of the table are the distances (m) between each plant.

	Plant 1	Plant 2	Plant 3	Plant 4	Plant 5	Plant 6	Plant 7	Plant 8	Plant 9	Plant 10
Sex	Male	Female	Female	Female	Male	Female	Male	Female	Male	Male
Number of open inflorescences	21	14	1	2	4	3	1	0	??	1
Plant 2	2334									
Plant 3	949	2534								
Plant 4	2975	745	3257							
Plant 5	3594	1564	4006	840						
Plant 6	1025	2745	215	3470	4213					
Plant 7	1055	2683	158	3415	4168	98				
Plant 8	2977	670	3068	660	1434	3285	3215			
Plant 9	4181	1857	4353	1234	1158	4572	4506	1298		
Plant 10	2551	596	2517	1109	1955	2742	2662	600	1885	

refractometer and nectar quantity was measured using 20 μl capillary tubes. Five bracts from different inflorescences were collected from three female and two male plants (a total of 25 bracts) for length measurement. The total length of each bract (an approximation of the distance from bract tip to floral nectar) was measured with a ruler. Floral scent was assessed by human observers who smelled male and female inflorescences at different times of day. While many scent components will be missed by this assessment, the human nose is usually able to detect the yeasty odours of rodent pollinated flowers (Rouke and Wiens, 1977; Wiens et al., 1983), the strong odours of carrion flowers (Faegri and van der Pijl, 1979), and the lack of a discernible odour for bird pollinated flowers (Johnson, 2010).

2.4. Observations of floral visitors

To determine whether vertebrates are common visitors to *T. sanguinea*, two camera traps (Panthera V4 model) were placed around a small *T. sanguinea* cluster (plant 10) for seven days, totalling 14 trap days and nights (i.e. two traps × 7 nights). Five traps were placed around plant 1 for a total of 46 trap days and nights (not all five traps were active for this entire duration). Four traps were placed around plant 2 for a total of 47 trap days and nights. These two plants (1 and 2) were the largest known infections. The cameras were set up to cover as many open inflorescences as possible and they were in operation during the day and night. The cameras were placed 0.6–1 m away from the inflorescences and at approximately 0.6 m above the ground. Pictures were taken automatically whenever movement was detected by the camera sensors. For nocturnal camera trapping, we recorded the number of rodents seen in photographs and whether they were interacting with the inflorescences or not. While it is possible that visitors could have been recorded more than once, we reduced this possibility by counting successive photographs in a single camera (separated by less than one minute) as single visits. For diurnal trapping, we recorded the number of birds seen in the photographs (rodents were not active during the day). Again, successive photographs of the same bird on the same inflorescence separated by one minute were counted as a single interaction. We also recorded the time of visitation, the activity of the bird (i.e. whether it was perching alongside an inflorescence or not, whether its bill was inserted in an inflorescence and what it was perching on while probing inflorescences).

We observed small diurnal insects by sitting at a distance of about 1 m from between three and six *T. sanguinea* inflorescences. One and three hours were spent observing ants and flies respectively. No observation time was allocated for butterflies, because individuals spent hours foraging from the same plant, without moving to other inflorescences, suggesting that they are probably poor pollinators. Observations of flies and ants took place on different days (one day each). Observation times were split equally among a male (plant 1) and a female plant (plant 2). During this time, we recorded the total number of visitations and the total number of inflorescences observed.

Six days (a total of 21.5 h) were spent observing bird activity. Most observations were conducted on the two largest known plants: 8.5 h were spent observing a male plant (plant 1) consisting of approximately 21 open, nectar producing inflorescences. Twelve hours were spent observing a female plant (plant 2) consisting of approximately 14 open inflorescences. These two plants were situated 2334 m apart. One hour was spent observing a small male plant (plant 10) consisting of one open inflorescence. This plant was relatively close to (596 m away) the large female plant (plant 1). To avoid disturbing potential bird visitors, we sat approximately ten meters away from the plants and consequently we were usually able to view only a small subset of the inflorescences. We recorded the number of inflorescences being observed. A visitation was recorded when a bird probed an inflorescence. If a bird moved to, and probed another inflorescence, this was recorded as another visitation. Each time an inflorescence was probed, we recorded the time. We also noted whether visiting birds could be identified using coloured rings on their legs (see below).

Visitation rates were calculated in the same way for visual and camera trap observations. Each camera trap was counted as a separate "observation" or replicate. Similarly, each separate period of visual observation was treated as a replicate. The visitation rate (visits per inflorescence per hour) was calculated separately for each camera trap or visual observation period as the number of visits divided by the total numbers of inflorescences being observed, divided by the total time spent observing. Visitation rates for visual and camera trap data are reported as means (over all camera traps or visual observation period) ± SD.

2.5. Pollen loads

Rodents were trapped using Sherman traps placed among *T. sanguinea* inflorescences in the largest male and female plants (plant 1 and 2). Six and seven different individuals were captured among the female and male inflorescences respectively. The nose and facial fur of the mice were swabbed with glycerine jelly containing fuchsin stain to check for the presence of pollen. In addition, the faeces from five different individuals were collected from the traps and examined for the presence of *T. sanguinea* pollen. Faeces were diluted in ethanol, treated with fuchsin stain and examined with a light microscope.

Insects present on the inflorescences were collected to check for pollen presence. A butterfly net was used to capture flying insects such as flies and butterflies, and flexible forceps were used to capture ant visitors. The insects collected were killed with ethyl acetate fumes and stored separately. Small insects were directly placed on a slide with glycerine jelly containing fuchsin stain, while larger insects were swabbed with glycerine jelly containing fuchsin stain

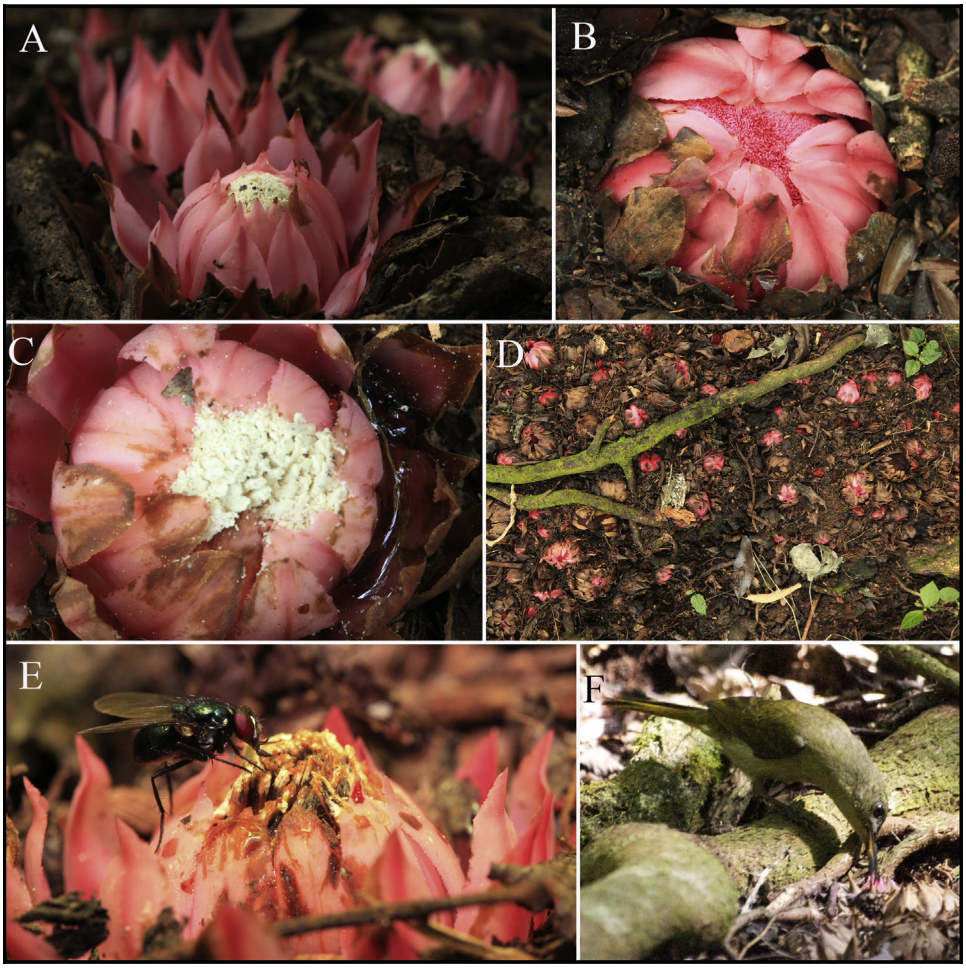

Fig. 1. The (A) male and (B) female inflorescences of *T. sanguinea*. (C) Nectar pooling around the bases of the bracts on a male *T. sanguinea* inflorescence. (D) A dense infection of female *T. sanguinea* inflorescences among the roots of a fig host. (E) A fly visiting a male *T. sanguinea* inflorescence. (F) An olive sunbird using a root to perch on while probing a female *T. sanguinea* inflorescence.

before melting the jelly on a slide. The number of pollen grains observed in each sample was counted using a light microscope.

Over the course of the study we also captured seven sunbirds using mist nets set up around a male and a female plant. Each bird was ringed with a unique colour code around its legs (Supplementary material 1), and the length of its bill was measured with a ruler from bill tip to skull (total culmen). Each sunbird was checked for pollen presence by rubbing glycerine jelly with fuchsin stain onto its bill, feet, and the feathers at the base of the bill. These gel samples were placed on separate glass slides and later examined with a light microscope. Pollen grains found on potential pollinators were identified as belonging to *T. sanguinea* by comparing them to a reference sample of *T. sanguinea* pollen.

2.6. *Pollinator effectiveness*

The effectiveness of a pollinator (in terms of female fitness) depends on the frequency with which it visits flowers and the numbers of pollen grains that it places on the stigmas of female flowers. The latter is likely to depend on the pollen loads that pollinators are carrying. Unfortunately, most of the pollinators were captured on male plants, and so it was not possible to determine the pollen loads of pollinators in the vicinity of female plants. To standardize the effectiveness of pollinators, we multiplied the average visitation rate of each kind of pollinator with the average pollen load carried by individuals captured on male inflorescences. This measures the effectiveness of pollinators in picking up pollen (an important aspect of male fitness, and a factor which is very likely to affect female fitness) but is a poor reflection of how effective pollinators are at moving pollen in between plants.

3. Results

3.1. *Inflorescence characters*

The inflorescences of *T. sanguinea* consist of hundreds of tiny, tightly packed flowers which form a sphere. This is closely surrounded by hard, pink bracts with sharp tips (Fig. 1A and B). As the inflorescence matures and the bracts part, copious amounts of pollen are exposed in the centres of the male inflorescences (Fig. 1A and C) and the velvety stigmas of the female inflorescences can clearly be seen (Fig. 1B). These inflorescences appear to last for many days. The inflorescences have no odour discernible to the human nose and they produce copious amounts of nectar which can sometimes be seen pooling around the bases of the bracts (Fig. 1C). The average ± SD nectar volume of female inflorescences was 120.8 ± 163.6 μl, while for male inflorescences, it was 321.7 ± 320.5 μl. The nectar concentration for female inflorescences was 16.8 ± 2.1%, while for male inflorescences it was 14.5 ± 1.1%. We were unable to determine whether there were significant differences in nectar concentration or volume between the sexes as replication was at the inflorescence level with only a few individual plants investigated. The average ± SD length of inflorescence bracts was 25.8 ± 2.9 mm. Of the ten traits examined, both rodent and sunbird pollinated plants commonly shared 7 traits with *T. sanguinea*. Only four traits were shared with butterfly pollinated plants, while five traits were shared with ant pollinated plants as well as plants pollinated by brood site-seeking flies (Table 2).

3.2. Pollinator observations

Nocturnal camera traps recorded the presence of Jackson's soft-furred mouse (*Praomys jacksoni*) close to *T. sanguinea* inflorescences on 38 occasions, but none were captured interacting directly with inflorescences. Diurnal camera traps captured footage of olive sunbirds (*Calamitra olivacea)* close to the inflorescences on 243 occasions. Of these, 76 actual interactions between birds and *T. sanguinea* inflorescences were recorded on camera (Supplementary material 1). During these interactions, birds foraged for nectar. In 27 cases, foraging occurred while the birds were perched on the ground, while in 49 instances birds were observed using roots (29 times) or twigs (20 times) to perch on while visiting inflorescences. Olive sunbirds actively visited *T. sanguinea* inflorescences throughout the daylight hours with the highest activity between 10:00 and 15:00 (Supplementary material 2). The visitation rate captured by cameras (using all 243 images of birds next to inflorescences) was an order of magnitude lower (0.06 visits per inflorescence per hour) than for visitation rates observed by human observers (0.6 visits per inflorescence per hour).

Observers saw very frequent visits (Table 3) from calliphorid and muscid flies, ants (Formicidae), sunbirds and also butterflies (Satyridae and Nymphalidae). The most frequent visitors were ants and flies (Table 3). Although butterflies were also frequent visitors (visitation rates not quantified), our preliminary observations quickly determined that individual butterflies spent hours foraging from the same plant, and seldom moved from the immediate vicinity. This suggests that they are probably poor pollinators and consequently we did not perform detailed observations on their foraging rates.

3.3. Pollen loads and pollinator effectiveness

Video footage of birds foraging on male inflorescences clearly showed that they accumulated very large pollen loads on their bills (Supplementary material 3). The viscous pollen adhered to the bills when they were inserted between the sphere of inflorescences and the bracts to obtain the nectar at the base of those bracts (Supplementary material 3). However, after catching birds close to male inflorescences using mist nets, most of this pollen was rubbed off and it could no longer be seen with the naked eye. Fuchsin gel swabs of bird bills revealed average ± SD pollen loads of 172.3 ± 227.1 grains per bird (Table 3). No pollen was observed in the feathers at the base of bird bills. The bills of olive sunbirds were 27.17 ± 1.8 mm long. Three birds were captured close to a female plant and these birds were carrying very low *T. sanguinea* pollen loads of zero, one and three pollen grains. Small pollen loads were observed on ants and flies foraging among male inflorescences and rodents captured in traps (Table 3). No *T. sanguinea* pollen grains were found in the faeces of rodents. No pollen was observed on two butterflies captured on male inflorescences. The most effective pollen removers (Table 3), as estimated from observer-based visitation rates multiplied by pollen loads of foragers in male populations, were birds (103.4), followed by ants (54.0) and then flies (26.9).

3.4. Bird movement

The seven ringed birds were observed on 91 occasions by a combination of human observations and camera traps. The birds were

Table 2
The pollinator syndrome traits which *T. sanguinea* shares with plants from other well described pollination syndromes. We detail 10 of *T. sanguinea's* traits which are likely to reflect adaptations to pollinator preference, morphology or dispersal abilities. Character traits which *T. sanguinea* share with other syndromes are presented in bold. The total number of traits which each syndrome shares with *T. sanguinea* is given in the bottom row.

Floral characters	Thonningia	Rodent	Sunbird	Sapromyophily	Butterfly	Ant
References		Wiens et al. (1983) and Johnson (2010)	Rebelo et al., 1984, Johnson 2010	Faegri and van der Pijl (1979)	Krömer et al. (2008) and Faegri and van der Pijl (1979)	Hickman (1974) and de Vega (2007)
Colour	**pink-brick red**	**red-brown, green**	**red/orange/yellow/pink**	usually blotchy, red-brown, orange	**pink, red/yellow**	**variable**
Nectar volume	**very high (236 ul/inflorescence)**	**very high (24–250 ul/inflorescence)**	**high (10–30 ul/flower)**	no nectar or very little nectar	low (<5 ul/flower)	very low (<3 ul/flower)
Nectar concentration	**13–18.5%**	19.7–68%	**15–25%**	nectar seldom present	19–40%	>20%
Concealment of nectar	**none**	**often none**	in long floral tubes	**none**	in long floral tubes	**often poorly concealed**
Perch	**no**	**no**	usually	**no**	**no**	**no**
Scent (to human nose)	**no**	yes – yeasty	**no**	yes – Rotting meat	**no**	**no**
Geoflory	**yes**	**usually**	seldom	**usually**	no	**yes**
Mate distance	**long distances**	short distances	**long or short distances**	**long or short distances**	short to medium distances	short distances
Display size	**large inflorescences**	**large inflorescences**	**large flowers/inflorescences**	**large flowers/inflorescences**	**Large flowers/inflorescences**	inconspicuous, small flowers/inflorescences
Robustness	**very robust**	**often robust**	**can be robust**	often fleshy	not robust	not robust
Total characters	10	7	7	5	4	5

Table 3
Mean ± SD rates of visitation to *Thonningia sanguinea* (visits per inflorescence per hour) using camera traps and human observers. Average pollen loads per individual were collected from animals captured foraging on male inflorescences, except for rodents which were captured in traps close to male *T. sanguinea* inflorescences. The effectiveness of each pollinator was calculated from the average pollen load per individual multiplied by the visitation rate. Numbers in parenthesis are the number of individuals examined.

	Fly observations	Ant observations	Sunbird observations	Sunbird trap data	Rodent trap data
Total visitations	70	150	70	243	0.0
Visitation rate	1.5 ± 1.2	13.5 ± 7.1	0.6 ± 1.0	0.06 ± 0.04	0.0
Pollen load per individual	17.8 ± 40.2 (6)	4 ± 4.5 (9)	172.3 ± 227.1 (4)	172.3 ± 227.1 (4)	0.6 ± 0.8 (7)
Effectiveness (Load × visitation rate)	26.9	54.0	103.4	10.3	0.0

all captured from two populations separated by 2334 m and no movement between these two populations was observed. However, one bird was observed three times on the female plant 2 and then once on the small male plant 10, which was a distance of 596 m away.

4. Discussion

T. sanguinea receives visits from numerous different potential pollinators, but to our surprise we did not gather any evidence of active visitation by rodents. Although many different taxa visit *T. sanguinea*, not all of them are likely to be effective pollinators. Indeed, ants and butterflies carried very small pollen loads and are unlikely to transfer any pollen between plants, even if male and female plants were very close. Based on visitation frequencies and pollen loads, sunbirds appeared to be the most effective removers of pollen, and flies which were half as effective as birds were the next most effective pollen removers. Sunbird visitation rates were much higher for human observers than for camera traps, perhaps suggesting that the camera traps are not always triggered or that the camera flash scares bird visitors away.

One weakness of this study is that we did not estimate the quantity of pollen deposited by visitors on the stigmas of female inflorescences, which is a much better measure of pollinator effectiveness than pollen loads. This is an important consideration because male and female plants were often separated by great distances, making it unlikely that some pollen carrying visitors were moving pollen from male to female plants. In particular, it is highly unlikely that either ants or rodents would regularly move the large distances between male and female plants. Flies on the other hand are known to move large distances between inflorescences that mimic carrion (Beaman et al., 1988). However, unlike *T. sanguinea*, flowers that attract flies over large distances usually have very powerful odours which are clearly detectable by the human nose (e.g. Beaman et al., 1988; Van der Niet et al., 2011). We also observed that individual flies spent hours foraging on the same *T. sanguinea* inflorescences, suggesting that they seldom move between plants. Their lack of movement may be due to the fact that the extremely high nectar loads of inflorescences are unlikely to be depleted to levels which make it unprofitable for flies to stay and continue foraging on the same plant. In contrast, pollinating sunbirds only spent a few minutes at a time on each plant before moving away. Bird pollinators are known to use memory, experience and their excellent flight capabilities to repetitively visit distantly spaced nectar sources (Ohashi and Thomson, 2009). In support, we observed one sunbird moving between distant male and female plants separated by nearly 600 m. We speculate that olive sunbirds are much better than flies at moving pollen between distant *T. sanguinea* plants. This, and the fact that sunbirds were more effective than flies in terms of their visitation rates × pollen loads, suggests that sunbirds are the primary pollinators of this plant. The only other pollination study conducted on this plant suggested flies as the primary pollinators and did not record sunbirds as visitors (Goto et al., 2012). We suspect that Goto et al. (2012) may have been observing inflorescences from too close to allow the approach of olive sunbirds which are widespread and common in all tropical African forests (Cheke et al., 2001). While flies may make some contributions to the pollination of this plant, the character traits of the plant and pollinator observations suggest that several of the floral traits are adaptations to sunbirds. Fly visitations may be explained by the fact that many of the other monoecious members of the family are pollinated by insects and appear to have brood site mutualisms (Borchsenius and Olesen, 1990; Kawakita and Kato, 2002). Brood site mutualisms could consequently be the ancestral state for the family, and hence insect visitations may reflect the ghosts of the evolutionary past. However, efficient brood site pollination is unlikely for dioecious species like *T. sanguinea* which do not appear to have strong odours and where male and female plants are far apart.

Given the large number of traits shared with rodent pollinated flowers (Table 2), one may have expected to find rodent visitors to *T. sanguinea* (as hypothesized). However, it appears as though certain traits are good syndrome diagnostics whereas others are not. For example, a yeasty odour may be an important trait for rodent pollination whereas some of the others (e.g. large, robust flowers, copious nectar) are traits which are shared with the bird pollination syndrome. Pollination by rodents and brood site-seeking flies are almost always associated with strong scent cues, which can usually by discerned by the human nose. Lack of discernible scent was one of the main reasons for our scepticism surrounding the importance of brood site mutualisms *T. sanguinea*. In retrospect, the absence of scent should also have made us question the importance of rodents as pollinators. In contrast, a true lack of detectable (using GC–MS) scent is a key feature of hummingbird pollinated flowers (Knudsen et al., 2004) and the lack of sent to the human nose in *T. sanguinea* should have been an indicator of bird pollination. Phenotypic characters such as the extremely high nectar loads, pink colouration, are also in-keeping with the sunbird pollination syndrome (Rebelo et al., 1984; Johnson, 2010). The high nectar loads are suggestive of large vertebrate pollinators (including birds and rodents), but they are not in-keeping with insect pollination as insects are unable to deplete the nectar sufficiently to encourage movement between plants. While a systematic tally of shared traits may have helped us to predict birds as important pollinators, it did not suggest that they were any more likely pollinators than rodents (Table 2).

Despite being frequently visited by sunbirds, *T. sanguinea* lacks two traits frequently associated with sunbird pollination: *T. sanguinea* has terrestrial inflorescences, but no structure for sunbirds to perch upon while foraging. One study (Anderson et al., 2005) provided evidence that sunbirds prefer to perch while foraging, and that many sunbird pollinated flowers appear to have evolved structures for birds to perch upon (e.g. De Waal et al., 2012a). However, this is not ubiquitous and some geoflorous sunbird pollinated plants do not have perching structures (e.g. Sakai et al., 1999; De Waal et al., 2012b; Hobbhahn and Johnson, 2015; Turner and Midgley, 2016). The evolution of most floral traits is often likely to be influenced by phylogenetic constraints and so the absence of a particular trait may simply mean that it was not easy for a species to evolve, or that the species has evolved a different evolutionary solution. In the case of *T. sanguinea*, sunbirds used the abundant roots of the host plant to perch on, making the evolution of a perch unnecessary. In addition, some close-up video footage (Supplementary material 1) revealed that olive sunbirds may often perch on surrounding *T. sanguinea* inflorescences when probing. Anderson et al. (2005) demonstrated that *Babiana ringens* plants with perches receive more frequent visits than plants without perches, but that plants without perches still received visits. This suggests that while a perch may increase fitness, it is not essential for sunbird visitation and may not evolve if there are strong phylogenetic constraints. *T. sanguinea* also lacks long, tubular flowers which is unusual among bird pollinated plants. However, the sharp bracts of *T. sanguinea* often lie close to the flowers of the inflorescences, perhaps making it hard for pollinators to gain effective access to the nectar if they do not have a long proboscis or bill, or if they are not very small. The lengths of these bracts are closely matched to the length of the olive sunbird's bill, and present a similar curvature. In two similar cases of non-conformity, the bird pollinated plants *Disa chrysostachya* (Johnson and Brown, 2004) and *Microloma sagittatum* (Pauw, 1998) also lack long floral tubes. In each case, the necessity for long tubes has been negated by adaptations that allow the placement of pollen on very unusual parts of the sunbird anatomy (feet- Johnson and Brown, 2004; and tongues- Pauw, 1998). Such unusual responses to pollinator-mediated selection may provide surprising cases of apparent non-conformity to predictions of pollinators from floral phenotype (Ollerton, 1998). However, these exceptions are frequently the surprises that show the importance of the link between pollinators and floral anatomy, and they are easily explained with a more intricate understanding of pollination ecology. For example, the unusual morphology of *M. sagittatum* appears to be a direct result of adaptation to sunbirds and by extension, Pauw (1998) predicted that several other similar looking flowers in the Apocynaceae family are also likely to be bird pollinated (these predictions remain untested). Continued research on pollination is likely to generate many further pollinator surprises. However, it is important that our reaction to these surprises is not to dismiss syndromes as a concept, but rather to fine-tune the existing syndromes.

One surprising feature of the *T. sanguinea* system is that although nine species of sunbird have been recorded in Kibale forest (Dranzoa, 1998; Sekercioglu, 2002) and several are commonly seen (CN, Pers. Obs.), only olive sunbirds were observed visiting *T. sanguinea*. Other sunbird species were frequently seen foraging in the forest canopy and sub canopy, suggesting that the foraging niches of sunbirds in Kibale may be stratified. In South Africa, the sunbird pollination guild is clearly divided by tube length morphology into two smaller guilds of species pollinated by long-billed sunbirds and species pollinated by short-billed sunbirds (Geerts and Pauw, 2009). It is likely that sunbird pollinated plants in African rainforests may similarly form different guilds based on their flowering height and we predict that olive sunbirds may be one of the only sunbird species to visit red, tubular flowers (e.g. *Impatiens bombycina*) in the forest understories. Olive sunbirds are unusual among sunbirds in that the males are dull in colour, perhaps allowing them to forage more freely on the ground where they would be more prone to predation (Anderson et al., 2005).

5. Conclusions

This paper highlights both the usefulness as well as the short-comings of the syndrome concept. If it were not for some knowledge on syndromes – we would never have questioned the importance of brood site-seeking flies as pollinators. While we were unable to explicitly predict that birds are likely important pollinators, it is easy to make the associations between birds and the floral phenology of *T. sanguinea* in hindsight. We suggest that many of the apparent mismatches between pollinators and plant traits are simply due to a lack of experience or a poor understanding of how floral phenotype is adapted to pollinators. Furthermore, this study highlights the fact that visitation rates alone are a very poor predictor of pollinator importance. We argue that similarities in plant traits are often the result of adaptations to similar pollinators. However we emphasize that predictions should remain working hypotheses until direct evidence is collected.

Acknowledgements

We are extremely grateful to the Tropical Biology Association for the opportunity to work at Makerere University Biological Field Station and to all of the staff there for maintaining the excellent facilities. We would like to thank David Mills for lending us camera traps for this project. Financial support was provided by the British Ecological Society and the BAT Biodiversity Partnership. We would like to express our gratitude to Jeff Ollerton, two anonymous reviewers and Stefan Dötterl whose edits improved the original manuscript substantially. We also thank Callan Cohen for advice on bird taxonomy. Lastly, we thank the elephants and hippos of Uganda for making our experiences so exciting.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.flora.2016.11.015.

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