A preliminary investigation into the avian pollinators of three tree species in a Nigerian montane forest

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Summary

Pollination mutualisms are essential for tropical forests, but are threatened by forest fragmentation and degradation, which can lead to decline and loss of pollinator species. We studied the avian pollinators of three West African montane forest tree species, *Anthonotha noldeae* (dependent on birds for pollination), *Anthocleista vogelii* and *Croton macrostachyus* (with flowers characteristic of moth and insect pollination respectively). At 15 individuals of each tree species, we recorded bird visits and identified visitors as Pollinators, Secondary Pollinators and Robbers. In total, 25 bird species visited at least one of the three tree species, and eight visited all three. The Northern Double-collared Sunbird *Cinnyris reichenowi* and Orange-tufted Sunbird *C. bouvieri* pollinated all three tree species. The Variable Sunbird *C. venustus* pollinated only *A. vogelii* and *A. noldeae*. The Village Weaver *Ploceus cucullatus* occasionally pollinated *A. vogelii*. Nineteen bird species were considered Secondary Pollinators, while three were Robbers only. The Village Weaver behaved sometimes as a Pollinator, sometimes as a Secondary Pollinator and sometimes as a Robber. The frequency of bird visitation was higher on *A. noldeae* than on *A. vogelii* or *C. macrostachyus*. Four species of sunbird are crucial for the pollination of *A. noldeae* but the possibility exists for its pollination by Secondary Pollinators should sunbirds decline. Despite having flowers characteristic of insect pollination, both *A. vogelii* and *C. macrostachyus* are pollinated by sunbirds and perhaps the Village Weaver.

Résumé

Une enquête préliminaire parmi les oiseaux pollinisateurs de trois espèces d'arbres dans une forêt de montagne du Nigéria. Les mutualismes de pollinisation sont essentiels pour les forêts tropicales mais ils sont menacés par la fragmentation et la dégradation des forêts, qui peut conduire au déclin et à la disparition d'espèces pollinisatrices. Nous avons étudié les oiseaux pollinisateurs de trois espèces d'arbres de forêts de montagne d'Afrique de l'Ouest, *Anthonotha noldeae* (qui dépend des oiseaux pour sa pollinisation), *Anthocleista vogelii* et *Croton macrostachyus* (aux fleurs caractéristiques d'une pollinisation par, respectivement, papillons de nuit et insectes). Pour 15 individus de chaque espèce d'arbre, nous avons enregistré les visites d'oiseaux et identifié les visiteurs Pollinisateurs, les Pollinisateurs Secondaires et les Voleurs. Au total, 25 espèces d'oiseaux ont visité au moins une des trois espèces d'arbres et huit ont visité toutes les trois. Le Souimanga de Preuss *Cinnirys reichenowi* et le Souimanga de Bouvier *C. bouvieri* ont pollinisé toutes les trois espèces d'arbres. Le Souimanga à ventre jaune *C. venustus* a pollinisé seulement *A. vogelii* et *A. noldeae*. Le Tisserin gendarme *Ploceus cucullatus* a pollinisé occasionnellement *A. vogelii*. Dix-neuf espèces d'oiseaux ont été considérées comme des Pollinisateurs Secondaires, tandis que trois l'ont été seulement comme Voleurs. Le Tisserin gendarme s'est parfois comporté comme un Pollinisateur, parfois comme un Pollinisateur Secondaire et parfois comme un Voleur. La fréquence des visites d'oiseaux a été plus élevée sur *A. noldeae* que sur *A. vogelii* ou *C. macrostachyus*. Quatre espèces de souimangas sont cruciales pour la pollinisation de *A. noldeae* mais la possibilité existe de sa pollinisation par des Pollinisateurs Secondaires en cas de raréfaction des souimangas. Malgré leurs fleurs caractéristiques de la pollinisation par insectes, *A. vogelii* et *C. macrostachyus* sont tous les deux pollinisés par des souimangas et peut-être par le Tisserin gendarme.

Introduction

Sodhi *et al.* (2004) highlighted the vulnerability of tropical forest avifaunas to habitat fragmentation and degradation. They lamented the lack of knowledge about tropical avian ecology and stressed its importance for effective forest management. For example, loss of plant–pollinator mutualisms can lead to reduced ecosystem function, extinctions and trophic cascades. The more specialised the mutualism, the more vulnerable it is to disruption through anthropogenic change (Bond 1994, Kearns *et al.* 1998, Sodhi *et al.* 2004, Aguilar *et al.* 2006, Anderson *et al.* 2011, Sekercioglu 2011). Floral morphology is not necessarily a good predictor of pollinator specificity (Waser *et al.* 1996, Ollerton, 1998, Fumero-Cabán *et al.* 2007) and careful observation and even experimentation may be necessary to comprehend the nature of mutualisms fully. While nectar-feeding insects have been well studied, this is not the case for passerine birds and we lack data on their function as cross-pollinators (Allen-Wardell *et al.* 1998).

The aim of this paper is to begin to address the gaps in knowledge identified above for the montane forests of eastern Nigeria. Situated along the Cameroon border, these forests belong to the Cameroon Highlands Forest Ecoregion (WWF Global 2000 classification). The area belongs within the "West African Forests" biodiversity hotspot (Myers *et al.* 2000) which has exceptionally high levels of endemism across all taxa, and is therefore designated a global conservation priority (Fishpool & Evans 2001). The montane forests are threatened by increasing human population pressure and lack of effective conservation (Beck & Chapman 2008, Chapman *et al*. 2004, Cheek *et al.* 2000, Ezealor 2002, Maisels *et al.* 2001). While the avian diversity of this area has been well studied, avian ecology and pollination mutualisms have received little attention.

Most Afromontane forest tree species have small, often inconspicuous, flowers indicative of pollination by non-specialized insect pollinators (Dowsett-Lemaire 1989). However in the Ngel Nyaki forest, Nigeria, nectarivorous sunbirds (Nectariniidae) and passerines such as the Common Bulbul *Pycnonotus barbatus*, flycatchers (Muscicapidae), white-eyes (Zosteropidae) and weavers (Ploceidae) are common, and all of these taxa have been recorded visiting a wide range of tree species (Ihuma 2006).

Here we ask which bird species visit the flowers of Nigerian Afromontane tree species, to what extent each of them acts as a pollinator or nectar robber, and whether bird species preferentially visit flowers with bird pollination syndromes (Fægri & van der Pijl 1979).

Methods

The research was conducted in and around the 46 km^2 Ngel Nyaki Forest Reserve (7°30′N, 11°30′E), located on the Mambilla Plateau in Taraba State, Nigeria (Fig. 1) at an elevation of approximately 1550 m a.s.l. (Chapman & Chapman 2001). The reserve comprises *c*. 7.2 km^2 of escarpment forest as well as associated riparian forest along streams. The Reserve is an Important Bird Area (Ezealor 2002).

Three trees species were chosen for this study: *Anthonotha noldeae* (Leguminosae), *Anthocleista vogelii* (Gentianaceae) and *Croton macrostachyus* (Euphorbiaceae). These species were chosen because they were common in Ngel Nyaki forest and were in flower at the time of this study. A voucher specimen of each species has been deposited at the Nigerian Montane Forest Project Herbarium located in the Project field station, on Mambilla Plateau. *A*. *vogelii* flowers have traits consistent with adaptation for bird pollination (flowers *c.* 3 cm long, 1.5 cm diameter at the top, which do not open significantly) while *A*. *noldeae* (flowers *c*. 2 cm diameter) and *C. macrostachyus* flowers have typical insect pollination syndromes (Fig. 2). The flowers of *C. macrostachyus* are small and clustered in spikes; for this species, bird visits to inflorescences were counted, not visits to individual flowers, and hereafter a "flower" of *C. macrostachyus* is taken to mean an inflorescence.

For each of the three tree species, 15 individual trees were monitored along forest edge and riparian forest habitat. Individual trees ranged from 450 m to 1 km distant were monitored between 6h30 and 9h30, and 15h30 and 17h30, which represented periods of peak visitation (CN pers. obs.). Individual trees were observed for periods of 20 min., at comparable stages of flowering. Birds were observed through 8 x 50 binoculars, at sufficient distance from the tree to avoid deterring them. We monitored 15 individuals of each of *A. vogelii* and *C. macrostachyus* for 6 h (making a total of 90 h per species) and 15 individuals of *A. noldeae* for 14.6 h (total 219 h for the species). Observations took place during May–Jun (*A. vogelii* and *C. machrostachyus*) and Oct–Nov (*A. noldeae*) 2008. This disparity in time of assessment and observation hours was due to the difference in flowering phenology among the three species. For each avian visitor, time of arrival on the flower, time of departure, number of flowers visited, other plant parts visited and overall bird behaviour, including nectar robbing, were recorded. from each other. The avian visitors to each of the 15 focal trees of each of the three species.

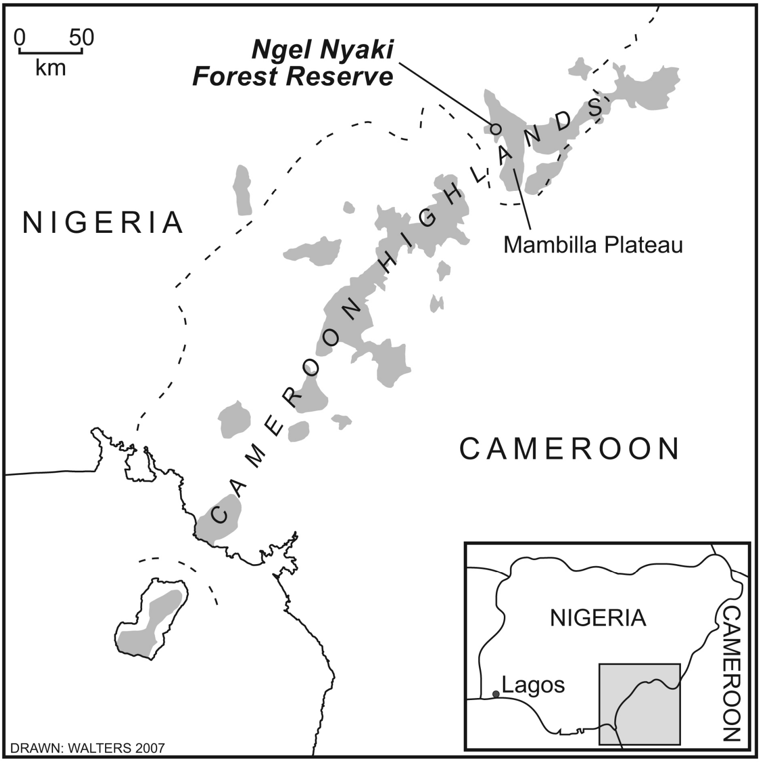

Figure 1. Map showing the position of Ngel Nyaki Forest Reserve on the Mambilla Plateau, Nigeria, and in relation to the Cameroon Volcanic Line.

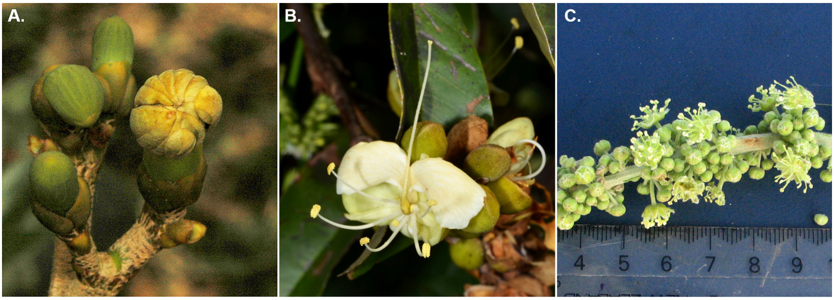

Fig. 2. Flowers of the three focal tree species. A *Anthocleista vogelii*; B *Anthonotha noldeae*; C *Croton macrostachyus.*

Avian visitors were categorized based on frequency of visitation and whether or not they used the flowers in a manner that would be likely to facilitate pollen transfer: a “Pollinator” was a frequent visitor which made contact with the flower in such a way that pollination could be effected, (the visitor’s bill and bristles reach into the flower so as to pass both the top of the pistil and the anthers); a “Secondary Pollinator” (*sensu* Stein 2011) was a visitor that made contact with flowers in a manner unlikely but possibly to result in pollen transfer (*e.g.* only brief contact with the flower, or eating pollen) and a “Robber” was a bird that treated the flower in such a way as not to pollinate it, *e.g.* piercing the base of the flower or using existing perforations to extract nectar (Coetzee & Giliomee 1985, Fumero-Cabán *et al*. 2007). For each focal tree observed, the visitation rate by each bird species was calculated as the number of visits/plant/h after the method of Anderson (2003).

Analysis of variance (ANOVA) was used to test focal observation data. The data were normally distributed and differences in bird visitation rate to each tree species were analysed using the Student’s t-test for equality of means. The statistical program SAS was used for all analyses.

Results

In total, 25 bird species from ten families visited at least one of the three focal tree species and eight of these (four families) visited all three tree species (Table 1). Of the five species of visitors classified as Pollinators of at least one of the three tree species, four were sunbirds (Nectariniidae) and the other was the Village Weaver *P. cucullatus* (Table1). Secondary Pollinators were more diverse, with 19 species recorded from eight families (Table 1). Of the four Robber species, three were weavers (Ploceidae) while the other was the Speckled Mousebird *Colius striatus*. The Village Weaver behaved variably, as a Pollinator, Secondary Pollinator or Robber, depending on tree species visited (Table 1). Similarly, the Green-headed Sunbird *C. verticalis* acted as a Secondary Pollinator on *A. vogelii* and *C. macrostachyus* but as a Pollinator on *A. noldeae*.

Table 1. The pollinator status of bird species observed on the focal tree species: P = Pollinator; SP = Secondary Pollinator; R = Robber (see text).

	Anthocleista vogelii	***Croton macrostachyus***	***Anthonotha noldeae***
Coliidae			
Colius striatus Speckled Mousebird	R	R	
Lybiidae			
Lybius bidentatus Double-toothed Barbet	SP		
Pogoniulus chrysoconus Yellow-fronted Tinkerbird	SP	SP	
Pycnonotidae			
Pycnonotus barbatus Common Bulbul	SP	SP	SP
Chlorocichla flavicollis Yellow-throated Leaflove	SP	SP	
Cisticolidae			
Apalis pulchra Black-collared Apalis		SP	
Muscicapidae			
Elminia longicauda Blue Paradise Flycatcher	SP	SP	
Zosteropidae			
Zosterops senegalensis Yellow White-eye	SP	SP	
Nectariniidae			
Anthodiaeta platura Pygmy Sunbird	SP	SP	SP
A. collaris Collared Sunbird	SP	SP	SP
Cinnyris bouvieri Orange-tufted Sunbird	P	P	P
C. cupreus Copper Sunbird	SP	SP	
C. pulchellus Beautiful Sunbird	SP		
C. reichenowi Northern Double-collared Sunbird	P	P	P
C. venustus Variable Sunbird	P		P
Cyanomitra verticalis Green-headed Sunbird	SP	SP	P
Malaconotidae			
Laniarius atroflavus Yellow-breasted Boubou	SP	SP	SP
L. aethiopicus Tropical Boubou	SP		SP
Ploceidae			
Ploceus bannermani Bannerman's Weaver	R	R	R
P. nigerrimus Vieillot's Black Weaver	SP	SP	
P. cucullatus Village Weaver	P/SP	SP/R	
P. ocularis Spectacled Weaver	SP		
P. pelzelni Slender-billed Weaver	SP		
P. baglafecht Baglafecht Weaver	R		
Estrildidae			
Estrilda nonnula Black-crowned Waxbill			SP

Two species, the Northern Double-collared Sunbird *C. reichenowi* and the Orange-tufted Sunbird *C. bouvieri*, were Pollinators of all three tree species but were most active on *A. noldeae*. For example we recorded 536 visits from Northern

Double-collared Sunbirds to *A. noldeae* but only 34 and five visits respectively to *A. vogelii* and *C. macrostachyus*, while Orange-tufted Sunbirds made 185 visits to *A. noldeae*, 200 to *A. vogelii* and only 59 to *C. macrostachyus*. These two sunbird species and the Variable Sunbird *C. venustus* together accounted for the majority of all bird visits to *A. noldeae* (94 %) and 50 % of those to *A. vogelii.* Only two sunbird species, Northern Double-collared Sunbird and Orange-tufted Sunbird, were Pollinators of *C. macrostachyus* and together accounted for 49 % of visits to this species (Table 2). Other common visitors to *A. vogelii* and *C. macrostachyus* were the Village Weaver (27 % and 14 % respectively) and Common Bulbul *Pycnonotus barbatus* (11 and 20 %).

The bird visitation rate (mean number of visits/tree/h by all species) to *A. noldeae* was significantly higher (4.74 ± 2.36 visits/tree/h) than to *A. vogelii* (2.21 ± 1.32 visits/tree/h; $t_{12} = 1.006$, $P = 0.045$) or to *C. macrostachyus* (0.54 ± 0.37 visits/tree/h; $t_{12} = 1.766$, $P < 0.006$).

A. noldeae was visited by 12 bird species of which four were Pollinators (Table 1). The most frequent visitor was the Northern Double-collared Sunbird, which accounted for 51 % of all visits, while the Variable Sunbird and Orange-tufted Sunbird accounted for 25 % and 18 %, respectively (Table 2).

A. vogelii was visited by 23 of the 25 bird species recorded during this study but its Pollinators were limited to the three *Cinnyris* species, of which Orange-tufted Sunbird was the most active (responsible for 41 % of all visits), plus occasional visits by the Village Weaver (Tables 1 and 2). Secondary Pollinators of *A. vogelii* included the Variable Sunbird (8 % of all visits) and Pygmy Sunbird *Anthodiaeta platura* (5 %), Village Weaver (27 %) and Common Bulbul (11 %). In addition, Robbers were common on *A. vogelii*, such that almost every flower examined had a hole pierced through the bottom of the floral tube. Robbers included Bannerman's Weaver *Ploceus bannermani*, Baglaflecht Weaver *P. baglafecht*, Speckled Mousebird and sometimes Village Weaver (Table 1).

Sixteen bird species were recorded visiting *C. macrostachyus* (Table 1). As with *A. vogelii*, the Orange-tufted Sunbird was the most frequent visitor (47 % of all visits), followed by Common Bulbul (20 %) (Tables 1 and 2). Robbers included Bannerman's Weaver, Village Weaver and Speckled Mousebird (Table 1).

There were significantly more visits in total (by all visitor species combined to all three tree species combined) during the morning observation sessions (862 visits) than the evening ones (595) (ANOVA $F_1 = 18.697$, $P < 0.001$).

Discussion

Our results illustrate that the flowers of each of the three Afromontane tree species studied in Ngel Nyaki forest are visited by a wide range of bird species with a variety of beak types, and whether or not their flowers have traits indicative of bird pollination.

Table 2. Bird visitors observed on 15 *Anthonotha noldeae,* 15 *Anthocleista vogelii* and 15 *Croton macrostachyus* during 14.6 h of observations per individual of *A. noldeae* and 6 h per individual of *A. vogelii* and *C. macrostachyus*. We include here only bird species that had cumulative visit counts > 25 across all three tree species. Means are given ± SE. OTS = Orange-tufted Sunbird; NDCS = Northern Double-collared Sunbird; VS = Variable Sunbird; PS = Pygmy Sunbird; GHS = Green-headed Sunbird; CB = Common Bulbul; VW = Village Weaver.

	OTS	NDCS	VS	PS	GHS	CB	VW
Anthonotha noldeae							
n trees visited	15	15	15	1	10	1	0
n (%) of visits to all trees	185 (17.6)	536 (50.9)	267 (25.0)	1 (0.1)	62 (5.9)	1 (0.1)	-
Mean visits/tree (n = 15)	12.3 ± 2.33	35.7 ± 4.96	17.8 ± 2.97	0.1 ± 0.06	4.1 ± 1.23	0.1 ± 0.06	-
Visitation rate (mean visits/tree/h)	0.85 ± 0.16	2.40 ± 0.33	1.20 ± 0.20	< 0.01	0.28 ± 0.08	< 0.01	-
Mean time spent in the tree per visit (min.)	1.65 ± 0.09	2.12 ± 0.07	1.50 ± 0.06	3	1.39 ± 0.12	1	-
Total number of flowers visited	2181	6872	3082	28	708	0	-
Mean flowers visited per visit	11.8 ± 0.56	12.8 ± 0.35	11.5 ± 0.46	28	11.4 ± 0.90	0	-

Anthocleista vogelii							
n trees visited	14	9	2	10	14	6	10
n (%) of visits to all trees	200 (40.7)	34 (6.9)	5 (1.0)	25 (5.1)	40 (8.1)	55 (11.2)	132 (26.9)
Mean visits/tree (n = 15)	13.3 ± 1.96	2.3 ± 0.83	0.3 ± 0.21	1.7 ± 0.45	2.7 ± 0.71	3.7 ± 2.57	8.8 ± 4.12
Visitation rate (mean visits/tree/h)	0.91 ± 0.13	0.15 ± 0.06	0.02 ± 0.01	0.11 ± 0.03	0.17 ± 0.04	0.25 ± 0.18	0.60 ± 0.28
Mean time spent in the tree per visit (min.)	1.62 ± 0.13	1.67 ± 0.33	1.14 ± 0.30	2.0 ± 0.53	1.29 ± 0.16	1.43 ± 0.19	1.95 ± 0.20
Total number of flowers visited	481	58	17	44	93	125	226
Mean flowers visited per visit	2.4 ± 0.21	1.7 ± 0.32	3.4 ± 1.40	1.8 ± 0.30	2.3 ± 0.40	2.3 ± 0.44	1.7 ± 0.25
Croton macrostachyus							
n trees visited	13	4	0	6	4	8	7
n (%) of visits to all trees	59 (47.1)	5 (4.0)	-	13 (10.4)	5 (4.0)	25 (20.0)	18 (14.4)
Mean visits/tree (n = 15)	3.9 ± 0.78	0.3 ± 0.15	-	0.9 ± 0.30	0.3 ± 0.15	1.7 ± 0.59	1.2 ± 0.41
Visitation rate (mean visits/tree/h)	0.26 ± 0.05	0.02 ± 0.01	-	0.05 ± 0.02	0.02 ± 0.01	0.11 ± 0.04	0.08 ± 0.02
Mean time spent in the tree per visit (min.)	1.49 ± 0.18	1.01 ± 0.27	-	2.09 ± 0.50	1.12 ± 0.32	3.71 ± 0.75	1.31 ± 0.20
Total number of flowers visited	70	6	0	17	9	9	4
Mean flowers visited per visit	1.2 ± 0.24	1.2 ± 0.58	–	1.3 ± 0.34	1.8 ± 0.91	0.4 ± 0.13	0.2 ± 0.12

However in each case just three *Cinnyris* species, Northern Double-collared Sunbird, Orange-tufted Sunbird and Variable Sunbird, were responsible for most pollination. It appears that sunbirds, particularly of this genus, are necessary for the pollination of *A. noldeae* and likely contribute to the pollination of *A. vogelii* and *C. macrostachyus* in montane forests of Nigeria and Cameroon.

While we found that only sunbirds behaved consistently as pollinators, and Village Weaver occasionally so, many more bird species visited flowers in a way that could effect pollination and therefore the importance of such Secondary Pollinators (*sensu* Stein 2011) cannot be discounted: they may introduce valuable redundancy into the system. Avian visitors that are less effective pollinators have been shown elsewhere to make significant contributions to seed production at times when the usual pollinators are scarce (Mayfield *et al.* 2001, Wolff *et al.* 2003). Future research to quantify pollen loads on visitors and bird movement patterns among trees will be necessary to confirm the importance of the different pollinators.

Most visitors and all Pollinators preferred to visit the “bird syndrome” flowers of *A. noldeae* rather than those of the “moth syndrome” *A. vogelii* and “insect syndrome” *C. macrostachyus*. The relative position of the stigma and anthers on *A. noldeae* is such that insects are unlikely to pollinate, and white flowers are known to attract bird polli-nators in Africa (Ley & Claßen-Bockhoff 2009). *A. noldeae* has been shown to be totally dependent on birds for outcrossed fruit set (Beavon & Chapman 2011) so its pollination mutualism with sunbirds, especially Northern Double-collared Sunbird, appears to be extremely important. However, rate of visitation does not necessarily imply pollination success (Castro & Robertson 1997, Ollerton 1998, Rivera-Marchand & Ackerman 2006). Several times during this study an individual bird spent up to 20 min. in the same *A. noldeae* crown. This type of behaviour would seem to lead to geitonogamous polli-nation (when pollen is transferred among flowers on the same plant). Future work is needed to determine the contribution of the different visitors to seed set in *A. noldeae*.

The contribution to seed set in *A. vogelii* and *C. macrostachyus* made by birds relative to insects is unknown and exclusion experiments will be necessary to determine this. However, bird visits were frequent, and Cheke & Mann 2001 reported three other species of sunbird (Collared Sunbird *Anthodiaeta. collaris*, Blue-throated Brown Sunbird *Cyanomitra cyanolaema* and Tiny Sunbird *C. minullus*) feeding on flowers of *Anthocleista* spp.. While undoubtedly these tree species have many more insect than bird visitors (K.P. Yoriyo pers. comm.), visiting taxa may vary with season and pollination by birds may be important (Cane & Payne 1993, Roubik 2001).

The fact that montane forests are threatened by increasing human population densities in Nigeria and Cameroon (Chapman & Chapman 2001, Chapman *et al*. 2004, Cheek *et al*. 2000, Maisels *et al*. 2001) puts sunbirds at risk of population decline. In order to predict the likely consequence on plant-pollinator mutualism more research is required. However our study suggests that while secondary avian pollinators may help compensate for *Cinnyris* on *A. noldeae* they are unlikely to substitute fully.

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