

— Short Communication —

AGGRESSIVE DISPLACEMENT OF CARPENTER BEES *XYLOCOPA NIGRITA* FROM FLOWERS OF *LAGENARIA SPHAERICA* (CUCURBITACEAE) BY TERRITORIAL MALE EASTERN OLIVE SUNBIRDS (*CYANOMITRA OLIVACEA*) IN TANZANIA

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Abstract— Male Eastern Olive Sunbirds (*Cyanomitra olivacea*) and *Xylocopa nigrita* carpenter bees in Tanzania both utilise the flowers of male plants of *Lagenaria sphaerica* (Cucurbitaceae) as a source of nectar. The sunbirds set up territories defending this nectar resource. Observations of interactions between the sunbirds and the carpenter bees show that the bees are aggressively displaced from flowers when spotted by the birds. Only the bees can be considered as legitimate pollinators as the birds do not contact the anthers of the male flowers and were never seen visiting nectarless female flowers of *Lagenaria sphaerica*. Such territory defence may have implications for the frequency of movement and composition of pollen being transferred from male to female flowers which warrants further research.

Keywords: Africa, Bee pollination, Birds, Mutualism, Territoriality, Tropical ecology

INTRODUCTION

Many animals are territorial and actively defend patches of habitat from individuals of the same and/or different species. The motivation for this aggression is varied and can include defence of mates and offspring, monopolisation of food resources, or combinations of these (e.g. Marler 1976). Although most pollinating animals are not strictly territorial, studies have shown that intra- and interspecific territorial aggression occurs in a wide range of flower visiting animals and that this may have implications for rates of pollen movement and reproductive success in the plants that they pollinate. Such territoriality has been observed in bees (e.g. Wirtz et al. 1988; Willmer et al. 1994; Johnson & Steiner 1994; Jürgens et al. 2009) and bats (Elmqvist et al. 1992), and there is an especially long and rich literature on hummingbirds (e.g. Stiles & Wolf 1970; Primack & Howe 1975; Stiles 1975; Boyden 1978; Carpenter 1979; Cotton 1998; Franceschinelli & Bawa 2000; Canela & Sazima 2003; Rocca & Sazima 2006; Jacobi & Antonini 2008; Lara et al. 2009).

In contrast there are relatively few published observations of such territoriality in Old World sunbirds and their relatives (Gill & Wolf 1977; Frost & Frost 1980; Akinpelu 1989; Lott & Lott 1991; Evans & Hatchwell 1992; Burd

1995; Larsson & Hemborg 1995; Symes et al. 2008; Geerts & Pauw 2009) and particularly scarce are examples of interspecific aggression, the only ones of which we are aware being Akinpelu (1989), Tropek et al. (in press) and Nuttman (unpublished data 2000) – see Conclusions. Territorial defence of floral resources can be considered a form of interference competition, as distinct from exploitative competition, both of which have been noted in bee-bird-flower systems (e.g. Hansen et al. 2002, Geerts & Pauw 2011).

During a period in the field in Tanzania we noticed that male Eastern Olive Sunbirds (*Cyanomitra olivacea* - Nectariniidae) feeding on flowers of *Lagenaria sphaerica* (Cucurbitaceae) would occasionally chase carpenter bees (*Xylocopa nigrita*) from those flowers. In this short communication we quantify the frequency of this interaction, and discuss resource use by the flower visitors and the potential negative impacts on pollination rate and seed set to *L. sphaerica*.

MATERIALS AND METHODS

Observations were made in secondary rainforest around the Amani Nature Reserve headquarters in the East Usambara Mountains, Tanzania (5° 6' 3.95" S, 38° 37' 45.26" E) between 26th July and 24th August 2011. *Lagenaria sphaerica* E. Mey. (Cucurbitaceae) is a climbing herb of forest edges with a distribution spanning Somalia to South Africa (Blundell 1987). At Amani, the plant is infrequently encountered at the edges of clearings, ponds and

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rivers, clambering up trees to a height of around 10 m. In common with many of the Cucurbitaceae the species is dioecious. We estimated the local population of *L. sphaerica* at Amani to comprise three male and three female plants within an area of approximately 2 ha; the only other plant observed was a fourth female individual some 1 km from the Amani Nature Reserve offices. The genders were spatially clustered but this was probably coincidental.

Eastern Olive Sunbirds *Cyanomitra olivacea* are resident endemics of East Africa and occur from Kenya east of the Rift Valley and southern Somalia, down to the Eastern Cape, westwards to Malawi and southeast Zambia, eastwards as far as the Tanzanian islands of Zanzibar, Pemba and Mafia (Fry & Keith 2000). They are common birds in the undergrowth and at higher levels of both mature and secondary forest, and may be encountered as individuals, in pairs, or as groups of 4 to 5 birds, with larger aggregations occurring in trees that are mass flowering. These sunbirds have a mixed diet of small fruit, invertebrates and nectar, visiting a wide range of both native and introduced species. At Amani we observed them feeding on flowers of African tulip tree *Spathodea campanulata* (Bignoniaceae), bananas *Musa* var. (Musaceae), *Thunbergia grandiflora* (Acanthaceae), *Syzygium* sp. and *Callistemon* sp. (Myrtaceae), and other species.

Male Eastern Olive Sunbirds are polygynous and territorial. Dominant individuals set up territories around plants in flower that provide sufficient nectar, aggressively displacing all other sunbirds except females who copulate with the resident male. Mated females then make nests within the male's territory (Fry & Keith 2000, Cheke et al. 2001). Birds are relatively sedentary with the longest

recovery distance of a ringed bird being only 4 km (Cheke et al. 2001).

The carpenter bees that we observed have been identified as female *Xylocopa nigrita* (Fabricius, 1775) (Apidae, Xylocopinae). A larger, reddish brown *Xylocopa* sp., observed only once, may be the male of this sexually dimorphic species. The females were only observed visiting *L. sphaerica* and a second species of Cucurbitaceae, as well as the non-native *Thunbergia grandiflora* (Acanthaceae) at Amani. We did not otherwise encounter it within the surrounding forest.

Observations of interactions between the flowers of *L. sphaerica*, Eastern Olive Sunbirds *C. olivacea* (A. Smith, 1840) and carpenter bees *Xylocopa nigrita* were carried out during daylight hours on a single, large male plant which was the most easily accessible of those that we located. We recorded the time, number of open flowers on the plant and the number of flowers foraged, as well as residence times of animals on flowers. Total observation time for the male plant was 1630 minutes over 18 days. Female plants in the vicinity were observed for flower visitors for a total of 480 minutes over 9 mornings, all between 0620 and 0915.

We also recorded the opening times of flowers and measured their dimensions. Nectar characteristics were assessed as standing crop from unbagged flowers at two time periods (0900-1000 and 1500-1600). Volume was measured using microcapillary tubes and concentration assessed using sugar refractometers (Kearns & Inouye 1993; Dafni et al. 2005). Data from the two time periods were not statistically significantly different and were therefore pooled. Statistical analyses were carried out using SPSS 17.0.

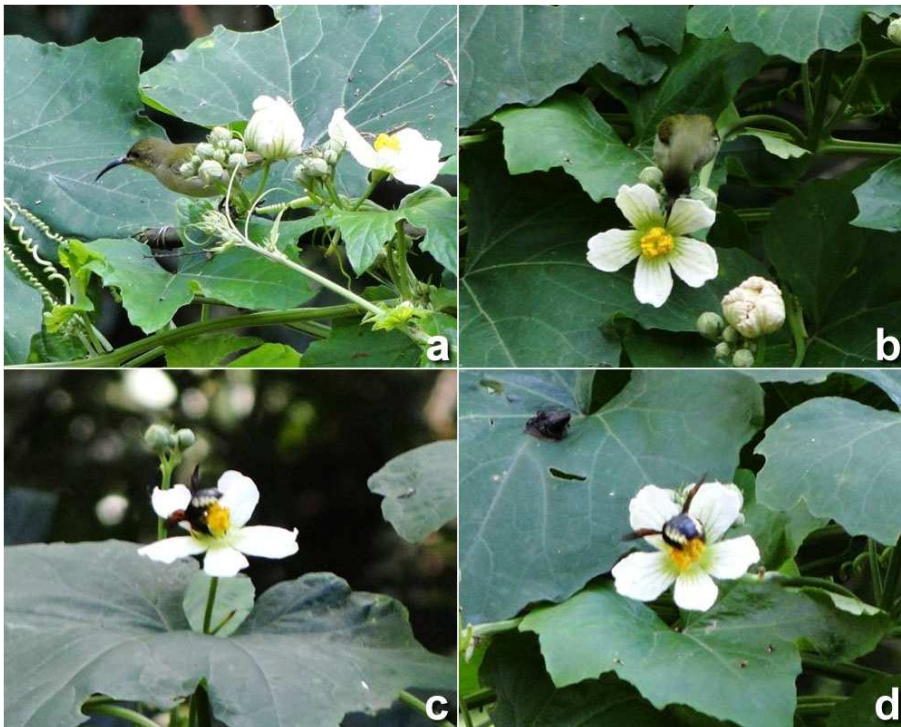


FIGURE 1: (a) Male Eastern Olive Sunbird in its territory within a patch of male *Lagenaria sphaerica*. (b) Male Eastern Olive Sunbird feeding on nectar in flowers of male *Lagenaria sphaerica*. Note that the head and body of the bird is not coming into close contact with the anther cone of the flower. (c) & (d) Female *Xylocopa nigrita* visiting flowers of a male *Lagenaria sphaerica*. Note that the underside of the body of the bee is coming into close contact with the anther cone of the flower. Photographs by Anna Rausch.



FIGURE 2 – Male (left – scale bar = 15 mm) and female (right – scale bar = 25 mm) flowers of *Lagenaria sphaerica* (Cucurbitaceae). Note the nectar chamber formed by the filament bases in male flowers; this is absent in the rewardless female flowers.

RESULTS AND DISCUSSION

Male sunbirds were observed to establish territories only around male *L. sphaerica* plants (Fig. 1a). This is explained by the fact that whilst male flowers produce significant quantities of rather concentrated nectar, female flowers do not produce nectar (Tab. 1, Fig. 2). Flower dimensions of males and females were similar, though highly variable within gender; the largest female flowers observed had much a wider corolla diameter than the largest males, though overall there was no statistically significant difference, perhaps because of the smaller sample size of female flowers (independent samples t-test for unequal variances: $t = -1.68$, $df = 8.4$, $P = 0.13$). However mean diameter of the androecium was larger than that of the gynoecium (independent samples t-test: $t = 7.37$, $df = 36$, $P < 0.001$; Tab. 1). Both male and female flowers were scented with a similar, fresh, sweet odour, though our perception was that female flower odour contained a citrusy component that was absent from the male flowers (see Ashman 2009 for a discussion of gender scent differences in dioecious species). The overall similarity of the two genders suggests that unrewarding female flowers are mimicking rewarding male flowers and relying on occasional visits by pollinators which are deceived into expecting nectar to be present. Deceit pollination by rewardless female flowers is known from other species (e.g. Bawa 1980; Willson & Agren 1989; Armstrong 1997) and may explain why female floral display was small compared to male display, as is expected in model-mimic systems (female range = 0 to 5 flowers per plant per day; male range = 12 to 36 flowers per plant per day). However during the review process one anonymous referee noted that “This is common in dioecious species since female plants need to invest more in eventually producing fruits. Common for example in *Leucadendron* in South Africa.” The small sample size and the slightly different growing conditions of male and female

plants in our study make any conclusions tentative and would require testing using a common garden experiment.

Male flowers opened in the early morning (before 0700) and closed in the early evening at dusk, then reopened once more the next day, before finally closing for good the second evening. Female flowers also opened in the early morning; in contrast, however, they always closed prior to midday and did not reopen.

Nectar in male flowers was exploited by a diversity of flower visitors of varying abundance (Tab. 2). The most common flower visitors were female carpenter bees (*Xylocopa nigrita* – Figs. 1c and d) followed by Eastern Olive Sunbirds (*Cyanomitra olivacea* - Figs. 1a and b) who collectively accounted for over 87% of all visits. The only observed visitor to a female flower was a single female individual of *Xylocopa nigrita* (Tab. 2). The remainder of this paper will focus on these two most abundant flower visitors.

Both *Cyanomitra* sunbirds and *Xylocopa* bees actively visited male flowers throughout the day (Fig. 3). If average visitation rates during four time periods (0700-0959; 1000-1259; 1300-1559; 1600-1859) are considered, average flower visitation across the day was relatively constant in sunbirds (Kruskal Wallis Test, $\chi^2 = 2.3$, $df = 3$, $P = 0.52$), whilst *Xylocopa* foraging was significantly higher in the morning (Kruskal Wallis Test, $\chi^2 = 16.9$, $df = 3$, $P = 0.001$). The two most frequent visitors also differed in their residence times on flowers, carpenter bees spending on average more than 60% longer than sunbirds (2.9 ± 1.1 s versus 1.8 ± 0.9 s; independent samples t-test: $t = -3.1$, $df = 31$, $P = 0.004$). During five-minute foraging bouts, *Xylocopa* individuals on average visited more flowers than sunbirds (10.7 versus 7.3 flowers per 5 minutes; two sample t test: $t = 2.9$, $df = 179$, $P = 0.004$).

TABLE 1: Flower sizes and nectar characteristics of male and female flowers of *Lagenaria sphaerica*. Samples sizes (number of flowers assessed) are given in brackets.

	Corolla diameter (mm)		Androecium/gynoecium diameter (mm)		Nectar volume (μ l)	Nectar concentration (%)
	Mean \pm SD	Range	Mean \pm SD	Range	Mean \pm SD	Mean \pm SD
Male	70.1 \pm 5.5 (29)	60 – 79	16.2 \pm 1.7	14 – 22	0.63 \pm 0.46 (22)	42.4 \pm 4.1 (20)
Female	82.9 \pm 21.3 (9)	55 – 115	11.5 \pm 1.7	9 – 14	0.0 (9)	-

	Male flowers	Female flowers
Carpenter bees (<i>Xylocopa nigrita</i>)	69.4	100
Eastern Olive Sunbirds (<i>Cyanomitra olivacea</i>)	18.1	0
Other bees (including some different <i>Xylocopa</i> spp.)	6.9	0
Lepidoptera (including Hesperidae)	3.2	0
Other insects	2.4	0
Total number of animals observed	216	1

TABLE 2: Proportional (%) abundance of the different visitors to male and female flowers of *Lagenaria sphaerica*

The sunbirds and the carpenter bees interacted aggressively throughout the day (Fig. 3) but at a low frequency: of 134 *Xylocopa* foraging bouts observed, only 21 (almost 16%) resulted in aggressive behaviour by sunbirds. In all cases the birds chased the bees from flowers and actively pursued them into the forest; the sound of their beaks striking the bees' bodies could sometimes be heard. Intraspecific aggression was less common; female bees chased female bees only twice, whilst the one observation of a putative male *Xylocopa nigrita* resulted in it being chased off by two female bees that were foraging in the same patch. The male sunbird was aggressive to another male twice in 49 foraging bouts (i.e. just over 4% of observations). Other birds and mammals that entered the sunbird's territory but did not feed on the *Lagenaria* flowers (e.g. Green Barbet *Stactolaema olivacea*, Square Tailed Drongo *Dicrurus ludwigii*, bush squirrel *Paraxerus* sp.) were ignored.

Although we did not explicitly test for pollinator effectiveness we are confident that the most important pollinators of *Lagenaria sphaerica* during our period of

observation at this site were the female *Xylocopa* bees. We draw this conclusion because: (1) bee visitation rate to male flowers was more than three times that of the sunbirds (Tab. 2); (2) when visiting male flowers, sunbirds appear to pick up little or no pollen on their bill or feathers, due to their long bills probing beneath the position of pollen release from the anthers (see Figs. 1 and 2) compared to the bees which grasp the androecium firmly with their legs and pick up pollen on their ventral surface (Figs. 1b, c and d); see also Janeček et al. (2007) for another very similar example; (3) crucially, bees are the only visitors to be observed on female flowers. The territoriality of the male sunbirds makes it unlikely that they would visit the female flowers and the very occasional visits by *Xylocopa* bees are probably by individuals moving between other nectar sources and testing these flowers to check if they contain nectar or pollen (though no obvious pollen collecting behaviour was observed by these bees on *L. sphaerica*).

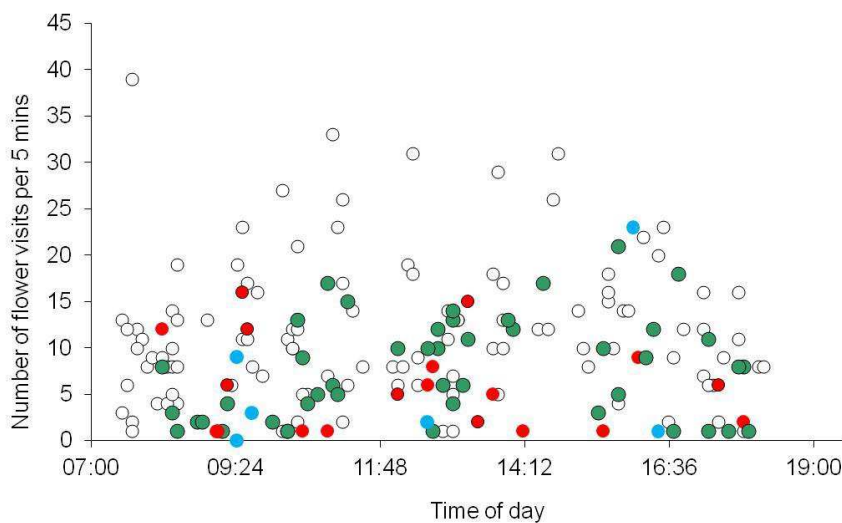


FIGURE 3: Rate of visitation to male *Lagenaria sphaerica* flowers by Eastern Olive Sunbirds (green markers) and carpenter bees (white markers). Intraspecific aggressive interactions between bees are coloured blue. Interspecific aggressive interactions between birds and bees are coloured red and have a nominal value of 1 when bees were chased away by birds before they could land on a flower. Where markers with different colours overlapped completely they have been slightly offset. Note that periods with zero visitation have been removed from the graph to aid interpretation but are included within the statistical analyses (see text).

Future work on this system should include pollinator exclusion and pollen addition experiments that specifically test for the effectiveness of these different flower visitors. A number of recent studies have demonstrated that plants with apparently mixed bird-bee pollination systems are in fact functionally specialized for bee pollination (e.g. Janeček et al. 2007, Watts et al. 2012, Padyšáková et al. 2013). However more such studies are required to assess the generality of these findings.

CONCLUSIONS

Only three other studies that we are aware of have noted interactions between sunbirds and bees on flower patches, but with conflicting results. In Nigeria, Akinpelu (1989) showed that honeybees (*Apis mellifera*) displace Western Olive Sunbirds (*Cyanomitra obscura* syn. *Nectarina olivacea*) from flowers of *Tecoma stans* (Bignoniaceae). However it is unclear whether these were male birds defending territories. In contrast, Nuttman (unpublished data 2000) observed aggressive interactions between Palestine Sunbirds (*Nectarinia osea*) and *Xylocopa pubescens*. The birds defended flowers of an *Erythrina* sp. (Fabaceae) and drove away bees that tried to access floral resources, as was found in our present study. Finally Tropek (in press) recently documented observations of *Cynniris* spp. sunbirds attacking *Xylocopa* spp. carpenter bees in patches of *Hypoestes aristata* (Acanthaceae) in Cameroon, with striking parallels to the present study. It seems likely that this phenomenon is widespread but unreported in the Old World.

Territorial defence of flowers by sunbirds may affect the frequency of movement of pollinators and the composition of pollen (in terms of paternal genotypes) that they carry. This could be particularly significant for dioecious species such as *L. sphaerica* in which the female flowers are unrewarding mimics of the males. If the male sunbirds are indirectly improving the likelihood of female flowers being pollinated by chasing away pollinators from male flowers and forcing them to explore the unrewarding female flowers, they could be engaging in a mutualistic relationship with *L. sphaerica* despite being ineffective pollinators. This would be an interesting question to follow up and warrants further research.

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The framework of this short paper was written at Emau Hill Campsite on Sunday 14th August 2011. Accompanying the trill and cry of the local bird fauna was the constant whine of a chain saw and the occasional crash of another falling tree as land is cleared for a sugar field or *shamba*. The East Usambaras are an area of incredible, unique biodiversity. But they have been, and continue to be, changed faster than they can be conserved or studied. People require food and food production needs land. But people also require the forest for a range of ecosystem services. Conservation of the whole of the Eastern Arc Mountains, including the East Usambaras, should be a Tanzanian (indeed an African) priority and needs to be carefully balanced against the requirements of local people who need the forest as well as land for crops. We say *asante sana* to the people of the East Usambaras for their warmth and hospitality, in the sincere hope that they can achieve such a balance. Thanks also to the staff and students of the Amani 2011 Tropical

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