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SHORT COMMUNICATION

Pollen movement by the bat *Artibeus jamaicensis* (Chiroptera) in an agricultural landscape in the Yucatan Peninsula, Mexico

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Abstract *Artibeus jamaicensis* is a medium-sized frugivorous microchiropteran bat that complements its diet with nectar and pollen during the dry season. We investigated which species of pollen are carried by *A. jamaicensis* in order to determine its potential role as a plant pollinator in the northern Yucatan Peninsula. We collected pollen from the fur of 192 individuals throughout the year from April 2004 to March 2005. We recorded pollen from nine plant species of eight families and found five unidentified pollen types, with the highest pollen species richness recorded in June. *A. jamaicensis* moved pollen of *Erythrina standleyana* and *Mimosa bahamensis*, which have not hitherto been reported as visited by this species. The most abundant pollen in the samples was found to be that of three tree species: *Ceiba pentandra*, *C. aesculifolia* and *Lysiloma latisiliquum.* Very few samples contained pollen in the rainy season, when the bats fed mainly on fruits. *A. jamaicensis* can fly several kilometres among foraging locations and dispersed large amounts of pollen from tree species growing near cenotes as well as those not present at cenotes but occurring in other forest fragments, highlighting its importance as a pollen vector among forest fragments in the largely deforested landscape of the Yucatan Peninsula, helping to reduce the negative effects of forest fragmentation. *Ceiba* appears to benefit from the role of *A. jamaicensis* as a pollen vector, and the species play an important ecological role in the Yucatán landscape, supplying shade, nectar and fruit for wildlife.

Keywords *Ceiba pentandra* · Cenotes · Chiroptera · Pastureland · Pollinator

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Tropical deforestation is one of the most important environmental threats of our time, causing habitat degradation and species extinction and contributing to global climate change (Vance and Geoghegan 2002). Animals that displace genetic material contained within pollen or seeds within fragmented landscapes can help to reduce the negative effects of forest fragmentation (Young et al. 1996). Plants and animals have both evolved a series of morphological, physiological and behavioural adaptations in order to facilitate dissemination of their genetic resources. Examples of these adaptations occur in phyllostomid bats within the subfamily Glossophaginae, which are adapted to nectar feeding and pollen movement (Fleming et al. 2009; Muchhala and Thomson 2010; Tschapka and Dressler 2002). However, bat visitors to flowers are not restricted to glossophaginaes, since some dietary generalists (e.g. the omnivorous *Phyllostomus discolor*, Lobo et al. 2005) or even insectivorous bats (e.g. *Antrozous pallidus*, Frick et al. 2014) supplement their diets with nectar and pollen as sources of water, calcium, protein and energy.

While studying the vegetation around cenotes (water-filled sinkholes formed by the dissolution of limestone) as a food source for frugivorous and nectarivorous bats, we observed some individuals of the Jamaican fruit bat *Artibeus jamaicensis* Leach with pollen coating their fur. This species is known to feed on a variety of plant resources, including mainly fruits and also flowers, leaves, pollen, nectar and occasionally insects or small vertebrates (Ortega and Castro-Arellano 2001; Ruiz-Velásquez et al. 2014). In particular, the role of *A. jamaicensis* as a seed disperser is well established, with records of consumption and seed dispersion in nearly 190 plant species from 43 families (Lobova et al. 2009). In contrast, the role of this species as a pollen vector is poorly known. The aim of this study was to investigate the species of pollen carried by *A. jamaicensis* in order to determine its potential role as a pollinator of trees in the fragmented remnant forest patches found within the extensive pastureland of the Yucatan Peninsula.

We sampled bats at two cenotes 3.5 km apart in Buctzotz County, Yucatan, Mexico, located approximately 100 km east of the capital Mérida. This county is almost entirely comprised by cattle ranches, with nearly 90% of the original forest now converted to pastureland (INEGI 2009). The dry season extends from November to April and the wet season from May to October. Cenote Azul (21° 13′ N, 88° 40′ W) and Cenote Buenavista (N 21° 11′ N, 88° 40′ W) are about 40–60 m in diameter with a 10–50-m-wide surrounding belt of vegetation. The predominant tree species are *Ficus cotinifolia* Kunth., *F. padifolia* Kunth., *F. tecolutensis* Miq. (Moraceae), *Piscidia piscipula* (L.) Sarg., *Lysiloma latisiliquum* (L.) Benth (Fabaceae), *Metopium brownei* (Jacq.) Urb. (Anacardiaceae), *Manilkara zapota* (L.) van Royen (Sapotaceae), *Vitex gaumeri* Greenman (Lamiaceae), *Bursera simaruba* (L.) Sarg. (Burseraceae) and *Gymnopodium floribundum* Rolfe (Polygonaceae). Keys were used to identify plant species (Pennington and Sarukhán 1998; Standley et al. 1946–1977), as well as consulting botanical specialists from the herbarium "Alfredo Barrera Marín" at the Autonomous University of Yucatan (UADY). Flowers were collected in order to establish a reference collection for comparison with the pollen recovered from bats. Plant vouchers were deposited at the herbarium.

Each site was sampled for two nights per month from April 2004 to March 2005. On each sampling night, four 12 × 2.6-m mist nets (AFO Mist Nets, Manomet, Inc.) were erected at ground level (0–3 m), in the vegetation that surrounds the cenotes. Nets were set at sunset, left open for an average of 7 h and monitored every 30 min. Bats were identified to species, measured and then released at the capture site. Due to the similarity in vegetation composition and bat species richness and abundance between sites, the data from both sites were pooled. Prior to initiation of trapping, a collecting permit was obtained from the Secretaría del Medio Ambiente y Recursos Naturales, Mexico (No. 02809).

We used a fine brush dipped in distilled water to collect pollen from the heads and bodies of a sample of 16 *A. jamaicensis* individuals per month. Pollen was stored in Eppendorf tubes containing 70% ethyl alcohol. A separate brush was used for each individual in order to avoid sample contamination. Samples were prepared according to the acetolysis method described by Erdtman (1960) and analysed with an Olympus Model Bx41 microscope (Olympus America Inc.). We used keys (Palacios-Chávez et al. 1991) and comparison with a palynological reference collection of flowers from our study sites and from other sites in the Yucatan in order to identify the pollen collected from captured bats. For samples with abundant pollen, we identified a maximum of 300 grains (Loveaux et al. 1978). We confirmed the presence of a pollen type when three or more grains were recorded in a sample (Heithaus et al. 1975). The most common pollen always accounted for more than 80% of the pollen grains in the sample (Lobo et al. 2003). Faecal samples were collected all year for a study of seed dispersal, but only the samples taken in January were analysed microscopically since these showed evidence of pollen content.

A total of 192 samples were taken from the fur of *A. jamaicensis*, 41 of which (21.3%) contained pollen. Eight families, nine species and five unidentified pollen types were recorded (Table 1). The highest pollen species richness was recorded in June, whereas the highest number of samples containing pollen was recorded in January (Fig. 1). Only one sample contained pollen during July and October whereas samples in August and November contained no pollen grains. Individuals of *A. jamaicensis* carried from one to four different pollen species. Three pollen species were most abundant in the samples: *C. pentandra*, *C. aesculifolia* and *L. latisiliquum* (Table 1). *A. jamaicensis* carried pollen of six plant families during the dry season. Very few samples contained pollen in the rainy season, when the bats fed mainly on fruits.

Fruits of *Ficus* trees were the main food resource for *A. jamaicensis* at our study sites. In January, however, only 7% (n = 68) of the *Ficus* trees around cenotes had fruits and most of these were immature and not typically eaten by frugivores (Korine and Kalko 2005). In contrast, the flowering period of *C. pentandra* was at its peak and *A. jamaicensis* almost exclusively consumed the pollen and nectar of this species. *C. pentandra* exhibits a massive production of flowers ("big bang" type according to Gentry 1974), which are pollinated in the Neotropics mainly by *Glossophaga soricina* and generalist bats like *P. discolor* (Lobo et al. 2005) and in the Paleotropics by *Eonycteris spelaea* (Bumrungsri et al. 2013). While we captured other species with pollen on their fur in the northern Yucatan, including *G. soricina* Pallas (n = 1), *Artibeus lituratus* Olfers (n = 1) and *A. phaeotis* (n = 2) Miller, the number of individuals encountered was very low in comparison to *A. jamaicensis* (n = 31). This suggests that *A. jamaicensis* may be the main bat pollinator of *C. pentandra* in the Yucatan.

Another pollen species found on the fur of *A. jamaicensis* but unrecorded in the vegetation surrounding the cenotes was

Table 1 Plant species whose pollen was found on the fur of *Artibeus jamaicensis* in the Yucatan Peninsula, Mexico, during April 2004 to March 2005. The matrix shows the number of samples in which the species was present/number of samples where the same species accounted for more than 80% of the pollen collected. Samples in August and November did not contain pollen

Family and species of visited plants	Apr	May	Jun	Jul	Sep	Oct	Dec	Jan	Feb	Mar
Agavaceae										
Agave fourcroydes Lem.							2/1	2/0		
Burseraceae										
Bursera simaruba (L.) Sarg.	1/0	2/1								
Cactaceae										
Hylocereus undatus (Haw.) Britton and Rose			2/1							
Fabaceae										
Erythrina standleyana Krukoff					1/1	1/1				
Lysiloma latisiliquum (L.) Benth.	1/0	4/3	2/1							
Mimosa bahamensis Benth.					1/1					
Malvaceae										
Ceiba aesculifolia (Kunth.) Britton and Rose	5/5	1/1	1/1							
Ceiba pentandra (L.) Gaertn.								12/12	1/1	1/1
Moraceae										
Maclura tinctoria (L.) D. Donn. ex Steud.			4/3							
Sapindaceae							3/3			
Vitaceae							3/2			
Unidentified pollen types										
Type 1			2/1							
Type 2				1/1						
Type 3							1/0			
Type 4								2/0		
Type 5									1/1	

C. aesculifolia. The nearest individuals of this tree were about 3 km away from the cenotes (B. Bolívar-Cimé, pers. Obs.). In

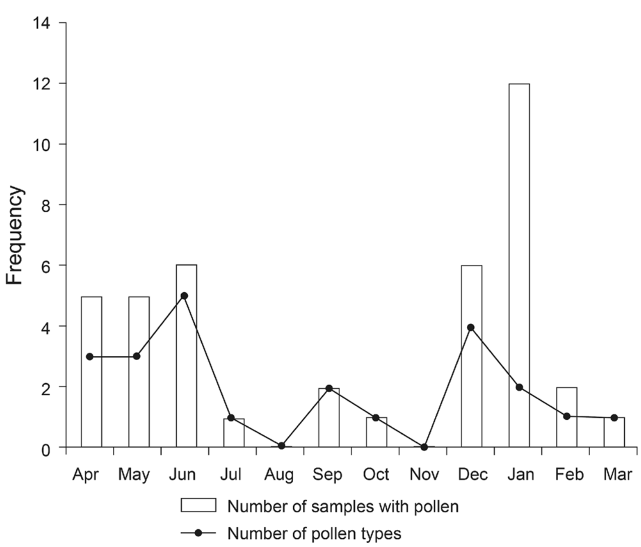

Fig. 1 Number of samples with pollen and species richness of plants whose pollen was carried by *Artibeus jamaicensis* in the Yucatan Peninsula, Mexico, during April 2004 to March 2005

Costa Rica, *A. jamaicensis* has been recorded carrying pollen of *C. aesculifolia* for distances greater than 1 km from known trees (Heithaus et al. 1975), while other authors have established that *A. jamaicensis* can fly up to 8 km per night in search of foraging locations (Morrison 1978). This is crucial for outcrossing tree species such as *C. aesculifolia*, which depends on pollinators for fertilization and fruit production (Herrerías-Diego et al. 2006).

Pollen of the Henequén agave *(Agave fourcroydes)* was found on the fur of *A. jamaicensis*. This plant species was not recorded in the vegetation belt surrounding cenotes but was present as abandoned cultivars in secondary growth fragments in the study area. Henequén is cultivated for its fibre and was domesticated during the pre-Hispanic Maya culture in the Yucatan Peninsula. During the nineteenth and twentieth century, cultivation of this plant was extensive in northern Yucatan but decreased considerably after the development of synthetic fibres. Agricultural practices that involved the removal of agave inflorescences and relied solely on vegetative propagation led to an accelerated loss of genetic diversity for *A. fourcroydes* in the Yucatan (Colunga-GarcíaMarín et al. 1999). The gene flow that now takes place is largely confined to wild populations of agaves, and the role of bats such as *A. jamaicensis* as pollen vector is likely to be important in conserving the genetic diversity of this species in the Yucatan.

One of our most significant findings was that *A. jamaicensis* dispersed pollen from plants that have not hitherto been reported as visited by this species during flowering periods. One plant, *Erythrina standleyana,* has tubular, pink flowers with diurnal anthesis and nectar with sugar ratios that correspond to those of plants pollinated by hummingbirds (Baker and Baker 1990). In our study site, *E. standleyana* pollen was found on the fur of *A. jamaicensis* during September and October in a small number of samples. However, a different study in the Yucatan Peninsula, carried out after the present study, found this species in a higher number of samples taken from the fur of *A. jamaicensis* and *G. soricina* in October, November, February and March (Tzab-Hernández 2012). *E. standleyana* thus seems to be a resource readily used by bats during the dry season in the north of the Yucatan Peninsula. The second species found in *A. jamaicensis* fur was *Mimosa bahamensis*, which was not recorded in the vegetation surrounding cenotes. While the genus is predominantly entomophilous, some species such as *M. lewisii* have been recorded as pollinated by bats (Vogel et al. 2005). Whether this dispersion of *Erythrina* and *Mimosa* pollen by *A. jamaicensis* is incidental, the result of bat pollination requires further investigation, since the flowers of some plants that are actually pollinated by bats do not conform to the classic “bat pollination syndrome” (Fleming et al. 2009). To our findings of the pollen of nine species and five unidentified pollen types, Tzab-Hernández (2012) adds *Crescentia cujete* as another species for which *A. jamaicensis* disperses pollen in the dry forests of the Yucatan Peninsula.

A. jamaicensis is mainly a frugivore but uses nectar and pollen to complement its diet, particularly during the dry season and thereby acts as the pollinator of many plants. Our results show that a single *A. jamaicensis* can visit up to four plant species in one night. A recent study has demonstrated that by placing pollen on different parts of the body of the bat (e.g. head, chest or wings), plant species can limit heterospecific pollen movement and reduce competition among bat-pollinated plant species that share a common pollinator (Stewart and Dudash 2015). *A. jamaicensis* is one of the most abundant and common bat species in the Neotropics; it tolerates disturbed areas and can be observed commuting and foraging in urban settings. In these modified habitats, this bat has the potential to replace disturbance-sensitive pollinator species; however, its role as a pollinator remains poorly understood and requires further investigation.

In the Yucatan Peninsula, cenotes and their heterogeneous vegetation attract many nectarivorous and frugivorous bats that use these habitats to roost and feed (Bolívar-Cimé et al. 2013; MacSwiney et al. 2007). Our results demonstrate that in the deforested agricultural landscape of the Yucatan, *A. jamaicensis* can move pollen from plant species that occur at the cenotes as well as those that are absent from there (i.e. *C. aesculifolia*, *A. fourcroydes, M. bahamensis*) but located in other, more distant forest fragments. The vegetation around cenotes, especially those derived from agriculture, must be conserved since it facilitates the movement of bats across deforested landscapes and promotes the movement of pollen from many Neotropical plants.

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