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ARTÍCULO DE INVESTIGACIÓN/RESEARCH ARTICLE

DIFFERENTIAL FRUIT CHOICE IN TWO SIMPATRIC MONKEY SPECIES AND FRUGIVOROUS BATS IN SOUTHERN MEXICO

Elección diferencial de frutos en dos especies simpátricas de monos y murciélagos frugívoros en el sureste de México

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ABSTRACT

In order to identify the role played by plant species as a food source in the fruit election of dispersing agents (*Alouatta pigra* Lawrence 1933*, Ateles geoffroyi* Kuhl 1820 and frugivorous bats), we developed a study in dry tropical forests in Yucatan, Mexico. We recorded the fruits consumed by frugivorous bats using collectors and, for monkeys, we implemented the focal animal method. The number of fruits consumed by primates (*A. pigra* and *A. geoffroyi*) and bats were recorded, 342 and 386, respectively. It was determined that bats deposited fruits with some percentage of pulp, while monkeys contributed more with a fruits without pulp (pairwise LSD contrast *p* < 0.05). Among the variety of fruit species in the diet of primates, we detected that *A. pigra* chose mostly not an abundant species such as *Enterolobium cyclocarpum* Jacq. Griseb. (1860) instead of those more abundant (*Manilkara zapota* (L.) P. Royen (1953) and *Brosimum alicastrum* Sw. subsp. *alicastrum* C.C. Berg (1972)). The type of fruit and seed handling caused by primates would be more beneficial to seed germination than those applied by bats. Moreover, this election and fruit handling could depend on the characteristics of fruits and space-temporal availability of plant species as a food source.

Keywords: *Alouatta pigra*, *Ateles geoffroyi*, seed handling, tree species, Yucatan.

RESUMEN

Con el objetivo de examinar el papel que juegan las especies vegetales como fuentes alimenticias en la selección de frutos de agentes dispersores (*Alouatta pigra, Ateles geoffroyi* y murciélagos frugívoros), se realizó un estudio en selvas secas en el sureste de Yucatán, México. Se registraron los frutos consumidos por murciélagos usando colectores y, en el caso de los monos, se implementó el método de animal focal. El número de frutos consumidos registrados para ambas especies de primates y murciélagos fueron 342 y 386, respectivamente. Se determinó que los murciélagos depositaron frutos con pequeñas cantidades de pulpa, mientras que los monos contribuyeron mayormente con frutos totalmente despulpados (contrastes por pares LSD *p* < 0.05). Entre la variedad de especies de frutos en la dieta de los primates se detectó que *A. pigra* eligió frutos de las especies menos abundantes como *Enterolobium cyclocarpum* Jacq. Griseb. (1860) en vez de aquellas más abundantes (*Manilkara zapota* (L.) P. Royen (1953) y *Brosimum alicastrum* Sw. subsp. *alicastrum* C.C. Berg (1972)). El tipo de manejo de frutos y semillas causado por los primates sería más beneficioso para la germinación de las semillas que los aplicados por los murciélagos. Además, esta elección y manejo del fruto podría depender de sus características y la disponibilidad espacio-temporal de las especies de plantas como fuente de alimento.

Palabras clave: *Alouatta pigra*, *Ateles geoffroyi*, manipulación de la semilla, especies arbóreas, Yucatán.

INTRODUCTION

Frugivory is a mutualistic ecological relationship, which is an important element of natural interactions in tropical areas around the earth (Fleming, 1988). Through frugivory, the plants have been related to groups of visitors that change over space and time. This relationship has originated a diffuse coevolution process, where the involved organisms have suffered a mutual specialization process and even some of them alter their population dynamics (Jordano, 2000).

Mammals, such as bats and primates, present morphological, physiological and behavioral specializations to locate, consume and digest food, while plants have phenological, morphological and physiological differences to attract and satisfy the seed dispersing agents (Fleming, 1988).

Mammals do not consume fruits randomly; it has been observed that the fruit selection is determined by intrinsic and extrinsic factors (anatomical and physiological characteristics) that affect the animal behavior directly (Fleming, 1988). With regard to the bats, they prefer to consume mature and big fruits with high visual exposition and with small seeds of strong odor. These attributes facilitate localization and consumption of fruits and are called chiropterocory syndrome (Jordano, 2000).

Primates tend to be highly selective in their diets; there is vast information about what a primate takes into account when choosing its food (McConkey and Chivers, 2007; Amato and Garber, 2014). It has been proposed that there are features that influence the food choice, such as the environmental and social conditions, as well as internal factors as: digestive system type, nutritional necessities depending on age, sex, physiological condition and energetic costs. The fruit physical characteristics as color, size, weight and type of seed, are considered as clues employed by primates to define whether a food is consumable or not (Dominy, 2004). Some studies suggest that the fruit color is the most important morphological and/or chemical feature (Howe and Miriti, 2004). Nevertheless, distinct plant and fruit species consumed are not different in color and structure, so the animals also use their other senses to evaluate the potential food (Dominy, 2004).

Bats as well as primates present similarities when choosing their food. However, we have to consider that during foraging, the time for search, handling and ingestion is included and it is relevant that in most of the studies the time consumed does not consider how much the individuals are really ingesting. This is so because of the handling given to each of the different plant parts, each of which requires a specific handling (Lambert et al., 2004). It has been determined that a good foraging efficiency depends on the individual's capacity for recognizing the condition of a given food (Dominy, 2004). Linked to the previous idea, it is suggested that the optimal foraging theory is based on three sections: costs, rewards and constraints. The costs are related to the time and energy spent in obtaining food, the reward is the nutrient gain and the constraints are the limiting factors that increase costs or reduce rewards (Stephens and Krebs, 1986). Such theory is the basis for determining what really influences the animal food selection.

Several studies have analyzed the manipulation of fruit by monkeys in Mexican tropical forests (Chaves et al., 2011; Benítez-Malvido et al., 2014); however, a few of them have studied the fruit choice simultaneously among primates and bats, even considering fruit and seed handling in the association with any particular plant species. The present study is focused on the fruit election of three dispersing agents (primates, A. geoffroyi and A. pigra and frugivorous bats). Three fruit election predictions and the fruit handling associated with frugivorous species were established: 1) based on the foraging behavior of each frugivorous species (Stephens and Krebs, 1986), it would be expected that undamaged fruits and spat-out seeds would be mainly generated by monkeys than by bats and inversely with the dropped bitten fruits. 2) In the absence of fruit that usually eat these dispersors, the main fruit handling associations found would depend of the easiness to eat the fruit (Dominy, 2004). 3) In case dominant plant species are present like Brosimum alicastrum and M. zapota, we would predict a high consumption of those species by the three frugivorous species, with a larger tendency of the bats towards M. zapota owing to the pulp softness (Lambert, 2002), and without expecting any difference between these fruit species for monkeys because of their jaws features (Di Fiore et al., 2008).

MATERIALS AND METHODS

The study was performed in two tropical forest sites: for bats, it was carried out in a deciduous tropical forest within the Environmental Management Unit of Telchac, Puerto Yucatán (16°11' – 42'S, 68°53' – 55'W) during May, 2013; for monkeys, it was carried out within the "Otoch Ma'ax Yetel Kooh" Flora and Fauna Protection Area (20° 38' N, 87° 37' W) (20° 38' N, 87° 37' W) during October, 2013. Different sampling sites were established to avoid the dependent effects of dispersing agents, for the outstanding presence of them in each place.

Sample design

To evaluate the fruit election of the bats, 12 trees of Ehretia tinifolia L were systematically selected (with previous identification of roost sites for bats) in the forest; the sampled trees were separated 10 m from each other. Four 1 m^2 collectors, 1 m high from floor level, were placed for each tree (total n = 96). Each collector was placed for inspection since 0700 to 1900 h, during two days. To evaluate the fruit election of the monkeys, five transects of 150 m, separated by 100 m were systematically selected and during five continuous days, we recorded the fruit election of each primate every time that was feeding. In addition to the transects we used the focal animal sampling method only

on adult monkeys; we decided to use both methods in order to avoid confusion to follow another monkey different from the focal one. Each transect was marked with biodegradable flagging tape which avoided confusing trees of different transect. Once the group of monkeys was located (*A. pigra* or *A. geoffroyi*) in the trees, a 2 m² quadrant was charted around the parental tree, then fruits, seeds and faeces produced by monkeys during the observation were collected immediately to avoid contamination; this procedure was carried out during seven continuous days. Samples were placed in plastic bags for transport to the laboratory where they were processed upon arrival. Each sample was washed with water from the tap and a sieve with holes of approximately 0.5 mm in diameter was used.

Fruit and seed handling categorization
We recognized three categories of seed handling in bats and primates: 1) undamaged fruit ("Uf") – intact fruit dropped under the parental tree; 2) dropped bitten fruit ("Dbf") – when monkeys ingest–only part of the fruit pulp and drop it under the parental tree; and 3) spat-out ("Sot") – when monkeys eat the fruit pulp or aril and spit out the seeds under the parental tree while eating. The whole assignment of category was based on visual characteristics. Finally, as the fruit species were not the same on both sites, we performed statistical analyses separately.

Data analysis
To evaluate if seed handling differed between bat and monkey species, we used generalized linear models- GLM (McCullagh and Nelder, 1989; Crawley, 1993). We estimated the proportion of records belonging to each category of seed handling per animal species, considering parental tree and collector as replicates within each animal species. Due to different seed handling occurred within each animal species, we nested seed handling within animal species, with the whole model being: PROPORTION OF RECORDS = SEED HANDLING + ANIMAL SPECIES + SEED HANDLING nested within ANIMAL SPECIES. Data of proportion were first transformed with arcsine of the square root, and tested for a normal distribution with a Shapiro-Wilk and Kolmogorov-Smirnoff tests (passed, $p > 0.05$). We then selected Normal distribution with an Identity link-function to the response variable. To identify which seed handling categories were statistically different among each other, we used post-hoc analyses with contrast (LSD; Least Significant Difference; Crawley, 1993). The analyses were run in SPSS 22.

The relationships among bats, monkeys and fruit species were assessed separately because the study sites were different in most of fruit species. Only common fruit species in both study sites such as *B. alicastrum* and *M. zapota* were analyzed together. To evaluate the relationship between seed handling and fruit species in bats, we ran a Canonical Correspondence Analysis- CCA (Legendre and Legendre,

1998). To test the relationship between seed handling and monkeys to fruit species, we used a Redundancy Analysis-RDA (Legendre and Legendre, 1998). To analyze the relationship among bats, monkeys and seed handling to fruit species, we ran an RDA also. Previous to run the analyses, we calculated the length of the gradient (ter Braak and Smilauer, 2002) of each matrix of fruit species, in all cases by Detrended Correspondence Analysis (DCA; Hill, 1979). In all cases, the statistical significance of each seed handling category as well of the four axes, were tested within the forward selection procedure using a Monte Carlo random permutation test (999 permutations, $p \leq 0.05$). The analyses were run using Canoco 4.5.

RESULTS

Fruit choice
We recorded in total 17 feces samples, twelve from four subgroups of *A. geoffroyi* and five from two groups of *A. pigra* during our study. Regarding the monkey's diet, we obtained 342 fruits belonging to six species: *B. alicastrum*, *Ficus cotinifolia* Kunth, *Ficus ovalis* (Liebm.) Miq., *M. zapota*, *Spondias purpurea* L. (1762) and *E. cyclocarpum* from the Moraceae, Zapotaceae, Anacardiaceae, and Fabaceae. With regard to bats, 386 fruits belonging to nine families were collected: Moraceae, Malpighiaceae, Poligonaceae, Boraginaceae, Solanaceae, Sapotaceae, Anacardiaceae, Combretaceae and Sapindaceae; and eleven species *B. alicastrum*, *Ficus benjamina* L., *Byrsonima crassifolia* L. Kunth (1822), *Coccoloba uvifera* L. (1759), *Cordia sebestena* L., *Solanum hirtum* Vahl, *M. zapota*, *S. purpurea*, *Talisia olivaeformis* (H.B.K.) Radlk and *Terminalia catappa* L. (Table 1).

All animal species showed differential fruit election records on three seed handling categories (Fig. 1). The proportion of feeding records differed significantly among primates and bats (χ^2 Wald = 66.9, df = 2, $p < 0.0001$). Black howler monkeys had a higher proportion of undamaged fruit records than spider monkeys as well as with bats (pairwise LSD contrast $p < 0.05$). A similar result was found in spat-out seed, although we only found significant differences between primate species and bats (pairwise LSD contrast $p < 0.05$) (Fig. 1). In contrast, dropped bitten fruit showed a higher proportion of records in bats than in both monkey species (pairwise LSD contrast $p < 0.05$; Table 1). On the other hand, we found not significant differences among the categories of seed handling nested within each primate species and bats (χ^2 Wald = 6.0, df = 4, $p > 0.1$), however, post-hoc test uncovered that the proportion of dropped bitten fruit was larger than the undamaged fruit and spat-out seeds among bats (Fig. 1).
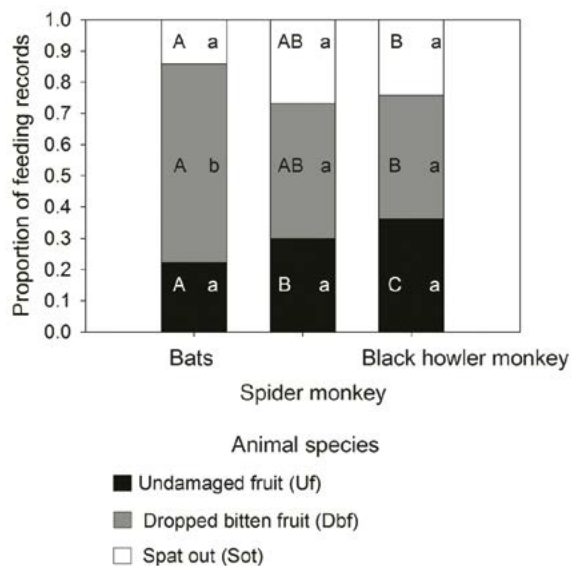
Seed handling
The relations among seed handling and bats were analyzed. The CCA triplot showed a fruit species separation on the

Table 1. Seed handling of bats and monkeys.

Plant species	Family	N	% Seed handling (no.)		
			Spat out	Dropped bitten fruit	Undamaged fruit
Bats					
B. alicastrum	Moraceae	108	39.81 (43)	47.22 (51)	12.96 (14)
F. benjamina	Moraceae	7	0	100 (7)	0
B. crassifolia	Malpighiaceae	28	3.57(1)	21.42 (6)	75 (21)
C. uvifera	Poligonaceae	15	0	0	100 (15)
C. sebestena	Boraginaceae	59	0	67.79 (40)	32.2 (19)
S. hirtum	Solanaceae	12	0	58.33 (7)	41.66 (5)
M. zapota	Sapotaceae	93	3.22 (3)	88.17 (82)	8.6 (8)
S. purpurea	Anacardiaceae	18	33.33 (6)	66.67 (12)	0
T. olivaeformis	Sapindaceae	33	3.03 (1)	96.97 (32)	0
T. catappa	Combretaceae	6	16.66 (1)	83.33 (5)	0
Unknowed species	Fabaceae	7	0	28.57 (2)	71.42 (5)
Monkeys					
B. alicastrum	Moraceae	75	22.66 (17)	44 (33)	33.33 (25)
F. cotinifolia	Moraceae	54	25.92 (14)	35.18 (19)	38.88 (21)
F. ovalis	Moraceae	34	32.35 (11)	38.23 (13)	29.41 (10)
M. zapota	Sapotaceae	46	15.21 (7)	43.47 (20)	41.3 (19)
S. mombin	Anacardiaceae	110	40 (44)	40.9 (45)	19.1 (21)
E. cyclocarpum	Fabaceae	23	0	43.47 (10)	56.52 (13)

Figure 1. Seed handling in tropical forest of Peninsula of Yucatan, produced by bats and spider monkey (*A. geoffroyi*) and black holder monkey (*A. pigra*). Different capital letters indicate significant differences among primate species and bats, and different lowercase letters indicate differences among seed handling categories within each animal disperser (pairwise contrast LSD, *p*<0.05).

axes (Table 2), and Monte Carlo permutation test was highly significant for the four axes (Table 2). In addition, seed handling categories as undamaged fruit and dropped bitten fruit were significant (F = 4, *p* = 0.001 and F = 3.14, *p* = 0.002, respectively). Although, spat-out seed was not significant, it showed certain influence on the model (F =1.69, *p* = 0.08; Fig. 2A). Seed handling categories were closely related to Axes 1 and 2: Axis 1 negatively to "Uf" (*r* = -0.98) and positively to "Dbf" (*r* = 0.81), while Axis 2 negatively to "Dbf" (*r* = -0.57) and positively to "Sot" (*r* = 0.94). Fruit species were mostly ordinated in Axis 1 with respect to seed handling (72.9 %), Axis 2 only explains the 27.1 % remaining. We identified three strong relations between seed handling and fruit species: 1) undamaged fruit was related mainly to *C. uvifera*, *B. crassifolia* and unknown plant species (Fabaceae); 2) dropped bitten fruit was related mainly to *T. olivaeformis* and *F. benjamina*; 3) spat-out seeds were related almost exclusively to *S. purpurea* (Fig. 2A).

In monkeys, fruit species showed narrow ordination on axes (Table 2). However, Monte Carlo permutation showed a significant influence of the first and rest of axes (F = 7.0, *p* = 0.004 and F = 3.06, *p* = 0.004, respectively). In addition, undamaged fruit ("Uf"; F = 3.21, *p* = 0.03), *A. geoffroyi* (F = 5.03, *p* = 0.006) and *A. pigra* (F = 5.03, *p* = 0.007) were highly

Table 2. Eigenvalues and Monte Carlo results for Canonical Correspondence Analysis (CCA) and Redundancy Analysis (RDA) of fruit choice associated to plant species in bats and monkeys in a neotropical forest, Mexico.

Axes	1	2	3	4
Bats and seed handling (CCA)				
Eigenvalues	0.476	0.177	0.978	0.737
Species-environment correlations	0.761	0.590	0.000	0.000
Cumulative variance of species data (%):	10.7	14.7	36.7	53.3
Cumulative variance of species-environment (%): (%)relation:	72.9	100.0	0.0	0.0
Significance of first canonical axis:	F ratio = 3.96		*p* value = 0.003	
Significance of all canonical axes:	F ratio = 2.64		*p* value = 0.002	
Primates and seed handling (RDA)				
Eigenvalues	0.124	0.024	0.007	0.463
Species-environment correlations	0.584	0.304	0.200	0.000
Cumulative variance of species data (%):	12.4	14.8	15.5	61.8
Cumulative variance of species-environment (%): (%)relation:	79.9	95.3	100.0	0.0
Significance of first canonical axis:	F ratio = 7.08		*p* value = 0.004	
Significance of all canonical axes:	F ratio = 3.06		*p* value = 0.004	
Bats, primates and seed handling (RDA)				
Eigenvalues	0.140	0.012	0.565	0.283
Species-environment correlations	0.496	0.167	0.000	0.000
Cumulative variance of species data (%):	14.0	15.2	71.7	100.0
Cumulative variance of species-environment (%): (%)relation:	92.2	100.0	0.0	0.0
Significance of first canonical axis:	F ratio = 19.75		*p* value = 0.001	
Significance of all canonical axes:	F ratio = 5.43		*p* value = 0.001	

significant. Moreover, relationships among *F. cotinifolia, F. ovalis* and *Spondias mombin* L. were clear, and related to *A. geoffroyi*. Instead, *E. cyclocarpum* was mostly related to *A. pigra* (Fig. 2B).

Fruit choice and seed handling in dominant tree species in Yucatan Peninsula

Separation of *M. zapota* and *B. alicastrum* data were no wide (Table 2), however Monte Carlo permutation showed a significant effect on the first and rest of axes (F = 19.75, *p* = 0.001 and F = 5.43, *p* = 0.001, respectively). Seed handling, spat-out seeds ("Sot"; F = 5.96, *p* = 0.003), dropped bitten fruit ("Dbf"; F =18.04, *p* = 0.001) and undamaged fruit ("Uf"; F =4.08, *p* = 0.01), also produced a significant effect. Despite narrow ordination, interestingly, *M. zapota* fruits were associated mostly with bats in the category of dropped bitten fruit, while *B. alicastrum* tended to associate to *A. geoffroyi* in the category spat-out seeds. *Alouatta pigra* showed low election for *M. zapota* and *B. alicastrum*, although the

main category of seed handling associated with them was undamaged fruit (Fig. 2C).

DISCUSSION

Fruit choice
In our first prediction, we expected that monkeys mainly produced undamaged fruit and spat-out seeds more than bats and inversely with dropped bitten fruits; our findings support these ideas. It is possible that these results have been determined by the high abundance and diversity of frugivorous bats, which influence on a larger amount of consumed units and, consequently, a major probability of fruit fall (Romo and Herrera, 2010). It has been registered that *Artibeus jamaicensis* Leach, 1821, holds the fruit with the thumbs and rotates it while consuming it. This behavior causes the bat to bite the fruit repeatedly and then abandon it (Romo and Herrera, 2010). A similar behavior but, with compact and hard fruits has been observed in a study by
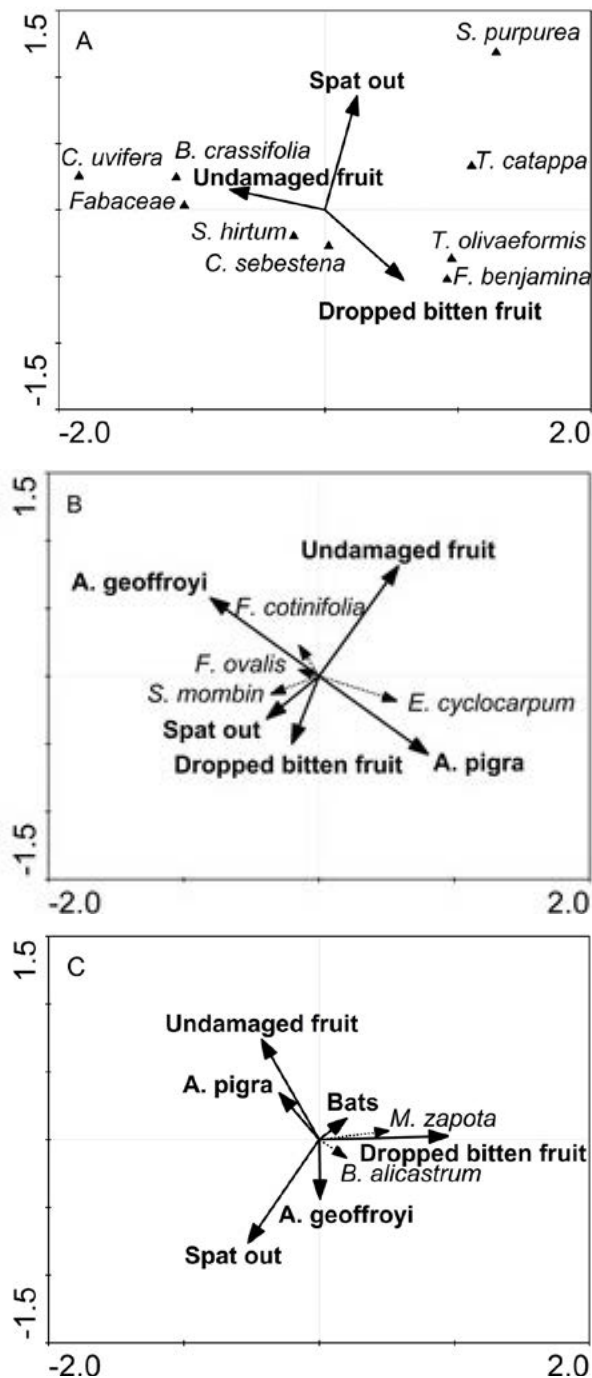
Figure 2. (A) Canonical Correspondence Analysis (CCA) scatterplot illustrating the relationships among nine fruit species to seed handling of bats: Undamaged fruit ("Uf"), Dropped bitten fruit ("Dbf") and Spat out ("Sot"), represented by arrows.

(B) Redundancy Analysis (RDA) scatterplot illustrating the relationships among four fruit species to seed handling (Undamaged fruit, "Uf"; Dropped bitten fruit, "Dbf"; and Spat out, "Sot"), represented by dot arrows in two monkey species, *A. geoffroyi* and *A. pigra*.

(C) Redundancy Analysis (RDA) scatterplot illustrating the relationships among two common fruit species to seed handling (Undamaged fruit, "Uf"; Dropped bitten fruit, "Dbf"; and Spat out, "Sot"), represented by dot arrows and monkey species, and bats.

Hernández and Medellín (2009) where bats bit only the fruit epicarp and then discard it.

In the present study, the fruit manipulation presented variations according to the mammalian study group, even among the monkeys, the black howler monkeys presented larger proportions of "Uf" than spider monkeys. Likewise, the latter showed larger proportions of "Dbf" with regard to the black howler monkeys. This pattern is consistent with other studies in which it was found that monkeys of the genus *Ateles* are highly frugivorous to the degree that they are specialists (Di Fiore *et al.*, 2008). Regarding the black howler monkeys, the results support the findings of other studies where *A. pigra* is considered mainly folivorous (which explains the high "Uf" proportion) (Wallis *et al.*, 2012), but opposite to Garber *et al.* (2015) who characterize this primate as one species with a balanced diet between leaves and fruits.

With regard to the absence of differences in the "Sot" by both monkey species, it is possible that the answer is based on the morphological structures of those animals that allow them to fully consume any kind of fruit (Di Fiore *et al.*, 2008).

Seed handling

It has been mentioned that the frugivorous species determine, from certain fruit traits and characters, if a given food is consumable (Dominy, 2004). Our findings are in accordance with what we previously mentioned. It is so that our second prediction also came true. We observed that the bats exhibited strong specific associations with the consumed species and somewhat varied diet. This phenomenon may be explained by the characteristics of foraging, as these bats are underbrush and canopy fruit consumers (Kalko and Handley, 2001). Although the bats used a wide source of the fruits of the Malpighiaceae, Poligonaceae, Boraginaceae, Anacardiaceae, Combretaceae and Sapindaceae families; other studies have registered the preference of the Urticaceae, Moraceae, Piperaceae and Solanaceae families (Lou and Yurrita, 2005; Da Silva *et al.*, 2008; Novoa *et al.*, 2011). This may suggest that the penetrating odors expelled by the fruits of the families above mentioned promotes and facilitates their location (Valenta *et al.*, 2013). An important-fact is that diversity of plants found in the bats diet was smaller (11 plant species), unlike what has been observed in studies with 19 (Galindo-González, 1998) and 22 (Novoa *et al.*, 2011) species of bats. In contrast, our results correspond to previous reports that establish a correlation of the floristic diversity with the fruit species amount present in the bats diet (Novoa *et al.*, 2011). We believe that plant diversity has been a result of the anthropogenic activities on the study site, although other factors as the environmental conditions variation and the space-time abundance of the fruits may have importantly modified the fruit selection (Gómez-Posada, 2012). We identified three principal fruit handling relations and fruit

species in bats: the undamaged fruit was related with *C. uvifera*, *B. crassifolia* and plant species belonging to Fabaceae. A shared feature between these species is the size of the seed (>50 % of fruit size). This trait causes the bat to bite the fruit superficially and then release it when feeling the hardness of the seed; this mechanism would explain the spat-out seeds of *S. purpurea* consumed entirely, despite its size (2 x 4 cm). The size variation of the fruit to be eaten may be overlooked (Dumont, 2003). After having eaten the pulp, the undigested big seeds are dropped directly to the nocturnal burrows and never swallowed (Galindo-González *et al.*, 2000; Galindo-González and Sosa, 2003; Novoa *et al.*, 2011).

Alouatta pigra mainly feeds on *E. cyclocarpum* fruits, and *Ateles geoffroyi* on *F. cotinifolia*, *F. ovalis* and *S. mombin* fruits. This preference has been reported for other Mexican southeastern populations of *Ateles* (Martínez and Galindo-Leal, 2002; Ramos-Fernández and Ayala-Orozco, 2002; González-Zamora *et al.*, 2009; Scherbaum and Estrada, 2013) in common and dominant plant families in tropical forests such as Fabaceae and Moraceae (Primack and Corlett, 2005). The diet of *Ateles* is mainly based on fleshy fruits and a variable proportion of leaves and blossoms (García-Orduña, 2003). The food election of *A. geoffroyi* over *S. mombin* fruits was outstanding and previously reported in Bolivia but with the *Cebuella pygmaea* (Spix, 1823) and *Callithrix argentata* (L.) 1771 monkeys. Apart from fruits, feeding from tree sap was also recorded (Grieser-Johns, 1997; Burgoa and Pacheco, 2008). These findings suggest that the choice of *S. mombin* fruit could be due to the advantage of primates for choosing a tree with several types of food resources (fruits, leaves, tree sap, etc.) instead of a single type (for example, fruits). Besides, fruit size and shape also had an important influence on the fruit election (Chapman, 1995), as *A. geoffroyi* tends to ingest and disperse big rather than small fruits (Oliveira and Ferrari, 2000; Dew, 2008) and rather ovoid than round (McConkey, 2000), features of *S. mombin* fruits.

Fruit choice and seed handling in dominant tree species in Yucatan Peninsula

When the fruit choice and seed handling in the three dispersing agents were analyzed together, we observed a high preference of the bats for the *M. zapota* and spider monkeys for the *B. alicastrum*, in both cases with the category of seed handling of dropped bitten fruit. Our results are partially adjusted to the third prediction as, even though, the bats preferred to feed on *M. zapota*, the *A. geoffroyi* monkey fed on *B. alicastrum* rather than both plant species as proposed at the beginning. The results showed by the monkeys agree with those discussed by Chaves *et al.* (2011), who reported that *A. geoffroyi* ate a small portion of the pulp when feeding on immature fruits, dropping the rest. Such foraging behavior induced the waste of much fruit, which fell under the progenitor tree (Estrada *et al.*, 1984). In another study, Morales (2003) observed that

monkeys of the genus *Ateles* based their diet in *B. alicastrum* in at least 50 %. Previous information has also suggested this relationship because *Brosimum* is an abundant and wide distributed genus (Russo *et al.*, 2005; Wallace, 2005; Di Fiore *et al.*, 2008; González-Zamora *et al.*, 2009). Likewise, a similar association has been observed, albeit with spat-out fruits in Punta Laguna, Yucatán (H. F. Dzul-Cauich, personal observation). Surprisingly, the black howler monkeys did not present preference for *M. zapota* nor for *B. alicastrum*, but they did for *E. cyclocarpum*, although generally with undamaged fruit, suggesting a possible fruit protection fallback effect (Lambert, 2002). This mechanism may indicate a niche partition owing to adaptive advantages of some species (Chapman *et al.*, 2005). For example, the monkeys *Cercopithecus ascanius* (Audebert, 1799) and *Lophocebus albigena* (Gray, 1850) did not present any difference in fruit selection during periods of abundant resource. However, when there was a shortage of resources, only *L. albigena* and not *C. ascanius*, could continue feeding on hard cover fruits. In this sense, it is possible that only *A. pigra* may have consumed *E. cyclocarpum* fruits, as a result of having a stronger mandibular bone system, unlike *A. geoffroyi* (Campbell *et al.*, 2000; Lambert *et al.*, 2004; Fleagle, 2013). The relation between *A. pigra* and *E. cyclocarpum* could be an energetic cost result because the displacement through the trees searching for sufficient food, generates a higher energy consumption; *E. cyclocarpum* is a tree generally bigger and taller than the rest of the plant community. This tree not only provides food for black howler monkeys, but also a physical substrate on which they perform activities such as social interactions and resting (Tobón *et al.*, 2012). In addition, it is possible that *E. cyclocarpum* has served as an alternative food source driven by group and forest size of the study site (Dias and Rangel-Negrín, 2015).

It is import to mention that the fruit handling will depend on morphological characteristics (seed size mainly) and on the primate species (Andresen and Feer, 2005). Generally, big primates tend to swallow and defecate a larger proportion of seeds, especially the large ones (>1 cm), while the smaller ones tend to spit them out. The primates, who have cheek pouches spit out a large proportion of seeds while those who lack them, defecate most of them (Chapman, 1995; Dew, 2008).

Despite our study presents space-time limitations, it analyzes data of frugivorous species of the Yucatan Peninsula in a novel way. Thereby, we highlight the fruit election of each of the frugivorous species described along the manuscript and show the specific associations by plant species and fruit handling caused by the dispersers as principal contribution. In a future follow-up on this study, it would be convenient to increase the monitoring time and evaluate the final destination of the handled fruit, in order to analyze the advantages of seed germination and the seedling recruitment in the understory of tropical forests.

CONCLUSIONS

The present study shows that bats dispersed a greater variety of plant species than monkeys, although the former did not completely consumed the fruit and the monkeys did. This food behavior in monkeys may promote the seed germinating success. Among the plant variety present in the diet of primates, we observed a high fruit choice for low abundant species such as *E. cyclocarpum* in the case of *A. pigra*, which showed lower fruit choice for abundant species such as *M. zapota* and *B. alicastrum*, a very uncommon behavior.

ACKNOWLEDGEMENTS

CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

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