Journal of Agricultural Research, Development, Extension and Technology, 1(1), 1-9 (2019) Full Paper

Fruit bats as natural foragers and potential pollinators in fruit orchard: a reproductive phenological study

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Received: 27 February 2019
Accepted: 10 June 2019

Abstract

Family Pteropodidae could consume either fruit or flower parts to sustain their energy requirement. In some species of fruit bats, population growth is sometimes dependent on the food availability and in return bats could be pollinators of certain species of plants. In this study, 152 female bats captured from the *Manilkara zapota* orchard of the University of Southern Mindanao were examined for their reproductive stages. Lactation of fruit bat species *Ptenochirus jagori* and *Ptenochirus minor* were positively correlated with the fruiting of *M. zapota.* While the lactation of *Cynopterus brachyotis, Eonycteris spelaea* and *Rousettus amplexicaudatus* were positively associated with the flowering of *M. zapota*. Together, thirty *M. zapota* trees were observed for their generative stage (fruiting or flowering) in 6 months. Based on the canonical correspondence analysis, only *P. jagori* was considered as the natural forager as its lactating stage coincides with the fruiting peaks and only *C. brachyotis* and *E. spelaea* were the potential pollinators since its lactating stage coincides with the flowering peaks of *M. zapota* tree. The method in this study can be used to identify potential pollinators and foragers in other fruit trees.

Keywords - agroforest, chiropterophily, frugivore, nocturnal, Sapotaceae

Introduction

Fruit bats belonging to the family Pteropodidae are volant mammals that provide important ecosystem services resulting to maintained interactions between species and ecosystems (Kunz et al. 2011). Fruit bats are said to be the major pollinators of most economically important plants such as *Durio* sp. (durian), *Musa* sp. (banana), *Mangifera* sp. (mango), *Psidium* sp. (guava), *Lansium* sp. (lanzones) (Kingston et al., 2006). Moreover, fruit bats efficiently disperse the seeds of the fruits they consume making them an important agent of habitat regeneration (Jones et al., 2009; Boyles et al., 2011). In spite of the ecological services provided by fruit bats, their nocturnal activity is perceived in different views by the farmers. Fruit bats are rather considered as a menace especially in fruit orchards. Locally, the farmers have a general understanding that all species of bats are eating fruits, and only a few knew the other functions of bats. Pollen could stick to the fruit bat body when fruit bat flies to the plant to obtain nectar from the flowers. As the bat flies to another plant for more food, the bat unintentionally transfers the pollen from its body to the new plant (Read, 2018) and this bat pollination process is called chiropterophily.

This research used the phenology schedules of different bat species to relate it to its foraging activities in the flowering and fruiting stages of *M. zapota*, a representative fruit species. Dinerstein (1986) stated that the reproductive activity, notably lactation of fruit bats, coincides with the seasonal peaks in fruit abundance. Lactation is the most energetically costly reproductive stage in bats, hence food availability appears to be one of the most important factors that influences a female's ability to reproduce, thus considered as the ultimate cause of reproductive timing (Heideman, 2000). This statement implies that the population growth of a certain bat species is supported by the tree species with seasonal peak in fruit abundance during lactation of female bats. Thus, this study used a presumption that peak of captures of lactating bats in flowering or fruiting of *M. zapota* are the potential pollinators or natural foragers, respectively. This study was limited on the fruiting and flowering peak of one fruit tree species in a mixed orchard. This study aimed to determine which bats species that visits the orchard are natural fruit foragers and which species are considered as potential pollinators.

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Methodology

Study Area

Data collection was carried out in the *M. zapota* (Family: Sapotaceae, local name: chico) orchard, the fruit bearing tree available during the time of the study at the University of Southern Mindanao (USM), North Cotabato, Philippines. The campus has variety of habitat types which include agro-forests, orchards, rice fields and disturbed habitats with infrastructures.

There are two *M. zapota* orchards in the campus specifically situated at the Agricultural Research Center (USMARC) and near the College of Agriculture Annex (approximately 1.6 km apart) with an area of 0.6 and 1.1 hectares, respectively. The vicinities of these two areas are dominated mostly by mixed orchards and crops. The vegetation was composed of fruit-bearing trees including *L. domesticum* (lanzones), *Citrus maxima* (pomelo), *Durio* sp. (durian), *Nephelium lappaceum* (rambutan), *Annona muricata* (guyabano), *Cocos nucifera* (coconut) and *M. zapota* (chico). Economically important plants such as *Oryza sativa* (rice), *Zea maize* (corn) and *Musa paradisiaca* (banana) were also present in the area.

Fruit Bat Sampling And Collection

Bats were captured using mono-filament mist nets. Four mist nets were strategically set in open areas, possible flight paths, and near the fruiting or flowering trees. The distances between each mist net ranges from 27 m to 70 m. The sampling period runs four nights per month starting from September 2017 to February 2018 for a total of 96 net nights.

Identification of captured bats was done through morphological examination and morphometric measurement supported by the keys of Ingle and Heaney (1992), and the photographic guide for the cave bats of the Philippines by Ingle et al. (2011). All individuals caught were marked using a nail polish for the recognition of recaptures over the same sampling period. Lastly, captured bats were released, if possible near the site of capture.

Reproductive Assessment

Reproductive status of female bats were assessed by visual inspection and palpation and were classified as non-reproductive, pregnant, lactating, and post lactating. Non-reproductive female bats were categorized based on non-enlargement of the reproductive organ (vagina or mammary gland). Juveniles were considered as non-reproductive. Pregnancy was determined by gently palpating the abdomen of the female bat. Lactating female bats were identified on the basis of attached juveniles or enlarged nipples without fur around them that secrete milk when gently pressed. Post-lactating bat was determined by observing loss of fur surrounding the enlarged nipple and the inability to express milk. If an individual was of uncertain status, the bat reproductive status was categorized as unknown and this data was not used in the analysis (Adams, 2010).

Plant Phenology Assessment

The *M. zapota* can produce flowers and fruits throughout the whole year but showed greatest reproductive display during the rainy season (Mizrahi et al., 2001). Accordingly, the sampling period of this study focused only during rainy season to ascertain reproductive peaks of *M. zapota* tree. The reproductive stage of 30 representative *M. zapota* trees in the orchard was checked every sampling session usually after the sample collection of bats in the morning. Individual plants were categorized as: inactive, flowering, and fruiting. Number of fruits and flowers in each tree were obtained by visual estimation per sampling period. Fruits were estimated in a section of the canopy and this was used as a reference to make an estimate for the full canopy (Pereira et al., 2010). The average fruits of *M. zapota* were obtained from the total fruits from all the *M. zapota* trees divided by the total number of fruiting *M. zapota* trees. Fruiting peak is defined the time when most *M. zapota* trees bear fruit. On the other hand, total flowering *M. zapota* trees every month were obtained by counting only the number of the flowering trees in the orchard (since number of flowers are difficult to quantify). Flowering peak is defined as the time when most *M. zapota* trees bear flowers.

Analysis

Statistical analysis was done using PAST software. Canonical correspondence analysis (CCA) was used to determine the relationship of the different reproductive stages of each bat species to the flowering and fruiting of *M. zapota* in the six months sampling. CCA (Ter Braak, 1986) was used in measuring the relationship between sets of multiple variables such as identifying the effect of fruits, flowers and rainfall to the reproductive pattern of fruit bats. Data on rainfall was also included in the analysis. Monthly average of rainfall (mm) was obtained from Smarter Approaches to Reinvigorate Agriculture as an Industry in the Philippines (SARAI) satellite of UPLB.

Results and Discussion

A total of 314 pteropodid bats belonging to three species (*Ptenochirus jagori, Ptenochirus minor* and *Cynopterus brachyotis*) of frugivorous and two species (*Rousettus amplexicaudatus* and *Eonycteris spelaea*) of nectarivorous bats (Figure 1) were captured and identified from *M. zapota* orchard. Among the captured bats (Table 1), 152 (48.41%) individuals were female. The most abundant species throughout the sampling

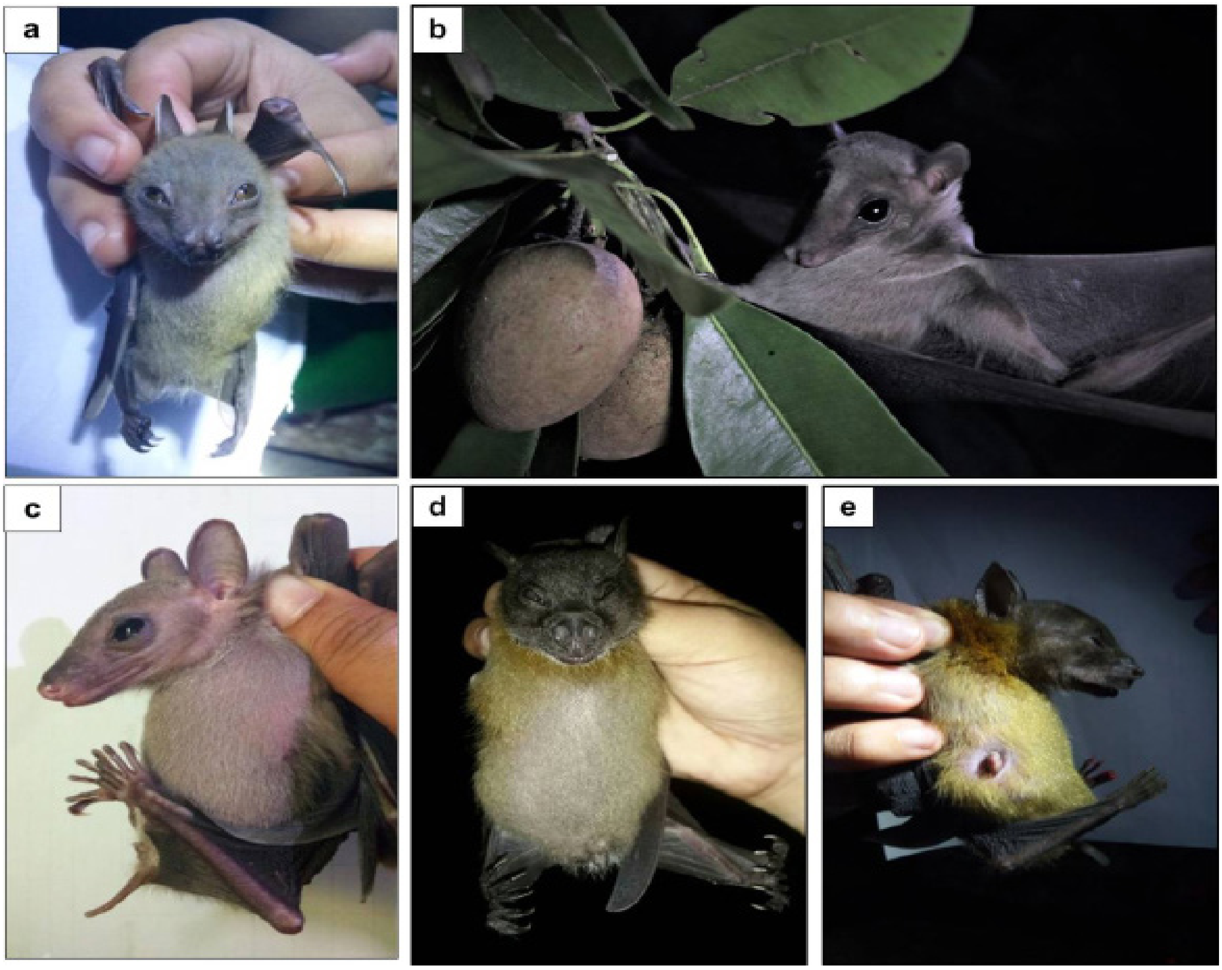

Figure 1. Five species of fruit bats captured in *Manilkara zapota* orchard, USMARC; September 2017 to February 2018; a. *Cynopterus brachyotis*; b. *Eonycteris spelaea*; c. *Rousettus amplexi-caudatus*; d. *Ptenochirus jagori*; e. *Ptenochirus minor*.

Table 1. Total number of female (XX) and male (XY) fruit bats in all species captured in every month from September 2017 to February 2018.

Month	*Cynopterus brachyotis*		*Ptenochirus jagori*		*Ptenochirus minor*		*Eonycteris spelaea*		*Rousettus amplexicaudatus*		Total
	XX	XY	XX	XY	XX	XY	XX	XY	XX	XY	
September	9	7	5	15	0	1	1	1	7	1	47
October	11	12	11	20	7	9	11	3	9	11	104
November	11	17	2	3	2	1	0	0	1	0	37
December	1	1	12	12	4	6	0	1	5	1	43
January	0	1	15	15	1	2	0	1	3	1	39
February	1	2	17	17	0	0	2	1	4	0	44
TOTAL	33	40	62	82	14	19	14	7	29	14	314
	=73		=144		=33		=21		=43		314

was the *P. jagori,* followed by the *C. brachyotis, R. amplexicaudatus*, *P. minor* and *E. spelaea*.

The abundance of *P. jagori* could be explained by their large population present in the area. Another possible reason is that this species could easily locate the fruit of *M. zapota* by olfaction (Luft et al., 2003) since *M. zapota* fruits were abundant during the sampling period. According to Ong et al. (2008), this bat species was considered endemic in the Philippines but listed as least concern because it is very common and widespread occasionally. *Ptenochirus jagori* forage in agricultural areas, tolerate degraded habitats including urban areas (Mickleburgh et al., 1992), and their population is thought to be stable.

The *C. brachyotis* or lesser dog-faced fruit bat was the second abundant species in this study and also a common frugivorous species in Southeast Asia. Throughout its range, this bat occupies a variety of habitats including primary forest, disturbed forest, mangrove, cultivated areas, orchards, gardens and urban areas (Zubaid, 1993).

On the other hand, *R. amplexicaudatus* is a locally abundant bat species in Southeast Asia and not limited to the Philippines (Heideman & Utzurrum, 2003). It was listed as least concern in view of its wide distribution (Csorba et al., 2008) and they usually forage in fruit orchards and other agricultural habitats for nectar and pollen (Marshall, 1983). However, this species is subject to intense hunting at some cave roosts (Utzurrum, 1992) but their overall number in the country remain abundant even populations in some areas of the Philippines appear to be declining (Mickleburgh et al., 1992).

Ptenochirus minor or the lesser musky fruit bat is often misidentified as *P. jagori* because of their similarity in appearance. The occurrence of this species in this study is somewhat uncertain because according to Ong et al. (2008) *P. minor* does not occur in agricultural or urban areas and apparently coexists with *P. jagori* at upper elevations. Similarly, Mickleburgh et al. (1992) believed that this species would persist in secondary forests. Its population is considered to be stable and the species occurs in a number of protected areas. As population of this species have declined due to destruction of lowland forest habitat, they are still considered to be common and widespread as it can adapt to some secondary habitats (Ong et al., 2008). This species is endemic to the Philippines and is found only in the Mindanao faunal region.

Eonycteris spelaea on the other hand is listed as least concern in view of its wide distribution, as it occurs in a number of protected areas, and has a tolerance to a degree of habitat modification (Francis et al., 2008). However, *E. spelaea* has the smallest sample size in this study which may be due to its small population in the area. In fact, this species was reported to have small captures on the orchard sites in the Philippines (Mickleburgh et al., 1992). This species is often found in colonies of thousands in caves in the Philippines, even in agricultural areas (Heaney & Regalado, 1998; Tanalgo & Tabora, 2015) but their populations undergone a significant decline due to hunting in their roosts. It is threatened by deforestation and conversion of land to agricultural and other uses (Molur et al., 2002). Another emerging threat to this species is cave tourism and lighting (Francis et al., 2008).

Reproductive Status of Demale Bats

Among the captured individuals *C. brachyotis* has a total of 33 females of which only 10 are lactating throughout the sampling period. Many lactating bats were captured on September and November during the peak of flowering of *M. zapota* trees and fruits were abundant (Table 2). Out of 62 female *P. jagori*, there were only 13 lactating bats captured. The highest proportion of lactating females occurred in October and December in which *M. zapota* fruits were plenty and on its fruiting peak.

Ptenochirus minor have only 14 females and all of these are non-lactating. Captured bats of this species from October to January were mostly juveniles or non-reproductive (Figure 2).

There were 29 females of *R. amplexicaudatus* captured in this study but only three individuals were lactating. Two lactating females were observed on September and only one on October. Of the 14 females of *E. spelaea*, only one lactating bat was captured on October. Overall, the most consistent reproductive stage captured from the five species of fruit bats throughout the sampling period is the non-reproductive or the juvenile.

The *M. zapota* trees started to flower on October and the flowering peaked on November (27 out of 30 trees). On the other hand, fruiting peaks were noted on December 2017 (73.8 ± 57.9 fruits) and January 2018 (70.7 ± 57.9 fruits) from all the *M. zapota* trees studied. Moreover, monthly average rainfall was observed to be low ranging from 0.13 mm to 2.27 mm (Table 2).

The data shows that all reproductive stages of *P. minor* and most of the *P. jagori,* except the

Table 2. Total Number of lactating bats, average fruits and numbers of flowering *M. zapota* trees every month (September 2017 to February 2018).

Species	2017				2018		
	Sept	Oct	Nov	Dec	Jan	Feb	Total
C. brachyotis	4	1	4	1	0	0	10
E. spelaea	0	1	0	0	0	0	1
P. jagori	1	4	0	4	3	1	13
P. minor	0	0	0	0	0	0	0
R. amplexicaudatus	2	1	0	0	0	0	3
Total	7	7	4	5	3	1	27
Flowering trees	1	15	27	8	2	3	56
Average fruits	27.5	61.2	65.9	73.8	70.7	48.3	347.4

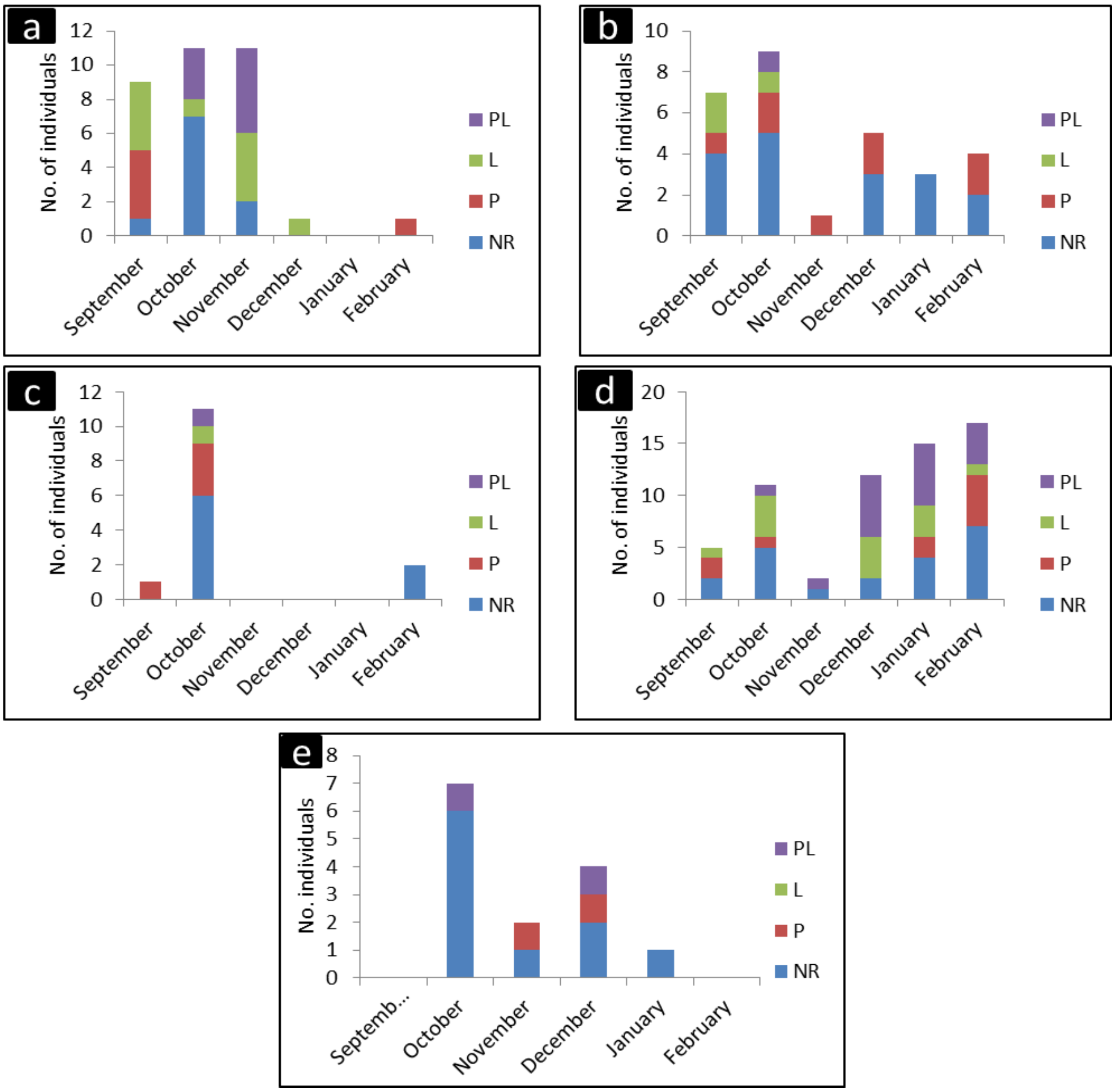

Figure 2. Proportion of the different reproductive stages of fruit bats in six months sampling, a. *Cynopterus brachyotis*; b. *Rousettus amplexicaudatus*; c. *Eonycteris spelaea*; d. *Ptenochirus jagori*; e. *Ptenochirus minor*. PL- post lactating; L- lactating; P- pregnant; NR- non-reproductive.

pregnant stage, were positively correlated with the fruiting of the *M. zapota*. All representatives of *E. spelaea*, and most of *C. brachyotis* and *R. amplexicaudatus* (except pregnant and lactating, respectively) were positively correlated with the flowering of *M. zapota* (Figure 3). This result was analyzed using CCA with an explained variation of 81.4%. In this study, data on rain has no significance because of the low amount of rainfall during the sampling period.

Natural Foragers and Potential Pollinators of *M. zapota* tree

The *C. brachyotis*, *E. spelaea* and *R. amplexicaudatus* were the common species captured during flowering peaks of *M. zapota*. The *C. brachyotis* was identified as frugivorous bat, but recognized also to feed on leaves and flower parts of some species of plants (Tan et al., 1998). Further, *E. spelaea* and *R. amplexicaudatus* are both nectarivore bats hence both obtained nectars produced by flowers to meet their energy requirement. With their presence in the orchard, these species could be the potential pollinators of the *M. zapota* tree through their consumption of nectars and flower parts.

On the other hand, *P. jagori* and *P. minor* were common foragers during fruiting peaks. They are frugivorous or known to eat primarily on fruits of different plant species. Droppings of partially eaten *M. zapota* fruit in the area is an evidence of their activity at night. *Ptenochirus jagori* was the most abundant species in this study implying that this bat species are good candidate for seed dispersal, or in other way, it could be a menace in fruit orchard if their population exceeds.

Unfortunately, these endemic species are not well documented, hence information on its reproductive cycle has not been established. Since there are no available literatures for the reproductive biology of *P. jagori* and *P. minor*, further researches on these species are needed. This data would serve as baseline to the future studies and could be used for their conservation.

Fruiting peaks of *M. zapota* was noted on

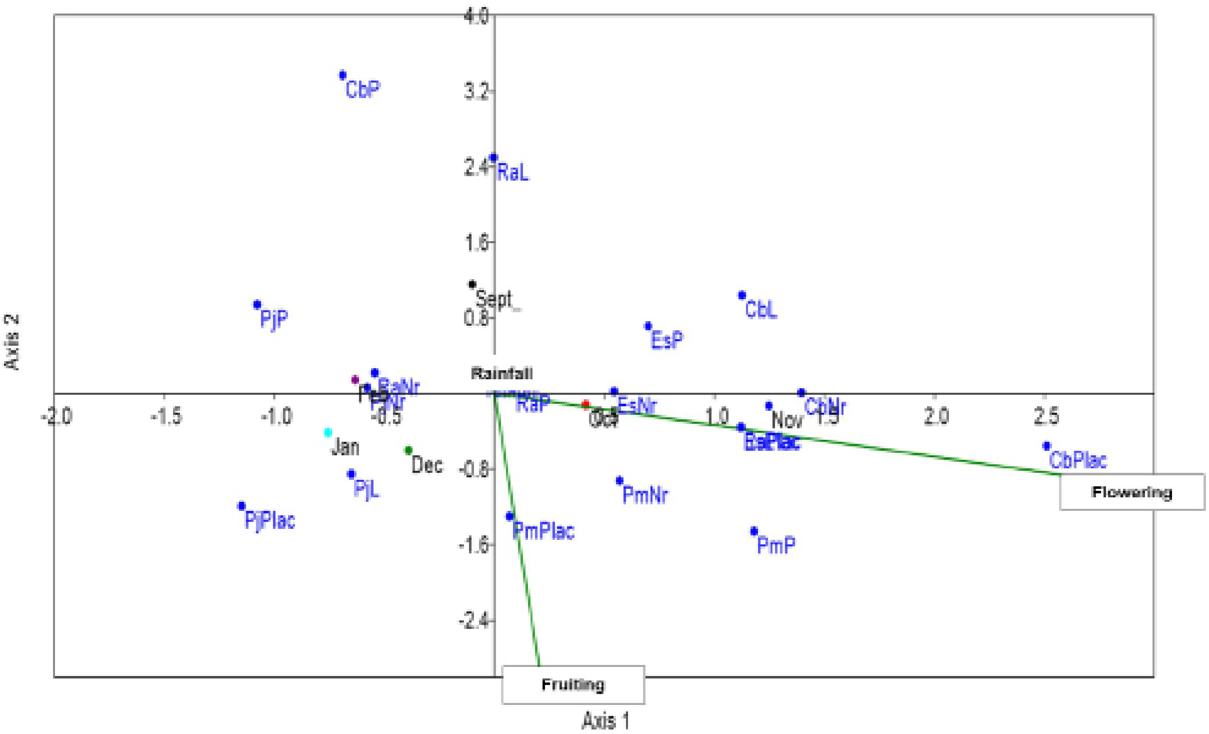

Figure 3. Influence of rainfall, fruiting and flowering of chico to the reproductive status in each species of fruit bats using Canonical Correspondence Analysis (CCA). CbNr, CbP, CbL, CbPlac- *C. brachyotis* non-reproductive, pregnant, lactating and post-lactating, respectively; EsNr, EsP, EsL, EsPlac- *E. spelaea* non-reproductive, pregnant, lactating and post-lactating, respectively; PjNr, PjP, PjL, PjPlac- *P. jagori* non-reproductive, pregnant, lactating and post-lactating, respectively; PmNr, PmP, PmL, PmPlac- *P. minor* non-reproductive, pregnant, lactating and post-lactating, respectively; RaNr, RaP, RaL, RaPlac- *R. amplexicaudatus* non-reproductive, pregnant, lactating and post-lactating, respectively. ($R2$= 81.4%).

December 2017 and January 2018 and the most abundant species in this period was the *P. jagori.* This could indicate that fruit of *M. zapota* can be considered as their main food source during the sampling period. Fruits are available during the sampling since *M. zapota* was known to produce flowers and fruits throughout the year (Salinas-Peba & Parra-Tabla, 2007), and this presumably the main reason why *P. jagori* commonly forage in this area. The present data indicates that *M. zapota* may be an important component in the diet of *P. jagori*.

Cynopterus brachyotis shows distinct food preferences at any one place and time if a choice is available (Tan et al., 1998). The *C. brachyotis* was a frugivore, but in this study it was positively affected more by the flowering rather than fruiting of *M. zapota*. They just prefer to feed on flowers since *C. brachyotis* was also observed to visit the orchard and consume nectars of flowers (Tan et al., 1998) similar to *C. sphinx* (Sudhakaran et al., 2012). Another possibility and also to avoid competition on fruits with *P. jagori* and *P. minor*. Tan et al. (1998) observed *C. brachyotis* to feed upon the fruits of 54 plant species, leaves of 14 plant species and stamens of 4 species. In addition to seasonal patterns of fruit availability, frugivorous bats face highly inter-specific variations in the timing and amount of food production (McKenzie et al., 1995). Although individual species of plants have restricted fruiting seasons, several species of bat eat fruits that are generally available at all the times of the year in tropical habitats (Fleming, 1982).

According to a study, bee species of Euglosa and Trigona (e.g. *Trigona nigra*), as well as members of Lepidoptera and Coleoptera are the usual floral visitors and potential pollinators of *M. zapota* (Salinas-Peba & Parra-Tabla, 2007). Remarkably, studies have shown that some species of bats feed on fruits and flowers from several species of Sapotaceae (e.g. Mickleburgh et al., 1992 and Fleming et al., 2009). They also carry off the delicious fruit, eventually dropping seeds that may grow into new trees.

Low rainfall has no profound effect on bat foraging activities. However, studies showed that rainfall could potentially change bat phenology and foraging (Molinari & Soriano, 2014).

Relationship Between Fruit Bats and the Flowering or Fruiting of *M. zapota*

The analysis shows that the species *C. brachyotis*, *E. spelaea,* and *R. amplexicaudatus* on different reproductive stages (non-reproductive, pregnant, lactating, and post lactating) were positively correlated with the flowering of *M. zapota.* This suggests that flowers of *M. zapota* could be their source of food that supports their energy requirement during child rearing. Meanwhile, these three species are not directly assumed as the main pollinator of the *M. zapota* because there might be other plants that they depend on. The concept is that those lactating fruit bats captured during fruiting and flowering peaks were considered as the foragers and pollinators, respectively, of *M. zapota,* since lactation stage is likely to be more dependent or influenced by the availability of their food. Lactation is considered as the most important stage because it requires more energy that will support the mother and its pup. It signifies that the survival of both lactating bat and its pup depends on the food availability, thus this could be the ultimate cause of reproductive timing (Heideman, 2000). Lactating *C. brachyotis* and the *E. spelaea* were captured during the flowering peaks of *M. zapota*, thus these species could be reflected as one of the pollinators of this plant. However, lactating females of the species *R. amplexicaudatus* were inversely correlated with the flowering of *M. zapota*, indicating that there might be other species of tree used as source of food during their child rearing.

On the other hand, species from genus *Ptenochirus* was positively correlated with the abundance of fruits during the sampling period. This could indicate that they are the natural foragers that consume fruits of *M. zapota*. However, lactating female of *P. minor* is not strongly dependent on the fruits of *M. zapota* but maybe on the fruits of other trees. Of the bat species captured, only *P. jagori* was observed to be lactating during the whole duration of the sampling period. It signifies that they might be considered to be more dependent consumer of *M. zapota.* It was mentioned previously that the timing of reproduction of bats especially lactation is influenced by food availability since it is the most energetically costly reproductive stage in bats. Thus, population growth of a certain species of bats is possibly determined more by its lactation stage that is influenced with fruiting or flowering peaks of fruit bearing tree. According to Tan et al. (1998), the major factor that presumably maintains the population of bats is the fruits that are available throughout the year or with a long fruiting ability.

All observed bat species visits the orchard not by chance but with a purpose. It was observed that of all the fruit bearing trees (e.g. rambutan, lanzones, mango and durian) in the orchard, only chico tree exhibit abundant flowers and fruits during the sampling period. Fruit bats in this case are opportunistic of which they tend to forage on the areas where fruits or flowers are available and abundant. It was obvious in this study that the five species of bats visits the chico trees daily. This observation is treated as a circumstantial evidence to the assumption that fruit bats are the natural consumer and potential pollinators of *M. zapota*.

It is evident in this study that there is a relationship between the *M. zapota* and the different species of bats. This tree could be a good model to identify potential pollinators and natural foragers in the orchard. Nonetheless, the *M. zapota* orchard should be conserved since its fruits and flowers were consumed by different species of fruit bats. The fruits of *M. zapota* tree are available throughout the year or with a long fruiting season and this is presumably a major factor in maintaining the population of fruit bats in the area.

Conclusion

This study reveals that *P. jagori* are the natural foragers that consume fruits of *M. zapota* because their lactation positively corresponds with the fruiting peaks of *M. zapota*. Meanwhile, the *C. brachyotis* and *E. spelaea* are the potential pollinators of *M. zapota* because their lactation was positively correlated with the flowering peaks of *M. zapota*. The timing of the reproduction especially during lactation of the bat species could be dependent on the availability of fruiting or flowering of the *M. zapota* since its fruits are available throughout the year and this suggests that this fruit bearing tree could support and maintain bat population. Although populations of these bat species are stable in this area, further studies among these fruit bats are needed to obtain a conclusive data and determine their connection with *M. zapota*.

Acknowledgement

We are grateful to Mr. Krizler Tanalgo for providing the mist nets and some materials used in this research, and also help us in bat identification. Special thanks to Bryan Lloyd Bretaña, Cromwel Jumao-as and to the USM Security personnel for their assistance and security during the field works. Lastly, we are grateful to the USM President for allowing us to conduct this study in the University.

References

Adams, R.A. (2010). Bat reproduction declines when conditions mimic climate change projections for western North America. *Ecology*, *91*(8), 2437–2445.

Boyles J.G., Cryan, P.M., McCracken G.F. & Kunz T.H. (2011). Economic importance of bats in agriculture. *Science*, *332*, 41–42.

Csorba, G., Rosell-Ambal, G. & Ingle, N. (2008). *Rousettus amplexicaudatus*. IUCN 2012. *IUCN Red List of Threatened Species*. Version 2012.1. www.iucnredlist.org.

Dinerstein, E. (1986). Reproductive ecology of fruit bats and the seasonality of fruit production in a Costa Rican cloud forest. *Biotropica*, *18*(4), 307–318.

Fleming, T.H. (1982). Foraging strategies of plant-visiting bats. In T.H. Kunz, (Eds.), *Ecology of bats* (pp. 287–325). New York: Plenum Press.

Fleming, T.H., Geiselman, C. & Kress, W.J. (2009). The evolution of bat pollination: a phylogenetic perspective. *Annals of Botany*, *104*(6), 1017–1043.

Francis, C., Rosell-Ambal, G., Tabaranza, B., Carino, P., Helgen, K., Molur, S. & Srinivasulu, C. (2008). Eonycteris spelaea. *The IUCN Red List of Threatened Species*. www.iucnredlist.org.

Heaney, L.R. & Regalado Jr, J.C. (1998). Vanishing treasures of the Philippine rain forest. The Field Museum. *Journal of Mammalogy*, *82*(1), 246–247.

Heideman, P.D. (2000). Environmental regulation of reproduction. In E.G. Crichton & P.D. Krutzsch (Eds.), *Reproductive biology of bats* (pp. 469–499). San Diego, CA: Academic Press,

Heideman, P.D. & Utzurrum, R.C. (2003). Seasonality and synchrony of reproduction in three species of nectarivorous Philippines bats. *BMC Ecology*, *3*(1), 11.

Ingle, N.R., Gomez, R.K., Mendoza, M., Paguntalan, L., Sambale, E., Sedlock, J. & Waldein, D. (2011). Status of the Philippine cave bats. *Proceedings of the Second International Southeast Asian Bat Conference, Bogor, West Java, Indonesia*.

Ingle, N.R. & Heaney, L.R. (1992). *A key to the bats of the Philippine Islands*. Field Museum of Natural History, USA.

Jones, G., Jacobs, D.S., Kunz, T. H., Willig, M.R. & Racey, P.A. (2009). Carpe noctem: the importance of bats as bioindicators. *Endangered Species Research*, *8*, 93–115.

Kingston, T., Lim, B.L. & Akbar, Z. (2006). Bats of Krau Wildlife Reserve. Bangi, Penerbit

Universiti Kebangsaan Malaysia. http://www.loc.gov/catdir/toc/fy0710/2006325297.html

Kunz T.H., Braun de Torrez E., Bauer D., Lobova T. & Fleming T.H. (2011). Ecosystem services provided by bats. *Annals of the New York Academy of Sciences*, *1223*, 1–38.

Luft, S., Curio, E. & Tacud, B. (2003). The use of olfaction in the foraging behaviour of the golden-mantled flying fox, *Pteropus pumilus*, and the greater musky fruit bat, *Ptenochirus jagori* (Megachiroptera: Pteropodidae). *Naturwissenschaften*, *90*, 84–87.

Marshall, A.G. (1983). Bats, flowers and fruits: evolutionary relationships in the Old World. *Biological Journal of Linnean Society*, *20*, 115–135.

McKenzie, N.L., Gunnell, A.C., Yani, M. & Williams, M.R. (1995). Correspondence between flight morphology and foraging ecology in some paleotropical bats. *Australian Journal of Zoology*, *43*, 241–157.

Mickleburgh, S.P., Hutson, A.M. & Racey, P.A. (1992). *Old World fruit bats. An action plan for their conservation*. Gland, Switzerland: IUCN.

Mizrahi, A., Salinas, L., Young, R., Hattam, C. & Parra-Tabla, V. (2001). Ecology report for the village of Poop and Poop state of Yucata´n, Mexico. Enhancing the role of forest fruits in sustaining livelihood of forest margin communities. DFID.

Molinari, J. & Soriano, P.J. (2014). Breeding and age-structure seasonality in *Carollia brevicauda* and other frugivorous bats (Phyllostomidae) in cloud forests in the Venezuelan Andes. *Therya*, *5*(1), 81–109

Molur, S., Marimuthu, G., Srinivasulu, C., Mistry, S., Hutson, A. M., Bates, P.J.J., Bates, S., Walker, S., Priya, K.P. & Priya, A.B. (2002). Status of South Asian Chiroptera: conservation assessment and management plan (CAMP) workshop report. Zoo Outreach Organisation, Conservation Breeding Specialist Group South Asia and Wildlife Information & Liaison Development Society, Coimbatore, India.

Ong, P., Rosell-Ambal, G. & Tabaranza, B., Heaney, L., Pedregosa, M., Warguez, D., Ramayla, S., Gomez, R., Gonzalez, J.C. & Pamaong, R. (2008). *Ptenochirus minor*. *The IUCN Red List of Threatened Species*.

Pereira, M.J.R., Marques, J.T. & Palmeirim, J.M. (2010). Ecological responses of frugivorous bats to seasonal fluctuation in fruit availability in Amazonian forests. The Association for Tropical Biology and Conservation. *Biotropica*, *42*(6), 680–687.

Read, M. (2018). *The echo bats love to pollinate. Bat Conservation International*. Retrieved March 2, 2019 from http://www.batcon.org/resources/media-education/news-room/the-echo/1184-pollinator-week.

Salinas-Peba, L. & Parra-Tabla, V. (2007). Phenology and pollination of *Manilkara zapota* in forest and home gardens. *Forest Ecology and Management*, *248*(3), 136–142.

Sudhakaran, M.R. & Doss, P.S. (2012). Food and foraging preferences of three pteropodid bats in southern India. *Journal of Threatened Taxa*, *4*(1), 2295–2303.

Tan, K.H., Zubaid, A. & Kunz, T.H. (1998). Food habits of *Cynopterus brachyotis* (Muller) (Chiroptera: Pteropodidae) in Peninsular Malaysia. *Journal of Tropical Ecology*, *14*, 299–307.

Tanalgo, K.C. & Tabora, J.A.G. (2015). Cave-dwelling bats (Mammalia: Chiroptera) and conservation concerns in South Central Mindanao, Philippines. *Journal of Threatened Taxa*, *7*(15), 8185–8194.

Ter Braak, C.J. (1986). Canonical Correspondence Analysis: a new eigenvector technique for multivariate gradient analysis. *Ecology*, 67(5), 1167–1179.

Utzurrum, R.C. (1992). Conservation status of Philippine fruit bats (Pteropodidae). *Silliman Journal*, *36*, 27–45.

Zubaid, A. (1993). A comparison of the bat fauna between a primary and fragmented secondary forest in Peninsular Malaysia. *Mammalia*, *57*(2), 201–206.