UNIVERSIDAD DE COSTA RICA

SISTEMA DE ESTUDIOS DE POSGRADO

FENOLOGÍA REPRODUCTIVA Y DISPERSIÓN DE SEMILLAS DE *POTALIA TURBINATA* (GENTIANACEAE) POR VERTEBRADOS EN UN BOSQUE HÚMEDO TROPICAL EN COSTA RICA

Tesis sometida a la consideración de la Comisión del Programa de Estudios de Posgrado en Biología para optar al grado y título de Maestría Académica en Biología

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DEDICATORIA

Dedico esta tesis a mi familia por el infinito apoyo que me han dado. No sería quien soy sin ellos.

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RESUMEN

Potalia turbinata (Gentianaceae) es un arbusto que se distribuye en la zona norte y caribe de Costa Rica. En general se sabe poco de esta especie, por ejemplo, se desconoce la fenología reproductiva y sus interacciones de dispersión. La dispersión de semillas es un proceso ecológico que involucra la remoción de las semillas de la planta progenitora para alejarlas y mejorar su valor adaptativo. Esta tesis tiene como objetivo describir la fenología reproductiva y el consumo de los frutos de *Potalia turbinata* por vertebrados. El estudio se lleva a cabo en la Reserva Biológica Tirimbina, ubicada en La Virgen de Sarapiquí, Heredia, Costa Rica, de 2016 a 2019 en un bosque tropical húmedo.

En el primer capítulo describo la fenología reproductiva de *Potalia turbinata* y determino si existe una correlación entre la producción de frutos y el clima para la producción de frutos y el vigor de la planta. Por medio de observaciones mensuales, se establece que la floración y la fructificación de la especie es anual a nivel de la población y supra-anual a nivel del individuo. Se presenta un pico de floración en marzo y un pico de fructificación en junio. La floración está correlacionada con la época menos lluviosa (r=-0.44, p=0.015). Además, se determina el promedio de número de semillas por fruto, así como las características morfológicas de frutos y semillas, tales como peso, tamaño (ancho y largo) y dureza. Encontré que la producción de frutos está relacionada con el vigor de la planta (altura y diámetro).

En el segundo capítulo, identifico a los vertebrados que visitan la planta y consumen los frutos (potenciales dispersores), detallo el comportamiento de animales en la planta, y compruebo si hay diferencias temporales en las visitas entre dispersores. Un total de 24 plantas con frutos fueron monitoreadas con cámaras trampa. Todas las interacciones observadas de planta-animal con *P. turbinata* fueron de mamíferos: un roedor (*Nyctomys sumichrasti*) y murciélagos (*Artibeus* spp., *Dermanura* spp., y *Carollia* spp). Los roedores a veces se alimentan de los frutos in situ y los murciélagos hacen vuelos exploratorios antes de remover frutos. Se encontraron diferencias temporales significativas entre los roedores y murciélagos en los meses de la remoción de frutos. Los murciélagos visitan la planta los últimos meses de la temporada de fructificación en comparación con *Nyctomys* que llega más temprano durante la temporada. Las características de los frutos de *P. turbinata* son típicas de la dispersión por mamíferos por su color verde y la posición del fruto en la planta. Los murciélagos generalmente son dispersores efectivos, ya que dispersan las semillas lejos de la planta madre, mientras que los roedores tienden a ser depredadores de semillas. Este proyecto aporta información sobre las interacciones planta-animal previamente desconocidas de *Potalia turbinata.*

ABSTRACT

Potalia turbinata (Gentianaceae) is a shrub that is distributed in the northeast of Costa Rica. Little is known about this species; for example, the reproductive phenology and its dispersal interactions are unknown. Seed dispersal is an ecological process that involves removing the seeds away from the parent plant to improve their adaptive value. This thesis aims to describe the reproductive phenology and consumption of *Potalia turbinata* fruits by vertebrates. The study is carried out in the Tirimbina Biological Reserve, located in La Virgen de Sarapiquí, Heredia, Costa Rica, from 2016 to 2019 in a tropical humid wet forest.

In the first chapter, I describe the reproductive phenology of *Potalia turbinata* and determine if there is a correlation between fruit production and climate, as well as fruit production and plant vigor. Through monthly observations, I established that the flowering and fruiting of the species is annual at the population level and supra-annual at the individual level. There is a flowering peak in March and a fruiting peak in June. Flowering is correlated with the less rainy season ($r = -0.44$, $p = 0.015$). In addition, I recorded the average number of seeds per fruit, as well as the morphological characteristics of the fruits and seeds, such as weight, size (width and length) and hardness. I found that fruit production is related to plant vigor (height and diameter).

In the second chapter, I identify the vertebrates that visit the plant and consume the fruits (potential dispersers), detail the behavior of animals at the plant, and check if there are temporal differences in visits between dispersers. A total of 24 plants with fruits were monitored with camera traps. All observed plant-animal interactions with *P. turbinata* were from mammals: a rodent (*Nyctomys sumichrasti*) and bats (*Artibeus* spp., *Dermanura* spp., and *Carollia* spp.). Rodents sometimes fed on the fruit in situ, and bats exhibited exploratory flights before removing fruit. Significant temporal differences were found between rodents and bats in the months of fruit removal. Bats visited the plant in the last months of the fruiting season compared to *Nyctomys* which arrived earlier in the season. The characteristics of *P. turbinata* fruits are typical of mammal seed dispersal due to their green color and the position of the fruit on the plant. Bats are generally effective dispersers, as they disperse seeds far from the parent plant, while rodents tend to be seed predators. This project provides information on previously unknown plant-animal interactions of *Potalia turbinata*.

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LISTA DE ABREVIATURAS

Chapter/Capítulo	Abbreviation/Abreviatura	Description/Descripción
I, II	m	Meter/Metro
I, II	N	North/Norte
I, II	W	West/Oeste
I, II	ha	Hectares/Hectáreas
I, II	C	Celcius/Celcius
I, II	a.s.l.	Above sea level/Sobre el nivel del mar
I, II	d.f.	Degrees of freedom/Grados de libertad
I,II	i.e.	It is/Es
I, II	km	Kilometers/Kilometros
I	mm	Millimeter/Milimetro
I	cm	Centimeter/Centimetro
I	PC1	Principal component 1/Componente principal 1
I	t	Variation in data/Variación en los datos
I	p	Probability/Probabilidad
I	r	Correlation coefficient/Coeficiente de correlación
I	e.g.	For example/Por ejemplo
II	sp.	Species/Especie
II	spp.	Species/Especies
II	X^2	Chi-square/Chi cuadrado

INTRODUCCIÓN GENERAL

Potalia turbinata es una especie de árboles del sotobosque y la única especie de 9 en total del género *Potalia* en Costa Rica. Existe poca información sobre la especie *Potalia turbinata* de la familia de plantas Gentianaceae, lo que podría deberse a que recientemente se la describió como separada de la especie *P. amara* (Struwe & Albert, 2004). No se describe la fenología de *P. turbinata* y, a su vez, existe poca información sobre la morfología de frutos y semillas a nivel de especie. No existe información sobre los dispersores de semillas de la especie. Asimismo, faltan descripciones fenológicas e interacciones planta-animal para las otras especies del género *Potalia*, que se encuentra desde el norte de Costa Rica hasta el sur de Bolivia (Frasier et al., 2008).

La fenología vegetal describe fenómenos periódicos que incluyen la floración y fructificación, así como la dispersión y el momento de estos eventos (Bustamante & Burquez, 2008). Varios factores influyen en los eventos fenológicos, incluida la precipitación y la temperatura, así como sus interacciones ecológicas con polinizadores y dispersores (Pires et al., 2018). Comprender las estrategias fenológicas y los ciclos de vida de las plantas nos permite comprender aspectos sobre su reproducción y supervivencia (Rathcke & Lacey, 1985) además de su efecto sobre los herbívoros o animales que utilizan las plantas (Van Schaik, Terborgh & Wright, 1993).

Las colecciones de herbario muestran que se han observado flores de *P. turbinata* en marzo y mayo, mientras que sus frutos se han observado en mayo, julio, septiembre y diciembre (Struwe & Albert, 2004) – un estudio formal no existe sobre la fenología de *P. turbinata* en términos de la producción de flores y frutos. Se sabe que los frutos de *Potalia* son utilizados como recursos por los animales, particularmente los murciélagos. Los murciélagos de la especie *Vampyriscus nymphaea* construyen tiendas de campaña cónicas en la planta de *P. turbinata* como refugio y lugar de alimentación. La construcción de estos retiros podría reducir el número de flores que produce la planta, ya que se reduce notablemente el área foliar expuesta a la poca luz que llega al sotobosque (Rodríguez-Herrera datos no publicados, Rodríguez-Herrera, Rodríguez & Fernández Otárola, 2018).

Los factores ambientales como la lluvia y la temperatura afectan las fenofases de las plantas como la floración y la fructificación. Los patrones fenológicos son más variables en los bosques tropicales húmedos que en los bosques templados, ya que el medio ambiente favorece la floración y la fructificación durante todo el año (Boyle & Bronstein, 2012), y dicha variación se refleja en los diversos patrones fenológicos que muestran las plantas: subanual (que se reproduce más de una vez al año), anual (se reproduce una vez al año), continua (floración y fructificación todo el año) y supra-anual (fases reproductivas superiores a ciclos de un año) (Newstrom et al., 1994). La intensidad de la fructificación aumenta con la precipitación en las selvas tropicales (Dunham et al., 2018), y en el noreste de Costa Rica, las especies del sotobosque muestran un pico de fructificación en la segunda mitad del año durante el período más lluvioso (Boyle & Bronstein, 2012). Las especies del sotobosque tienen floración irregular en bosques húmedos, pero más comúnmente, mayor abundancia de flores durante la estación menos lluviosa al comienzo del año en un bosque húmedo de Costa Rica (Opler et al., 1980).

La fructificación de la planta a menudo se ve influenciada por el tamaño de la planta (Ollerton y Lack, 1998; Fernández Otárola, Sazima y Solferini, 2013), y la investigación de la relación entre el tamaño de la planta y el cultivo de la fruta proporciona información sobre las estrategias implementadas por la planta (es decir, la asignación de recursos y tamaño en la madurez reproductiva). Las plantas más grandes tienden a tener más frutos y/o frutos más grandes (Herrera, 1993). Un estudio sobre especies de leguminosas *Lotus corniculatus* mostró que las plantas más grandes producían más frutos y tenían menor depredación de semillas (Ollerton & Lack, 1998). Asimismo, en un bosque tropical húmedo de Costa Rica, 17 especies mostraron el mismo patrón, produciendo más frutos en árboles más grandes; el tamaño del árbol también predijo si una planta se reproducía (Minor y Kobe, 2019).

La dispersión de semillas es la remoción de semillas de la planta madre para mejorar su valor adaptativo (Stoner & Henry, 2009). Las semillas que se dispersan lejos de la planta madre tienen una mayor tasa de supervivencia debido a una menor competencia intraespecífica y depredación; evitando así la mortalidad conespecífica dependiente de la densidad (Janzen, 1970; Connell, 1971; Comita et al., 2014; Lu et al., 2015; Zhu, et al., 2015; Kellner & Hubbell, 2018; Jia et al., 2020). Además, la dispersión de semillas ayuda a regenerar bosques fragmentados (Wunderle, 1997; González-Zamora et al., 2012; Carlo & Morales, 2016).

Muchos animales son dispersores de semillas en los bosques tropicales, como aves, murciélagos, primates y roedores, en ese orden de importancia (Abrahamson, 1989). Los vertebrados dispersan las semillas dejándolas caer mientras consumen la pulpa de la fruta, o ingiriéndolas junto con la fruta y luego defecándolas (David, Manakadan & Ganesh, 2015). Es importante estudiar las interacciones de dispersión debido a la inmensa cantidad de relaciones existentes y redes ecológicas que aún no se han entendido.

Los patrones de alimentación temporales proporcionan información sobre la eficacia de la dispersión. La remoción de frutos inmaduros impone un efecto negativo sobre el éxito reproductivo de la planta (Niederhauser & Matlack, 2015). Además, los frutos inmaduros dificultan la digestión, lo que también puede influir en la dispersión y uso del recurso (Abrahamson, 1989). Saber cuándo un fruto está madura y observar si el dispersor quita el fruto antes de que alcance la madurez puede ayudar a determinar si un dispersor es eficaz o actúa como un depredador al remover los frutos antes de que las semillas sean viables. El tiempo que un dispersor permanece en el mismo lugar también contribuye a la eficiencia de la dispersión y si las semillas se asientan debajo o cerca de la planta madre. Cuanto más tiempo permanezca el dispersor alimentándose de la planta, mayor será la probabilidad de que la semilla se asiente cerca de la planta madre (Abrahamson, 1989).

Las características de la semilla, incluido el tamaño y la toxicidad del fruto y la semilla, afectan las interacciones de dispersión entre animales y plantas (Kuprewicz y García-Robledo, 2019). Además, muchas plantas tienen síndromes de dispersión que atraen a los dispersores, incluido el color, tamaño, forma, posición, olor y tiempo de maduración de la fruta (Abrahamson, 1989). Un síndrome de dispersión puede interpretarse como una adaptación de la planta para atraer a los dispersores (van der Pijl, 1982). Según la hipótesis de los síndromes de dispersión, las características de los frutos deberían predecir su tipo de dispersor (Lomáscolo et al., 2010). De esta forma, los dispersores más efectivos producen una presión selectiva sobre las características fenotípicas del fruto (Lomáscolo & Schaefer, 2010). Flörchinger et al. (2010) encontraron que la selección de frutos de primates se vio afectada por el número de frutos y el tamaño de la planta y no fue afectada por el color; en el mismo estudio, la selección de frutos por aves estuvo más influenciada por el color. Las aves prefieren frutos más pequeños a los más grandes (Muñoz et al., 2016).

Los frutos de *Potalia turbinata* tienen varias características relacionadas con el síndrome de quiropteronchoria (dispersión por murciélagos). Los síndromes de quiropteronchoria incluyen frutos expuestos por encima del follaje, lo que los hace fácilmente accesibles a los murciélagos y un color verde (Mahandran et al., 2018), y los frutos cambian poco de color en la madurez (es más común que permanecen verdes) (Van der Pjil, 1982). Todas estas características están presentes en *Potalia turbinata*, en la que los frutos verdes permanecen adheridos al árbol en la madurez y se agrupan de tal forma que potencialmente pueden ser removidos en vuelo. Los frutos que consumen las aves suelen ser de color rojo o negro, mientras que los de los mamíferos son de color verde, amarillo, marrón o naranja (Abrahamson, 1989). En *Potalia*, las semillas están sumergidas en poca pulpa y generalmente son pequeñas (típicamente menos de 5 mm; Lobova et al., 2009). La descripción de *P. turbinata* no se ajusta al síndrome de dispersión del mono, pero los murciélagos y los roedores posiblemente podrían actuar como dispersores. Los murciélagos generalmente se consideran dispersores efectivos debido a su alta movilidad y capacidad para mover semillas a largas distancias (Bernard & Fenton, 2003). Aunque los roedores pueden ser dispersores eficaces, son principalmente depredadores de semillas (Abrahamson, 1989; Weighill et al., 2017).

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CAPÍTULO 1. Do weather and plant vigor affect the reproductive phenology of the treelet *Potalia turbinata* (Gentianaceae) in a Tropical Humid Wet Forest of Costa Rica?

(Con formato para Revista Biología Tropical)

Do weather and plant vigor affect the reproductive phenology of the treelet *Potalia turbinata* (Gentianaceae) in a tropical humid wet forest of Costa Rica?

Rachel Salazar

Resumen: *Potalia turbinata* (Gentianaceae) es un arbusto que se distribuye en el caribe y la zona noreste de Costa Rica. Es una especie que cuenta con poca información y de la que se desconoce la fenología reproductiva. Este estudio tiene como objetivo describir la fenología reproductiva de *Potalia turbinata* y determinar si existe una correlación entre la producción de frutos y el clima tanto como la producción de frutos y el vigor de la planta. El estudio se llevó a cabo en la Reserva Biológica Tirimbina, Sarapiquí, Costa Rica. Por medio de observaciones mensuales, se determinó que la floración y la fructificación de la especie es anual a nivel de la población y supra-anual a nivel del individuo. Se presenta un pico de floración en marzo y un pico de fructificación en junio. La floración está correlacionada con la época menos lluviosa (r=-0.44, p=0.015). Además, se determinó el promedio del número de semillas por fruto, así como las características morfológicas de frutos y semillas, tales como peso, tamaño (ancho y largo) y dureza. Se determina que la producción de frutos está relacionada con el vigor de la planta (altura y diámetro).

Palabras clave: fenología reproductiva, *Potalia turbinata,* Reserva Biológica Tirimbina, bosque tropical, Gentianaceae, morfología de frutos

INTRODUCTION

Phenology can be described as the study of life cycle events and the seasonal timing of each event for individuals, populations, species, and communities (Rathcke & Lacey, 1985). Phenological events are influenced by abiotic factors such as precipitation and temperature, as well as their ecological interactions with pollinators and dispersers (Pires et al., 2018). Understanding the phenological strategies and life cycles of plants allows us to understand aspects about their reproduction and survival (Rathcke & Lacey, 1985) in addition to their effect on herbivores or animals which use the plants (Van Schaik, Terborgh & Wright, 1993).

The plant family Gentianaceae has 16 genera and 30 hermaphroditic species in Costa Rica, which are mostly herbs, in addition to some shrubs or trees, a few saprophytes (e.g., *Voyria* spp.), and epiphytes (Sánchez, 2010). *Potalia turbinata* is an understory treelet species and the only species from the *Potalia* genus in Costa Rica. Flowers of *P. turbinata* have been observed in March and May, while fruits have been observed in May, July, September, and December (Struwe & Albert, 2004), but there is no formal description on the phenology of this plant; nor for the other 8 species in the genus, which is found from northern Costa Rica to southern Bolivia (Frasier et al., 2008).

The phenological information of *Potalia turbinata* in terms of flower and fruit production, along with the timing of such phases, would provide information for the use of these resources by pollinators and fruit-eating animals (of which information is scarce). *Potalia* fruits are known to be used as resources by animals, particularly bats. Bats of the species *Vampyriscus nymphaea* build conical tents in *P. turbinata* as refuge and feeding sites. The construction of these roosts could reduce the number of flowers the plant produces, since foliar area exposed to the little light that reaches the forest understory is notably reduced (Rodríguez-Herrera unpubl. data, Rodríguez-Herrera, Rodríguez & Fernández Otárola, 2018).

Environmental factors such as rainfall and temperature affect plant phenophases such as flowering and fruiting. Temperate species are more seasonal and predictable than tropical species and often follow temperature and precipitation patterns closely (Ting et al., 2008). However, tropical climates are presumably less variable throughout the year, though precipitation influences growth in tropical environments as it separates the dry season from the wet season (Brearley et al., 2007). Furthermore, phenological patterns are more variable in wet tropical forests than temperate forests as the environment supports flowering and fruiting year-round (Boyle & Bronstein, 2012), and such variation is reflected in the diverse phenological patterns plants show: subannual (reproducing more than once a year), annual (reproducing once a year), continuous (flowering and fruiting all year), and supra-annual (reproductive phases longer than one-year cycles) (Newstrom et al., 1994). Fruiting intensity increases with precipitation in tropical rainforests (Dunham et al., 2018), and in northeastern Costa Rica, understory species show a fruiting peak in the second half of the year during the rainier period (Boyle & Bronstein, 2012). Understory species have irregular flowering in wet forests, but more commonly, higher flower abundance during the less rainy season at the beginning of the year in a wet forest of Costa Rica (Opler et al.,1980). Thus, considering that *Potalia turbinata* is an understory treelet, I expected it to flower during the early months of the year when precipitation decreases at the study site, while fruiting would correlate with the onset of heavier rains. Temperature, which is less variable during the year, should not correlate to either of the phenophases (flowering and fruiting).

Plant fruiting is often influenced by plant size (Ollerton & Lack, 1998; Fernández Otárola, Sazima & Solferini, 2013), and investigating the relationship between plant size and fruit crop provides insight about the strategies implemented by the plant (i.e., resource allocation and size at reproductive maturity). Larger plants tend to have more and/or larger fruits (Herrera, 1993). A study on legume species *Lotus corniculatus*, showed that larger plants produced more fruits and had lower predation of seeds (Ollerton & Lack, 1998). Likewise, in a wet tropical forest of Costa Rica, 17 species showed the same pattern, producing more fruits in larger trees; tree size also predicted whether a plant reproduced (Minor & Kobe, 2019). Therefore, I expected plant vigor (height, basal diameter, and number of leaves) to correlate to the number of fruits and to have a relationship with the reproductive success of *P. turbinata* plants.

The aim of this study was: 1) to describe the reproductive phenology of *P. turbinata*, 2) to detail the morphological characteristics of its fruits and seeds, 3) to correlate weather data (rainfall and temperature) and reproductive output, and 4) to relate the influence of plant vigor (height, basal diameter, and number of leaves) to fruit crop size and the probability of reproduction (plant produces flowers and fruits).

MATERIALS AND METHODS

Study site and species: I conducted this study at the Biological Reserve Tirimbina (hereafter Tirimbina), Heredia, Costa Rica (10°25' N; 84°47' W). I collected data from January 2017-March 2019. I located, marked, and quantified the plants of *P. turbinata* in an area where their high density was known along an 805 m trail; all plants within 10 m on each side of the trail were included in this study.

Tirimbina has 345 ha mostly covered by mature humid tropical wet forest (Holdridge et al., 1971). The average annual temperature and precipitation are 24.3°C and 3 777 mm respectively, with an elevation of 180-220 m a.s.l. (Ley-López & Avalos, 2017). The rainy season ranges from May through November, while the dry season extends from December through April.

Potalia turbinata is endemic to Central America and has a restricted and sporadic distribution in the east of Costa Rica and also in Panama near Bocas del Toro (Sánchez, 2010), from sea level to 350 m a.s.l. (Struwe & Albert, 2004), where it has a patchy distribution. *Potalia turbinata* is an understory shrub or treelet with a single trunk and a height of 1-4.5 m. The leaves are simple and grouped distally on branches. The flowers are on a compact inflorescence, with up to 30 flowers that vary in color from white, yellow, pale green, yellow-green, or green (Struwe & Albert, 2004). The green fruits are turbinate with a horizontal ring and may darken slightly as they mature (Sánchez, 2010).

Phenology: I surveyed all of the plants in the selected area monthly for 27 months. The sampling frequency may affect the interpretation of phenological patterns, and for tropical trees, sampling is recommended every two weeks, and in the case that sampling is monthly, at least 25 trees are recommended (Morellato et al., 2010). Fournier and Charpantier (1975) comment that monthly observations are appropriate to obtain a good representation of tree phenology. *Potalia turbinata* shows slow changes from flowering to fruiting and fruit maturation (Rodríguez-Herrera unpubl. data). Hence, I considered that monthly sampling is likely appropriate for this slow-changing species.

During each sampling, I counted the flower buds, flowers, and fruits for each plant; immature and mature fruits were grouped together due to subjective separation of the categories (cryptic color and size changes over the months). This information allowed me to determine duration and peak of the flower and fruit phenophases. In addition, I determined the flowering frequency and fruiting cycles and the extension of those phenophases at the population and individual level. I also implemented a t-test to compare fruit production between years (2017-2018). Monthly precipitation and temperature data provided by Tirimbina were also considered in order to evaluate the correlative effect (Pearson's correlation) of rainfall and temperature on flowering and fruiting phases during the study period.

Plant vigor and effects on fruit crop size and reproductive success: Several measurements were taken to characterize each individual of *P. turbinata*. Firstly, I measured the height of each plant from the ground to the top of the plant and the basal diameter at 10 cm from the ground. Then, I counted the number of leaves. Furthermore, to describe the morphological characteristics of the fruits and seeds, I collected fruits from plants surrounding the study area where I took up to 10 fruits per plant when possible and as little as 2 from one plant. I weighed all fruits and measured their length and maximum diameter. The hardness (strength required to perforate the exterior and access the seeds) was estimated using a penetrometer with a 2 mm chisel (Chatillon, model DPPH-100). I weighed the seeds, and measured their length, width, and thickness.

In order to specify whether the plant measurements of *P. turbinata* (height, basal diameter, and number of leaves) have a relationship with maximum fruit crop size, I did an analysis of principal components to combine plant size variables into one variable (PC1) that would represent plant vigor. I then correlated the first principal component and number of fruits. To evaluate the relationship of plant vigor with the number of plants that produce flowers and fruits, I performed a t-test using the data from year 2018 (the closest complete year to the date the plant measurements were recorded) and ran the test with each plant size variable. I conducted all statistical analysis in the statistical analysis program JMP version 7.0.

RESULTS

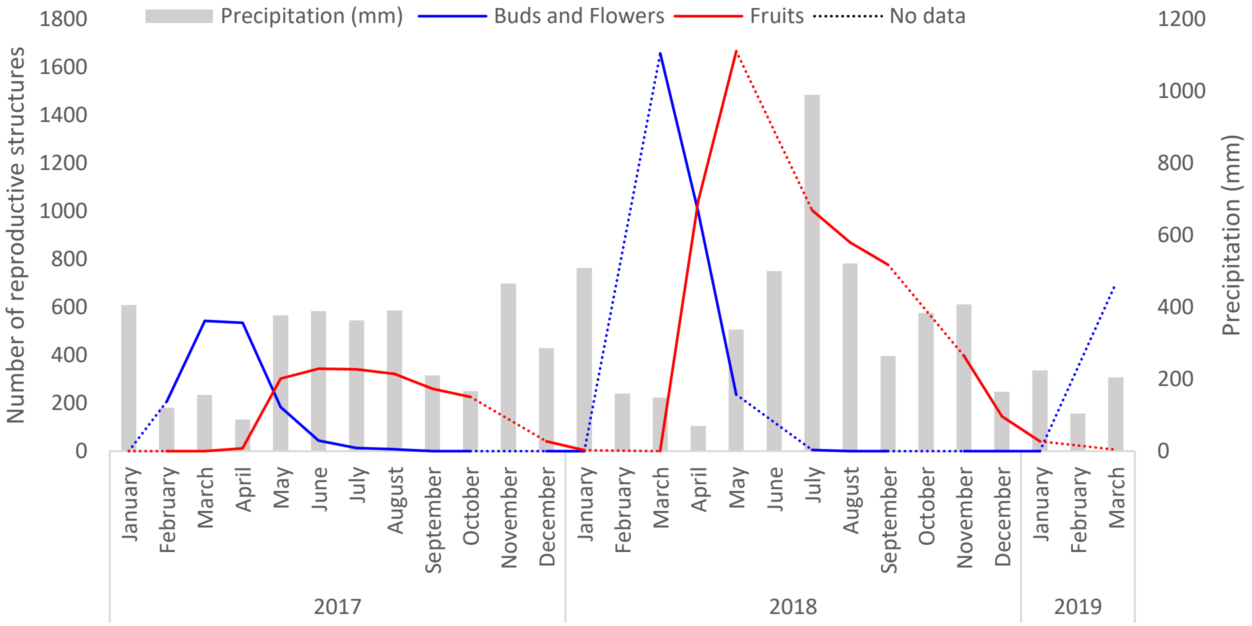
Phenology: I sampled 83 *Potalia turbinata* plants in 2017 and 86 plants in 2018. Budding started in February with a flowering peak in March, while the presence of fruits peaked in June as the fruits started maturing. The presence of fruits lasted up to 10 months from the date the fruiting phase was first detected in the population to the date all fruits had been dispersed or fallen in the population. Immature fruits were observed as early as April and some plants still had some mature fruits as late as January of the following year. The fruiting period of an individual plant averaged of 7.05 months with a range of 3 to 10 months. Figure 1 shows the total number of buds and flowers along with the number of fruits present for the entire population in the study January 2017- March 2019 with monthly precipitation (mm) at Tirimbina.

The timing of phenophases was similar in 2017 and 2018; however, in 2017 there were less reproductive plants than 2018. There were 12 reproductive plants in 2017, 46 in 2018, and 20 by March 2019. From 2017, only eight plants (66.67%) reproduced subsequently in 2018, and from 2018 to March 2019, 18 plants (39.13%) reproduced again. Only four plants that reproduced in 2017 also budded in 2019, three of which flowered all three years. As a population, *P. turbinata* follows an annual phenological pattern, whereas at the individual level, it is more irregular with a small fraction of the individuals exhibiting annual patterns and the majority, supra-annual.

The average maximum count of fruits per fruiting plant was 29.83 ± 21.27 in 2017 and 43 ± 27.16 in 2018, which is significantly different between years (t=1.79, DF=21.63, p=0.044). In 2017, the range of number of fruits on an individual plant was 10 to 81 fruits at the peak count of fruits during the study. The range for 2018 was 4 to 136 fruits. The median value of the maximum count of fruits during the study was 37 fruits. In 2017, the peak fruit count across the population was 344 fruits. In 2018, the peak fruit count was 1667.

FIGURE 1

Total number of buds and flowers along with the number of fruits for all plants in the study per month from January 2017 through March 2019 with monthly precipitation (mm) at Tirimbina.



The number of flowers correlated negatively with monthly precipitation (r=-0.442, p=0.040), so the number of flowers increased when precipitation decreased (Figure 1). Fruits did not show a correlation with precipitation (r=0.359, p=0.101). The average monthly temperature during the study was 25.49°C, with a narrow range from 22.39 to 31.71. Neither flower (r=0.017, p=0.939), nor fruit production (r=0.170, p=0.449) correlated with temperature.

Plant vigor and effects on reproductive success: I recorded the height, basal diameter, and number of leaves for 82 plants in January 2019, and I collected and measured a total of 185 fruits from 27 plants (19 fruits in August 2017, 106 fruits in October 2017, and 60 fruits in November 2018). I measured the hardness for 132 fruits. Seed measurements (weight, length, width, and thickness) came from a total of 150 seeds extracted from 30 fruits taken from 10 plants, from which 3 fruits per plant had 5 seeds randomly selected. The values of the plant, fruit, and seed measurements are summarized in Table 1.

For the correlations that involved plant vigor, height and diameter were highly correlated (r=0.686, p<0.0001), and they were combined in a principal components analysis to create a variable that represents plant vigor (PC1). I ran the number of leaves in a separate analysis because those values did not correlate with height. PC1 explained 84.31% of the variance in the data (Eigenvalue=1.68). The analysis included only reproductive plants because at the individual level, plant reproduction was supra-annual, and some reproductive plants did not reproduce every year. There was a significant correlation (r=0.334, p=0.011) between the number of maximum fruits produced and the PC1. Number of leaves and fruit crops did not show a significant relationship (r=0.195, p=0.146).

TABLE 1

Description of: a) plants, b) fruits, and c) seeds of *Potalia turbinata*.

a)

	Plant Height (cm)	Basal Diameter (cm)	Number of Leaves
Average	245.69 ± 80.36	10.09 ± 2.48	16.85 ± 6.23
Range	60-450	6-16	4-38

b)

	Weight (g)	Length (mm)	Width (mm)	Hardness (neutrons)
Average	2.74 ± 0.50	18.93 ± 1.09	21.28 ± 1.60	44.58 ± 8.10
Range	1.43-3.93	16.00-21.50	16.10-24.70	16.00-68.00

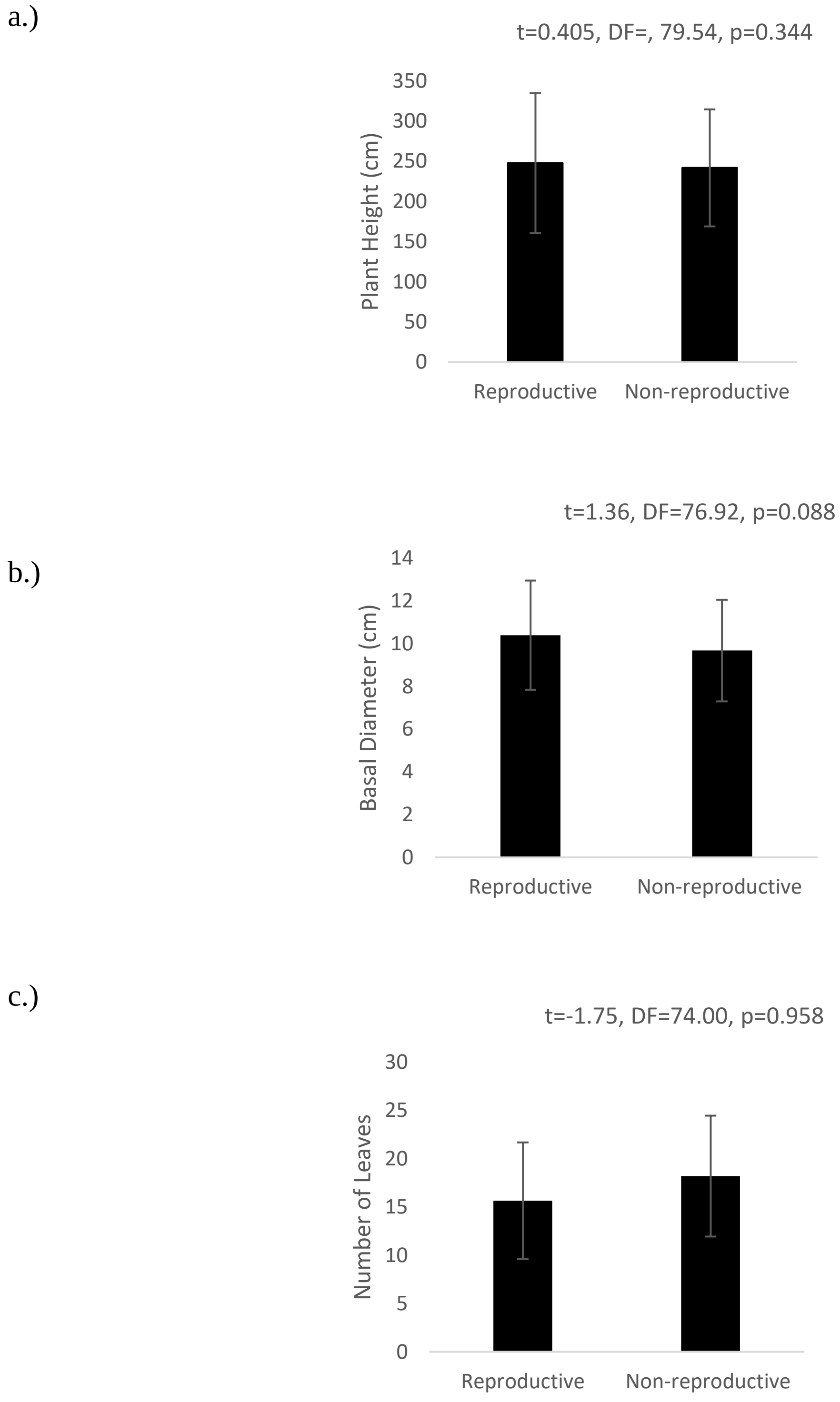
c)

	Seeds per Fruit	Weight (mg)	Length (mm)	Width (mm)	Thickness (mm)
Average	36.17 ± 7.34	13.78 ± 2.77	4.84 ± 0.35	2.88 ± 0.33	1.38 ± 0.23
Range	11.00-46.00	1.26-20.40	3.60-5.60	1.80-3.80	0.80-1.90

Of the 82 plants measured in 2018, there were 46 reproductive plants and 36 non-reproductive plants. As seen in Figure 2, no significance ($p>0.05$) was found for the effect of height, basal diameter, and number of leaves on whether *P. turbinata* was reproductive in 2018. Figure 2 also shows the average height, basal diameter, and number of leaves for reproductive plants and non-reproductive plants in 2018.

FIGURE 2

Average measurements of a.) height b.) basal diameter and c.) number of leaves for reproductive and non-reproductive plants of *Potalia turbinata* in 2018 (all p>0.05).



DISCUSSION

Phenology: Sakai (2001) studied phenological diversity in La Selva (20 km from Tirimbina) and noted that many trees follow an annual cycle at the community level in accordance with precipitation levels; *Potalia turbinata* follows this pattern at the population level. Phenological patterns in flowering and fruiting often differ from the population level to individual level (Sakai et al., 2005); individual plants have been known to have more irregular strategies than at the population level (Fenner, 1998; Boyle, & Bronstein, 2012). At the level of individuals, *P. turbinata* is supra-annual with only a few plants following an annual pattern. Subannual phenological patterns were highest at the individual level in La Selva, subsequently, annual patterns followed, and rare strategies included continuous and supra-annual (Newstrom et al., 1994; Sakai et al., 2005), making *P. turbinata* a rare exception to the norm at the individual level.

Understory species frequently differ from canopy species in their phenological patterns since they are smaller, present shorter lifespans, and have light limitations for allocating resources to flower and fruit development (Boyle & Bronstein, 2012). In La Selva, phenological patterns were studied in 168 treelets and shrubs of 29 species, which showed irregular phenological patterns between species that resulted in an aseasonal pattern at the community level; contrary to *P. turbinata*, the individual level phenological patterns usually reflected the population level patterns (Boyle & Bronstein, 2012). Some species of plants need to store enough resources in order to reproduce, and insufficient resources may cause a supra-annual fruiting pattern, because plants require longer periods of time to replenish between fruiting years (Fenner, 1998).

Several factors influence fruit and seed production, including resource allocation, predation of flowers, and effective pollination (Cunningham, 2000). Boyle and Bronstein (2012) mentioned light variation, rainfall, and nutrient availability to a plant as possible factors affecting flowering and fruiting patterns; although, in their study, precipitation was not an influencing factor. Other contributing factors to variation include competition and herbivory (Sakai et al., 2005). Cunningham (2000) studied an understory plant and found that floral predation was the main limiting factor on fruit production followed by the proportion of flowers visited by pollinators. In *P. turbinata,* all flowering plants produced fruits, and more than half of the flowers produced fruits in 2017, and in 2018, the majority of flowers appear to have produced fruits across the population. Due to the high production of fruit from flowers in *P. turbinata* and the variation from one year to the next, resource allocation and environmental factors seem more probable limiting factors than floral predation. Successful reproduction is more likely for plants that had high flowering synchrony as they satiate florivores and attract more pollinators (Bruno, Massi, Vidal & du Vall Hay, 2019). Though synchrony is not specifically measured in this study, *Potalia turbinata* shows a pattern of peak flowering in March across 3 years, and plants which flowered also bore fruits, indicating successful pollination. The influencing factors on fruit production need to be further explored in future studies on *P. turbinata,* and pollination strategies should be identified.

Tropical plants tend to have longer fruiting periods, averaging four months (Jordano, 1992). *Potalia turbinata* is one example in which we can see a lengthy fruiting period at the population level (ten months) and at the level of an individual plant (approximately seven months).

In this study, immature and mature fruits were considered together due to subjective separation of the categories during later months as a result of cryptic color and size changes. Immature fruit in early development present an underdeveloped turbinate ring. In future studies, to avoid ambiguity while deciding whether fruits are immature or mature, color could be measured and the diameter of the fruit ring across the months could be considered. Though it could be more demanding in the field, a higher resolution of the timing of important phenological events could be achieved, such as a more exact moment of fruit maturation. Additionally, the start of fruit dispersal could be used as an indicator of fruit maturity.

Potalia turbinata only had one flowering period per year in Tirimbina. Flowering took place at the beginning of the year and fruiting during the rainy season closer to the middle to second half of the year, which is consistent with patterns reported by Opler et al. (1980)—a lowland wet forest in Panama had maximum fruiting later in the year and flowering was more prominent in the first months. Flowering periods were shorter for supra-annual species and tended to occur in the dry season more than for annual or subannual plants (Bawa et al., 2003), which is similar to *P. turbinata* with a flowering period of four to five months during a period of less rainfall. Though the onset of the rainy season was not a significant determiner in the *P. turbinata* fruiting cycle, the flowering significantly correlated with less rain which in turn lead to the presence of fruit during the rainier months. Seed germination facilitation is one factor that may influence fruiting occurring during the rainy season (Garwood, 1983).

Plant measurements: The measurements taken of *P. turbinata* in this study support previously reported measurements of the plant and fruit. Height and basal diameter were consistent with Struwe and Albert (2004). *Potalia turbinata* was stated to have up to 30 flowers (Struwe & Albert, 2004), and there were no fruit counts reported before this study. The average fruit size in this study is slightly larger than previously reported by Struwe and Albert (2004); however, those measurements were taken from dry material which could lose 10-15% of its mass. Sanchez (2010) described the seeds as 4–5.5 mm which is in accordance with my findings. Additionally, number of seeds, weight, width, and thickness were measured, as well as fruit hardness. All of these measurements are noteworthy when investigating a resource for dispersal or consumption by animals, which should be investigated in further studies of *P. turbinata*.

The seeds of Neotropical woody species are primarily dispersed by vertebrates (Howe, 2014), and the size of the seeds influences whether they are ingested (Sebastián-González, 2017). Smaller seeds are more likely to be swallowed by a disperser and pass through the digestive tract; larger seeds (> 12 mm) tend to only be swallowed by large vertebrates including primates, tapirs, and peccaries (Fuzessy, Janson & Silveira, 2018). Seed weight in addition to length can influence whether a seed is swallowed or dropped as well as which frugivores act as dispersers; birds, bats, and small mammals are less likely to consume from large-seeded fruits (Fuzessy et al., 2018). Although, it has been shown that bats can disperse large-seeded fruits (Melo, Chazdon, Medellín, Ceballos & Rodriguez-Herrera, 2009). *Potalia* seeds are small and numerous, making them more likely to pass through the gut in order to be dispersed, although dispersion needs to be further investigated due to a lack of information.

Fruit hardness, which was measured in this study, may also affect fruit consumption. Dumont (1999) documents changing behaviors of phyllstomid bats when they consume fruits of varying hardness and indicates that some species have morphological traits that aid in consumption. Whichever strategy is implemented to consume fruit, there is a limit to the hardness that can be handled by some species. According to Dumont (1999), New World fruit bats' feeding behavior is related to fruit hardness. Additional studies on *Potalia turbinata* could contribute information on animal diets, considering the fruit hardness of this plant.

Plant vigor effects: The vigor of *P. turbinata* correlated with maximum crop size per reproductive plant, which concurs with other reports in which tree size is often related to reproductive output or has an influence on initial reproductive activity (Susko & Lovett-Doust, 2000; Fernández Otárola et al, 2013; Herrera, 1991). This trend has also been shown in other plants such as a cactus species studied by Bustamante and Búrquez (2008), which had higher flowering intensity and larger fruit crops from larger plants. A study in a lowland conifer forest investigated the effect of plant size, plant age, site factors, and canopy density on flower and fruit production of 9 understory shrubs; the study stated that plant size (closely followed by plant age) was the best factor in predicting reproductive output (Wender et al., 2004).

Light availability created by gaps may influence the resource environment which in turn influences plant size (Wender et al., 2004). Competition can also affect plant size, and a larger growth of a plant may show that it has more access to resources; crowding affects the plant reaching its maximum potential size and in turn affects its crop size or fecundity (Tracey & Aarssen, 2011). The effects of the resource environment and light availability should be studied in the future for *P. turbinata.* Fig tree fruit production may be influenced by the amount of time the trees are able to restore nutrients between reproductive cycles (Huang et al., 2019), which is another factor in addition to plant size that could be considered in future studies on *P. turbinata*.

Differing from the other plant size variables, the number of leaves did not correlate with plant height nor fruit crop size. Plants with higher leafing intensity commonly have higher fruiting intensity when the leaves are smaller in size, whereas plants with larger leaves produce large individual fruits or fruit clusters with a lower leafing intensity and also present a negative trade-off relationship between the two factors (Dombroskie, Tracey & Aarssen, 2016). *Potalia turbinata* has large leaves with a low count, which may explain the lack of correlation; however, there was not a negative relationship. The characteristics of the *P. turbinata* (height, diameter, and number of leaves) also did not determine whether a plant reproduced. A study in La Selva of approximately 2,000 trees from 17 species showed that the likelihood of reproduction could be predicted by plant size (Minor & Kobe, 2019), contrasting the results for *P. turbinata.*

Previously, specific phenological information was lacking for the genus *Potalia* apart from knowing in which months herbarium specimens were collected. I found that *Potalia turbinata* reproduces annually at the population level with irregularities at the individual level. Higher flower abundance coincides with drier months as predicted. The hypothesis of the fruiting phenophase correlating with rainfall was not supported. *Potalia turbinata* reproductive output correlates with plant vigor, concurring with initial predictions. This study provides information about phenological patterns of *P. turbinata* and its different measurements. The information gathered serves as a base for further investigation on *P. turbinata.* Next steps include identifying pollinator and disperser interactions with the plant as well as the abiotic factors that influence phenological strategies.

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CAPÍTULO 2. Seed Dispersal of *Potalia turbinata* (Gentianaceae) in a Tropical Humid Wet Forest of Costa Rica

(Con formato para Revista Biología Tropical)

Seed Dispersal of *Potalia turbinata* (Gentianaceae) in a Tropical Humid Wet Forest of Costa Rica

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Resumen: La dispersión de semillas es un proceso ecológico que implica la remoción y transporte de las semillas lejos de la planta madre. *Potalia turbinata*, es una especie endémica de Costa Rica y Panamá, de la cual no se cuenta con información sobre las interacciones con sus polinizadores y dispersores. El objetivo de este estudio fue identificar a los vertebrados que visitan la planta y consumen los frutos (potenciales dispersores), detallar el comportamiento de animales en la planta, y comprobar si hay diferencias temporales en las visitas entre dispersores. La recolección de datos se realizó durante los años 2016-2019 en la Reserva Biológica Tirimbina, en La Virgen de Sarapiquí, Heredia, Costa Rica, en un bosque tropical húmedo. Un total de 24 de plantas con frutos fueron monitoreadas con cámaras trampa. Todas las interacciones planta-animal con *P. turbinata* observadas fueron de mamíferos: un roedor (*Nyctomys sumichrasti*) y murciélagos (*Artibeus* spp., *Dermanura* spp., y *Carollia* spp). Los roedores a veces alimentan de los frutos in situ y los murciélagos hacen vuelos exploratorios antes de remover frutos. Se encontraron diferencias temporales significativas entre los roedores y murciélagos en los meses de la remoción de frutos. Los murciélagos visitan la planta los últimos meses de la temporada de fructificación en comparación con *Nyctomys* que llega más temprano durante la temporada. Las características de los frutos de *P. turbinata* son típicas de la dispersión por mamíferos por su color verde y la posición del fruto en la planta. Los murciélagos generalmente son dispersores efectivos, ya que dispersan las semillas lejos de la planta madre, mientras que los roedores tienden a ser depredadores de semillas. Este estudio aporta información sobre las interacciones planta-animal de *Potalia turbinata* que antes se desconocían.

Palabras clave: Gentianaceae, frugivoría, dispersión de semillas, interacciones planta-animal, síndromes de dispersión

INTRODUCTION

Seed dispersal is an ecological process that involves the removal of the seeds from the parent plant to improve their adaptive value (Janzen, 1984; Stoner & Henry, 2009). Seeds that are dispersed away from the parent plant have a higher survival rate due to less intraspecific competition and predation; thereby avoiding conspecific density-dependent mortality (Janzen, 1970; Connell, 1971; Comita et al., 2014; Lu et al., 2015; Zhu, et al., 2015; Kellner & Hubbell, 2018; Jia et al., 2020). In addition, dispersion of seeds helps to regenerate fragmented forests (Wunderle, 1997; González-Zamora et al., 2012; Carlo & Morales, 2016). In neotropical forests of Costa Rica, there have been several studies related to seed dispersal, seed rain, forest regeneration influenced by animal seed dispersion, important dispersal agents, and seed species diversity consumed by dispersers (Hunter, 1989; Guariguata et al., 2000; Barrantes & Pereira, 2002; Lopez &Vaughan, 2007; Zamora & Montagnini, 2007; Villalobos-Chaves et al., 2020b). Dispersal interactions are important to study due to the immense number of existing relationships and ecological networks yet to be understood.

While studying dispersion, several factors need to be considered such as the identity of the disperser, the behavior of the disperser (time remaining on the plant, and mobility for example), the timing of consumption, and the dispersers' effectiveness. Birds are the most important dispersers, followed by mammals, such as bats, primates, and rodents (Abrahamson, 1989). In Costa Rica, one study showed that birds, mammals, and wind were the most important agents of dispersal across plantations and abandoned pastures (Zamora & Montagnini, 2007). More than 80% of Neotropical plants depend on vertebrate frugivores for seed dispersal (Howe & Smallwood, 1982). Vertebrates disperse seeds by dropping them while consuming the pulp of the fruit, or by ingesting them together with the fruit and then defecating them (David, Manakadan & Ganesh, 2015). To further illustrate the importance of vertebrates as dispersers, Aliaga-Rossel & Fragoso (2015) showed that heavy hunting (defaunation) in a sub-montane tropical forest in Bolivia significantly affected seed removal of *Astrocaryum gratum*; with heavy hunting, 48.5% of the seeds remained as compared to no hunting with 1.75%. A similar trend was observed between sites in Costa Rica where a protected forest had a seed removal rate double that of an unprotected forest (Guariguata et al., 2000).

It is also important to consider temporal foraging patterns and the moment of fruit removal by a disperser during the fruiting cycle of a plant because immature fruit removal imposes a negative effect on the reproductive success of the plant (Niederhauser & Matlack, 2015). Additionally, immature fruits make digestion difficult, which can also influence the dispersal and use of the resource (Abrahamson, 1989). Niederhauser and Matlack (2015) studied the consequences of the consumption of *Podophyllum peltatum* fruits by *Odocoileus virginianus* and *Procyon lotor* and determined that not all frugivores are equal in their effectiveness. *Odocoileus virginianus* is a seed predator, while *P. lotor* increased the germination rate of ingested seeds; furthermore, the deer removed the immature fruits (82%) and decreased the possibility of the raccoon to consume fruits and seeds in their mature state. The survival of the seeds in the digestive tract varies according to the disperser species (25% in raccoons and 1% in deer). Only 5.5% of the fruits reached maturity due to premature consumption. Knowing when a fruit is mature and observing whether the disperser removes the fruit before it reaches maturity can aid in determining whether a disperser is effective or acting as a predator by removing fruits before the seeds are viable.

The time that a disperser remains in the same place also contributes to dispersal effectiveness and whether the seeds are deposited under or near the parent plant. The longer the disperser remains feeding on the plant, the higher the probability that the seed will settle near the mother plant (Abrahamson, 1989). Birds generally stay for a short time at feeding plants which helps them visit various species; some studies find numerous species of seeds in the feces and regurgitations of different birds (Abrahamson, 1989). Most species regurgitate or defecate after a range of 20 minutes to three hours (Abrahamson, 1989).

In Neotropical forests, bats are the most important dispersal mammals, dispersing at least 549 species, 191 genera, and 62 plant families (Lobova, Geiselman & Mori, 2009). Bats usually disperse mature seeds by consuming the fruits in their roosts or by defecating the seeds in flight (Lobova et al., 2009). However, there is little information on the dispersal (distance, ingestion benefits, etc.) of most species of fruit-eating bats, with the exception of *Carollia perspicillata* and *Artibeus jamaicensis* (Lobova et al., 2009). According to Abrahamson (1989), the spatial memory of the dispersers affects the success of dispersal, so that the dispersers return to the plants that provide the best benefits, either due to plant density in a field or the number of fruits exposed. Few species of bats have been recorded preying on seeds: Nogueira and Peracchi (2003) observed individuals of the genus *Chiroderma* (*C. doria* and *C. villosum*) destroying *Ficus* seeds; *Centurio senex* consumes *Sideroxylon capiri* seeds (Villalobos-Chaves et al., 2016); and *C. perspicillata* preys on the seeds of *Anacardium excelsum* (Bonoccarso, 1979).

Although rodents can be effective dispersers, they are primarily seed predators (Abrahamson, 1989; Weighill et al., 2017). In many cases, they are also considered secondary dispersers (moving the seeds after initial dispersion) (Chambers & MacMahon, 1994). In Costa Rica, Janzen (1982) showed that *Liomys salvini* removes at least 88.53% of the seeds under the Guanacaste tree, and accumulates them for consumption. Brewer and Rajmenek (1999), studied the granivory process of *Heteromys desmarestianus* which effectively disperses the seeds, since a significant proportion of the seeds that it buries, are not eaten by being forgotten or left by the disperser that dies or migrates, or because germination occurs before the disperser recovers the seed. This small percentage of neglected seeds becomes a significant amount of seedling recruitment during the life of a tree.

In addition to disperser characteristics and behavior, plant characteristics affect their interactions. Seed characteristics, including size and toxicity of fruits and seeds, affect dispersal interactions between animals and plants (Kuprewicz & Garcia-Robledo, 2019). Moreover, many plants have dispersal syndromes which attract dispersers, including color, size, shape, position, odor, and fruit ripening time (Abrahamson, 1989). A dispersal syndrome can be interpreted as an adaptation of the plant to attract its dispersers (van der Pijl, 1982). According to the hypothesis of dispersal syndromes, the characteristics of the fruits should predict their type of disperser (Lomáscolo et al., 2010). In this way, the most effective dispersers produce a selective pressure on the phenotypic characteristics of the fruit (Lomáscolo & Schaefer, 2010). Flörchinger et al. (2010) found that the selection of fruits by primates was affected by the quantity of fruits and the size of the plant and was not affected by the color; in the same study, birds ate from a wider variety of fruits, and fruit selection was more influenced by color. Conversely, the foraging decisions of primates with trichromatic vision may be influenced by color whereas monkeys with dichromatic vision rely more on fruit scent (Hogan et al., 2018; Melin et al., 2019). A comprehensive study on seed dispersal by birds showed that generally, smaller fruits were favored over larger fruits, and larger birds removed more fruits than smaller birds, making them more functionally important dispersers (Muñoz et al., 2016).

Dispersal agents of the plant *Potalia turbinata* have not previously been identified, and plant-animal interactions are lacking in information. The fruits of *Potalia turbinata* have several characteristics related to the chiropterochory syndrome (dispersal by bats). Chiropterochory syndromes include fruits exposed above the foliage, which makes them easily accessible to bats, and a green color (Mahandran et al., 2018), and the fruits change little in color at maturity (it is more common for them to remain green) (Van der Pjil, 1982). All of these characteristics are present in *Potalia turbinata,* in which the green fruits remain attached to the tree at maturity and are grouped in such a way that they can potentially be removed in flight. Fruits consumed by birds are usually red or black, while those of mammals are green, yellow, brown, or orange (Abrahamson, 1989). In *Potalia,* the seeds are immersed in little pulp and are generally small (typically less than 5 mm; Lobova et al., 2009).

The purpose of this study was to identify the vertebrates that remove fruits (an indication of dispersal) from *Potalia turbinata*, to detail the behavior of the dispersers as they visit the plant in the field, and to speculate on their dispersal effectivity as related to temporal segregation of arrival to the plant throughout the year and daily foraging times. Assuming the characteristics of a fruit can predict the type of dispersers it has, I expected mammals to remove *Potalia turbinata* fruits for consumption. Due to the known characteristics of *Potalia turbinata* (plant size, green fruits, and fruit position), I predicted that the fruits would be removed by bats.

MATERIALS AND METHODS

Study site and species: I collected data from 2016-2019 at the Biological Reserve Tirimbina (hereafter Tirimbina), in La Virgen de Sarapiquí, Heredia, Costa Rica (10°25' N; 84°47' W). Tirimbina is a humid tropical wet forest (Holdridge et al., 1971) with mainly mature forest. The area includes 345 ha with an elevation of 180-220 m.a.s.l. and presents an average annual temperature and precipitation of 24.3°C and 3777 mm respectively (Ley-López & Avalos, 2017). Rainier months occur May through November with a reduction of rainfall from January through April.

Potalia turbinata is an understory shrub or small tree with a height of 1-4.5 m restricted to the Caribbean slope of Costa Rica and Panama near Bocas del Toro; the species is possibly present in the region of Río San Juan in Nicaragua (Sánchez, 2010). This species has been observed from 5 to 350 m.a.s.l. (Struwe & Albert, 2004). In Tirimbina, the distribution is aggregated with a higher density in some areas of the forest. The leaves are simple, opposite, decussate, and oblanceolate. The flowers are on a compact inflorescence and have low variation in their color—they can be white, yellow, pale green, yellow-green, or green (Struwe & Albert, 2004). Individual plants produce an average of approximately 30 fruits ranging from 4 to 136 (R. Salazar, unpub. data). The green fruits are turbinate with a horizontal ring and may darken slightly as they mature. The peak of flower and fruits production is in March and June respectively (R. Salazar, unpub. data).

Identification of visitors to *Potalia turbinata* and behavior at the plant: I located and quantified the plants of *P. turbinata* in an area with high density of plants along an 805 m trail; I marked all plants within 10 m on each side of the trail. The total study area was 1.6 ha and included 83 plants 2016-2017 and 86 plants in 2018-2019. I recorded fruit visitors from the onset of fruit maturation in June until all fruits were removed by January of the following year. More specifically, the data collection periods ran from June 2016 – January 2017, June 2017 – January 2018, and June 2018 – January 2019.

In order to identify the vertebrates visiting *P. turbinata*, I placed camera traps with infrared triggers in the direction of fruiting plants (Bushnell, model 119476). I programmed the cameras to function 24 hours continuously and record 60-second videos at one-second intervals once triggered by movement. There were 24 cameras placed during the study—3 in 2016, 10 in 2017, and 11 in 2018. I lost the data from 3 cameras that disappeared. There were 2216 trap nights in total after excluding lost data. The visitors were identified to the species level when possible, and the interaction with the plant was noted between 3 categories: approaches fruits, removes fruits, and consumes fruits on site. Approaching includes an animal walking or flying over the fruits without removing a fruit. Removing a fruit included taking the fruit from the plant out of the view of the camera. Consumption on site includes the visitor consuming parts of the fruit while sitting at the plant.

I used the recording of visitors to the plants to describe animal behavior at the plant. I counted the number of approaches in each video before the removal of a fruit and I considered the direction of the approach, from below the plant or from a neighboring branch, or from flight. I also identified where on the fruits animals were biting to remove them. The description serves as an overview of the way a disperser removed the fruit.

Temporal variation of visitors at *Potalia turbinata:* In order to determine the temporal differences of visitors, I conducted two Pearson Chi-Square tests. The first test determined whether there were differences between dispersers in the time of year of visits to the plant, and I ran another test to compare if there were differences in the daily time arrival to the plant (24-hour periods). The time of the year was split between 2 time periods with known fruit presence with the assumption that the first period would have more immature fruits and the second period would have more mature fruits, in turn giving some indication of whether the fruits are removed as immature more frequently by any particular disperser. Furthermore, the sample size was not large enough to run a test by month of fruit removal. I also separated the hours of fruit removal into two groups. In both tests, I included the number of observations of animals removing fruits and consuming fruits on site; I did not include approaches without fruit removal. I used the program JMP version 7.0 for all analysis.

RESULTS

Identification of visitors on *Potalia turbinata*: Evidence of animals at *Potalia turbinata* was captured at 17 plants of 24 total plants monitored across the study. The cameras captured 122 videos with evidence of animals interacting (or potentially so) with this species. In 33 of the videos, the animals approached the fruits without removing any. In 89 of the videos, animals removed a fruit, 17 of which consumed parts of the fruit at the plant.

All of the approaches to the fruit, fruit removal, and fruit consumption of *P. turbinata* were from mammals. Neither birds nor reptiles visited the monitored plants. The animals that visited were Rodentia (*Nyctomys sumichrasti*), Chiroptera (*Artibeus* spp., *Dermanura* spp., and *Carollia* spp.), and Didelphimorphia (*Marmosa zeledoni*); however, Didelphimorphia was not seen removing or consuming fruits. Considering the 122 animal observations at the plant, mice represented 59.84%, bats 38.52%, and the mouse opossum 1.64%. In the 33 videos where the visitors only approached the fruits, mice represented 54.55%, and bats 39.39%, and 6.06% the mouse opossum. From the 89 videos in which fruits were removed or consumed on site, 61.80% were removed by mice and 38.20% by bats. Only rodents consumed the fruits on the plant—*Nyctomys sumichrasti* is the only rodent identified consuming fruits, while 4 videos remain unidentified due to poor video quality. TABLE 1 shows a list of orders, families, and species that approached the fruits, removed them, or consumed them on site and the corresponding number of observations.

TABLE 1

List of orders, families, and species that visited Potalia turbinata and the number of observations per interaction type (approaches fruit, removes fruit, consumes fruit on site)

Order	Family	Species	Approaches Fruit	Removes Fruit	Consumes Fruit on Site
Rodentia	Cricetidae	*Nyctomys sumichrasti*	17	38	13
	NA	NA	1	0	4
Chiroptera	Phyllostomidae	*Artibeus* spp.	4	9	0
		Dermanura spp.	7	23	0
		Carollia spp.	2	2	0
Didelphimorphia	Didelphidae	*Marmosa zeledoni*	2	0	0

Nyctomys sumichrasti arrived by climbing up the trunk of *P. turbinata* or occasionally from a neighboring branch. They removed fruits by biting the turbinate ring of the fruit and pushing upwards or by biting the fruit at the base and pulling. After removing a fruit, they left the same way they arrived – down the trunk or on a neighboring branch respectively. Mice which handled fruits on site selected and removed the fruits before feeding on them. They ate from their selected fruit over the infructescence or on a leaf next to the fruits; mice moved under the leaves of the plant to consume the fruits only on a few occasions. In 3 videos, rodents are seen spitting out what appears to be pieces of the fruit. By video observation, it is not clear whether they are only consuming seeds. In the field, a few fruits were found with the top of the fruit bit through and the seeds missing.

Bat foragers showed approach behavior through exploratory flights (low flights above the infructescence) and approaches to the fruits (hovering and making contact with fruits in flight) 0-8 times before removing a fruit with an average number of approaches observable by camera at 2.26 ± 2.40. Since I positioned the cameras close to the fruits, cameras did not capture potential search and orienting flights farther above the plant prior to approach behavior. The bats removed the fruits after landing on the infructescence in 73.52% of the videos and removed the fruit in flight on 26.47% of occasions. In flight removal of fruits was almost exclusively by *Dermanura* spp. on 7 occasions and twice by *Artibeus* spp. On 5 occasions, bats landed after the exploratory flights in what appeared to be failed attempts at fruit removal before flying away, returning, landing, and removing a fruit. *Dermanura* spp. also moved their bodies or heads over the fruits in 6 videos before selecting and removing a fruit. Bats bit the turbinate ring or the tips of the fruits in order to remove them.

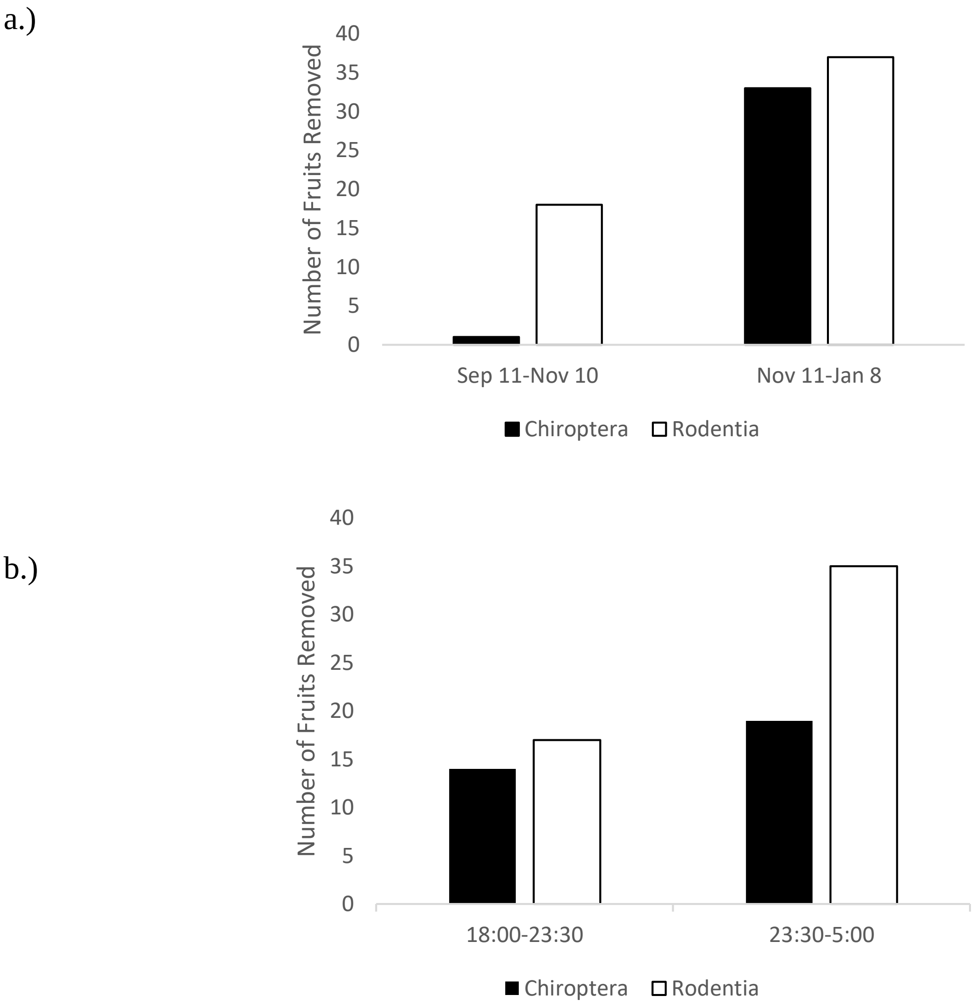
Temporal segregation of visitors of *P. turbinata*: September 11 was the earliest date throughout the study years in which I observed a fruit being removed from *Potalia turbinata*. Likewise, the latest date to record an animal removing a fruit was January 8. The majority of videos captured was from 18:00 to 5:00. The hour with the most videos was between 2:00 and 3:00 with 21 videos and representatives of the 3 orders. There were no observations between 12:00-17:00.

I divided the fruiting period into two groups: September 11-November 10 and November 11-January 8, from the day with the first fruit removal to the last day a fruit was removed. A total of 89 videos with fruit removal were included in the analysis. I also divided the hours into two groups: 18:00-23:30 and 23:30-5:00. Outliers of visits between 7:00 and 11:00 were not included, which left a total of 85 interactions in the analysis of foraging times. Didelphimorphia was not a part of the analysis since they did not remove fruits.

Mice arrived more frequently and earlier in the fruiting period of *Potalia turbinata* than bats, and there was a significant difference between in their arrival times (χ^2 = 11.02, df=1, p = 0.001). I did not find differences between the behavior of mice and bats between early or late at night (18:00-23:30 and 23:30-5:00) foraging on *Potalia turbinata* (χ^2 = 0.820, df = 1, p = 0.365). Mice and bats arrived more frequently in the second time group than the first. The number of fruits removed per group by dates and hours can be seen in FIGURE 1.

FIGURE 1

The number of fruits removed by Chiroptera and Rodentia during the fruiting of Potalia turbinata by a.) dates (September 11-November 10 and November 11-January 8) and b.) by hours of the night (18:00-23:30 and 23:30-5:00)



DISCUSSION

Fruit removal from *Potalia turbinata*: This study supports my original prediction of mammals removing fruits from *Potalia turbinata*, as well as bats removing fruits from the plant. Mammals exclusively removed fruits at the monitored plants; 3 genera of bats (*Carollia*, *Artibeus*, and *Dermanura*) and 1 species of rodents (*Nyctomys sumichrasti*). The bats in this study could be *A. jamaicensi* or *A. lituratus*, *C. perspicillata* or *C. sowelli*, and *D. watsoni* or *D. phaeotis*. The species mentioned within the same genus must be captured to identify the species level with certainty due to their similarities (i.e., their size). All of the bat species in this study are primarily fruit generalists but may consume floral parts and insects (Cretekos et al., 2005; LaVal & Rodríguez-Herrera, 2002; Baker et al., 1977*). Carollia perspicillata* disperses *P. amara* by passing them through their gut (Lobova et al., 2009), therefore a relationship between the genus *Carollia* and *Potalia* was already known and further observed in this study with *Potalia turbinata*. *Artibeus* spp and *Dermanura* spp are newly identified dispersers of *Potalia*, as is Sumichrast's vesper rat *Nyctomys sumichrasti*, which besides this plant consumes *Ficus* fruits, seeds, and other vegetative matter (Hunt et al., 2004), but otherwise has little known dietary information (Villalobos-Chaves et al., 2020a). *Marmosa zeledoni* only approached the fruit of *Potalia turbinata* but did not remove any fruit. No bird species approached fruits of *Potalia turbinata* during this study despite frugivorous birds being the most important seed dispersers (Abrahamson, 1989). Primates are also important dispersers but were not a mammal that visited *Potalia turbinata*.

The characteristics of *Potalia turbinata* are typical for mammal dispersers with its green color and fruit position, which supports the hypothesis of dispersal syndromes (fruit characteristics should predict their dispersers) (Lomáscolo et al., 2010). Birds tend to consume redder fruits with a contrast against the foliage (Valenta & Nevo, 2020; Lomáscolo & Shaefer, 2010; Abrahamson, 1989). Though primates consume greener fruits than birds (Valenta & Nevo, 2020), primates select higher trees that offer higher quantities of fruits (Flörchinger et al., 2010). *Potalia turbinata* only measures up to 4.5 m (R. Salazar, unpub. data) and does not fit the primate plant syndrome for its height, and although birds select smaller plants (Flörchinger et al., 2010), the color and contrast to surrounding foliage do not support typical bird plant syndromes. The position of the fruits allowed bats to grab fruits in flight or land on the fruit and take off in flight again quickly. Consumption of fruits with smaller seeds and later defecation of those seeds is characteristic of bats (Hodgkison et al., 2003). The seeds of *Potalia turbinata* are small (average length of 4.84 ± 0.35) and numerous (average count of 36.17 ± 7.34) (R. Salazar, unpub. data), which could pass through the digestive tract of bats offering an effective dispersal route.

Behavior of Sumichrast's vesper rat: *Nyctomys sumichrasti* is an arboreal species and rarely at ground level, preferring to stay 3-22 m high in trees (Timm and LaVal 2000). The maximum 4.5 m height of *Potalia turbinata* is within the species' preferred range, though Perez-Lustre et al. (2010) reported about 46% of captures even higher, between 9-21 m. Inhabiting an arboreal niche lowers risks of predation by terrestrial predators (Abreu et al., 2010). *Nyctomys sumichrasti* was the only species of Rodentia to remove fruits from *Potalia turbinata* and the only species in the study to feed on fruits in situ. Villalobos-Chaves et al. (2020a) also described

Nyctomys sumichrasti as a seed predator feeding on arils of *Tabernaemontana glabra* seeds in situ at 4 m high in Costa Rica. On the other hand, Sumichrast's vesper rat has also been observed feeding on just the pulp of palm fruits with a pulpy mesocarp and leaving the seeds (Bessesen & Saborío-R, 2009). Consumption at the plant and observations of the species spitting out fruit pieces provide evidence that this rodent is a seed predator of *Potalia turbinata*; furthermore, the fruits of this plant species are not pulpy.

The question remains of how mice treat *Potalia turbinata* seeds after taking fruits away from the plant; the fruit may be stored or consumed immediately. *Potalia turbinata* seeds, due to their small size may not be worth caching; larger seeds are preferred for hoarding since they are more valuable than smaller seeds in terms of higher nutrition, lower toxicity, and facility of digestion (Shimada et al., 2015). Upon feeding, some of the small seeds could fall during handling even if the fruits are removed for immediate consumption of seeds. A study conducted in a Costa Rican tropical premontane wet forest showed that agoutis dispersed larger seeds farther away from the parent plant in comparison to smaller seeds which were primarily consumed at the parent plant (Kuprewicz & Garcia-Robledo, 2019). The majority of observations of *Nyctomys sumichrasti* showed the fruit being taken away from the site, but the exact distance and fruit handling decisions remain to be explored. In another study, *Nyctomys sumichrasti* males and females travelled an average of 35.42 m (range 10.3-75.1 m) and 34.86 m (range 20.1-60.32 m) respectively (Perez-Lustre et al., 2010). Perhaps the behavior and home range of Sumichrast's vesper rat influence the clustered distribution of *P. turbinata.*

Behavior of bats: *Potalia turbinata* is an understory plant species. *Carollia perspicillata* and *Dermanura watsoni* are understory foragers (Bernard, 2001; Ripperger et al., 2013) while *Artibeus jamaicenses* is typically a canopy frugivore (Bonaccorso, 1979). All 3 species showed approach behavior to *Potalia turbinata* fruits in exploratory flights before removing one.

These bats have been found to use olfactory cues as the main method of detecting ripe fruits and their general location paired with echolocation in order to determine more exactly the orientation of the fruits (Korine & Kalko, 2005; Thies & Kalko, 1998; Kalko et al., 1996). *Carollia* is described as using scent in exploratory flights as a detection tool, swooping over fruit several times before employing echolocation in a final approach—this experiment also controlled for light exposure to rule out sight detection (Thies & Kalko, 1998). Fruit position influences the combination of scent and echolocation use (Thies & Kalko, 1998). Korine and Kalko (2005) exposed *Dermanura watsoni* to ripe and unripe fig fruits of various sizes and it used a combination of scent and echolocation to locate the fruit—large ripe fruits were preferred. The species exhibited an orienting call and approach call, echolocating continuously as it foraged, but it did not use a terminal phase call and usually removed fruits in flight (Korine & Kalko, 2005). Even though orienting flights and echolocation were not examined, the general overview of bat behavior at *P. turbinata* plants is consistent with other studies except that *Dermanura watsoni* removed fruit more frequently during a brief landing versus in flight. Possibly, *Potalia turbinata* fruits are more difficult to remove than fig fruits and require a brief landing.

Although it was not measured in this study, the distances travelled by each disperser after fruit removal can provide insight to the dispersal of this plant. In Costa Rica, the average travelled distance by *Carollia perspicillata* between forage and refuge sites was observed at 1.6 km and 1.6 and 1.5 km between feeding sites and within feeding sites respectively (Heithaus & Fleming, 1978). Fleming (1988) observed the species flying as far as 3.7 km from its refuge in Santa Rosa National Park, Costa Rica. *Artibeus jamaicensis* showed a similar niche distance in Panama at 1.61 km (Ortega & Castro-Arellano, 2001) but has several reports of longer flight distances such as 1-4 km on average and 3-10 km frequently (Handley et al. 1991), and up to 21 km for *Artibeus literatus* (Esbérard, 2003). Foraging areas are smaller for *Dermanura watsoni*, with an average of 2 ha (Albrecht et al., 2007). Even so, the species was observed flying distances of 25-180 m between foraging areas in a fragmented neotropical landscape (Albrecht et al., 2007), and another small bat, *Artibeus phaeotis* flew 650 m over grassland (Montiel et al., 2006). The high mobility of the phyllostomid species show the value they can have as dispersers. Bats have the potential to move seeds far from the parent plant and deposit the seed in new geographic locations.

Temporal segregation of dispersers: Bats and rodents did not have the same temporal intensity—rodents began more intense foraging on *P. turbinata* at an earlier time during fruiting months than bats. It is possible that rodents were consuming fruits prematurely. Frugivores can be negatively affected by immature fruit due to secondary metabolite concentrations (Mahandran et al., 2016), and fruits consumed by bats have fewer secondary metabolites than fruits consumed by other mammals (with considerable overlap) (Cipollini & Levey, 1997). Hovering behavior over the infructescence of a plant aids bats in determining ripeness of fruits through smell (Muchhala & Serrano, 2015). Seed predators, especially those which arrive before a fruit is ripe, cause less fruit availability for higher quality dispersers (Niederhauser & Matlack, 2015).

Bat arrival may indicate fruit ripeness of *Potalia turbinata.* Fruit counts peak in June with approximately 1,600 fruits counted at Tirimbina in 2018; nearly half of the fruits still remained on the plants in September, long after assumed fruit maturation in July, and did not completely disappear until January of the following year (R. Salazar, unpub. data). Further studies should explore why fruits were left on the plants and whether it is related to fruit maturation, plant location, a particular plant characteristic such as height, or other available resources more pertinent to its visitors' diets. The nutritional values of the fruits and seeds should also be detailed to explore what role *P. turbinata* plays in the diets of its consumers.

Foraging activity at *P. turbinata* does not differ by hour between bats and mice; however, activity differs more notably for mice between early and late at night. Rodentia is represented by one species (*Nyctomys sumichrasti*) vs Chiroptera which is represented by 3 species (*Artibeus* spp, *Dermanura* spp, *Carollia* spp). Risks of predators during the day may favor nocturnal patterns of foraging by rodents and select against diurnal patterns (Weighill et al., 2017). The majority of bats are also nocturnal, and their foraging times vary across species—some appear around sunset and subsequently around dawn whereas others may forage all night (Rydell et al., 1996). *Carollia perspicillata* emerges about 24 minutes after sunset on average according to one study (Bonaccorso et al., 2006). *Artibues jamaicenses* also emerges after dark, about 45 minutes after sunset and forages through the night until dawn –returning to its day roost during high moonlight hours (Morrison, 1978); *Artibeus lituratus* exhibits this habit as well (Morrison, 1980). *Dermanura* *watsoni* similarly begins to forage at 18:00 hours (Chaverri et al., 2007). The month and hour data provide information for when to put up cameras or nets for trapping in future studies.

It is important to note that consumption does not define whether seeds are dispersed effectively (Howe, 2016). Bats do not necessarily provide a benefit to seeds by passing them through the gut, but bats act as a medium for dispersing seeds far from the parent plant (Saldaña-Vázquez et al., 2019). Phyllostomid bats are known to be valuable in providing pollination and seed dispersal services and aiding in habitat connectivity in fragmented landscapes (Ripperger et al., 2015; Ghanem & Voigt, 2012). Further testing should be done to determine dispersal effectivity by all dispersers and whether passing through the gut of Chiropteran species enhances germination rates in the case of *Potalia turbinata*.

The results of this research support the dispersal syndrome hypothesis and my initial predictions that mammals would be the sole removers of fruits at *Potalia turbinata.* Based on the differences in behavior, temporal segregation, and potential dispersal distance, I conclude that bats are more effective potential dispersers of *Potalia turbinata* seeds than Sumichrast's vesper rat. This study provides new information about *P. turbinata* and animals which remove its fruits. The information presented here also provides a baseline for future studies to further enlighten the plant-animal relationships of *P. turbinata* and its role in mammal diets.

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