

**IMPACT OF EDGE EFFECT ON DIVERSITY
AND DIET OF INSECTIVOROUS BATS IN
PENANG ISLAND**

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PENANG ISLAND**

by

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IMPAK KESAN PINGGIRAN KEPADA KEPELBAGAIAN DAN DIET KELAWAR INSEKTIVOR DI PULAU PINANG

ABSTRAK

Kehilangan habitat di Pulau Pinang telah meningkat baru-baru ini disebabkan perubahan tumbuh-tumbuhan semulajadi akibat pertanian dan urbanisasi. Kesan pembentukan pinggir hutan terhadap populasi kelawar di Pulau Pinang masih belum dikaji. Tesis ini bertujuan mengisi jurang penyelidikan berkaitan kelawar insektivor di pinggir hutan Pulau Pinang, sekaligus meningkatkan pemahaman ilmiah tentang bagaimana kesan pinggir mempengaruhi kelawar Paleotropik. Pertama, impak kesan pinggir pada komposisi komuniti kelawar insektivor dikaji. Jaring kabut dan perangkap harpa digunakan dari Januari hingga Disember 2019 bagi merekodkan kelimpahan, kekayaan dan kepelbagaian spesies dalam kumpulan kelawar di dua lokasi di pinggir hutan. Keseluruhan Shannon bagi kepelbagaian yang dianggarkan adalah tidak tinggi secara relatif ($H' = 1.38$), tetapi 13 spesies yang dijumpai, 15–19 spesies yang dianggarkan dan kadar tangkapan yang lebih tinggi (4.18/ perangkap-malam) menunjukkan bahawa kesan pinggir mungkin mempengaruhi kepelbagaian dalam himpunan kelawar Paleotropik. Tidak ada perbezaan dalam kepelbagaian spesies antara lokasi gelap dan terang di pinggir (masing-masing 11 spesies), tetapi beberapa spesies secara individu cenderung ditangkap pada satu lokasi lebih banyak daripada yang lain. Kedua, diet spesies kelawar insektivor biasa di kawasan kajian (*Hipposideros armiger*, *Hipposideros kunzi*, *Rhinolophus affinis*, *Rhinolophus lepidus*, *Rhinolophus pusillus* dan *Rhinolophus steno*) diperiksa menggunakan analisis tinja. Kumpulan serangga utama yang terdapat dalam diet termasuk Coleoptera, Isoptera, Hemiptera, Lepidoptera, Hymenoptera dan Diptera. Kumpulan-

kumpulan ini mencerminkan ketersediaan serangga di persekitaran berdasarkan perangkap cahaya dan berkorelasi secara kuat dan positif dengan diet kelawar ($P < 0.05$). Ini menunjukkan perlakuan pemakanan oportunistik kepada semua spesies kelawar yang dikaji. Lebar nic trofik spesies kelawar kebanyakannya tinggi ($B = 0.5-1$) kecuali bagi *Hipposideros armiger* ($B < 0.5$). Pertindihan nic berkisar antara sederhana hingga tinggi ($P_{jk} = 40-90\%$) dengan tahap persaingan rendah (perbezaan interspesifik dalam diet, $P < 0.05$). Dari kajian ini, ketersediaan dan kepelbagaian makanan yang berterusan ($H' \geq 1.50$) menunjukkan bahawa kawasan pinggir hutan mampu menyediakan kawasan pencarian makanan yang sesuai untuk kelawar insektivora di Pulau Pinang yang membenarkan pembahagian sumber dan memainkan peranan penting dalam kelestarian kelawar. Namun, keadaan hujan mungkin mempengaruhi dan membatasi pemilihan mangsa kelawar kepada jenis mangsa tertentu. Akhir sekali, analisis diet spesies kelawar menunjukkan bahawa ia berpotensi sebagai kawalan biologi untuk serangga perosak.

IMPACT OF EDGE EFFECT ON DIVERSITY AND DIET OF INSECTIVOROUS BATS IN PENANG ISLAND

ABSTRACT

Habitat loss in Penang Island is recently rising due to the changes in the natural vegetation cover resulting from the agriculture and urbanization. The effect of edge formation has not been studied on bat population in Penang Island. The purpose of this thesis is to fill multiple research gaps related to the insectivorous bats in the forest edges of Penang Island, thereby increasing scientific understanding of how edge effects impact Paleotropical bats. First, the impact of edge effects on an insectivorous bat community composition was studied. Mist nets and harp traps were employed from January through December 2019 to record species abundance, richness and diversity in an assemblage of bats in two sites of a forest edge. The overall Shannon estimate of diversity was relatively not high ($H' = 1.38$), but the 13 discovered species, 15–19 estimated species and a higher capture rate (4.18/ trap-night) indicated that edge effects probably influence the diversity in Paleotropical bat assemblages. There was no difference in species diversity between dark and light sites of the edge (11 species each), but some species individually captured in one site more than the other. Second, diets of common insectivorous bat species in the studied area (*Hipposideros armiger*, *Hipposideros kunzi*, *Rhinolophus affinis*, *Rhinolophus lepidus*, *Rhinolophus pusillus* and *Rhinolophus steno*) were examined using the fecal analysis. The main insect groups found in the diets including Coleoptera, Isoptera, Hemiptera, Lepidoptera, Hymenoptera and Diptera. These groups reflected the insect availability in the environment based on light trapping and strongly-positively correlated with bat diets ($P < 0.05$). This suggested opportunistic feeding behavior to all studied bat species.

Trophic niche breadths of bat species were mostly high ($B = 0.5-1$) except *Hipposideros armiger* ($B < 0.5$). Niche overlaps ranged from moderate to high ($P_{jk} = 40-90\%$), but the competition levels were low (interspecific differences in diet, $P < 0.05$). From this study, the constant food availability and diversity ($H' \geq 1.50$) suggested that forest edges may provide suitable foraging areas for insectivorous bats in Penang Island that allow for resource partitioning and play essential roles for bat sustainability. Yet, rainfall conditions likely impacted and limited the prey selection of bats toward specific prey types. Lastly, dietary analyses of bat species indicated that they are potentially become biological control for pest insect.

CHAPTER 1

INTRODUCTION

Chiropterans or bats, with more than 1,400 species, form a major component of mammalian biodiversity, and makes up about 22% of mammals worldwide and 50% of mammals in tropical forests (Simmons, 2005; Simmons & Cirranello, 2020). Bats are key to the ecosystem as they are responsible for services such as seed dispersal (Florens *et al.*, 2017), pollination (Ober & Tsang, 2019), recycling of nutrients (Kunz *et al.*, 2011) as well as pest insect control (Burgiełł, 2018). Yet, bats are naturally and anthropogenically threatened, and these threats locally and regionally affect their distribution and diversity, experiencing high rates of extinction (Mickleburgh *et al.*, 2002; Fleming & Racey, 2010; Frick *et al.*, 2019). In Southeast Asia alone, about 20% of bat species are expected to be extinct by the year 2100 (Lane *et al.*, 2006). One of the most daunting problems not only to bats but also to the global biodiversity is the increasing losses of natural habitat as a result of land fragmentation and incessant changes to how lands are used (Russo & Ancillotto, 2015). The problem is more pronounced in Southeast Asia region, exacerbated by the loss of tropical forests. Therefore, the region has the fastest rate of forest loss in the tropics (e.g., Stibig *et al.*, 2014), fuelled by large scale logging, rapid expansion of cash crop cultivation and currently booming construction projects (Laurance *et al.*, 2015; Sloan & Sayer, 2015). Lasting forest loss and fragmentation means that much remaining forests potentially subject to what are called *edge effects* (Barber *et al.*, 2014; Haddad *et al.*, 2015).

The edge-effect phenomenon forms if continuous habitats are breaking up (Yoh, 2018). Deforestation process principally leads to creating a mosaic of smaller

fragments. Another effect is the concomitant decline and local extinction of species due to the loss of natural habitats. This is also compounded by reduced habitat connectivity (Didham, 2010; Yoh, 2018) and “crowding effects” (Turner, 1996). Nevertheless, the remaining ecological communities in created fragments are not in any way fixed. They are subjected to biotic and abiotic changes arising out of these fragments (Laurance *et al.*, 2017). These changes are known as *edge effects*. The effects are some of the most significant factors influencing the dynamics as well as displaced fauna and flora (Broadbent *et al.*, 2008; Laurance *et al.*, 2017) as they overshoot inherent natural changes in conditions. Therefore, they adversely affect the ecosystems and their suitability for species they adequately supported before (Murcia, 1995; Rocha *et al.*, 2017). Due to the diversity in edge-related phenomena, adding the sheer complexity of bio-interactions and mechanisms underlining, the edge-effect phenomenon is not fully understood yet despite it is being one of the most studied ecological phenomena in the last century (Ries *et al.*, 2017; Yoh, 2018).

Physical consequences of edge creations can affect the capacity of biodiversity in fragmented and continuous forests through increased light penetration (Haddock *et al.*, 2019), amplified temperature fluctuations (Murcia, 1995), exposed wind stress (Laurance *et al.*, 2017) and reductions in relative humidity (Cochrane & Laurance, 2002). The effects could reach to 15–500 m within the fragment or forest (Laurance, 1991; Villaseñor *et al.*, 2015), according to the type of forest and the extent of degradation out of the fragment or forest. For bats, edge effects are most likely to reduce at 50 m, which is a threshold where many abiotic effects show decline (Rocha da Silva *et al.*, 2013). Notwithstanding, yet, there is no globally reliable estimate regarding how long the distance from an edge is a particular species, functional group

or guild can be impacted (Hansbauer *et al.*, 2008; Yoh, 2018). Studies agreed that edge formations significantly affect bats in fragmented and continuous forest (reviewed in Meyer *et al.*, 2016). However, how tropical bats respond to edges is adequately studied yet, particularly in Paleotropics (Meyer *et al.*, 2016). In Neotropics, tropical bats displayed variable responses to edge formations and do not support a unifying theory (Morris *et al.*, 2010; Pettit, 2011; Meyer *et al.*, 2016).

In Paleotropics, bat assemblages are often dominated by species of the following families: Rhinolophidae, Hipposideridae and Vespertilionidae, particularly subfamilies Kerivoulinae and Murininae (Kingston *et al.*, 2003; Furey *et al.*, 2010). These species are all insectivorous and many of them are not found in Neotropics. The majority of these species are well-adapted to forage in forest interiors (“narrow-space” bats, *sensu* Schnitzler & Kalko, 2001). As such, they are far more sensitive to the loss of forests and keenly avoid open and disturbed environments (Kingston *et al.*, 2003). Therefore, a clear pattern of negative response to edge habitats likely occurs in assemblages of Paleotropical bats. The first objective of this thesis focused on the impact of edge effects that may have on the community composition of Paleotropical insectivorous bats by measuring species abundance, richness and diversity of a bat assemblage in a forest edge of Penang Island.

Artificial light adjacent to forest edges is one pressure that may drive the diverse responses of bats to edge habitats. Ultraviolet radiation attracts high numbers of insects and could offer suitable feeding grounds for many bat species that are adapted to exploit this resource (Blake *et al.*, 1994; Haddock *et al.*, 2019). Ecologically, insectivorous bats are a diverse group (Simmons, 2005), and respond in

variety ways to different resource types of habitats and food taking in the account their own morphological characteristics and echolocation systems (Norberg & Rayner, 1987; Fenton, 1990; Threlfall *et al.*, 2011). For example, some faster flying open-space adapted bat species are able to dive through the lit cone when foraging (Blake *et al.*, 1994) and perhaps able to evade aerial predators that use the lit areas as hunting grounds. Conversely, slower flying clutter adapted species often avoid artificially lit areas (Stone *et al.*, 2012) and may be constrained by light patch edges, spending the majority of their foraging time within dark edge patches (Threlfall *et al.*, 2013), and thereby reducing the overall functional of edge habitats. In this study, the impact of light and dark edges on species diversity of insectivorous bats was also targeted.

Knowledge of animal diets is imperative for inferring their roles in ecosystem as predators and their effects on the surroundings. Such information is particularly significant as natural habitat is being subjected to change due to increased urbanization, modernistic agricultural applications and deforestation (Kunz *et al.*, 2011; Kemp *et al.*, 2019). Bats worldwide have a broad range of food preferences, generally they may feed on or have a combination of the following: insects, fruits, blood, fish and small vertebrates (Kunz *et al.*, 2011). Hence, bats can be useful as primary, secondary and tertiary consumers to ecosystems that benefit and support both natural and anthropogenic ecosystems, varying from simple to complex ecosystems. Thus, obtaining knowledge on bat diets is essentially important for appropriate management to promote their conservation (Vaughan, 1997; Kunz *et al.*, 2011). Knowledge on diets of different bat species can be also helpful when a study on a bat community is targeted, as it may give insight into how food resources are distributed within that community (Salinas-Ramos *et al.*, 2015; Gordon *et al.*, 2019).

The study of insectivorous bats feeding habits is important as they are believed to play an essential role in influencing insect populations both in agriculture and forest areas, where they act as a biological control agent for many of major insect pests that badly affect agricultural sectors and forest trees (Kunz *et al.*, 2011; Burgieł, 2018). Such services postulate to provide important economic benefit. For example, in USA, the approximation of bat services as a result of drop application of pesticides costs due to pest suppression by predation is in the range of 3.7–53 billion dollars annually, not including the cost of impacts of insecticide and pesticides on ecosystems (Boyles *et al.*, 2011). However, the magnitude of prey consumption by insectivorous bats can be influenced by numerous factors, including time of nocturnal emergence (Milne *et al.*, 2005), seasonally changing energy and nutrient demands (Kunz *et al.*, 1995), temporal distribution and spatial distribution of prey (Hayes *et al.*, 2019) and prevailing climatic and meteorological conditions (Kaupas & Barclay, 2018). Thus, knowledge on the local diets of insectivorous bats is basically required to make informed conservation decisions. The knowledge is also necessary to define food compositions, understand partitioning and ecological interactions of bats in a particular habitat (Salinas-Ramos *et al.*, 2015) and highlight the functioning in insect suppression (Kunz *et al.*, 2011).

Since bats provide a considerable function in controlling insect populations, having information on insect prey is, otherwise, significant in evaluating the possible value of bats in controlling insect pests, particularly in areas where urban and cultivated lands have substituted natural habitat (Kemp *et al.*, 2019; Kolkert *et al.*, 2020). Further, insectivorous bats feed on insects of various groups with different methods, at different altitudes and from non-flying insects on the ground or water surfaces to airborne insects flying as high as 3000 m over the ground (Sales & Pye,

1974; Vaughan, 1997; Kunz *et al.*, 2011). On the other hand, insects are available year-round, and in any case, they might be affected by changing of climatic conditions. For example, in tropical regions, aerial insect activity changes directly and indirectly with precipitation, humidity and temperature (Pereira da Silva *et al.*, 2011; Kishimoto-Yamada & Itioka, 2015). Therefore, a well-understanding of insect prey used by insectivorous bats requires an understanding of prey availability and diversity in the foraging areas.

1.1 Rationale of Research

Penang Island is among the most populated Islands in the world with 1,663 people per square kilometer (Department of Statistics Malaysia 2010, Leen *et al.*, 2019). It has 1.77 million people on the 1,032 km²-state, and the average population growth rate is 1.3% (Penang Institute 2017, Leen *et al.*, 2019). The population of the Island is predicted to increase significantly in the next 15 years (Chee *et al.*, 2017). Moreover, the urbanized parts of the Island have exponentially increased since 1960, resulting in the loss of natural habitats (Chee *et al.*, 2017), which in turn, could significantly affect the population of wildlife or even outright extinction (Hong & Chan, 2010). In the same vein, the Island still witnesses an alarming rate of deforestation in Southeast Asia. It is also considered by the National Aeronautics and Space Administration (NASA) as one of the hotspots of deforestations in Peninsular Malaysia (Masum, 2017). These issues can make Penang Island an ideal case study to learn about impacts of habitat loss and change on the wildlife in order to facilitate feasible conservation actions, if necessary (Leen *et al.*, 2019).

The current bat fauna of Penang Island is relatively higher with 36 species presents compared to the other coastal Islands of Peninsular Malaysia such as Langkawi Island (25 species) and Singa Besar Island (29 species), for example (Roslan *et al.*, 2016). The number also seems to be higher compared to the regional-urbanized Island, Singapore (25 species, Simmons, 2005). The higher number of bat species on Penang Island could be due to the good record of bats since the year 1900 by Flower, with expectations that some species might be extinct due to the rapid industrialization (Roslan *et al.*, 2016). Even so, bat communities in Penang Island are still one of the least studied animals, but information on diversity, ecology and behavior has been recently provided (Nur-Juliani, 2016; Nur-Izzati, 2018; William-Dee *et al.*, 2019). Given the ongoing threats facing the biodiversity-rich of Penang Island ecosystem, particularly in the form of deforestation and habitat degradation and their consequences of fragmentations and edges, there is an urgent need for understanding to what extent these consequences affect bat diversity and ecology. The results would certainly lead to better conservative planning and management of bats in Penang Island.

1.2 Objectives and hypotheses

The objectives of this research are:

1. To test the impact of edge effects on a community composition of Paleotropical insectivorous bats in dark and light sites of a forest edge in Penang Island by studying species abundance, richness and diversity in an assemblage of bats.
2. To identify diet compositions, measure trophic niche breadths and overlaps of bats, and examine the partition of food resources among bat species.
3. To investigate influence of food resource availability and the rainfall condition gradients: no rainfall (NR), light rainfall (LR) and heavy rainfall (HR), on the dietary ecology of insectivorous bats.

The objectives will be addressed following three hypotheses:

- i. Paleotropical assemblages of bats are often dominated by species that are susceptible to forest disturbance. Therefore, forest edges might not support the diversity in an assemblage of Paleotropical bats. The light edge in comparison with the dark one should relatively increase species diversity by providing additional food resources (i.e., streetlights).
- ii. In tropical wet regions, food supplies (insects) are available throughout the year for insectivorous bats. Edge habitats are also known for higher insect richness. Therefore, insectivorous bats in this study are expected to be opportunistic feeders, with high food niche breadths and overlaps.
- iii. The expected opportunistic foraging behavior should highly reflect the local prey availability, with strongly positive correlations, but the rainfall condition gradients (NR; LR; HR) are expected to affect the prey selection of bats and limit it toward specific prey types.

CHAPTER 2

LITERATURE REVIEW

2.1 Bat of Southeast Asia

Chiroptera is the second on the list of species richness among orders of mammals after rodents, showing great ecological and physiological diversity (Kunz *et al.*, 2011). In their present form, bats have been living on the planet for over 52 million years (Simmons *et al.*, 2008), and through this period they have diversified into 1,430 extant species (Simmons & Cirranello, 2020). The 1,430 species are subcategorized into Megachiroptera (Old-World fruit bats) and Microchiroptera (Insectivorous bats) belonging to 18 families. However, the phylogenetic relationship that exists between bat species, depending largely on morphological traits, has underlined the veracity of conventional sub-division and suggested that the Chiroptera order could be subcategorized into two new suborders, namely, Yinpterochiroptera and Yangochiroptera (Simmons & Geisler, 1998). The flight property is very significant in bat diversity and distribution. Bats are found all over the world, except in the Arctic region, Antarctica, extremely dry areas (or deserts) and some Oceanic Islands (Mickleburgh *et al.*, 2002; Fleming & Racey, 2010). Despite most bat species can be found in the tropics, the majority of bat species were found in the areas around the equator, including three broader regions of biodiversity, which the Southeast Asia region is part of (Jones, 2006).

Southeast Asia is one of the dominated areas by the tropical rainforests. Bats are the most ubiquitous group of mammals in Southeast Asia region and the key to the rainforest community (Furey *et al.*, 2010; Kingston, 2013). The region is also known

as one of the world-biodiversity hotspots of bats, with about 330 described species, comprising 25% of overall bats' species in the world (Kingston, 2013). Assemblages of bats in Southeast Asia mostly characterize by insectivorous species, especially from the families Hipposideridae and Rhinolophidae as well as Vespertilionidae, particularly the subfamilies Kerivoulinae and Murininae (Kingston *et al.*, 2003; Furey *et al.*, 2010; Lim *et al.*, 2017). These species of bats over the years become so adept to forage in the interiors of forests. They have equally unambiguous and foreseeable ensembles depending on eco-morphological traits such as wing loading, aspect ratio and echolocation signal design (Schmieder *et al.*, 2012; Senawi & Kingston, 2019), as well as roosting ecology such as foliage, tree cavities and caves (Struebig *et al.*, 2008; 2009). Notwithstanding, these special features and lifestyles reveal that many interior-forest species of bats are especially vulnerable to disturbances arising out of habitat loss and fragmentation.

Four “biodiversity hotspots” overlap in Southeast Asia: Indo-Burma, Sundaland, the Philippines and Wallacea (Sodhi *et al.*, 2004). Malaysia is a part of Sundaland and is recognized as one of 12 mega-biodiversity countries in the world (Giri *et al.*, 2001; Jamadon *et al.*, 2007), with over 15,000 species of flowering plants, 1,500 species of terrestrial vertebrates and 150,000 species of invertebrates (Fong *et al.*, 2006). Among the 290 mammal species known in Malaysia, there are about 133 species of bats, representing about 10% of the bat population in the world (Kingston *et al.*, 2006; Kingston *et al.*, 2012). Meanwhile, there are 110 bat species recorded in Peninsular Malaysia belonging to eight families (Lim *et al.*, 2017). The most common families in Peninsular Malaysia are Vespertilionidae (n = 44, 36%), Hipposideridae (n = 20, 18%) and Pteropodidae (n = 18, 16%) (Lim *et al.*, 2017). Various research related

to populations and assemblages, ecology and behavior of different groups of bats have been undertaken on the mainland of Peninsular Malaysia, especially in Krau Wildlife Reserve (Kingston *et al.*, 2003; Struebig *et al.*, 2008; 2009; Nurul-Ain *et al.*, 2017; Senawi & Kingston, 2019). However, little is known about bats in coastal islands of Peninsular Malaysia (Roslan *et al.*, 2016).

According to the Department of Survey and Mapping, Malaysia (JUPEM, 2020), there are hundreds of islands in Malaysia spread out the coasts of Peninsular and East Malaysia. The coastal islands of Peninsular Malaysia are interesting areas for scientific studies since they are likely to receive high impacts from anthropogenic sea-based and land-based activities. For example, the terrestrial habitats in the main islands of coastal Peninsular Malaysia are suffering due to the massive tourism industry that threatens bat populations, especially the island specialist flying fox, *Pteropus hypomelanus* (Roslan *et al.*, 2015). According to Roslan *et al.* (2016), the coastal islands of Peninsular Malaysia are rich with bat species, in which 62 species of bats have been recorded in 23 coastal islands of Peninsular Malaysia (=5.50% of total coastal islands) (Roslan *et al.*, 2016). This number of species constitutes about 56% of total bats species recorded in Peninsular Malaysia mainland, making islands as important as mainland area in Peninsular Malaysia in the diversity of bat species.

The most challenging problem regarding bats in Southeast Asia is indeed the loss of their habitat (Kingston, 2013). The rate of deforestation in the region is relatively higher compared to other tropical regions, which could invariably lead to the total extinction of many bat species (Lane *et al.*, 2006; Kingston, 2013). It is feared that with increasing deforestation, up to 20% of Southeast Asian bat population could

be lost by 2100 (Lane *et al.*, 2006). Specifically, Malaysia has a far higher rate of deforestation than all other tropical countries combined (Pirker *et al.*, 2016; Masum, 2017). This could be attributed to the exponential increase in the demand for palm oil that precipitated an unprecedented level of deforestations in the country since 1990. By some estimate, about 17% of all plantations in Malaysia have been converted from tropical forests (Pirker *et al.*, 2016). Because of the high level of biodiversity in the Malaysian forest ecosystem and the large amount of carbon found in the forest biomass (up to 3,212 million metric tons); therefore, the level of deforestation in Malaysia could lead to huge regional and global disturbance. Further, the consequence of deforestation is critical to both fauna and flora in Malaysia. To date, about 9.3% of all Malaysian known species of amphibians, birds, mammals and reptiles are all facing extinction (Masum, 2017). Bats seem to be no exception to this susceptibility as the deforestation and fragmentation of forest are suspected to lower abundance, diversity and species number of bats (Zubaid, 1993; Struebig *et al.*, 2008).

2.2 Edge habitat

One of the consequences of deforestation is, evidently, edge formation or habitat. Of all elements of the landscape, edges may be the most ubiquitous. Edges come into being at the interface of two or even more discrete habitat formations, meaning they form in both human and natural places (Luck, 2007). This also means that different species respond positively, negatively, or neutrally to edges and they may as well show different strengths and directions of responses at varying types of edges. Many species appear in literature as edge specialists, including white-tailed deer (Williamson & Hirth, 1985), cowbirds (Gates & Giffen, 1991), and tiger sharks (Heithaus *et al.*, 2006). Scientists have also been included bats in this group, as bats

maintain high activity levels in forest-edge habitats (Crome & Richards, 1988; Grindal & Brigham, 1999; Struebig *et al.*, 2008; 2009).

2.2.1 History of edge in ecology

Early examinations of edge habitats compared the number of animal species in edges to the number of similar species in interiors (Lay, 1938), or on the distribution of species relative to the amount of edge habitat (Beecher, 1942). Lay's work focused on forests, discussing edges in terms of forest clearings and interfaces between forests and meadows. He used the terms "edge" and "margin" interchangeably, but favored margin, probably due to the connotation of a wider space than the term "edge" implies. Lay noted that birds in general seemed to make use of margins around clearings at a higher rate than interior habitats, evidenced by higher overall abundance of individuals and greater species richness. Not all bird species were found in edges, as some termed "interior species" were not observed in margin habitat. However, more species were found in the edges surrounding forest clearings than anywhere else in the forest (Pettit, 2011).

Beecher's (1942) definition of edge habitat was subtly different from Lay's approach, defining edge as "...the amount of border around any plant community in a given complex of communities. It is measured as closely as possible along the "zone of tension" or ecotone between adjacent communities." Beecher's use of the phrase "zone of tension" here actually denotes a boundary, it is a line drawn between two habitat types. This zone likely refers to the interaction between the different habitat types that share a particular border, with the interaction creating the gradient effect, or "ecotone". Though "gradient" still finds common use for small-scale edge

descriptions, modern discussions of edge using Beecher's "ecotone" usually refer to large-scale habitat changes over a scale of kilometers instead of meters (Winemiller & Leslie, 1992; Pettit, 2011).

2.2.2 Edge habitat and fragmentation

In the wake of massive deforestation, knowing more about how habitat loss and fragmentation change or affect ecological communities is of the utmost importance facing conservation ecology (Laurance *et al.*, 2017). Ecologists often associate the term "edge" with the habitat fragmentation phenomenon, where disturbance events cause contiguous habitat to become interrupted and patchy in distribution. These disturbance events may include human activities (Murcia, 1995; Barber *et al.*, 2014) and landscape-level processes related to hydrology, soil distributions and weather patterns (Harrison, 1997; Hargis *et al.*, 1999; Laurance *et al.*, 2017). Bat ecologists have found that human-caused habitat fragmentation is generally exploited by forest species of bats (Crome & Richards, 1988; Grindal & Brigham, 1999).

2.2.3 Edge effect

The characteristics of edges differ by habitat type, though they typically share characteristics of both adjoining habitats ("zone of tension", *sensu* Beecher, 1942). Human-created edges often affect interior habitats by introducing processes, conditions, and organisms that previously were not present. For example, forest remnants adjacent to areas where humans have removed trees exhibit decreased soil moisture due to increased solar radiation; greater windthrow (tree falls from wind) and

windborne particle deposition due to greater amounts of exposed surface area; and water flow changes across denuded landscapes, often contributing to increased erosion, and nutrient flow changes (Murcia, 1995; Barber *et al.*, 2014). These processes, conditions, and species interactions are generally referred to as “edge effect” in the scientific literature (Beecher, 1942, Murcia, 1995; Morris *et al.*, 2010; Meyer *et al.*, 2016; Laurance *et al.*, 2017), though other types of edge effects may exist (Pettit, 2011).

Beecher (1942) used the term “edge effect” to describe the effects of edge propagation on related wildlife. He described edge effect as “[t]he influences of...animal constituents on the population density that is exerted when the ratio of edge in any plant community is increased relative to its area.” This definition is useful for explaining effects of edge as they relate to population density, though it does not explain many other factors contributing to the role of edges in a system. Such interactions change the character, and even definition, of edge habitat on a per-taxon, or per-species basis. For example, edges may increase predation along an agriculture-forest interface, though predators only make superficial incursions to the forest edge (Lima & O'Keefe, 2013). Similarly, what to some species is an edge to be exploited may serve as an impenetrable barrier to other species, depending on the ability of a species to pass through an edge and the spatial configuration of the habitat (Pettit, 2011; Meyer *et al.*, 2016).

Magnitude and extent are the two measures with which edge effects are determined (Ewers & Didham, 2006; Ries *et al.*, 2017; Yoh, 2018). The magnitude of an edge effect is the proportional strength of effect, while the extent is the distance for

which variations in natural conditions underlying habitat boundaries are found in habitat interiors (Ewers & Didham, 2006). Based on the type of the edge effect as well as the species involved, there are varying estimations about the distance that edge phenomena penetrate interiors of forests. Many of these effects occur between 100–300 m from the edge (Laurance *et al.*, 2002; Rocha da Silva *et al.*, 2013). However, some researchers have suggested an estimated effect distance of 1–10 km into forest interiors (Murcia, 1995; Delaval & Charles-Dominique, 2006). The estimate could be changed relative to the focal taxonomic group (Yoh, 2018). For example, Villada-Bedoya *et al.* (2017) observed that related edge variations affected dung beetle abundance over a maximum extent of 420 m in Colombian Andes. Zurita *et al.* (2012) found that *Thamnophilus caerulescens* (a neotropical bird species) was greatly affected over an extent of 1300 m. Subsequently, there is no globally agreed estimate regarding what distance from a forest edge that a particular species or functional group can be impacted (Hansbauer *et al.*, 2008).

The surrounding matrix or close to the edge as such is also very significant in deciding an edge effect magnitude as well as the extent (Meyer *et al.*, 2016). In a situation where there are low-contrast matrices such as secondary forest enables higher dispersal rates than in high contrast matrices (e.g., pasture; Laurance *et al.*, 2002). In addition, animals in or around urban edges where the extent ranges between habitat patches and edge matrices differ substantially, including access to nearby forest patches and the chance for dispersal, are more likely to experience human disturbance (Barber *et al.*, 2014), noise pollution (Ortega, 2012) and artificial light (Haddock *et al.*, 2019), changes to abiotic, e.g., warmer ambient temperatures (Murcia, 1995) and biotic conditions, e.g., vegetation structure and composition (Laurance *et al.*, 2017).

Essentially, over activation of the acute stress response from such a variety of stressors can engender chronic stress and a far higher level of vulnerability to disease and, thereby reduce the level of fecundity and the chance for survival (Sapolsky *et al.*, 2000). Therefore, a specific physiological and ecological response to edge habitats, with a changing degree of contrast to the nearby disturbed urban matrix such as major vis-a-vis minor roads, could give insight into the process of survival in fragmented urban landscapes.

2.2.4 Edge habitat and bat

Generally, bats are regarded as not adversely affected by fragmentation or edges because of their utmost mobility as well as their capability to utilize some matrix habitats (Groenenberg, 2012). However, there are evidences that edges can have fundamental effects on abundance and activity pattern of bats (higher pattern, Delaval & Charles-Dominique, 2006; Groenenberg, 2012; Grindall & Brigham, 1999; Morris *et al.*, 2010) and species richness (lower pattern, Faria, 2006; Meyer & Kalko, 2008). There are four principal mechanisms that may explain differential patterns in bat richness and abundance as they relate to edges (Groenenberg, 2012).

- i. Access to spatially separated resources

The abundance of species could be increased at edges if habitats at the two sides of the edge offer complementary resources to a particular species, and the edge habitats allow full access to both resources. For instance, those species of bats which forage in open areas but roost in the forest habitat proliferate in abundance at the forest borders since they always cross borders to exploit both resources.

ii. Resource mapping

Resource mapping takes place when the abundance of bat species matches the abundance of resources. For bats, like edges as flyways over structurally complex and dense interior vegetation, they also avail themselves protection from predation and wind, in addition to the use of edges as a landmark for their orientation. However, the last proposition comes into effect only when compared to open areas, and not to interior habitat. Mixing could happen when resources of both the matrix and interior habitat mix at the edge, meaning “species mixing” could happen. Upon that distinct matrix and interior species map onto resources at the edge and richness is further increased.

iii. Species interactions

Both, the increase and decrease of some species could indirectly flow to the community level via the species’ interaction like parasitism, predation, mutualism and competition. Bats could, therefore, interact with insects (predation) and pioneer fruit species (mutualism) which precipitate increase at edges.

iv. Geometric edge effects

It is only recently that the often ignored “geometric edge effects” offers insight into abundance and species decreases at edges. The proposition submits that areas in the middle of habitat patches will naturally get more individuals far more than areas near the edge since the centre gets individuals from all directions. However, edges do not have individuals from outside the patch. While demonstrated for birds, the role play by geometric edge effects has not

so far been well studied. A lot of species of bats are known for their high mobility and can as such fly through different habitats in a night. As such, it appears highly unlikely that edges could have lower richness or abundance since they do not receive individuals from outside of the patch.

There are four different Palearctic bats based on their foraging ensembles. In the Pteropodidae family, there are the plant-visiting bats who are principally frugivorous with few other species specialized for nectars. The eight other families are insectivorous. These bats could be placed into any of the three foraging ensembles depending on where they forage in relation to background vegetation: (1) “open-space” bats forage in open spaces above forests or land cleared for agricultural purpose. (2) “edge/gap” bats hunt insects often along the edge of vegetation stands and sometimes in small clearings in forests or over water. (3) “forest-interior” bats can find prey in densely vegetative habitats (Kingston, 2013). Each ensemble involves several echolocation and wing features, which ensures performance in their preferred foraging habitat, yet it inhabits performance in other habitats (Norberg & Rayner, 1987; Schmieder *et al.*, 2012; Senawi & Kingston, 2019). As such and arising from this are differences among different bat responses to edge habitats.

2.3 Feeding ecology of insectivorous bat

Studies on feeding ecology of animals can provide knowledge about their feeding location, feeding method, feeding time, feeding pattern, quantity of food and food preferences of animals. Tropical insectivorous bats are perhaps the most interesting group because they present a variety of feeding habits due to insect availability throughout the year compared to temperate bats. Generally, insectivorous bat species of the world are almost exclusively fed on different insects during different foraging times at a single night from various habitat types. Insectivorous bats mostly capture insects from the air, but some may glean from foliage, ground or even water surface. The feeding patterns of insectivorous bats can show that some of the bats are selective feeders, which are restricted to certain prey, others are generalist feeders, which feed on a wide diversity of insects according to their availability within a foraging habitat. Most food of insectivorous bats consists of around 30–40 main types; however, they do not eat different kinds of insects at one time and that a fecal pellet often contains only one to four types of insects (Whitaker *et al.*, 2009).

2.3.1 Feeding time

Insectivorous bats start feeding in the early evening and may continue until dawn, but the peak activity time of insectivorous bat species varies considerably. The feeding time of each night can be considered as before midnight and after midnight foraging period. The food intake late in the night is less than during the first foraging session. More than 60% of all-night food intake takes place before midnight, the time when there are a lot of insects (Anthony & Kunz, 1977). Change in emergence time is one method for ensuring there is no competition among different species of bats (Swift

& Racey, 1983). Though bats are nocturnal, yet many species come out of their roost to forage in early morning and just before dark despite there is a supposedly high risk of predation at that particular time (Pavey *et al.*, 2001; Chua & Abdul Aziz, 2018). During daytime insectivorous bats complete their process of food digestion and absorption. They start the night feeding with stomachs completely free of foods, but there may be fecal matter content in the gut as remnants of the previous meal. Therefore, the fecal matter collected during the daytime may be of previous days feeding (Anthony & Kunz, 1977).

2.3.2 Feeding habitat

During the night, bat forage and by so doing large cover distances. They are also more likely to come into contact with food resources from both terrestrial and aquatic habitats as well as from a variety of trophic levels (Kunz *et al.*, 2011). The selection of habitat depends on many aspects of an organism ecology, which may be different over a variety of spatial scales (Orians & Wittenberger, 1991). Habitat structure for bats may be one of the most critical features in determining and selection of foraging habitat since most bats forage while flying, so structural habitat characteristics may determine their flight paths (Norberg & Rayner, 1987; Brigham *et al.*, 1997). For instance, the structural characteristic of forest habitats is clutter; therefore, foraging process of bats depends on the amount of clutter found in a particular habitat (Senawi & Kingston, 2019). Complex habitats have structural clutter, which may not be suitable for foraging for those bats that have greater wing loading ratios and narrow band echolocation calls. Hence, they find it manoeuvrability difficult (Norberg & Rayner, 1987; Fenton, 1990; Senawi & Kingston, 2019) although prey

availability could be higher in those habitats (Brigham *et al.*, 1997). Open and edge habitats may be alternatively suitable foraging areas for many species of these bats.

According to Schnitzler & Kalko (2001), bats forage largely in any of the three outlined habitats: uncluttered space, background-cluttered space or highly cluttered space, meaning they can be divided into open-space foragers, edge and gap foragers and narrow-space foragers. The first one is the aerial insectivores in uncluttered space. Bats can hunt in open or uncluttered spaces, which are located high up or canopy and even far from any obstacle. These species are often found in four families: Molossidae (e.g., *Molossus* spp., *Promops* spp. and *Tadarida* spp.), Rhinopomatidae (*Rhinopoma* spp.), Emballonuridae (e.g., *Diclidurus* spp., *Peropteryx* spp. and *Taphozous* spp.), and Vespertilionidae (e.g., *Lasiurus* spp. and *Nyctalus* spp.). The following is the aerial or sometimes trawling insectivores in background-cluttered space. Hunting for insects in backgrounds, which are cluttered space, like forest edges and gaps, including: Vespertilionidae (e.g., *Eptesicus* spp., *Myotis* spp. and *Pipistrellus* spp.), Mormoopidae (e.g., *Mormoops* spp. and *Pteronotus* spp., except *Pteronotus parnellii*), and Emballonuridae (e.g., *Saccopteryx* spp.). The final type of aerial insectivores in highly cluttered space. Bats are looking to catch insects in highly cluttered space adjacent to vegetation or even ground. These bats are Horseshoe and Old-World leaf-nosed bats (Rhinolophidae, Hipposideridae and the New-World mustached bat, *Pteronotus parnellii* (Mormoopidae)).

Species-specific wing morphologies and echolocation call characteristics may bias bat species activity toward different habitat types (Fenton, 1990; Threlfall *et al.*, 2011). Species-specific differences in wing morphology affect flight speed and

maneuverability (Norberg & Rayner, 1987), while the differences in echolocation calls result in variable detection of both obstacles and prey when moving across landscapes (Fenton *et al.*, 1995). Therefore, bat ecomorphological relationships are strongly influenced by wing and echolocation call structures (Crome & Richards, 1988; Schnitzler & Kalko, 2001; Müller *et al.*, 2012; Senawi & Kingston, 2019). Different combinations of echolocation call characteristics and wing traits form the core functional groups of bats that are expected to differentially use three structural habitat types: cluttered areas, open areas and edges (Fenton, 1990), are discussed herein.

Insectivorous bats that forage in cluttered areas commonly have low intensity and calls that occur across large frequency (broadband calls) that happen within a short period of time (Threlfall *et al.*, 2011). Also, bats that forage in such habitats often possess wings that have low aspect ratios ($\text{wing span}^2/\text{wing area}$) and usually low wing loading ($\text{body-mass}/\text{wing-area}$) (Norberg & Rayner, 1987). These permit a powerful flight mobility with full of energy in cluttered areas (Fenton, 1990). Insectivorous bats that hunt in open areas, on the other hand, generally have high-intensity, low-frequency, and narrow-band calls that occur within a long period of time (Fenton, 1990). Such bats are usually characterized by wings with high aspect ratio and wing loading that influence faster and powerful flying patterns (Norberg & Rayner, 1987; Fenton, 1990; Threlfall *et al.*, 2011). The last category, which comprises edge-foraging bats, possess moderate features as compared to the first two categories (i.e., bats that forage in open and cluttered habitats). Insectivorous bats that forage at edges are usually characterized by high-intensity echolocation calls with a combination of both narrowband and broadband elements. They possess wings as aspect ratios are high

while having low wing loading that supports flexible flight and provide efficient energy and maneuverable flight (Fenton, 1990).

2.3.3 Feeding method

Bats that feed on insects have different modes for hunting their prey. There are basically five foraging methods used by bats, which are defined by Norberg & Rayner (1987) and reviewed in Vaughan (1997) and Kunz *et al.* (2011). (1) Bats that forage by fast hawking are known to move in fast manner towards their prey and they require a highly rapid and quick motion with the use of loud-long-ranging echolocation calls of low frequency. (2) The slow hawking bats as the name implies use slow-motion to detect and hunt prey within its vicinity. (3) Trawling bats are characterized by using their hind legs and tail membranes to catch insects in aquatic environment by using frequency-modulated calls that echoes to discern details in the background and target. (4) Gleaning bats hunt insects that perch or do not fly, on leaves or the ground. Short echolocation calls of low intensity are used in order to prevent the overlapping of their pulses and the echoes of targets that are around them. (5) Perch-hunting or fly-catching bats takes a lot of time perched and searching for insects, and flies as soon as an insect is being detected. A lot of bats are capable of receiving echoes as insects move through the use of flutter detection by long, constant-frequency echolocation calls. Lastly, it should be mentioned that these foraging methods occur simultaneously, and it is not easy to identify which category a species belongs (Habersetzer & Vogler, 1983).

2.3.4 Feeding behavior