DISTRIBUTION, METHODOLOGICAL VALIDATION AND ECOLOGY OF NOCTURNAL ISLAND MAMMALS IN PENINSULAR MALAYSIA

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DISTRIBUTION, METHODOLOGICAL VALIDATION AND ECOLOGY OF NOCTURNAL ISLAND MAMMALS IN PENINSULAR MALAYSIA

by

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"What you do makes a difference, and you have to decide what kind of difference you want to make"

Jane Goodall

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TABLE OF CONTENTS

ACKNOWLEDGEMENT……………………………………………………………ii

TABLE OF CONTENTS……………………………………………………………..iii

LIST OF TABLES…………………………………………………………………...viii

LIST OF FIGURES………………………………………………………………... x

LIST OF ABBREVIATIONS AND SYMBOLS……………………………...xiv

ABSTRAK……………………………………………………………………….... xvi

ABSTRACT………………………………………………………………………..xix

CHAPTER 1 INTRODUCTION……………………………………………….. 1

1.1 General introduction………………………………………………………………..1

1.2 Problem statement…………………………………………………………….3

1.3 Chapter outline: Objectives and hypotheses……………………………......4

CHAPTER 2 LITERATURE REVIEW………………………………………...6

2.1 Mammals and their variability……………………………………………….. 6

2.2 Adaptation to nocturnality in mammals……………………………………7

2.2.1 Evolution of nocturnality and advantages……………………………7

2.2.2 Nocturnal vision in mammals……………………………………... 8

2.2.3 Impact of artificial light…………………...…………………………10

2.3 Nocturnal mammal research……………………………………………... 11

2.4 Research on nocturnal mammals in Malaysia………………………………12

2.4.1 General knowledge………………………………………………..12

2.4.2 Habitat uses and ecological importance of nocturnal mammals……. 13

2.4.3 Conservation status of nocturnal mammals in Malaysia…………….15

2.5 Species of interest……..…………………………………………………. 18

2.5.1 Sunda slow loris (*Nycticebus coucang*) ……………………………. 18

2.5.2 Sunda colugo (*Galeopterus variegatus peninsulae*) ………………..19

2.5.3 Red giant flying squirrel (*Petaurista petaurista*) …………………...20

CHAPTER 3 GENERAL METHODOLOGY……………………………….. 22

3.1 Sampling sites………………………………………………………………22

3.1.1 General overview………………………………………………… 22

3.1.2 Description of the two main study sites…………………………….. 24

3.1.3 Description of the secondary study sites……………………………27

3.2 Sampling methods…………………………………………………………...29

3.2.1 Transect survey on the islands……………………………………… 29

3.2.2 Transect surveys on the mainland…………………………………...30

3.2.2 Study period……………………………………………………… 31

3.3 Statistical analyses………………………………………………………….. 32

3.3.1 Transect survey on the islands……………………………………… 32

3.3.1(a) Densities and diversity indices…………………………….. 32

3.3.1(b) Canopy cover per site……………………………………… 33

3.3.1(c) Species Distribution Model………………………………... 35

3.3.2 Analyses for the secondary sampling sites………………………...35

CHAPTER 4 METHODOLOGICAL ASSESSMENT OF DEVICES AND PATH TYPES TO DETECT NOCTURNAL MAMMALS……………………38

4.1 Introduction……………………………………………………………….38

4.2 Methods……………………………………………………………………...40

4.2.1 Sampling sites……………………………………………………. 40

4.2.2 Sampling methods…………………………………………………...43

4.2.3 Statistical analysis…………………………………………………... 44

4.2.3(a) Number of surveyed transects………………………………44

4.2.3(b) Type of transect path used……………………………………44

4.2.3(c) Devices used to detect animals……………………………..45

4.3 Results…………………………………………………………………46

4.3.1 Number of surveyed transects…………………………………………46

4.3.2 Type of transect path used……………………………………………...48

4.3.3 Devices used to detect nocturnal mammals………………………… 50

4.3.3(a) Detection of species and individuals………………………. 50

4.3.3(b) Species-specific detection…………………………………. 53

4.4 Discussion……………………………………………………………... 56

4.4.1 Number of surveyed transects…………………………………………56

4.4.2 Type of used transect path……………………………………………...56

4.4.3 Devices used to detect nocturnal mammals………………………… 57

4.4.3(a) Detection of species……………………………………….....57

4.4.3(b) Detection of individuals……………………………………..58

4.4.3(c) Species-specific detection…………………………………..59

CHAPTER 5 RAPID MAINLAND NOCTURNAL MAMMAL SURVEYS AND FURTHER METHOD EVALUATION……………………………………61

5.1 Introduction……………………………………………………………61

5.2 Methods……………………………………………………………….....63

5.3 Results…………………………………………………………………63

5.3.1 Sites surveyed on the mainland……………………………………...63

5.3.2 Segari Melintang, Perak…………………………………………….. 66

5.4 Discussion……………………………………………………………... 70

5.4.1 Sites surveyed on the mainland……………………………………...70

5.4.2 Segari Melintang, Perak……………………………………………..70

CHAPTER 6 ANTHROPOGENIC EFFECTS ON DISTRIBUTION AND DENSITIES OF NON-VOLANT NOCTURNAL ARBOREAL MAMMALS ON TWO ISLANDS……………………………………………………………….72

6.1 Introduction…………………………………………………………………..72

6.2 Methods……………………………………………………………………...74

6.3 Results………………………………………………………………………74

6.3.1 Distribution and encounter rates of nocturnal, non-volant mammals. 74

6.3.2 Diversity of each survey site on islands.……………………………76

6.3.3 Factors influencing nocturnal mammal detection…………………... 79

6.3.4 Factors influencing nocturnal mammal distribution………………... 79

6.4 Discussion…………………………………………………………………... 83

6.4.1 Distribution and encounter rates of nocturnal, non-volant mammals. 83

6.4.2 Diversity of each survey site………………………………………... 84

6.4.3 Factors influencing non-volant nocturnal mammal detection……….85

6.4.4 Factors influencing non-volant nocturnal mammal distribution…… 86

CHAPTER 7 ECOLOGY OF THE SUNDA COLUGO IN LANGKAWI ISLAND…………………………………………………………………………….89

7.1 Introduction…………………………………………………………………89

7.2 Methods……………………………………………………………………..93

7.2.1 Sampling sites……………………………………………………… 93

7.2.2 Sampling methods…………………………………………………..95

7.2.3 Statistical analysis………………………………………………… 100

7.3 Results……………………………………………………………………...101

7.3.1 Activity budgets of *Galeopterus variegatus*……………………… 105

7.3.2 Behavioural difference at night between habitats…………………. 108

7.3.3 Behavioural difference at night depending on sex………………… 110

7.3.4 Home ranges………………………………………………………..112

7.3.5 Coloration variations of *Galeopterus variegatus*…………………..116

7.3.6 Diet of *Galeopterus variegatus*……………………………………119

7.4 Discussion………………………………………………………………122

7.4.1 Activity budgets of *Galeopterus variegatus*………………………. 122

7.4.2 Behavioural difference at night between habitats…………………. 123

7.4.3 Behavioural difference at night depending on sex………………… 124

7.4.4 Home ranges……………………………………………………..124

7.4.5 Coloration patterns of *Galeopterus variegatus*……………………125

7.4.6 Diet of *Galeopterus variegatus*……………………………………126

CHAPTER 8 SUMMARY AND CONCLUSION…………………………...129

REFERENCES………………………………………………………………133

APPENDICES

LIST OF PRESENTATIONS

LIST OF PUBLICATIONS

LIST OF TABLES

Page

Table 2.1	Records of arboreal and terrestrial nocturnal, non-volant mammals in Peninsular Malaysia and their protection status (Wildlife Conservation Act 2010)…………………………………	16
Table 3.1	Transect area names by location and GPS coordinates in Penang and Langkawi islands, Malaysia…………………………..	26
Table 3.2	Location surveyed with number of days surveyed and method used..……………………………………………………...	31
Table 3.3	List of confirmed nocturnal mammal species occurring at the four mainland sites surveyed (ticks √indicate confirmed presence).…………………………………………………….....	37
Table 4.1	Generalized linear models (GLM) of the influence of the method on detection of species and individuals' nocturnal mammals during transect survey………………………………...	51
Table 5.1	Non- volant nocturnal mammal species sighted at each site and number of individuals detected……………………………...	64
Table 5.2	Comparison of the number of nocturnal mammal species sighted versus the number known to occur in each area..………….	64
Table 5.3	Nocturnal non-volant mammal species sighted in Segari Melintang and their encounter rates………………………………..	68
Table 5.4	Generalized linear models (GLM) of the factors affecting the presence and detection of nocturnal mammals in Segari Melintang.……………………………………………………...	68
Table 5.5	Parameter estimate of the Generalized linear model for each species in Segari Melintang.……………………………………...	69
Table 6.1	Nocturnal non-volant mammal species on Penang and Langkawi islands and their encounter rates.………………………...	75
Table 6.2	Diversity of each survey site in Penang island with biodiversity indexes and Canopy cover Index (CI) representing the percentage of area with low canopy cover per site.………………………………………………………....	77
Table 6.3	Diversity of each survey site in Langkawi island with biodiversity indexes and Canopy cover Index (CI) representing the percentage of area with low canopy cover per site.………………………………………………………………	78

Table 6.4 Generalized Linear Models (GLM) of the factors affecting the presence and detection of nocturnal mammals in Penang and Langkawi Islands.……………………………………………81

Table 6.5 Parameter estimate of the Generalized Linear Model (GLM) for each species on Penang and Langkawi islands.…………………82

Table 7.1 Ethogram used to record the behaviour of Sunda colugos (*Galeopterus variegatus)*.…………………………………………...97

Table 7.2 Identification of plant species of some items consumed by *Galeopterus variegatus*.…………………………………………121

LIST OF FIGURES

Page

Figure 2.1 Differences in eye forms of mammals with different activity patterns. Letters indicate (a) the retina, (b) the lens (source: Schroer & Hölker, 2014).. 8

Figure 2.2 Different ratios of rods and cones inside the eye of a diurnal animal (left) and nocturnal animal with *tapetum lucidum* (right).. 9

Figure 2.3 Anatomy of a nocturnal mammal's eye and how the light is reflected on the *tapetum lucidum* (source: Trissler, 2016).. 9

Figure 3.1 Map of two main field sites (♦) and secondary survey sites (●) in Peninsular Malaysia.. 23

Figure 3.2 Map of Segari Melintang with the location of the survey points (Left) and the habitat (Right) of the area surveyed............ 28

Figure 3.3 Example of Canopy cover index map of one survey site (i.e. Youth Park in Penang Island) showing the survey points and the convex hull drawn around them (left); the same area with the polygons created for the vegetation (here: forest in green) and the disturbed area (human settlements in brown) (right).
Calculation of Canopy cover index (CI): Total area convex hull: 1.5826 km^2**;** size of the disturbed area with low canopy cover (brown): 0.2794 km^2 and size of the vegetation area (green): 1.3032 km^2. CI [in %]: CI= (disturbed area*100)/ convex $hull_{total}$ = (0.2794*100)/ 1.5826= 17.65%. This number represents the area of low canopy cover in percentage in the area.................................. 34

Figure 4.1 Map of the two sites surveyed in Peninsula Malaysia (left: top - Cable Car in Langkawi Island, bottom - Taman Rimba in Penang Island) and the two sites surveyed in Brunei Darussalam (right top: Kiudang and Temburong National Park; right bottom: overview of Peninsular Malaysia and Borneo).. 42

Figure 4.2 Nocturnal mammal species accumulation curves for Penang Island (left) and Langkawi Island (right) produced by 100 random re-orderings (R Studio 2017, *Vegan* package). The different lines represent different survey sites. One site was removed on each island for this analysis as they had both only one detected species............................ 47

Figure 4.3 Comparison of the number of species and individuals sighted on different type of paths. Species: X2 (3) = 13.68, p <0.01; Individual: X2 (3) = 39.44, p <0.01. (Error bars represent SEM). *** p<0.01 49

Figure 4.4 Mean number of species sighted during transects per site with different detection devices (Thermal= FLIR + red light; Red= red light; White= white light). ***p<0.01. Sites (CB: Cable Car Langkawi; TR: Taman Rimba Penang; KDG: Kiudang Brunei; UTNP: Ulu Temburong National Park Brunei)........ 52

Figure 4.5 Mean number of individuals sighted during transects per site with different detection devices (Thermal= FLIR + red light; Red= red light; White= white light). ***p<0.01 Sites (CB: Cable Car Langkawi; TR: Taman Rimba Penang; KDG: Kiudang Brunei; UTNP: Ulu Temburong National Park Brunei)........ 52

Figure 4.6 Species detected by Observer 1 (Expert: Peninsular Malaysia) using different methods. The species assemblages are different between the two countries studied. (Thermal = FLIR + red light, Red = red light, White = white light). (Error bars represent SEM). *Arctogalidia trivirgata* (Small-toothed palm civet), *Galeopterus variegatus* (Sunda colugo), *Hylopetes spadiceus* (Red-cheeked flying squirrel), *Nycticebus coucang* (Sunda slow loris), *Otter* sp. (Unidentified), *Paradoxurus hermaphroditus* (Common palm civet), *Petaurista petaurista* (Red giant gliding squirrel), *Sus scrofa* (Eurasian wild boar), *Tragulus kancil* (Lesser mousedeer), *Trichys fasciculata* (Long-tailed porcupine)........ 54

Figure 4.7 Species detected by Observer 2 (Novice: Brunei Darussalam) using different methods. The species assemblages are different between the two countries studied. (Thermal = FLIR + red light, Red = red light, White = white light). (Error bars represent SEM). *Aeromys tephromelas* (Black flying squirrel), *Arctictis binturong* (Binturong), *Arctogalidia trivirgata* (Small-toothed palm civet), *Cephalopachus bancanus borneanus* (Horsfield's tarsier), *Galeopterus variegatus* (Sunda colugo), *Hystrix brachyura* (Malayan porcupine), *Nycticebus menagensis* (Philippine slow loris), *Paradoxurus hermaphroditus* (Common palm civet), *Petinomys setosus* (Temminck's flying squirrel), *Prionailurus javanensis* (Sunda leopard cat), *Ptilocercus lowii* (Pen-tailed treeshrew), *Sus scrofa* (Eurasian wild boar), *Tragulus kanchil* (Lesser mousedeer), *Tragulus napu* (Greater mousedeer), *Trichys fasciculata* (Long-tailed porcupine), *Viverra tangalunga* (Malayan civet)........ 55

Figure 5.1 Number of survey nights surveyed to successfully sighted targeted species. Overall $X^2(9)=9.5651$, n=19, p=0.3868. Chi-square test results per category: *** p ≤0.01, p ≤0.05, * p ≤0.1. (Error bars represent SEM)…………………………………65

Figure 7.1 Phylogenetic relationships of colugos (Dermoptera) within the superorder Euarchontoglires. Source: Moritz et al. 2013……………………………………………………………...90

Figure 7.2 Literature search on Google Scholar with the terms: 'colugo', 'flying lemur', '*Galeopterus*'……………………………… 92

Figure 7.3 Map of Langkawi Island with the location of the three field sites of the survey……………………………………………………..94

Figure 7.4 Two individuals of *Galeopterus variegatus* with different shades of brown and white markings on their body (identified as mixed-coloured individuals).…………………………98

Figure 7.5 Sex identification of *Galeopterus variegatus*. Left a female defecating (no testes visible); middle a male defecating (testes visible), and right a male gliding (testes visible)……………... 99

Figure 7.6 Location of animals sighted at The Datai Resort (6.4260°N, 99.6714°E), Langkawi.………………………………...102

Figure 7.7 Locations of animal sighted at the ELS Teluk Datai Golf course (6.4283°N, 99.6855°E), Langkawi.………………………...103

Figure 7.8 Location of the animals sighted at Temoyong village (6.2975°N, 99.7376°E), Langkawi………………………………..104

Figure 7.9 Proportion of behaviour of *Galeopterus variegatus* recorded by 1-min individual focal sampling at The Datai Resort, Langkawi with differences between day and night (n(day)= 4273; n(night)= 7,591)…………………………………..106

Figure 7.10 Proportion of behaviours of *Galeopterus variegatus* recorded by 1-min individual focal sampling at night at The Datai Resort (n = 7,591)……………………………………...107

Figure 7.11 Behaviour differences at night of *Galeopterus variegatus* between the three sites (n=17,493). Overall results: X^2 (12) = 74.097, p <0.01, n= 17,493. Chi-square test results per category: *** p ≤0.01, ** p ≤0.05, * p ≤0.1. (Error bars represent SEM)……………………………………………………109

Figure 7.12 *Galeopterus variegatus* male and female behaviour differences at night (n=3,425). Overall X^2 (6) = 21.038, p <0.01, n=3,425. Chi-square test results per category: *** p ≤0.01, ** p ≤0.05, * p ≤0.1. (Error bars represent SEM)…………111

Figure 7.13 Home ranges of four individuals of *Galeopterus variegatus* based on the minimum convex polygon method (95%

MCP) at Temoyong, Langkawi. Sex of the individuals (Females: Colugo A, B; Males: Colugo C; Juvenile unidentified sex: Colugo D). Home ranges sizes: between 0.041ha (Colugo D) and 0.68ha (Colugo B)……………………….113

Figure 7.14 Home ranges of 25 individuals of *Galeopterus variegatus* based on the minimum convex polygon method (95% MCP) at ELS Club Teluk Datai, Langkawi. The individuals represented by points have not been followed sufficiently to create a home range. Sex of the individuals (Females: Colugo 3, 4, 9, 12; Males: Colugo 2, 5, 7, 8, 11, 13; Unidentified sex and age: Colugo 1, 6, 10, 14 - 25)…………..114

Figure 7.15 Home ranges of females (left) and males (right) of *Galeopterus variegatus* based on the minimum convex polygon method (95%MCP) at ELS Club Teluk Datai, Langkawi. These individuals were selected as it was the ones that had enough GPS point to analyse and could also identify the sex. Age of the individuals could not easily be identified and differences between juvenile and adult was not assessed. Females' home ranges size: 0.13ha - 0.50ha (mean of 0.31 ha). Males' home range sizes: 0.053 - 0.83ha (mean of 0.47 ha).…………………………………………………115

Figure 7.16 Fur colouration differences of *Galeopterus variegatus*. Type a: grey variation (left); type b: mixed colour variation (both individuals in the middle); and type c: reddish-brown variation (right).…………………………………………………117

Figure 7.17 Fur colouration of male and female *Galeopterus variegatus* in Langkawi Island. Overall $X^2(2)=138.19$, n= 26, p<0.01. Chi-square test results per category: *** p ≤0.01, ** p ≤0.05, * p ≤0.1. (Error bars represent SEM). Type a: grey variation; type b: mixed colour variation; and type c: reddish-brown variation.…………………………………...118

Figure 7.18 Food items consumed by *Galeopterus variegatus* in Langkawi Island. Overall X^2 (8) = 35.574, n= 1,132, p<0.01. Chi-square test results per category: *** p ≤0.01, ** p ≤0.05, * p ≤0.1. (Error bars represent SEM).………………...120

LIST OF ABBREVIATIONS AND SYMBOLS

%	Percentage
α	Alpha
X^2	Chi-square test
AIC	Akaike Information Criterion
am	ante meridiem (before midday)
ANSI	American National Standards Institute
asl	above sea level
B	B coefficient (partial regression coefficient)
°C	degree Celsius
ca.	circa (“around”)
cd/m^2	Candela per square metre
CI	Confidence Interval
CCI	Canopy Cover Index
cm	centimetre
D	Simpson Diversity Index
df	Degree of freedom
DWNP	Department of Wildlife and National Parks, Peninsular Malaysia
°E	degree East
f	focal ratio
g	gram
GLM	Generalized Linear Model
GPS	Global Positional System
h	hour
H’	Shannon- Wiener Index
ha	hectare

IUCN	International Union for Conservation of Nature
i.e.	id est (“that is”, “in other words”)
ind/km	individual per kilometre
ind/km^2	individual per kilometre square
J’	Pielou's evenness
kg	kilogram
km	kilometre
km^2	kilometre square
m	metre
mK	milliKelvin
mm	millimetre
°N	degree North
n	number
nm	nanometre
NTSC	National Television Standards Committee
p	p-value
pm	post meridiem (after midday)
S	Species richness
SDI	Species Diversity Indices
SEM	Standard Error of the Mean
Std.	Standard
t	tonne
µm	micrometre
USM	Universiti Sains Malaysia
VHF	Very High Frequency
VOx	Vanadium Oxide
vs.	Versus

TABURAN, PENGESAHAN METODOLOGI DAN EKOLOGI MAMMALIA NOKTURNAL PULAU DI SEMENANJUNG MALAYSIA

ABSTRAK

Penyelidikan nokturnal yang semakin berkembang dalam beberapa tahun kebelakangan ini telah memberi sinar baru kepada haiwan elusif yang aktif pada waktu malam dan perilakunya. Namun begitu, model kajian yang lebih efektif perlu dibangunkan untuk mamalia nokturnal berdasarkan keperluan biologi spesifik haiwan ini. Hal ini kerana lampu putih yang biasaannya digunakan dalam penyelidikan mendatangkan mudarat kepada penglihatan haiwan nokturnal. Oleh itu, penyelidikan ini bertujuan untuk menguji beberapa kaedah pengesanan yang berbeza dengan menggunakan jenis lampu berbeza untuk mengesan mamalia nokturnal tidak terbang dan menilai diversiti, taburan dan jumlah individu di lokasi yang dipilih di utara semenanjung Malaysia. Tiga spesis yang menjadi fokus ialah: kongkang Sunda (*Nycticebus coucang*), tupai terbang (*Petaurista petaurista*), dan kubung Sunda (*Galeopterus variegatus*) dengan kajian terperinci terhadap ekologi pemakanan dan perilaku. Kajian transek malam dilakukan mengikut set berikut, jalan sedia ada untuk menaksir kehadiran mamalia nokturnal dan densiti populasi. Untuk menguji dan mengesahkan metodologi, kajian malam dilakukan di Segari Melintang, Perak dan Brunei Darussalam. Metodologi diuji dengan 1) menggunakan lampu berbeza, 2) kebolehlaksanaan transek (keluk ketepuan spesis mengikut bilangan transek), dan 3) bias pemerhati. Untuk kajian taburan dan jumlah individu yang mendalam, dua lokasi kajian utama di semenanjung Malaysia telah dikaji, i.e. Pulau Pinang dan Pulau Langkawi, masing-masing mengandungi tujuh 500m transek di setiap plot kajian

(berjumlah 24 plot), termasuk hutan hujan dara yang tidak diganggu dan kawasan luar bandar (diganggu). Sebanyak 24 plot kajian di Pulau Pinang dan 11 di Pulau Langkawi ditinjau diantara September 2017 dan Jun 2019. Lampu suluh kepala dengan lampu putih dan penapis merah, dan peranti haba Flir (FLIR Scout III model 640) digunakan untuk meningkatkan kadar pengesanan haiwan. Dengan menggunakan teknologi ini, mamalia nokturnal lebih mudah dilihat walaupun ketika tidak bergerak kerana peranti ini mengesan dan memaparkan haba badan tanpa sumber pencahayaan lain. Penggunaan lampu yang berbeza menghasilakan keputusan yang memberangsangkan dan bias pengesanan boleh ditolak kerana haiwan dikesan di habitat yang berbeza. Penggunaan FLIR dan lampu merah meningkatkan pengesanan spesis dan individu dengan ketara berbanding menggunakan lampu putih untuk semua lokasi. ($\chi 2(2)=31.114$, $p<0.01$). Oleh itu, lampu merah dan peranti haba perlu digunakan bukan hanya untuk meningkatkan pengesanan tetapi untuk melindungi mata mamalia nokturnal yang sensitif. Kaedah kajian transek terbukti efiksyen untuk mengesan mammalia nokturnal apabila menghasilkan keputusan yang memberangsangkan terhadap lokasi kajian dalam hanya masa yang pendek (1-2 minggu) tanpa perlu diulang. Penyelidikan ini telah mendedahkan bahawa menggunakan laluan atau jalan yang telah ditentukan adalah sesuai untuk mengesan spesis dan menilai individu yang terdapat dalam kawasan yang dinyatakan. Kajian di pulau menunjukkan bahawa pengesanan mammalia nokturnal dipengaruhi oleh jenis laluan yang digunakan untuk penyelidikan, masa penglihatan selepas matahari terbenam dan angin; dan taburan haiwan ini dipengaruhi oleh jenis habitat yang dikaji, altitud, sambungan kanopi, jarak titik tinjauan ke laluan dan saiz kawasan vegatasi yang dikaji. Fokus istimewa diberikan kepada salah satu mammalia nokturnal, kubong Sunda. Sebanyak 29 individu yang dikenal pasti dan tidak dikenal pasti diikuti di Langkawi untuk maksimum lima bulan bergantung kepada lokasi kajian (dari November 2018 hingga Ogos 2019) untuk menaksir corak aktiviti, diet dan system sosial haiwan ini. Keputusan kajian ini menunjukkan pencanggahan dengan rujukan yang sediada. Kubong hidup dalam kumpulan yang mengandungi 25 individu dalam kawasan yang kurang dari 3 ha, menunjukkan sosialiti. Namun begitu, kajian lanjut diperlukan bagi komposisi kumpulan ini. Kubong Sunda ini kelihatan mampu menyesuaikan diri dan bertahan dalam habitat yang terganggu dan boleh dijumpai berdekatan dengan tempat tinggal manusia dimana kumpulan yang mengandungi lima individu dikesan disekitar tepi jalan yang sangat terganggu. Penyelidikan ini adalah yang pertama menunjukkan penilaian tingkahlaku yang menyeluruh terhadap individu kubong Sunda yang dikenalpasti di dua jenis habitat yang berbeza. Walaubagaimanapun, secara umumnya masih terdapat kekurangan pemahaman yang besar terhadap spesis mamalia nokturnal dan adalah sangat penting untuk menambah baik metodologi di masa hadapan dengan menggunakan kaedah yang telah disahkan seperti menggunakan lampu merah untuk meningkatkan pengesanan dan kebajikan haiwan.

DISTRIBUTION, METHODOLOGICAL VALIDATION AND ECOLOGY OF NOCTURNAL ISLAND MAMMALS IN PENINSULAR MALAYSIA

ABSTRACT

Nocturnal research has developed in recent years, shining more light on the elusive animals that are active at night, and their behaviours. However, more efficient survey designs for nocturnal mammals according to their specific biological needs should be developed, as the commonly used artificial white light harms animals' eyesight. Therefore, this study was aimed to test different detection methods by using different types of light to spot nocturnal, non-volant mammals and to assess their diversity, distribution and abundance in selected localities in Northern Peninsula Malaysia. Three main species were focused on; Sunda slow lorises (*Nycticebus coucang),* red giant flying squirrels (*Petaurista petaurista*), and Sunda colugos (*Galeopterus variegatus*) with a detailed study on its feeding ecology and behaviour. Night transect surveys were conducted following set, pre-existing paths to assess nocturnal mammal presence and population density. For testing and validating the methodology, night surveys were conducted in Segari Melintang, Perak and Brunei Darussalam. The methodology was tested by 1) the use of different lights, 2) transect feasibility (species saturation curves according to number of transects) and 3) the type of paths used for the survey. For in-depth distribution and abundance studies, two main study areas in Peninsular Malaysia were surveyed, i.e. Penang and Langkawi islands, comprising a minimum of seven transects of 500 m each per study plot (total of 24 plots), including non-disturbed virgin rainforests and rural (disturbed) areas. A total of 13 study plots in Penang Island and 11 in Langkawi Island were surveyed between

September 2017 and June 2019. A head torch with either white light or red filter, and a FLIR thermal device (FLIR Scout III model 640) were used to enhance detection rates of the animals. By using FLIR technology, nocturnal mammals are easily visible, even when they are not moving, as it picks up and displays the heat of the body without any external light source. The use of different lights brought significant results and detection bias could be ruled out as animals were detected in different habitat types. The use of the FLIR combined with a red light head torch significantly enhanced the detection of the number of species and the number of individuals compared to using white light head torch for all sites. ($\chi^2(2)=31.114$, $p<0.01$). Therefore, red light and thermal devices should be used to enhance detection but also to protect the sensitive eyes of nocturnal mammals. The transect survey method proved efficient to detect nocturnal mammals yielding significant results to study an area in a short period of time (1-2 weeks) without having to do repeated surveys. This study revealed that the use of pre-determined paths or roads was feasible to detect species and to count individual numbers occurring in a defined area. The survey on the islands showed that nocturnal mammal detection was influenced by the type of path used for the survey, time of sightings after sunset and wind; and their distribution was influenced by the type of habitat surveyed, altitude, connectivity of the canopy, distance of the point surveyed to road, and the size of the surveyed vegetation patch. Special focus was put on one nocturnal mammal, the Sunda colugo and 29 identified as well as several non-identified individuals were followed in Langkawi for a maximum of five months depending on the survey site (from November 2018 to August 2019) to assess their activity patterns, diet and social system. The results showed that, contradicting existing literature, colugos live in groups of up to 25 individuals in an area of less than 3 ha, indicating sociality, but their group composition needs further research. They seem to adapt to and persist in disturbed areas and can be found near human habitation where a group of five individuals was detected at a heavily disturbed roadside. This study presents the first comprehensive behavioural assessment of identified individuals of Sunda colugos in two different habitat types. However, in general there is still a major lack of understanding of some nocturnal mammal species and a vital need to further improve methodology and to apply validated methods, like red light, for enhanced detection and animal welfare.

CHAPTER 1

INTRODUCTION

1.1 General introduction

Over 6,495 species of mammals have been identified on earth (Burgin et al., 2018) with 96 species just recently becoming extinct, and 6,399 still extant. These species belong to 1,314 genera, 167 families, and 27 orders (Burgin et al. 2018). This number is bound to change as new species are being described every year. In their study, Burgin et al. (2018) found that in only 13 years, 1,079 species of mammals have been described, which equals ca. 83 species per year. These changes in taxonomy are made possible by more field research, an improved understanding of geographic barriers, more precise genetic analyses, and many other technological advances (Burgin et al., 2018).

Most mammals are nocturnal (44%), while only 26% are diurnal and 29% are crepuscular or cathemeral (Jones et al., 2009). Mammals are amongst the most studied groups of animals, but the ecology of many nocturnal species still remains understudied (Clark & May, 2002; Jayasekara et al., 2007). Nocturnality is thought to be an ancestral trait of mammal evolution, thus explaining the high number of animals active at night or near night-time (Crompton et al., 1978; Gerkema et al., 2013; Heesy & Hall, 2010). Nocturnality minimizes contact with humans and may enhance survival of certain species but more studies are needed to evaluate if this adaptation also enables to cope with highly fragmented habitats (Bennie et al., 2014).

Most nocturnal animals have night vision adapted to see in the dark and some studies suggest that animals avoid power lines due to an ability to see UV light (Tyler et al., 2014). This may be the case for some mammals, but sightings of dead animals electrocuted on power lines is also occurring often, which seems to disagree with the earlier statement (Katsis et al., 2018). Many forest animals also persist in highly disturbed areas and increase their nocturnality to cope with disturbance (Gaynor et al., 2018). Animals are adapting their movement and behaviour in cities (Beier, 2006) and agricultural landscapes (Shamoon et al., 2018) by reducing their movements frequency (Tucker et al., 2018) or using artificial structures like pipelines or power lines as a replacement for trees to navigate in their habitat (Birot et al., 2019).

Most research in the past focused on nocturnal mammals in intact forests or protected areas, at the neglect of human impacted landscapes as generally nocturnal mammals seem to be more abundant in densely and forested areas (Rickart et al., 2007). However, this might be a biased view due to a fundamental lack of studies in highly disturbed areas where food availability is higher regarding certain items such as insects or fruits. Several studies have shown that some animals who consume insects (Rode-Margono et al., 2014) may be more flexible and adapt well to highly disturbed areas (Voskamp et al., 2014), such as the Javan slow loris, *Nycticebus javanicus*.

This study focused its research on all habitat types in the study sites, i.e. primary forests, secondary forests, village, plantations, and orchards. The main study was conducted on two Malaysian islands, Penang and Langkawi, but secondary survey sites included the mainland of the peninsula (i.e. Segari Melintang in Perak) and sites in Brunei Darussalam for method comparison and validation. The islands where chosen as primary sites due to the high abundance and presence of many recorded species, making them highly suitable sites for behavioural observations. One species, *Galeopterus variegatus*, the Sunda colugo, was studied in detail, assessing its activity budgets, sociality and feeding ecology as it was highly abundant and easily observable on Langkawi Island.

1.2 Problem statement

Commonly used methods to study nocturnal mammals (e.g. by illuminating the area with white torch lights) are not adapted to the needs of nocturnal animals and have not changed for the past century. Research has shown that these mammals are highly sensitive to light disturbance, which may alter behaviour and induce detection bias in research results (Beier, 2006). Artificial white light is also harmful to the eyesight of most nocturnal animals, inducing long-lasting visual impairment (Beier, 2006; Weldon et al., 2020). So far, only few researchers have started to use non-harmful red light and new technologies (e.g. infrared cameras) to enhance detection rates of nocturnal mammals while being less invasive, and to better observe more natural behaviours, but research on the feasibility and effects of these methods on animals is still lacking.

Here, an adapted methodology to study nocturnal mammals by using new technologies, i.e. a thermal imaging device and red light, and testing how efficient these are in detecting the animals, is presented (Chapter 4). In Chapter 5, the survey of sites on the mainland presents the problems with nocturnal mammal detection. In Chapter 6, the findings of a wide distribution assessment of nocturnal mammals in Penang and Langkawi islands were analysed, and how anthropogenic activities in both sites influenced their distribution in regard to their specific ecological needs. An updated behavioural and ecological study of the Sunda colugo in both, a natural and disturbed environment, is presented in Chapter 7.

1.3 Chapter outline: Objectives and hypotheses

This study was aimed at addressing the following four research objectives, which represent each working chapter of this thesis:

Objective 1 was to evaluate how different species of nocturnal mammals can be accurately detected by different standardized nocturnal survey methods. Amongst these was an assessment of the minimum amount of 500 m-long transects required in an area to sample all present species and individuals. A second test was conducted don the type of paths used and influence of path-type on detection rate. The third assessment was to specifically analyze the use of different light sources, i.e. white light, red light and a thermal imaging device (FLIR), and how they affected the detection rate of nocturnal mammals. The last assessment was to test observer bias and compare results between a novice and an experienced researcher. The first hypothesis for this objective was that a number of eight 500 m-long transects would be sufficient to study an area. For the second hypothesis, it was expected that paths with a more open canopy are more efficient to survey nocturnal mammals who are mostly arboreal. The third hypothesis was that the use of red light and a thermal imaging device would significantly enhance nocturnal mammal detection over the commonly used white light. It was also expected that there would be no observer bias for using this method. Further, it was expected that the survey design is efficient to survey all present species in a short period of time and by covering a large area.

Objective 2 was to evaluate transect survey accuracy in nocturnal mammal detection by using both short and more in-depth surveys in several sites on the mainland of Peninsular Malaysia. This provided baseline data to validate the methodology, to present the problem with animal detection, and to compare the results with the island sites. The hypotheses for this objective were that short surveys are inefficient to detect all present mammal species and that mainland results would be different than islands.

Objective 3 was to assess the composition and distribution of the nocturnal mammal community in Penang and Langkawi islands with focus on three species, i.e. Sunda slow loris, (*Nycticebus coucang)*, Sunda colugo (*Galeopterus variegatus)*, and red giant flying squirrel (*Petaurista petaurista*) to assess their relative abundance in relation to different habitat characteristics. The second aim was to examine how anthropogenic disturbance affects the distribution of nocturnal mammals. Based on the knowledge and biology of the species of interest, the hypothesis was that they would occur at higher densities in forested environments than in disturbed areas (Bernard et al., 2014; Lim et al., 2013; Rode-Margono et al., 2014). It was also hypothesized that certain habitat characteristics, such as level of disturbance, habitat type or canopy cover explain species abundance.

Objective 4 was to investigate the activity budgets, home ranges, sociality and diet of Sunda colugos (*Galeopterus variegatus)* and their behavioural differences between two sites, an urban area and a forested area. Another aim was to test for differences between males and females in activity budgets and habitat use. The fur colouration variation in both sexes was analysed to confirm sex-dimorphism. There have not been any intensive or long-term surveys on Sunda colugos that lasted for more than three months, and the hypothesis was that colugos can be found at higher densities in forested areas compared to more disturbed areas.

CHAPTER 2

LITERATURE REVIEW

2.1 Mammals and their variability

Extant mammals are described as animals with certain characteristics specific for this group such as fur, mammary glands, a neocortex in the brain, a vertebral column, and a single bone in the lower jaw, only to name few (Kemp, 2005). Other characteristics can be defined, but are not specific to mammals, such as endothermy, which also occurs in birds, or the presence of an enlarged brain (Kemp, 2005). Mammals can be classed in three groups regarding their reproductive biology (Kemp, 2005); Monotremata, also known as the egg-laying mammals; Marsupialia known as the pouched mammals, and the most abundant placental mammals, Placentalia.

Mammals are highly variable in size, from very small (<2g) to large (ca. 140t for some marine mammals; Lacher et al., 2019). They also have different lifespans from less than one year to more than 200 years (Kemp, 2005). They live in a wide variety of habitats and this is what makes their impact on the environment significant (Davidson et al., 2012; Ripple et al., 2014). Mammals have adapted to their respective ecological niches (Walls, 1942), which include four major activity patterns: nocturnal, crepuscular, diurnal and 24-hours (Halle & Stenseth, 2012). Nocturnal mammals are by definition only active at night, crepuscular species have activity peaks around sunset and sunrise, diurnal species are only active during the day, and 24-hour active species are mostly predators and carnivorous species such as cats who have adapted to hunting at night but are also active during the day. These species have excellent vision both during the day and night (Beier, 2006).

2.2 Adaptation to nocturnality in mammals

2.2.1 Evolution of nocturnality and advantages

A hypothesis was described by Walls in 1942 known as the ‘nocturnal bottleneck’. This concept explains that most mammal species evolved to be active at night to avoid the dominant predators at that time, the dinosaurs who were active during the day (Hut et al., 2012; Walls, 1942). Most mammals during that period were small, nocturnal and mostly insectivorous (Gerkema et al., 2013).

Nocturnality has been widely studied regarding the night vision of animals as the eye structure has to adapt to the amount of light that it is mainly exposed to (Hall et al., 2012; Heesy & Hall, 2010; Schwab et al., 2012; Walls, 1942). Nocturnal animals do not usually need to protect their retina from UV light from the sun allowing a high transmission (Hut et al., 2012). Their general anatomy and physiology has evolved to a nocturnal lifestyle (Crompton et al., 1978; Gerkema et al., 2013; Young, 1950), including endothermia for certain groups of species to maintain a constant body temperature, and thus, do not dependent on the sun for heating up, like diurnal reptiles for example (Crompton et al., 1978). Other senses also have to be adapted to compensate for a low light environment such as increased olfactory sensitivity (Striedter, 2005), hearing high frequencies (Coleman & Boyer, 2012), and the development of tactile whiskers (Muchlinski, 2010).

2.2.2 Nocturnal vision in mammals

Nocturnal mammals have generally adapted their vision to seeing better at night. The structure of the eye varies in different mammals affecting how they respond to light. Those differences are in the pupil, type of lens, number of photosensitive cells in the retina, and the ratio of rods and cones (Beier, 2006). Nocturnal mammals have large pupils to allow more light to enter, big lenses, and retinas rich in rod cells (Walls, 1942; Figure 2.1 and 2.2). Some species have also developed a *tapetum lucidum* at the back of the retina (Figure 2.3). This photosensitive tissue layer is highly reflective and allows more light to reach the retina (Beier, 2006).

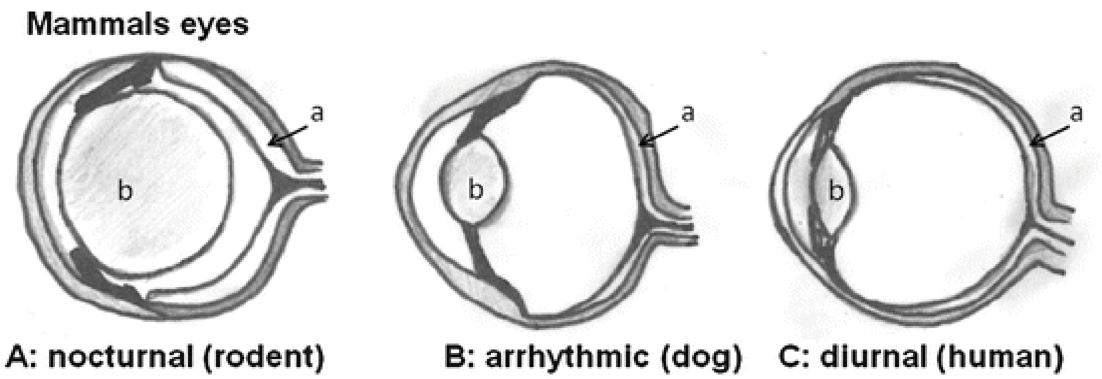

Figure 2.1 Differences in eye forms of mammals with different activity patterns. Letters indicate (a) the retina, (b) the lens (source: Schroer & Hölker, 2014).

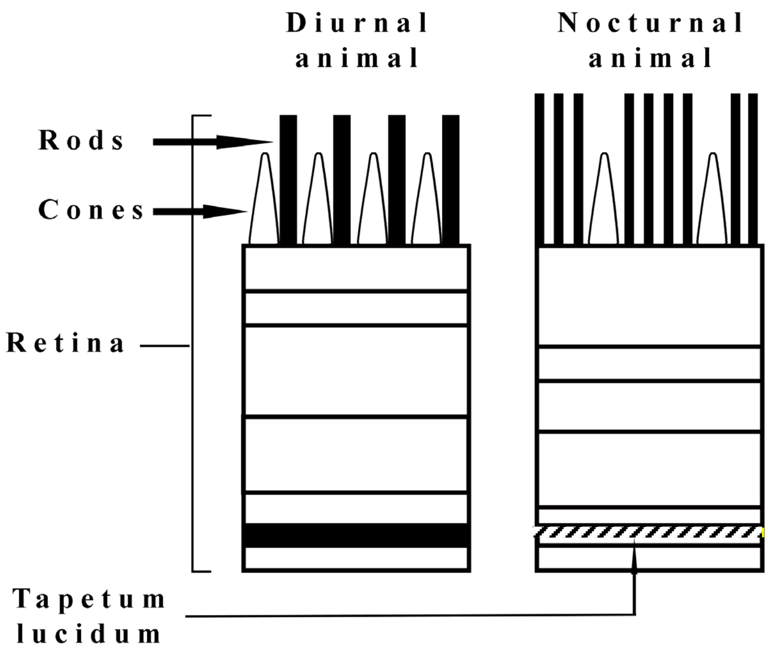

Figure 2.2 Different ratios of rods and cones inside the eye of a diurnal animal (left) and nocturnal animal with *tapetum lucidum* (right).

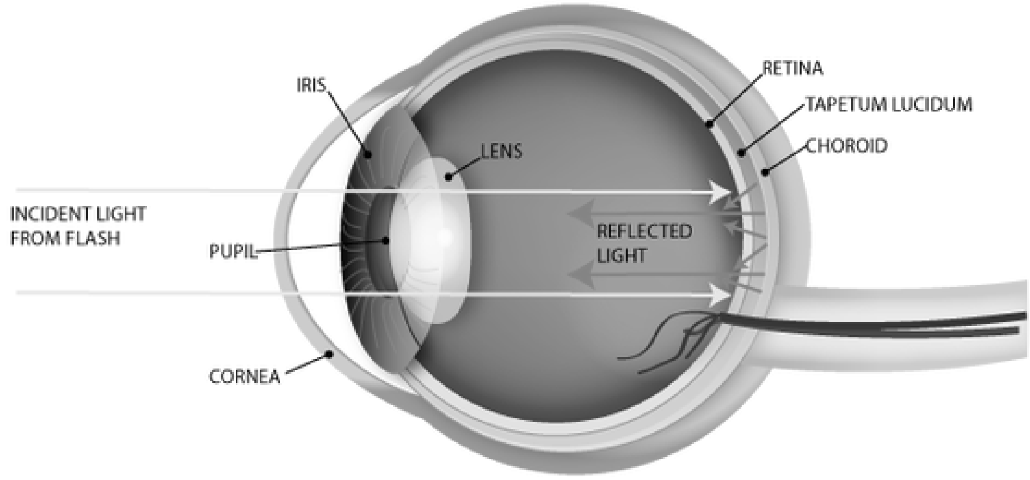

Figure 2.3 Anatomy of a nocturnal mammal's eye and how the light is reflected on the *tapetum lucidum* (source: Trissler, 2016).

2.2.3 Impact of artificial light

Most nocturnal mammals have few cone cells and the rods become saturated above 120 candela per square metre (cd/m^2; light level at twilight) and this explains why these animals can be blinded by bright lights such as artificial night lightings and flashlights or head torches (Beier, 2006). Some studies have already shown that most species of nocturnal mammals are impacted by moonlight by staying in denser areas, reducing foraging and movement during high light intensity nights (Beier, 2006; Rode-Margono & Nekaris, 2014). But some species also increase their activity or do not show any changes in their activity patterns due to changing light conditions; particularly the 24-hours carnivorous species have equally good day and night vision to catch prey (Beier, 2006; Gursky, 2003).

Light intensity reflected from the moon ranges between 0.1 lux (half-moon) to 0.3 lux (full moon; Beier, 2006). These subtle changes of light intensity can already bring changes in the behaviour of nocturnal mammals. Most roads in the United States, and potentially around the world, have a constant lighting with an average of 4–17 lux and with a maximum value around 3 times higher if exposure is directly under the light source (IESNA, 2000). With values that high, it can be suggested that artificial lights may impact the foraging behaviour of light-sensitive nocturnal mammals and increase their risk of predation (Beier, 2006).

The wavelength and intensity of light also affects mammalian biological clocks. This can influence the production of hormones, such as melatonin, which influence the activity patterns of mammals and their behavioural and physiological rhythm (Bartness & Goldman, 1989). Studies by Halle & Stenseth (2012) have demonstrated that 15-minute stimuli of around 1,000 lux (bright twilight) can change the circadian clock up to 2 hours.

Another effect of artificial lighting is the potential increase in road kills of nocturnal mammals through the headlights of oncoming vehicles. When looking into a bright light, their eye structure allows them to change from rods to cones if needed but this will take few seconds during which the animal is almost blind. If the illumination is long, it will take the animal between 10 to 40 minutes to fully recover (Beier, 2006; Weldon et al., 2020). Special types of lights could be used for vehicles, such as low-pressure sodium lights (emission at 589nm) that provide safety for drivers but also for mammals crossing roads at night (Beier, 2006)

Most research on effect of light on eyesight of nocturnal mammals is done in laboratory conditions and thus, more *in situ* studies are needed to fully understand how animals react to artificial lightning. However, some potential effects were highlighted such as disrupting foraging, increasing predation risk, disrupting biological clocks, increasing mortality on roads, and disrupting dispersal movements (Beier, 2006).

2.3 Nocturnal mammal research

Nocturnal mammals are represented by a variety of distinct animals that can be aquatic, terrestrial and aerial. All bat species, badgers, most smaller carnivores, and rodents, along with 20% of primates are nocturnal (Walls, 1942). There is also a large number of other species that are active both at night and day and considered either crepuscular or 24h-pattern (Walls, 1942).

Various techniques exist to study nocturnal mammal distribution and abundance in the forest (de Thoisy et al., 2008). These survey methods are important to give an estimation of population trends and to investigate the importance of nocturnal species for the ecosystem (de Thoisy et al., 2008; Keeping & Pelletier, 2014). All these methods need to be adapted to species of interest, cost involved for the study, limitation of resources, but also habitat and environmental conditions of the surveyed sites (Silveira et al., 2003). One of the most commonly used sampling techniques is trapping for smaller species, both nocturnal and diurnal such as rats, squirrels, and treeshrews (Barros et al., 2015; Ruppert et al., 2015). However, this method is time consuming and the trapping success can be rather low for some nocturnal species (Barros et al., 2015; Ruppert et al., 2015). Another frequently used method is direct observation by using transect survey walks (Silveira et al., 2003). This method is widely used but might underestimate species abundance as detection rates of certain animals can be low because some species are cryptic or rare and therefore hard to detect (Duckworth, 1998; Nekaris et al., 2014). Camera trapping has been widely used to study a variety of terrestrial species but was also recently adapted to study arboreal animals (Gregory et al., 2014; Silveira et al., 2003). This method is also time consuming and rather expensive, with detections depending on the species' use of the habitat (Silveira et al., 2003). Telemetry, or radio-tracking via VHF or GPS devices, is used to uncover the general ecology and behaviour of some nocturnal species as observers may be able to follow certain individuals over prolonged periods of time (Rode-Margono et al., 2014) to collect behavioural data. Without these instruments, following nocturnal wild mammals may otherwise be difficult or almost impossible (White & Garrott, 2012).

2.4 Research on nocturnal mammals in Malaysia

2.4.1 General knowledge

In Malaysia, 65% of wild mammals are nocturnal (with exclusion of bats in this species count; Barret, 1985), translating into 307 recorded species. But this number could rise as taxonomic studies still uncover new species every year (Ministry of Natural Resources and Environment Malaysia, 2015). Studies related to nocturnal mammals in Malaysia are limited and were conducted either by big scale fauna expeditions or smaller-scaled wildlife inventories (e.g. Azlan & Sharma, 2006; Azlan, 2006; Bahir, 2014; DWNP, 2000; Kawanishi, 1999; Lo et al., 2018; McShea et al., 2009; Sompud et al., 2016). However, only few studies have looked in more detail into the general ecology and behaviour of most of these animals.

2.4.2 Habitat uses and ecological importance of nocturnal mammals

Every species has its specific role in the ecosystem in order to maintain a balance through a diversity of mechanisms. Some examples of these roles are as seed dispersers, pest control agents, component of the nutrient cycles and food webs, pollinators, granivores, ecosystem engineers, herbivores, or predators (Lacher et al., 2019). The habitat stratum used by nocturnal mammals can be classified as either terrestrial or arboreal. Some species will only use one type of stratum while others may use both (Lacher et al., 2019). The actual range of most nocturnal species is not well known as most of our knowledge comes from single sightings and not from intensive surveys on their habitat preferences (Dzulhelmi & Abdullah, 2010; Sanamxay et al., 2015). For example, our knowledge on slow lorises (eight species are currently recognized worldwide) is based on intensive surveys of Javan slow lorises in Indonesia (Cabana et al., 2017; Nekaris et al., 2017; Rode-Margono et al., 2014) and Sunda slow lorises in Peninsular Malaysia (Wiens, 2002; Wiens et al., 2006; Wiens & Zitzmann, 2003).

The ecological roles of most nocturnal mammals are generally known to a certain extent. A majority are important primary or secondary seed dispersers by eating fruits or scatter-hoarding seeds in the rainforest (Fleming & Kress, 2013; Lacher et al., 2019). Once the fruit is eaten and seeds are ingested intact, animals will move and defecate and thus disperse the seed, which sometimes can be several kilometres away (Heymann et al., 2017). This is for example the case in most civet species, fruit bats and flying squirrels (Lacher et al., 2019) that forage in the canopy, as well as for some species that forage on the ground, such as wild boar and deer (Lacher et al., 2019).

Nocturnal mammals are also important pest control agents (Lacher et al., 2019). This role is mostly carried out by predators such as felid species that regulate populations of small mammals (Silmi et al., 2013). Other animals like tarsiers, slow lorises or insectivorous bats are feeding on large numbers of insects every year (Cabana et al., 2017; Gursky, 2015; Lacher et al., 2019). A study by Kunz et al. (1995) demonstrated that bats can eat up to two thirds of their body mass in insects every night, bringing the number of devoured insects per bat colony to billions of insects eaten in a single night (Leelapaibul et al., 2005). By doing so, bats protect crops, plantations and farms from destructive impacts of phytophagous insects.

One of the most important roles played by nocturnal mammals is pollination (Lacher et al., 2019). These animals pollinate up to 94% of plant species in tropical communities (Ollerton et al., 2011) by feeding on the nectar of flowers and attaching pollen to their fur that they transfer to other flowers. Without most species of nectivorous bats, the abundance of fruits for human consumption, for example durians in Malaysia (Aziz et al., 2017), would not be as high today (Lacher et al., 2019). This role is also played by other animals such as slow lorises and rats who are known to eat the nectar of certain plants (Cabana et al., 2017; Wiens et al., 2008).

2.4.3 Conservation status of nocturnal mammals in Malaysia

Peninsular Malaysia's latest amendment to the Wildlife Conservation Act was passed in 2010 with a revision currently in process. Under this law, most larger mammal species occurring in Malaysia are either Protected or Totally Protected. The laws in Peninsular Malaysia and the two Malaysian states in Borneo are regulated differently. Sabah and Sarawak have semi-independent laws, and both have their own regulations regarding wildlife. In Sabah, the regulation is under the Wildlife Conservation Enactment 1997 and in Sarawak, the regulation is under the Wildlife Protection Ordinance 1998 (Lappan & Ruppert, 2019).

In Peninsular Malaysia, 73% of non-volant nocturnal mammal species are Totally Protected, 18% Protected and 9% without any protection status (Table 2.1). The differences between the status is that certain licences can be obtained for Protected species such as hunting, taking, keeping, collecting, import and others. Those licences are unavailable for Totally Protected species and it is illegal to undertake any activities regarding those species (Lappan & Ruppert, 2019).

Table 2.1 Records of arboreal and terrestrial nocturnal, non-volant mammals in Peninsular Malaysia and their protection status (Wildlife Conservation Act 2010).

Order	Family	Scientific Name	Common Name	Protection status
Artiodactyla	Bovidae	*Bos gaurus*	Malayan gaur	Totally Protected
	Cervidae	*Muntiacus muntjak*	Barking deer	Protected
		Rusa unicolor	Sambar deer	Protected
	Suidae	*Sus barbatus*	Bearded pig	Totally Protected
		Sus scrofa	Eurasian wild boar	Protected
	Tragulidae	*Tragulus kanchil*	Lesser mouse deer	Protected
		Tragulus napu	Greater mouse deer	Protected
Carnivora	Felidae	*Neofelis nebulosa*	Clouded leopard	Totally Protected
		Panthera tigris jacksonii	Malayan tiger	Totally Protected
		Panthera pardus	Leopard	Totally Protected
		Pardofelis marmorata	Marble cat	Totally Protected
		Prionailurus bengalensis	Leopard cat	Totally Protected
		Prionailurus planiceps	Flat-headed cat	Totally Protected
	Herpestidae	*Herpestes brachyurus*	Short-tailed mongoose	Totally Protected
	Ursidae	*Helarctos malayanus*	Malayan sun bear	Totally Protected
	Viverridae	*Arctictis binturong*	Binturong	Totally Protected
		Arctogalidia trivirgata	Small-toothed palm civet	Totally Protected
		Hemigalus derbyanus	Banded palm civet	Totally Protected
		Paguma larvata	Masked palm civet	Totally Protected
		Paradoxurus hermaphroditus	Common palm civet	N/A
		Prionodon linsang	Banded linsang	Totally Protected
		Viverricula indica	Small Indian civet	Protected
		Viverra megaspila	Large spotted civet	N/A
		Viverra tangalunga	Malay civet	N/A
		Viverra zibetha	Large Indian civet	Totally Protected

Table 2.1 Continued

Order	Family	Scientific Name	Common Name	Protection status
Dermoptera	Cynocephalidae	*Galeopterus variegatus*	Sunda colugo	Totally Protected
Perissodactyla	Tapiridae	*Tapirus indicus*	Malayan tapir	Totally Protected
Pholidota	Manidae	*Manis javanica*	Pangolin	Totally protected
Primata	Lorisidae	*Nycticebus coucang*	Sunda slow loris	Totally protected
Proboscidea	Elephantidae	*Elephas maximus*	Asian elephant	Totally Protected
Rodentia	Hystericidae	*Atherurus macrourus*	Brush-tailed porcupine	Protected
		Hystrix brachyura	Malayan porcupine	Protected
		Hystrix crassispinis	Thick-spined porcupine	N/A
		Trichys lipura/ fasciculata	Long-tailed porcupine	Totally protected
	Sciuridae	*Aeromys tephromelas*	Large black flying squirrel	Totally protected
		Hylopetes lepidus	Gray-cheeked flying squirrel	Totally protected
		Hylopetes spadiceus	Red-cheeked flying squirrel	Totally Protected
		Iomys horsfieldii	Horsfield’s flying squirrel	Totally protected
		Petaurista elegans	Spotted giant flying squirrel	Totally protected
		Petaurista petaurista	Red giant flying squirrel	Totally protected
		Petinomys genibarbis	Whiskered flying squirrel	Totally protected
		Petinomys setosus	Temminck's flying squirrel	Totally protected
		Petinomys vordermanni	Vordermann's flying squirrel	Totally protected
		Pteromyscus pulverulentus	Smoky flying squirrel	Totally protected

2.5 Species of interest

2.5.1 Sunda slow loris (*Nycticebus coucang*)

The Sunda slow loris (*Nycticebus coucang)* is one of the species of slow lorises occurring in Peninsular Malaysia (Appendix A; Groves, 2005) including its islands (i.e. Langkawi, Penang, Tioman, and Perhentian) (Groves, 2005). New taxonomic and genetic research suggests that another species of slow lorises (potential name: *Nycticebus tanamensis*) might occur in northern Peninsular Malaysia and Southern Thailand, potentially including Langkawi island (K.A.I. Nekaris, personal communication, July 2019). Slow lorises are nocturnal and arboreal primates of the family Lorisidae and are classified as Vulnerable, Endangered and Critically Endangered depending on the species in the IUCN Red List (Nekaris et al., 2020). They are also totally protected by law in Malaysia but are often illegally kept as pets (Lappan & Ruppert, 2019).

They measure between 27 to 38 cm from head to tail and weigh between 599 and 685g (Ankel-Simons, 2010; Rigel, 2004). They mostly feed on specific plant sap known as gum, on nectar, fruits and arthropods (Wiens, 2002). They have a special teeth structure called toothcomb, normally used for grooming that they also use to remove bark to eat gum (Martin, 1979). They are mainly monogamous and form small groups with other individuals (Wiens, 2002; Wiens & Zitzmann, 2003). They prefer forested habitat but can adapt to disturbed habitats as long as some canopy connectivity exists. They rarely go down to the forest floor as they are not well adapted to walking on the ground (Nekaris & Bearder, 2007). They have the particularity to be the only venomous primate in the world, and one of the few venomous mammals (Nekaris et al., 2013). Their bite can take months to heal and can be fatal to allergic people following an anaphylactic shock (Madani & Nekaris, 2014).

2.5.2 Sunda colugo (*Galeopterus variegatus*)

The Sunda colugo (*Galeopterus variegatus*) is a nocturnal mammal belonging to the family Cynocephalidae and order Dermotera (Appendix B; Boeadi & Steinmetz, 2008). It is one of only two species of colugos recognized, with the other one occurring in the Philippines (*Cynocephalus volans*). Both are listed as Least Concern in the IUCN Red List (Boeadi & Steinmetz, 2008; Gonzalez et al., 2008). Although only two species are currently recognized, at least eight more species are suggested to exist throughout South-East Asia (Mason et al., 2016). Uncertainties in their taxonomy is due to a lack of research on these animals and the difficulty to observe them. Four subspecies are currently recognized: *G. v. variegatus* (Java), *G. v. temminckii* (Sumatra), *G. v. borneanus* (Borneo), and *G. v. peninsulae* (Peninsular Malaysia and mainland of Southeast Asia; Stafford & Szalay, 2000). Recent studies by Janečka et al. (2008) provide evidence that the mainland, Javan, and Bornean subspecies may be recognised as three distinct species in the genus *Galeopterus*. They are Totally Protected by law in Malaysia (Boeadi & Steinmetz, 2008) but they are sometimes killed by fruit farmers because they are considered as pest (personal observation, 2018).

Colugos are gliding mammals also known as flying lemurs, but to avoid confusion, as they are neither flying, nor lemurs, only the name colugo should be used. They are not primates but are closely related and recognized as sister-clade to the order Primata (Janečka et al., 2007; Mason et al., 2016) whereas lemurs are true primates, only occurring in Madagascar (Mittermeier et al., 2008).

They have a particular anatomy with a wide membrane attached to all limbs and tail, called a patagium (Feldhamer et al., 2015). This membrane allows them to glide efficiently but does not allow for specialized movement or change of direction, like in flying squirrels who steer with their tails. They are strictly arboreal and feed on young leaves, shoots, flowers, and rarely fruits (Agoramoorthy et al., 2006). They also lick tree bark for water, salts, nutrients, and minerals (Lim, 2007). They measure 33 to 42 cm body length with a tail of 18 to 27 cm, and they weight between 0.9 to 1.3 kg (Shepherd & Shepherd, 2012). They are known to communicate in audible sound (Dzulhelmi & Abdullah, 2009a) but also in ultrasound (Miard et al., 2019).

2.5.3 Red giant flying squirrel (*Petaurista petaurista*)

The red giant flying squirrel (*Petaurista petaurista*) is a species of gliding squirrels from Asia belonging to the order Rodentia and the family Sciuridae (Appendix C; Thorington et al., 2012). They are listed as Least Concern in the IUCN Red List (Duckworth, 2016) due to their broad geographic range from Indonesia to China and up to Afghanistan (Thorington et al., 2012). However, taxonomic research has shown the occurrence of multiple subspecies that could potentially be elevated to species level throughout South-East Asia (Duckworth, 2016; Sanamxay et al., 2015). In Peninsular Malaysia, there are three recognized subspecies: *P. p. melanotus* (mainland), *P. p. penangensis* (Penang island) and *P. p. terutaus* (Langkawi island) (Duckworth, 2016).

Petaurista petaurista is one of the largest flying squirrels with an average body length of 38 cm, and its tail can be as long. It can weigh up to 1.3 kg (Lee et al., 1993). These animals can glide over large distances of up to 75 m, with one record of 150 m (Krishna et al., 2016; Thorington & Heaney, 1981). They can be found in a variety of habitats such as mountain temperate forests, wet tropical lowlands, evergreen broadleaf forests, hardwood forests, coniferous forests, orchards, plantations and limestone hills (Miard et al., 2020; Thorington et al., 2012). A study by Lin et al.

(1988) showed that the home range of adult females of the subspecies *P. p. grandis* was 3.2 ha and that they are mostly active between sunset and midnight. They are herbivorous and their diet consist of conifer cones, leaves and branches. They also eat nuts, fruits and insect (Phillipps & Phillipps, 2018). Flying squirrels use nests during the day, which are mostly tree cavities or external leaf nest such as ferns (Hackett & Pagels, 2003; Holloway & Malcolm, 2007; Miard et al., 2020). They can also use subterranean nests, but it is rare and probably species dependent (Hackett & Pagels, 2003; Holloway & Malcolm, 2007).

CHAPTER 3

GENERAL METHODOLOGY

3.1 Sampling sites

3.1.1 General overview

The main sites for this study were Penang Island, state of Penang (5.3673°N, 100.2486°E) and Langkawi Island, state of Kedah (6.3500°N, 99.8000°E) (Figure 3.1). Islands were chosen due to the high abundance of some mammal species, probably due to a lower predation rate compared to the mainland. Those two islands were chosen as they have a similar size but are different in anthropogenic development with Penang being highly developed compared to the more rural Langkawi.

Additionally, shorter surveys were also conducted in other sites on the mainland for methodological validation and to assess nocturnal mammal distribution here: Batu Caves, Selangor (3.2425°N, 101.6873°E); Genting Highlands, Pahang (3.4125°N, 101.7926°E); Merapoh, Pahang (4.6930°N, 102.0038°E); Ulu Muda, Kedah (6.1574°N, 100.9483°E), and Segari Melintang, Perak (4.3112°N, 100.5774°E; Figure 3.1).

To compare results for the methodological testing with Peninsular Malaysia, two sites located in a pristine rainforest in Brunei Darussalam, Borneo (see Chapter 4 for detailed site description) were also surveyed. Those sites where chosen due to an existing research collaboration and the opportunity for a Master student to compare the results of this study with her study. It is important to compare methodological results between observers to validate the findings.

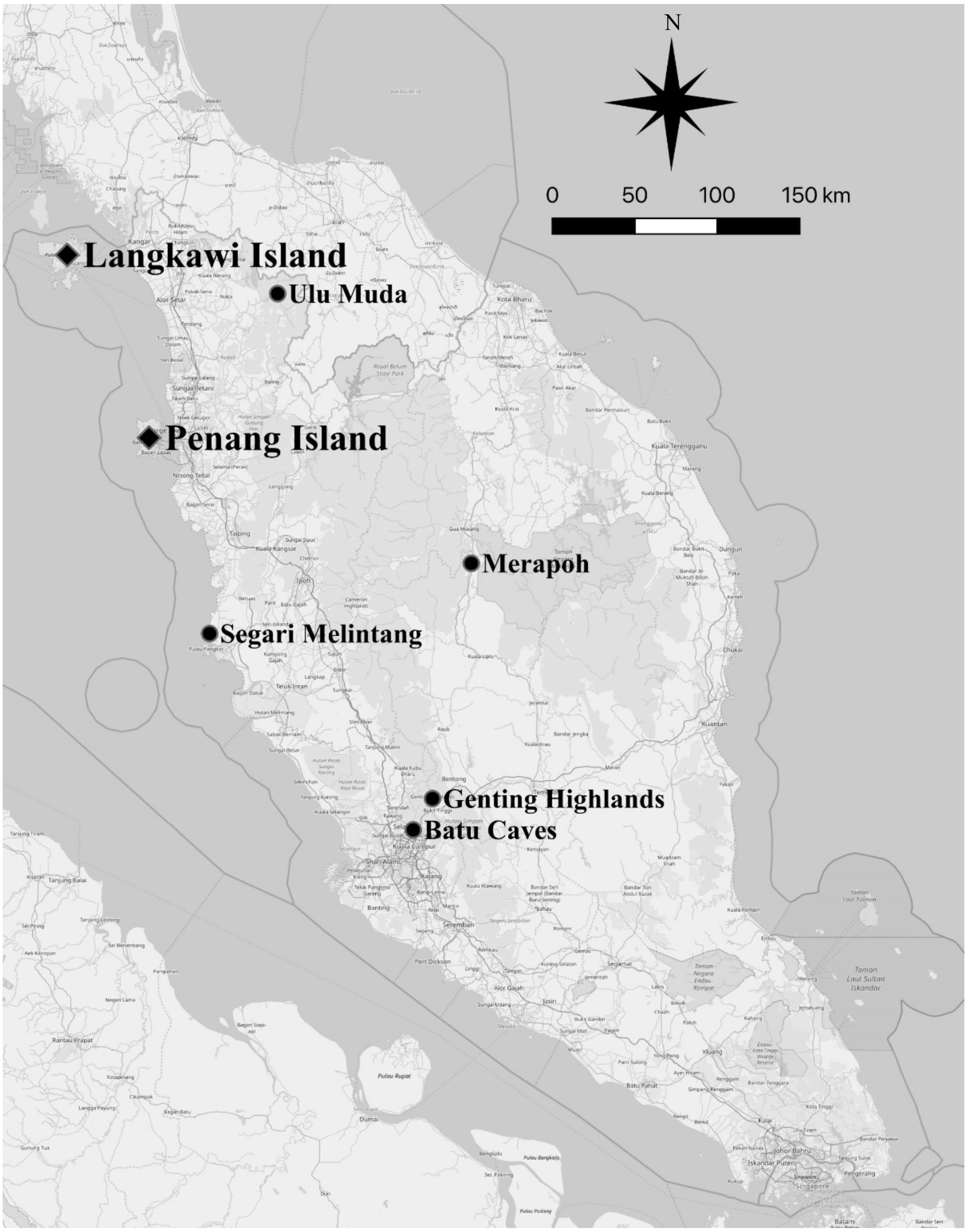

Figure 3.1 Map of two main field sites (♦) and secondary survey sites (●) in Peninsular Malaysia.

3.1.2 Description of the two main study sites

Penang Island is located on the North-West of Peninsular Malaysia (Table 3.1). It is one of the most developed states in Malaysia, with Malaysia's second largest city, Georgetown. The population of Penang island comprises ca. 722,000 habitants with a population density of ca. 2,500 people per km^2 (Department of Statistics Malaysia, 2010; Deuskar et al., 2015; MNS, 1999). The island comprises an area of 293 km^2 with the central area consisting of lowland tropical rainforest and hill forest. The elevation on the island ranges from 0 up to 833 m asl. The average temperature is relatively constant throughout the year (26.4°C – 27.7°C) with an average variation of 7.8°C during the day (NOAA, 2015). Annual precipitation is at a total of 2,477 mm with monthly variations of 68.7 - 383 mm (NOAA, 2015). The rapid development of the island over the last three decades has brought significant changes to its landscape (Masum et al., 2017). Most of the pristine land has been converted for urban development and agricultural use (Deuskar et al., 2015; Chan, 1998).

Langkawi is an archipelago of 99 islands located on the North-West of Peninsular Malaysia near the Thai border (Table 3.1). The total land surface is covering 478.5 km^2 and the main island, Langkawi Island being 320 km^2. The total population comprises 85,588 inhabitants of which 65,000 occupy the main island (Department of Statistics Malaysia, 2010). Due to its particular landscape, this archipelago is recognized as a UNESCO Geopark. Its karst landscape has been formed during multiple geological events bringing a special floral and faunal composition (Leman et al., 2007, 2008). The vegetation consists of alluvial plains punctuated with limestone ridges. It is also dominated by dipterocarp forest-covered mountains. The elevation on the island ranges from sea level to 881 m asl. The average temperature is constant throughout the year (26.9°C – 28.3°C) with average variation