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Dramatic decline in bat species richness in Singapore, with implications for Southeast Asia

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ABSTRACT

Literature searches and recent surveys of the bat fauna of Singapore indicate that of the 24 species of Microchiroptera and six species of Megachiroptera documented for this small equatorial island just 15 and 5, respectively, are still present. These recorded declines in chiropteran species richness almost certainly understate the true losses as extensive land transformation/habitat loss (>95%) and biota loss occurred early in Singapore's colonial history before comprehensive surveys of bats were made. In an effort to reconstruct the pre-settlement bat fauna, we inferred an upper bound of pre-settlement species richness using a checklist from a well-known bat assemblage in neighbouring Peninsular Malaysia, and a lower bound based on species common to Peninsular Malaysia, Borneo and Sumatra. The Singapore records were compared with these two species list predictions. Based on this analysis, we infer that between 60 and 72 species would have inhabited Singapore before 1819. We also estimate that between 33% (based on the confirmed inventory) and 72% of the species (based on the upper-bound estimate of species richness) are now locally extinct. For Microchiroptera the data suggest that the documented local extinction rate of 38% may project to between 69% and 75%. Forest-dependant bats are particularly affected and comprise a much lower proportion of the bat fauna than is seen in intact forest in Peninsular Malaysia. All hipposiderids and 40% of the documented rhinolophid taxa have been lost and almost half (6) of the surviving microchiropteran species are locally endangered. Projected local extinction rates for Megachiroptera raise the documented value (17%) to about 60%, with most of the survivors being widespread species known to forage in cultivated or secondary forest habitats or to commute long distances between fragmented resources. The dramatic decline in Singapore bat species richness and a concomitant change in chiropteran guild and trophic structure (Microchiroptera vs. Megachiroptera) reflect patterns of diversity change seen elsewhere in the region in response to loss of forest habitat. In Singapore, the decline in diversity (species richness and abundances) for both mega- and microbats may also relate to urbanisation and deliberate or accidental destruction of bats and their roost sites in a land that has one of the highest human population densities on the planet. Although these losses (actual and inferred) represent a microcosm of mainly local extinctions, a wider geographical extrapolation over the 21st century indicates that heavy deforestation in progress in Southeast Asia might be expected to lead to extinction of many bat taxa, with upper-bound estimates of regional species losses exceeding 40% and global extirpation anticipated for at least 23% of Southeast Asia's bat fauna by 2100.

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1. Introduction

The Republic of Singapore is located about 1°N of the equator in a humid, tropical environment at the southern tip of Peninsular Malaysia, from which it is separated by the narrow Johore Straits. Prior to the arrival of Sir Stamford Raffles in 1819 and the founding of modern Singapore, the main island of this 591 km^2 territory (pre-land reclamation) was almost entirely covered in primary, mixed dipterocarp rain forest and wetland forest. Dramatic land use changes resulted in more than 90% of the forest being cleared, mainly for agriculture, over the next 60 years, followed by increasing urbanisation (Corlett, 1992). Near the end of the 20th century nearly 50% of the island was built-up with 45% modified in other ways for human use (Chia et al., 1990). Less than 5% remains as primary or secondary (re-growth) forest (Corlett, 1992). Much of this forest now lies within Nature Reserves that, in 2003, constitute 4.8% of Singapore's enlarged land area of 697 km^2 (unpublished data, Singapore National Parks Board). The island has consequently undergone considerable ecological transformation in the last two centuries, including significant losses of the original biota (Corlett, 1992; Castelletta et al., 2000; Brook et al., 2003). Vertebrates are considered to have become depauperate with native non-bat mammals known to be severely impoverished (observed and inferred extinctions rates of 42% and 78%, respectively, – Brook et al., 2003). In particular, all the larger terrestrial mammals have become locally extinct (Corlett, 1992).

Bats constitute the second largest order of mammals worldwide and they peak in species richness in the equatorial tropics (Findley, 1993; Willig et al., 2003). Neighbouring Peninsular Malaysia supports in excess of 100 species (Simmons, 2005), with local species richness of insectivorous bats, which can exceed 50 species, being one of the highest in the world (Kingston et al., 2003). In contrast, recent surveys of Singapore bats report just 15 species of Microchiroptera (Pottie, 1996; Pottie et al., 2005), and 5 Megachiroptera (Rajathurai, 1995; Teo and Rajathurai, 1997) remaining from total inventories of 24 and six for these suborders (Table 1). Seven microchiropteran species, namely: *Rhinolophus sedulus, Rhinolophus stheno, Hipposideros bicolor, Hipposideros cervinus, Hipposideros ridleyi, Pipistrellus javanicus* and *Chaerephon plicatus* are considered locally extinct (Pottie et al., 2005). Another species, *Pipistrellus stenopterus*, is indeterminate (possibly extinct) and one other, *Myotis oreias*, known only from the Singaporean holotype, may be globally extinct unless other records in the region emerge (Pottie et al., 2005). Prior to the 1990s, Singapore bats had not been surveyed systematically, thus the decline in chiropteran species richness is likely to be greater than existing inventories indicate. The objective of the present study was to quantify and characterise this decline, based on likely projections of the original, unknown diversity of bats present in pre-colonial Singapore, and to use these data to predict bat diversity loss in Southeast Asia. Three methods were used to generate estimates of the historical species pool for Singapore: an inventory approach based on a combination of historical records and recent surveys; an estimate derived from an evaluation of the best-known bat fauna in neighbouring Peninsular Malaysia; and a conservative, geographic range estimate including only those additional species common to Peninsular Malaysia, Sumatra and Borneo.

2. Methods

2.1. Historical and recent surveys

The early literature has been comprehensively summarised in Yang et al. (1990) which, together with an additional species recorded by Harrison (1966), gave a historical inventory of 21 microchiropteran and six megachiropteran taxa. Recent intensive surveys of the Microchiroptera, including the use of harp traps and acoustic monitoring, provided a more comprehensive and current account of the status of this suborder of bats in Singapore and revealed three additional species, namely *Nycteris tragata*, *Rhinolophus lepidus* and *Murina suilla* (Pottie, 1996; Pottie et al., 2005). The combined historical and recent records are, however, likely to be an underestimate of pre-settlement bat diversity as systematic surveys were not conducted until after much of the large-scale habitat changes had occurred, and the early ad hoc surveys in the late 19th and early 20th centuries (Yang et al., 1990) were conducted prior to the advent of survey techniques (mist nets, harp traps and acoustic monitoring) that greatly improve the detection of species.

2.2. Species richness in neighbouring Peninsular Malaysia

Given the present day proximity (0.6–2.6 km) and historical continuity (pre-Holocene transgression) of Singapore land and, presumably, forest cover with that of Peninsular Malaysia, the bat diversity of pre-settlement Singapore is likely to have been comparable with Peninsular Malaysia. Brook et al. (2003) used checklists of freshwater and terrestrial species (excluding bats) from Peninsular Malaysia to infer pre-settlement species richness for Singapore, but several bat species are limited to the north of the Peninsula (Corbet and Hill, 1992), and their inclusion here would lead to an overestimate of inferred species richness. Indeed, inventories for Peninsular Malaysia (Medway, 1983; Lekagul and McNeely, 1988; Koopman, 1989; Corbet and Hill, 1992; Zubaid, 1993; Francis, 1995; Kingston et al., 2003) suggest a decrease in microchiropteran diversity towards the southern end of the Peninsula, but this southern region, adjacent to Singapore, has been surveyed less intensively compared to central and northern Peninsular Malaysia. Moreover, early surveys did not deploy harp traps, which are particularly effective in catching insectivorous species of the forest interior (Francis, 1989; Kingston et al., 2003). In central Peninsular Malaysia, Krau Wildlife Reserve (Pahang State, 3°43′N, 102°10′E) has been the subject of at least nine published bat surveys and recent research using an extensive array of survey techniques (i.e. harp traps, mist nets, roost surveys, acoustic monitoring) indicates that the Reserve supports the highest diversity of insectivorous bats known for a single locality in the Old World (Kingston et al., 2003, 2006). The Reserve is similar in extent to Singapore, encompassing 620 km^2 of largely undisturbed dipterocarp

Table 1 – Documented inventories and predictions of original diversity for Chiroptera in Singapore

Taxon	Historical and recent records							Predicted fauna	
	Harrison (1966)	Medway (1983)	Yang et al. (1990)	Rajathurai (1995)	Teo and Rajathurai (1997)	Pottie et al. (2005)	Cumulative Singapore inventory	P. Malaysia (KWR) predictions	Geographic range predictions
Pteropodidae									
Cynopterus brachyotis brachyotis (Müller)	C	+	C		C		x	x	x
Cynopterus horsfieldii Gray								x	x
Balionycteris maculata (Thomas)								x	x
Chironax melanocephalus (Temminck)								x	x
Dyacopterus spadiceus (Thomas)								x	
Eonycteris spelaea (Dobson)	+	+	I		C		x	x	x
Macroglossus minimus minimus (Geoffroy)		+	I	+			x	■	x
Macroglossus sobrinus K. Andersen								x	
Megaerops ecaudatus (Temminck)								x	x
Megaerops wetmorei (Taylor)								x	x
Penthetor lucasi (Dobson)	+	+	I		U		x	x	x
Pteropus hypomelanus Temminck									x
Pteropus vampyrus (Linnaeus)	C	+	U		V		x	■	x
Rousettus amplexicaudatus (Geoffroy)	+						x	x	x
Pteropodidae total							6	13	12
Emballonuridae									
Emballonura monticola Temminck	+	+	I			En	x	x	x
Saccolaimus saccolaimus (Temminck)	+	+	I		C	C	x	■	x
Taphozous longimanus Hardwicke									x
Taphozous melanopogon Temminck	+	+	I			R	x	x	x
Emballonuridae total						3	3	3	4
Nycteridae									
Nycteris tragata (Andersen)						En	x	x	x
Nycteridae total						1	1	1	1
Megadermatidae									
Megaderma spasma (Linnaeus)	+	+	I			En	x	x	x
Megadermatidae total						1	1	1	1
Rhinolophidae									
Rhinolophus acuminatus Peters								x	x
Rhinolophus affinis Horsfield								x	x
Rhinolophus lepidus Blyth					C	C	x	x	■
Rhinolophus luctus Temminck	+	+	I			En	x	x	x
Rhinolophus macrotis Blyth								x	
Rhinolophus pusillus Temminck									x

Rhinolophus robinsoni K. Andersen								x	
Rhinolophus sedulus Andersen	+	+	I			Ex	x	x	■
Rhinolophus stheno Andersen	+					Ex	x	x	■
Rhinolophus trifoliatus Temminck	+	+	I		R	En	x	x	x
Rhinolophidae total						3	5	9	8
Hipposideridae									
Coelops robinsoni Bonhote								x	
Hipposideros armiger (Hodgson)								x	
Hipposideros ater Templeton									x
Hipposideros bicolor (Temminck)[a]		+	I			Ex	x	x	x
Hipposideros cervinus (Gould)		+	I			Ex	x	x	x
Hipposideros cineraceus Blyth								x	x
Hipposideros diadema (E. Geoffroy)								x	x
Hipposideros doriae (Peters)								x	x
Hipposideros galeritus Cantor								x	
Hipposideros larvatus (Horsfield)								x	x
Hipposideros lylei Thomas								x	
Hipposideros ridleyi Robinson and Kloss		+	I			Ex	x	x	■
Hipposideridae total						0	3	11	8
Vespertilionidae									
Arielulus societatis (Hill)								x	
Hesperoptenus blanfordi (Dobson)								x	
Glischropus tylopus (Dobson,)								x	x
Myotis adversus (Horsfield)	+	+	I		C	C	x	■	■
Myotis ater (Peters)								x	x
Myotis hasseltii (Temminck)								x	x
Myotis horsfieldii (Temminck)								x	
Myotis muricola (Gray)	C	+	C		C	C	x	x	x
Myotis oreias (Temminck)	+		I			Ex	x	■	■
Myotis ridleyi Thomas								x	x
Myotis siligorensis (Horsfield)								x	
Pipistrellus javanicus (Gray)	+	+	I			Ex	x	x	x
Pipistrellus stenopterus (Dobson)		+	I			I	x	x	x
Pipistrellus tenuis (Temminck)									x
Philetor brachypterus (Temminck)									x
Scotophilus kuhlii Leach	C	+	C		C	C	x	x	x
Tylonycteris pachypus (Temminck)		+	I		En	En	x	x	x
Tylonycteris robustula Thomas	+	+	U		C	U	x	x	x
Vespertilioninae total						5	8	16	14
Miniopterus magnater Sanborn									x
Miniopterus medius Thomas and Wroughton								x	

Table 1 – *continued*

Taxon	Historical and recent records							Predicted fauna	
	Harrison (1966)	Medway (1983)	Yang et al. (1990)	Rajathurai (1995)	Teo and Rajathurai (1997)	Pottie et al. (2005)	Cumulative Singapore inventory	P. Malaysia (KWR) predictions	Geographic range predictions
Miniopterinae total						0	0	2	2
Harpiocephalus mordax Thomas								x	
Murina aenea Hill								x	
Murina cyclotis Dobson								x	x
Murina rozendaali Hill and Francis								x	
Murina suilla (Temminck)						En	x	x	x
Murininae total						1	1	5	2
Kerivoula hardwickii (Horsfield)								x	x
Kerivoula intermedia Hill and Francis								x	
Kerivoula papillosa (Temminck)								x	x
Kerivoula pellucida (Waterhouse)								x	x
Kerivoula picta (Pallas)									x
Kerivoula sp.								x	
Phoniscus atrox Miller								x	x
Phoniscus jagorii (Peters)								x	
Kerivoulinae total						0	0	7	5
Molossidae									
Cheiromeles torquatus Horsfield	+	+	I		+	En	x	x	x
Chaerephon johorensis (Dobson)								x	
Chaerephon plicatus (Buchannan)	+	+	I			Ex	x	■	x
Mops mops (de Blainville)								x	x
Molossidae total						1	2	4	3
Microchiroptera cumulative totals						15	24	59	48
All bats							30	72	60

The KWR prediction is based on the combined Krau Wildlife Reserve and Singapore fauna, while the geographic range prediction extends the historical Singapore list to include additional species common to Peninsular Malaysia, Borneo and Sumatra. Filled squares denote Singapore species not in the KWR or Malaysia/Borneo/Sumatra faunal lists but added for the combined predictions. For published Singapore inventories, + denotes unquantified presence. The abundance categories C (common), U (uncommon), R (rare) and En (endangered) are quantified in Pottie et al. (2005) for that study. Ex = local extinction; *I* = indeterminate; *V* = visitor. Nomenclature follows (Simmons (2005)).

a – *Hipposideros bicolor* in Peninsular Malaysia comprises a pair of cryptic species that are genetically and acoustically distinct but show substantial morphological overlap (Kingston et al., 2001). It cannot be determined which of the two phonic types were considered present in Singapore by Medway (1983), but neither was detected by Pottie et al. (2005).

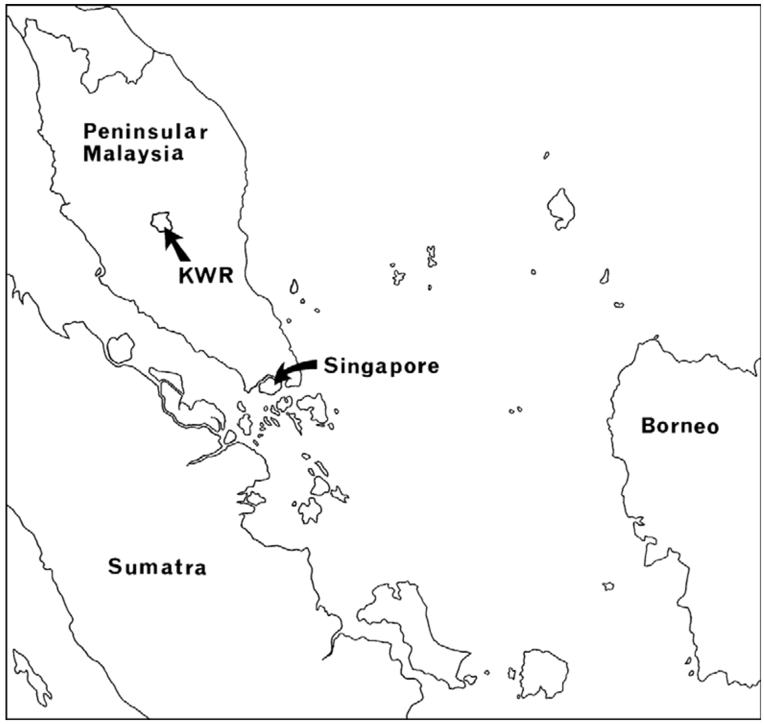

Fig. 1 – Map of Southeast Asia showing the position of Singapore within the Sumatra – Peninsular Malaysia – Borneo region, and the location of the Krau Wildlife Reserve (KWR) in Malaysia.

rainforest, and is effectively a forest 'island' in a 'sea' of development and land transformation. Its location (Fig. 1) is such that many of the species currently restricted to the north of the Peninsula (species that would have been unlikely to have occurred in Singapore) have not been recorded. Although the Reserve list, at 68 species (Kingston et al., 2006), may still be incomplete, the combined Singapore-Krau total provides a credible upper-bound limit of expected species richness for pre-settlement Singapore (Table 1).

2.3. *Geographic range estimate*

As a lower bound of estimated historical bat species richness in pre-settlement Singapore, we included, with the Singapore records, only those additional species currently known to be distributed across Peninsular Malaysia, Sumatra and Borneo, a region within which Singapore is centrally located (Fig. 1). Singapore would in fact have been land-locked within the emergent Sunda Shelf and connected terrestrially not only with Malaysia but with Sumatra and Borneo too, during low sea levels (~50–120 m or more below present levels) of the Pleistocene glacial maxima (Chappell and Shackelton, 1986; Fairbanks, 1989; Pirazzoli, 1991; Gvirtzman, 1994). This range estimate of bat diversity is a conservative one as some bat species are common to Peninsular Malaysia and Borneo but not Sumatra, while others are shared by the Peninsula and Sumatra but have not been recorded on Borneo. Consequently, species that are currently present in all three localities are highly likely to have occurred historically on Singapore.

2.4. *Future projections for Southeast Asia*

Based on observed and inferred Singapore extinction rates, estimates of future biodiversity loss of bat species in Southeast Asia were derived using the species-area relationship $S = cA^z$ and the methodology of Brook et al. (2003) to define the impact of forest loss. S and A represent, respectively, ratios of present to original species complements, and present to original forest areas. Values of S are calculated from the observed and inferred losses and values of z subsequently derived. With A set at 0.043 for Singapore, values of z and S (observed; upper-bound inferred; lower-bound inferred) were as follows: Microchiroptera, $z = (0.15, 0.44, 0.37)$ and $S = (0.63, 0.25, 0.31)$; Megachiroptera, $z = (0.06, 0.30, 0.29)$ and $S = (0.83, 0.39, 0.42)$; all bats, $z = (0.13, 0.41, 0.35)$ and $S = (0.67, 0.28, 0.33)$. Computation of extrapolated regional species losses assumed, as in Brook et al. (2003), a regional deforestation rate (Achard et al., 2002) of 0.71% yr^{-1}, giving a forest area in 2100 of 26% of its original extent.

3. Results

Compared with the documented Singapore inventory for Microchiroptera and Megachiroptera of 24 and six species, respectively, the Peninsular Malaysia extrapolation gives an upper limit prediction of 59 insectivorous species and 13 Megachiroptera (Table 1). The geographic range estimate method produces a more conservative expected historical pool of 48 Microchiroptera and 12 Megachiroptera species for Singapore (Table 1).

Table 2 – Extinction rates and patterns for Chiroptera in Singapore

Taxonomic category	Percentage species loss		
	Documented	P. Malaysia (KWR) predictions	Geographic range predictions
Emballonuridae	0	0	25
Nycteridae	0	0	0
Megadermatidae	0	0	0
Rhinolophidae	40	67	63
Hipposideridae	100	100	100
Vespertilioninae	38	69	64
Miniopterinae	–	100	100
Murininae	0	80	50
Kerivoulinae	–	100	100
Molossidae	50	75	67
All Microchiroptera	38	75	69
All Megachiroptera	17	62	58
All species	33	72	67

The KWR (Krau Wildlife Reserve) predictions are upper-limit losses based on a presumed extension of the Malaysian fauna to Singapore. The geographic range predictions are based on an extrapolation of the original Singapore fauna to include species common to Peninsular Malaysia, Sumatra and Borneo.

Estimates of the loss of chiropteran diversity in Singapore since pre-settlement range from approximately 33% of the documented fauna to, conservatively, a projected local extinction rate of 67% based on a geographic range estimate (Table 2). Projected local extinction rates for Megachiroptera raise the documented value (17%) to around 58–62% (Table 2). Similarly, the documented microchiropteran extinction rate of 38% extrapolates to a conservative 69% based on regional geographic ranges, or to an upper limit of 75% based the well-known Peninsular Malaysia fauna (Table 2). The inferred extinction rates for particular microbat families or sub-families show wide variation. While 40% (two species) of the documented rhinolophid taxa are considered locally extinct, Malaysian and regional range predictions raise this extinction value for Rhinolophidae to 67% and 63%, respectively (Table 2). All hipposiderids, perhaps as many as 11 species (Table 1), have been lost. Estimated losses of the vespertilionid sub-family Vespertilioninae ranged from 38% (documented fauna) to an upper limit of 69% (based on additional species recorded in Krau Wildlife Reserve). Two of the remaining three vespertilionid sub-families (Kerivoulinae and Miniopterinae) found in the region have never been recorded historically, or in recent surveys, in Singapore, and geographic range or Malaysian extrapolations (Table 1) suggest that between seven and nine species may have become locally extinct. The other vespertilionid sub-family, the Murininae, represented by a single record of two individuals of *Murina suilla* on the offshore island of Pulau Tekong (Robert Teo, pers. comm.), may have lost up to five species based on Malaysian fauna predictions. In contrast, the Emballonuridae, with inferred extinction rates of 0–25%, are less impacted in diversity terms although numbers for some taxa are low (Pottie et al., 2005).

Species-area projections of percentage losses for chiropteran species in Southeast Asia over the 21st century, based on upper-bound, lower-bound and observed extinction rates in Singapore, are 42, 38 and 16, respectively. For Microchiroptera and Megachiroptera separately, the projected extinctions are similar with corresponding sets of values being 44, 39, 18 and 34, 31, 8, respectively.

4. Discussion

For Microchiroptera, a reduction from 24 to 15 species in the Singapore inventory represents a documented extinction rate of 38%, which is almost certainly an underestimate. Reconstructed microchiropteran faunas, based on the geographic range estimate method, and the neighbouring Malaysian inventory, indicate, respectively, former species complements of 48 or 59 (Table 1). Island effects during interglacial, high sea-level stands may have limited pre-settlement species richness of Microchiroptera on Singapore, but the narrowness of the Strait separating Singapore from Malaysia (0.6–2.6 km) and the volant, sometimes migratory, habits of bats make it not unreasonable to assume the past diversity in Singapore to be similar to the species composition in neighbouring Malaysia. Inferred extinction rates of 69–75% for Microchiroptera (Table 2) suggest a catastrophic decline in diversity that is similar to extinction rates inferred (using a similar approach) for forest-specialist, non-bat mammals (78%) and birds (59%) in Singapore (Brook et al., 2003).

Possible causes of a decline to endangered status and local extinction of microbats in Singapore are numerous and currently speculative, but all hinge on the dramatic change in land-use patterns and the increase in human population density [currently >6000/km^2 (Tan, 2002)] that this small island state has undergone. The decline is a pattern that has been noted as symptomatic of urbanisation elsewhere (Racey and Entwistle, 2003). More than half (62%) of the documented locally extinct microbats (Table 1, Ex) belong to the families Rhinolophidae and Hipposideridae. The hipposiderids have completely disappeared and all three surviving rhinolophids have been recorded almost exclusively in remnant primary or secondary forest (Pottie et al., 2005). Rhinolophid and hipposiderid bats are typically characterised by specialisations of wing morphology and echolocation signal design that equip them to forage for insects in dense stands of vegetation, but greatly constrain their ecological flexibility (Kingston et al., 2003). They are ill-suited for foraging in the more open habitats that arise from forest loss and degradation and are thus dependant on intact stands of forest (Meijaard et al., 2005). The loss of two out of five (documented) or five out of nine (inferred) species of *Rhinolophus* and all *Hipposideros* species (documented or inferred) thus suggests a correlation with loss of primary forest habitat. Similarly, Brook et al. (2003) found that documented and inferred extinction rates of terrestrial (non-bat) and freshwater taxa were highest among forest specialists. However, loss of primary forest habitat may not be the sole reason for the relatively recent, documented local extinctions in these two bat families since most deforestation took place very early on in Singapore's colonial history (Corlett, 1992). Many hipposiderids and rhinolophids tend to roost gregariously and in consequence may be vulnerable to incidental or deliberate destruction by human disturbance, even if forest habitat suitable for foraging is available.

Also conspicuous by their absence are members of the forest-dependent vespertilionid sub-families Kerivoulinae and Murininae (except for an isolated record of *Murina suilla*). There are 16 species of these two sub-families in Peninsular Malaysia (Simmons, 2005) where up to 10 species may co-occur in intact forest. Moreover, they can comprise over a third of all species captured in harp traps set in undisturbed forest (Kingston et al., 2003). Although Kerivoulinae and most Murininae have never been recorded in Singapore, they are adept at avoiding mist nets and are not known to roost in caves or houses, limiting their detection in early survey work prior to the advent of harp traps.

Kingston et al. (2003) and Meijaard et al. (2005) predict that species that tend to forage in less structurally complex habitats, that is at the forest edge, or above the forest canopy, may be better able to adapt to the more open environments arising from anthropogenic disturbance. The present study provides some support for this: 58% of insectivorous species in the undisturbed lowland forest of Krau Wildlife Reserve are narrow-space foragers (*sensu* Schnitzler and Kalko, 1998), foraging in the highly cluttered space within the forest interior, with open-space and edge/gap guilds combined constituting the remaining 42% of species (Kingston et al., 2003, 2006). In contrast, the open-space and edge/gap species comprise 67% of Singapore insectivorous species, with the narrow-space guild reduced to 33%. Moreover, the Emballonuridae, Molossidae and Vespertilioninae (taxa that are typically open-space or edge/gap foragers) appear to have experienced fewer local extinctions and include four of the five insectivorous species considered locally common and at least six species that were regularly recorded foraging in anthropogenically modified habitats (Pottie et al., 2005). Nonetheless, many species are rare or endangered and details in Pottie et al. (2005) suggest that survival of species in the open-space and edge/gap guilds may also hinge on their ability to roost in man-made structures and habitats, particularly given the limited number of caves in Singapore.

With regard to the Megachiroptera, five of the six species in the historical record (Harrison, 1966; Yang et al., 1990) have been recorded in Singapore in recent years (Rajathurai, 1995; Teo and Rajathurai, 1997; see Table 1). Three of these, namely *Cynopterus brachyotis brachyotis*, *Penthetor lucasi* and *Eonycteris spelaea*, are confirmed (Teo and Rajathurai, 1997) as residents of mainland Singapore and a fourth, *Macroglossus minimus*, originally known only from Pulau Ubin – a northern Singapore island in the Johore Straits – (Rajathurai, 1995), is now known to occur on the mainland at Sungai Buloh Wetland Reserve (Anon, 2003). *Pteropus vampyrus* used to be seen in large numbers in Singapore (Chasen, 1925) but is now recorded only as a visitor. *Pteropus vampyrus* is believed to be transmigratory (Hutson, 2002) and a dramatic decline of populations of this species in Peninsular Malaysia, attributed to habitat loss and fragmentation, and hunting (Mohd-Azlan et al., 2001), may account for their reduced representation on Singapore.

Although the documented extinction rate for the Megachiroptera (17%) is less than half that for the Microchiroptera (38%), the projected rates, which exceed 55%, are closer to the projected microchiropteran extinction rates (Table 2). The surviving Megachiroptera in Singapore are widespread species (with the exception of *Penthetor lucasi*) and are known to forage in cultivated or secondary habitats and/or to commute long distances between fragmented resources (Medway, 1983; Payne and Francis, 1985). Moreover, bats historically identified as *Cynopterus brachyotis* in Peninsular Malaysia have recently been shown to comprise two divergent mitochondrial DNA lineages. The lineages are broadly sympatric but appear to be ecologically and morphologically distinct, with one generally confined to primary and mature secondary forest and the other more widely distributed in disturbed and agricultural habitats (Campbell et al., 2004). Currently only the latter has been confirmed for Singapore. The historical/geographical pool of pteropodid species distributed across Peninsular Malaysia, Borneo and Sumatra suggests that at least another five species (*Balionycteris maculata, Chironax melanocephalus, Megaerops ecaudatus, Megaerops wetmorei, Cynopterus horsfieldii*) might have occurred on pre-settlement Singapore. Although *C. horsfieldii* in Malaysia may persist in cultivated habitats if these are adjacent to forest (P. Campbell, pers. comm.), the other four species are largely dependant on intact stands of mature forest (Medway, 1983; Payne and Francis, 1985) that, except for small remnants, have not existed on Singapore for over a century.

The trophic structure of Chiroptera assemblages can be another indicator of habitat disturbance. Bat diversity studies in a logged and fragmented secondary forest in Peninsular Malaysia indicate a dramatic decline in the proportion of insectivorous microchiropteran species to 54% (Zubaid, 1993) compared with much higher percentages of 85% (Francis, 1990) and 82% (Kingston et al., 2003) reported for undisturbed lowland forests. Conversely, the plant-visiting Megachiroptera show a corresponding increase from 15% to 18% of species (Francis, 1990; Zubaid, 1993) in undisturbed forest to 46% in logged forest (Zubaid, 1993). Microchiropteran diversity in palaeotropical forests is therefore particularly vulnerable to disturbance by logging and forest clearance. Combining the data of Rajathurai (1995), Teo and Rajathurai (1997), Anon (2003) and Pottie et al. (2005), the relative proportions of insectivorous Microchiroptera and plant-visiting Megachiroptera (mainly frugivorous) species (including *P. vampyrus*) in the present Singapore inventory are 75% and 25%, respectively. Assuming that the three new microchiropteran records (Pottie et al., 2005) have always been present, this represents a slight decline in the proportion of insectivores compared with data

(80% insectivores and 20% frugivores) derived from either the cumulative Singapore inventory or from the geographic range prediction of species representation (Table 1). In urban Singapore, the shift to greater frugivorous representation is thus not so dramatic and may indicate that habitat degradation has been so severe that both trophic groups have been almost equally affected.

The confirmed species counts for Singapore Microchiroptera and all bats are, respectively, 15 and 20. From a conservation viewpoint, several species of insectivorous bats in Singapore, namely *Emballonura monticola, Megaderma spasma, Nycteris tragata, Rhinolophus trifoliatus, Rhinolophus luctus, Tylonycteris pachypus*, *Cheiromeles torquatus* and *Murina suilla* have very low abundances and are highly endangered (Pottie et al., 2005). Two of these locally endangered taxa, *N. tragata* and *Murina suilla* have only recently been discovered in Singapore, in very low numbers, which in itself suggests that other taxa may have become locally extinct before they could be detected. Despite the welcome addition of three new microchiropteran taxa to the fauna list, the low population numbers for many of Singapore's aerial insectivores (and many megachiropteran species) indicate that residual bat diversity in this 'garden-city' State is hanging by a thread and that, without further conservation measures and full legal protection, a continued decline in bat diversity for Singapore is likely.

The implications of local plant and animal extinctions in Singapore for the loss of biodiversity from tropical forests across Southeast Asia were considered for several taxonomic groups by Brook et al. (2003). Based on observed Singapore extinctions, projected biodiversity losses for Southeast Asia by the year 2100 ranged from 2% of all reptile species to 21% of non-bat mammals. Inferred extinctions generated higher predicted losses ranging from 25% (reptiles) to 58% (freshwater fish), with inferred non-bat mammal losses being 48%. Following their methodology, projected losses for bat species across Southeast Asia by 2100 range from 16% using observed extinctions to 42% based on extinctions inferred by comparison with the Krau Wildlife Reserve (KWR) dataset. Inferred KWR-based extinctions derived separately for the Microchiroptera (44%) and Megachiroptera (34%) are likewise high and are comparable to those predicted by Brook et al. (2003) for birds (32%) and non-volant mammals (48%). Regional deforestation and degeneration thus represents a dramatic threat to bat diversity in Southeast Asia, and with at least 168 species endemic to region (Simmons, 2005) such losses equate to the global extinction of up to 23% of Southeast Asia's bat fauna by 2100. The regional and global extinction rates for forest-dependant bats may however turn out to be greater than indicated above, for several reasons. First, the annual deforestation value of 0.71% (Achard et al., 2002) actually represents a year on year reduction in the rate of loss of forest area, an unlikely scenario. Second, as noted by Brook et al. (2003), biological hotspot areas, such Central Sumatra and S.E. Kalimantan, record significantly higher annual rates of deforestation (1.0–5.9%, Achard et al., 2002) than the average. Finally, in addition to deforestation, a high annual forest degeneration rate (0.42%, Achard et al., 2002) has further conservation implications for forest-dependant taxa.

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