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Conservation importance of limestone karst outcrops for Palaeotropical bats in a fragmented landscape

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ABSTRACT

Limestone karst landscapes are important for biodiversity yet are increasingly threatened by development activities such as mining. Furthermore, karsts are often scattered and isolated by agriculture, and are rarely considered in landscape planning because of a paucity of biodiversity data. We determined the conservation significance of an isolated limestone karst outcrop for insectivorous bats by quantifying the influence of this roosting resource on local assemblage structure across a fragmented landscape in peninsular Malaysia. Using a combination of rank abundance, gradient and randomisation analyses, we demonstrate that bat assemblages at nine forest sites are structured following a spatial gradient of increasing distance from a karst roosting resource. The assemblage at our karst site was dominated by a superabundance of three cave-roosting species, two of which were also found to dominate assemblages up to 11 km away. Cave-roosting bats exhibited a significant decay in abundance related to the distance from karst, with sites closest to karst also characterised by a rarity of tree cavity/foilage-roosting species that were otherwise common. Gradient analysis revealed that differences in assemblage composition were largely associated with the distance from the karst and, to a lesser extent, forest isolation and area. Our findings suggest that isolated karst outcrops can serve as important population reservoirs for cave-roosting bats, which subsidise diversity levels in forest fragments that might otherwise be expected to decline over time. While conservation efforts need to focus on maintaining large areas of connected forest, landscape management needs to ensure protection of karsts as point resources for cave-roosting bats.

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1. Introduction

'Conservation landscapes' should ideally include areas that support high biodiversity, as well as the key landscape features that sustain it (Sanderson et al., 2002). This is particularly important in the human-dominated landscapes of Southeast Asia, where forests are becoming increasingly disturbed and fragmented, and commercial pressures on remaining habitats have far reaching consequences for wildlife (Sodhi et al., 2004; Laurance, 2007). Conservation strategies designed to influence the locations and mitigation of land developments require an understanding of how features within these landscapes maintain wildlife populations; yet this information is often scarce or lacking (Meijaard and Sheil, 2007).

Among the forested landscapes in Southeast Asia, those that contain limestone karst systems are internationally recognised as

areas of huge biological importance, with aesthetic qualities and groundwater value (Wong et al., 2003; Gillieson, 2005). Limestone karsts are defined as sedimentary rock outcrops that were created millions of years ago by calcium-secreting marine organisms, and have been subsequently uplifted and eroded (Clements et al., 2006). They are prominent features of much of Southeast Asia, covering over 40 million hectares, of which only 13% is nominally protected (Day and Urich, 2000). Most karsts are scattered and isolated as small limestone hills, but nonetheless many of them support high levels of species diversity and endemism of plants, vertebrates and invertebrates (Schilthuizen et al., 2005; Clements et al., 2006, 2008). Unfortunately, not only are karst outcrops frequently isolated by urban and agricultural areas, but they are also under immense pressure from commercial mining interests, as well as the local harvest of guano and collection of bird nests (Hutton et al., 2001; Hobbs, 2004; Clements et al., 2006). This has led to revived efforts to both include karsts in conservation planning, and by using scientifically sound criteria, promote their biological importance in land-use decisions (Clements et al., 2006, 2008).

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Amongst the many biological attributes of karst outcrops, one that is often neglected in tropical conservation research is the importance that these landscape features have as roosting resources for bat populations. The availability of suitable roosting sites is essential in determining bat distributions (Lewis, 1995), and most bat families and genera contain species that roost in caves, which are typical features of karst areas. Cave networks can host large aggregations of bats, and although systematic documentation is lacking, karst sites often support substantial bat diversity (Arita, 1996; Niu et al., 2007; Kingston, 2009). Cave preservation is therefore important if we are to maintain viable bat populations. Indeed, cave disturbance is recognised as a major threat to bat diversity (Hutson et al. 2001; Niu et al., 2007; Racey, 2007), and may be a more important threat than landscape changes in some regions (Goodman et al., 2005). How these key roosting resources actually influence bat diversity elsewhere in a landscape, however, remains largely undocumented. Caves are a rare and unevenly distributed feature of most landscapes, and cave-roosting species appear to commute large distances to forage each night (Pavey et al., 2001; Bontadina et al., 2002; Struebig et al., 2008). Beyond these distances, however, cave-roosting species are expected to be rare, or absent (Lewis, 1995). Anecdotal reports attribute low levels of bat diversity at sites in Southeast Asia to disturbance at local caves and their surrounding habitat (Robinson and Webber, 2000; Suyanto and Struebig, 2007), yet the extent to which local assemblage structure is influenced by cave resources at distant sites has yet to be addressed. This is a simple, yet important question, because if bat assemblages are strongly shaped by the presence of a major roosting resource, then their long-term conservation over a landscape requires protection of this resource as well as the habitat in which they forage.

We assess the conservation importance of an isolated outcrop of limestone karst in Southeast Asia by quantifying its impact as a roosting resource on the assemblage structure of bats in the surrounding landscape. Our study was based in peninsular Malaysia, where more than 800 karsts have been reported, the majority isolated by agriculture and under pressure from commercial mining interests (Clements et al., 2008). We focused on the 'narrow-space' ensemble of insectivorous bats (sensu Schnitzler and Kalko, 2001), which are highly adapted to foraging in the forest interior, and predicted to be sensitive to land-use changes (Kingston et al., 2003). In the Palaeotropics, this ensemble is dominated by members of the families Rhinolophidae and Hipposideridae, and Vespertilionidae subfamilies Kerivoulinae and Murininae, which exhibit varying sensitivities to land-use change (Kingston, 2009). We have previously shown that tree cavity/foilage-roosting species are particularly susceptible to area-dependent effects of forest fragmentation (Struebig et al., 2008). Cave-roosting species, on the other hand, appear more resilient to fragmentation, but their long-term persistence in a landscape may be more dependent on the stability of a few major cave roost sites.

We predict that major cave systems will influence the composition and abundance of bat assemblages across a landscape, and that these trends will vary with proximity to the roosting resource. Specifically, we hypothesised that (1) the abundance of cave-roosting bat species will be higher at sites nearer to a karst outcrop, and lower further away and (2) the karst site will act as a population 'source', so that assemblages nearer to the site will be characterised by the same species that dominate the karst assemblage (leading to a similarity gradient). With Southeast Asian karsts facing unprecedented pressures from mining activities (Clements et al., 2006), it is vital to document their role in supporting wildlife populations, if we are to develop practical approaches to conserve biodiversity over large spatial scales (Meijaard and Sheil, 2007; Struebig et al., 2009).

2. Methods

2.1. Study landscape and sampling design

We sampled bats at the Gunung Senyum Recreation Park and other forested sites as part of a forest fragmentation study in the Krau landscape of central Pahang (3°40'N, 102°10'E) between May 2002 and June 2007 (Struebig et al., 2008). The park encompasses 1356 ha of lightly-logged lowland dipterocarp forest and comprises two limestone karst hills with at least 20 caves. The outcrops have Permian/Lower Triassic origins and are considered large and isolated from other karst areas according to Clements et al., (2008). Gunung Senyum and the surrounding forest fragments are relics of formerly continuous forest that was mostly cleared for plantation development in the late 1960s. The matrix is dominated by plantations of oil palm (*Elaeis guineensis*) and rubber (*Hevea brasiliensis*), in a low-contrast fragmentation system that is described more fully in Struebig et al., (2008). There are no additional karst outcrops within 18.8 km (see Clements et al., 2008).

In order to minimise the influence of other karst outcrops in the landscape, analyses were restricted to assemblages from eight forested sites that were within 25 km of Gunung Senyum and at least 20 km from other karst outcrops. Each site was a minimum of 500 m from other forested sites. We undertook a minimum sampling effort of 15 harp trap nights (HTN) per site based on favourable weather conditions, which yielded at least 50 individuals. Sites were situated along a distance gradient (Euclidean) from the karst outcrop (range 3.3–24.4 km, mean 13.4), but they also ranged in forest area (range 300–130,000 ha, mean 44,000), and isolation from each other (range 0.6–1.9 km, mean 1.0) and continuous forest (range 0.0–17.6 km, mean 6.6). We used ArcView version 3.2 to derive these metrics from digitised land-use maps, and log-transformed them to approximate normal distributions for subsequent analyses.

2.2. Bat sampling

We restricted our sampling to insectivorous species that are readily captured by harp traps set in the forest understorey, in order to minimise capture bias and methodological heterogeneity. We used a standardised sampling protocol using up to 15 four-bank harp traps set each night across trails or logging skids, and then moved to a new position every day (for further details see Kingston et al., 2003; Struebig et al., 2008). At Gunung Senyum, traps were placed along a trail in between the two limestone hills at least 500 m from either outcrop. All bats were marked with wing biopsies so that recaptures at a site could be recognised from scar tissue and excluded from analyses, and all were released at the capture point following identification. We classified species into three classes based on aspects of dispersal and roosting ecology criteria, as follows: (1) narrow-space foraging species that roost in tree cavities or foliage; (2) narrow-space foraging species that roost in caves; and (3) edge/open-space foraging species (Struebig et al., 2008).

2.3. Statistical analyses

We adopted a rigorous three-step procedure to determine whether bat assemblage structure at a given forest site was influenced by multiple landscape variables, including the distance to source populations of cave-roosting bats in the karst outcrop. Removing rare species from analyses can sometimes enhance the detection of signals in otherwise noisy assemblage data (McCune and Grace, 2002). Therefore, we initially included all species in analyses, but also repeated them with rare (defined here as

Gunung Senyum (*R. affinis* and *R. lepidus*) also dominated forest assemblages up to 11 km away from the karst (sites F20, F15, F10 and F24; Fig. 1), after which point cave-roosting species tended to decline down assemblage abundance rankings. Conversely, tree cavity/foilage-roosting species became more dominant in assemblages with increasing distance from the karst outcrop. As a result, the abundance rankings of cave- and tree cavity/foilage-roosting

species were more even at sites distant from the karst (F24, F04, S05, S01, S02; Fig. 1).

3.2. Determinants of bat assemblage composition

NMDS ordinations revealed an identical pattern regardless of whether they were based on all species, or only narrow-space

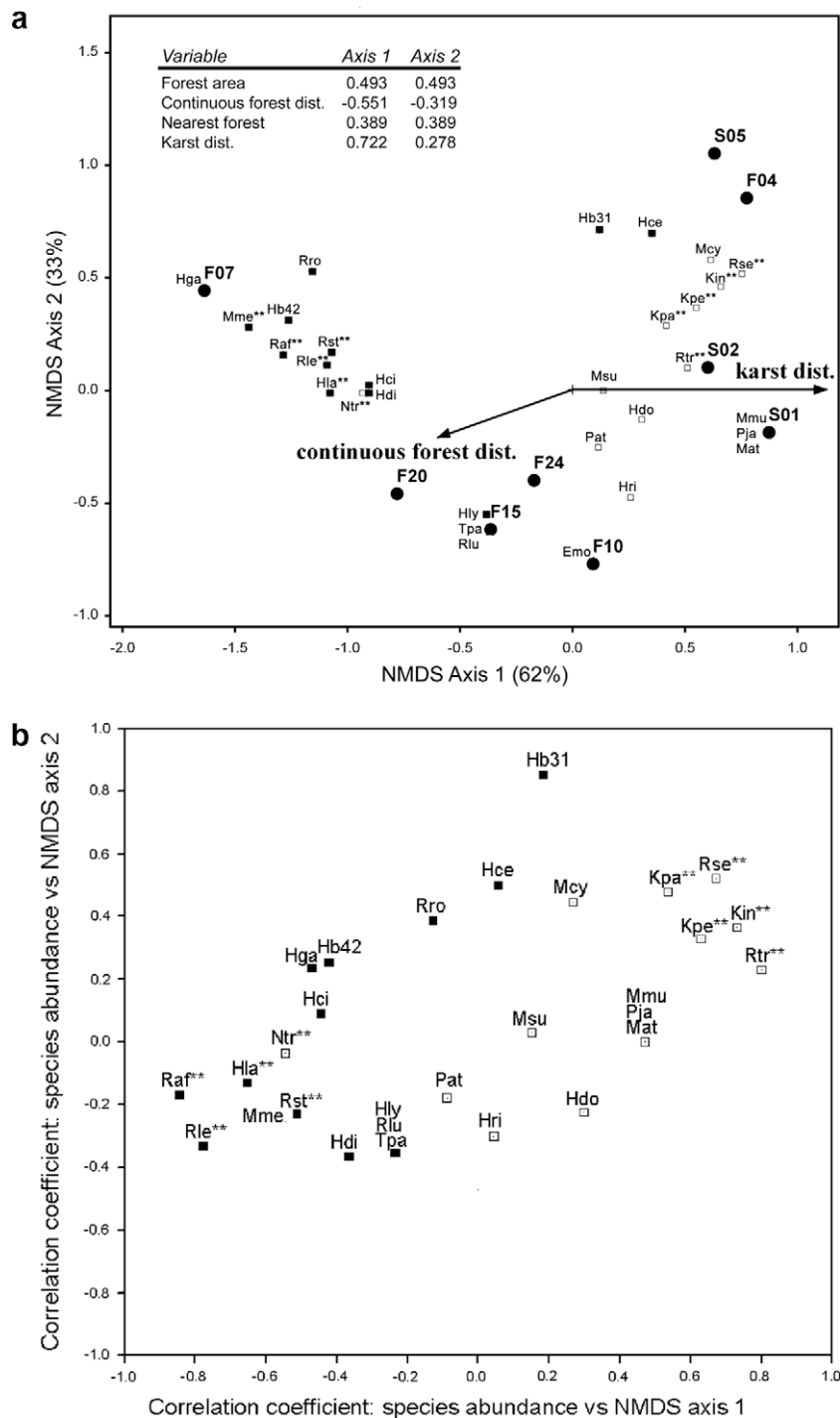


Fig. 2. (a) Triplot based on non-metric multidimensional scaling (NMDS) of bat assemblages at a karst site (F07) and eight other forested sites in the Krau landscape (all species included). The NMDS represented 95% of the variance in assemblage dissimilarity, with the majority (62%) represented in axis 1. Distances between sampling sites (circles) on the ordination reflect dissimilarity in bat species composition using Bray-Curtis coefficients. The tau coefficients for the sample site scores in axis 1 that correlate with each of the landscape metrics are presented, and those metrics with high association (less than -0.5 or greater than 0.5) are presented as vectors. The angle and length of vector loadings indicate the direction and strength of associations, respectively. The average position of species in sample space, reflecting their dominance in geographical space, is overlaid. (b) Correlation coefficient between species abundance and the sample site scores. See Appendix A for species and site abbreviations; crosses and squares represent tree/foilage-roosting and cave-roosting species respectively. Species with abundance associated with axis 1 are denoted by asterisks.

foraging species: large differences in bat assemblage structure among sites were associated with multiple landscape variables and characterised by differences in the abundance of a core group of species (Fig. 2). When samples were presented in species space, ordination distances between sites near to karst and those further away were large, illustrating sizeable differences in species composition between the sites (Fig. 2a). Plotting vectors of landscape metrics illustrated that sites in the right side of the ordination were highly associated with increasing geographic distance from karst (tau correlation with NMDS axis 1 = 0.722), while those sites in the left side were associated with increasing isolation distance from continuous forest (tau coefficient = -0.551). Associations with assemblage composition were positive but relatively weak for the other landscape metrics; namely forest area (tau coefficient = 0.493) and the distance to nearest forest (tau coefficient = 0.389).

The abundances of cave-roosting species were typically negatively correlated with NMDS axis 1 scores, indicating that these species were more abundant in assemblages nearer to the karst (Fig. 2b). Our null model analysis confirmed this trend; the observed decay in cave-roosting bat abundance over the karst distance gradient was greater than expected by chance ($p = 0.034$, randomisation test). Six species (*Hipposideros larvatus*, *Miniopterus medius/schreibersii*, *N. tragata*, *R. affinis*, *R. lepidus* and *R. stheno*) exhibited low correlation coefficients with NMDS axis 1 (ranging from -0.845 to -0.514), suggesting that it was mainly the abundances of these species that decreased across the distance gradient. Conversely, the abundances of tree cavity/foilage-roosting species were typically positively correlated with NMDS axis 1 scores, indicating that these species were more abundant in forests far away from karst. Five species (*Kerivoula intermedia*, *K. papillosa*, *K. pellucida*, *Rhinolophus sedulus* and *R. trifoliatus*) exhibited high correlation coefficients (ranging from 0.535 to 0.800), illustrating that these species were absent or rare near the karst site and that abundance increased across the distance gradient. However, overall, when tree cavity/foilage-roosting species were pooled into a single group, the observed increase in abundance over the distance gradient was not significant ($p = 0.063$, randomisation test).

4. Discussion

We found that bat populations in an isolated limestone karst outcrop had a substantial influence on assemblage structure elsewhere in our study landscape. Several lines of evidence indicated that the local structure of insectivorous bat assemblages at forested sites was in part determined by the distance to a karst outcrop. The bat assemblage at our karst site was dominated by a superabundance of three cave-roosting species, two of which were also found to dominate assemblages at sites up to 11 km away. Sites closest to karst were also characterised by the absence or rarity of tree cavity/foilage-roosting species that were otherwise common at sites further away from the karst. In the face of multiple spatial influences, gradient analysis revealed that differences in assemblage composition were largely associated with the geographic distance from this roosting resource. Comparisons with null models revealed that the observed decay in cave-roosting bat abundance with distance from karst was significant. Conversely, the abundance of tree cavity/foilage-roosting bats appeared to follow the opposite trend, however, this was not significant, possibly due to a lack of power resulting from the comparatively lower number of individuals available for this analysis.

Although increasing dissimilarity in bat assemblage composition across the karst distance gradient was typically associated with decreases in the abundance of cave-roosting species, and in-

creases in tree cavity/foilage-roosting species, not all taxa showed this trend. We suspect that the high abundance of two cave-roosting species (*H. bicolor* 131 kHz and *H. cervinus*) at two sites far from the karst outcrop (S05 and F04; Fig. 2a) was due to the presence of a small cave within 2 km of these sites that is known to contain these taxa; no other caves have been identified in the landscape in over 10 years of bat research (Kingston et al., 2006). In addition, the low correlation between karst distance and the abundance of one tree cavity/foilage-roosting species (*N. tragata*) is likely to be a statistical artefact of rank-based correlations, as this species was absent or rare at all sites. Overall, 30% of cave-roosting species exhibited decreases in abundance strongly associated with the distance from karst, and 39% of tree cavity/foilage species followed the opposite pattern.

Changes to assemblage composition are frequently related to environmental, anthropogenic and spatial gradients, because species tend to be most abundant around their environmental optimum (Ter-Braak and Prentice, 2004; Fukami and Wardle, 2005). Aquatic studies, for example, have revealed that species assemblages respond to gradients of nutrient enrichment and habitat quality (Johnson and Hering, 2009), and community change can occur over a distance gradient from a pollution source (Clarke and Ainsworth, 1993). However, regional processes, such as spatial gradients that describe landscape position, may be of overriding importance in determining species dispersal patterns, and hence local assemblage structure (Heino and Muotka, 2006). In order to fully determine the strength of these processes, foraging and commuting individuals would need to be distinguished in analyses. This was not possible in our study, but it remains most plausible that the distance that bats travel from their roosts to foraging areas plays a key role in determining assemblage structure.

Although the distance to the karst site appeared to be the dominant variable shaping bat assemblages in this study, several other gradients occur and may not have been fully assessed by our sampling regime. First, forest disturbance is likely to have shaped bat assemblages in some way. Other studies have demonstrated that some bat species are negatively affected by logging (Zubaid, 1993; Clarke et al., 2005a), but in the Neotropics at least, assemblages tend to recover across a gradient of vegetation regeneration (Medellín et al., 2000; Clarke et al., 2005b). In the Krau landscape, sites most distant from the karst in our study (S01 and S05, both in Krau Wildlife Reserve) were relatively undisturbed, and so may have provided ideal habitat to support greater abundances of tree cavity/foilage-roosting species. However, all other sites had comparable logging histories, and so it seems unlikely that variation in disturbance could explain such large differences in assemblage structure.

Perhaps the most obvious confounding variables in our study system are those related to forest fragmentation itself, since sites exhibited variation in their area and isolation histories in addition to their distance to the karst. Isolation from continuous forest was also identified as a correlate of assemblage structure (Fig. 2a), however, due to its covariation with distance to karst, it was not possible to determine fully which variable was most important. However, in a wider analysis over the Krau landscape in which fragments near to karst sites were excluded, we found that fragment area rather than isolation was the main determinant of bat diversity and assemblage composition (Struebig et al., 2008). Area was also found to correlate with assemblage dissimilarity in our gradient analysis, albeit more weakly than isolation and karst distance. Forest area is likely to reflect the prey base available to insectivorous bats, but perhaps most importantly it reflects viable roosting opportunities for tree cavity/foilage-roosting bat species. Indeed, the numbers of potential roost sites in foliage, hollows and standing tree cavities may decline in small forest fragments

because of sampling- (Schulze et al., 2000) and edge-effects (Laurance et al., 2002). This is supported by our previous finding that larger fragments support more species and larger populations of tree cavity/foilage-roosting bats (Struebig et al., 2008). The fact that cave-roosting species often rely on roost resources outside of their foraging habitat (Lewis, 1995), and are capable of commuting relatively long distances (Pavey et al., 2001; Bontadina et al., 2002; Struebig et al., 2008), means that fragmentation per se is unlikely to have such negative impacts on this group of bats.

Although fragment area and isolation appear to have limited influences on cave-roosting bats, the association of these animals with major cave sites elsewhere in a landscape could have important implications for fragmentation impacts and the long-term maintenance of species richness in forest fragments. Recently isolated fragments are expected to exhibit declines in abundance and species over time because they cannot sustain all surviving individuals that are initially crowded within them (see Ewers and Didham, 2006). This 'extinction debt' of fragment assemblages was initially considered to be determined by the competitive abilities of species (Tilman et al., 1994). Hence, tree cavity/foilage-roosting could be outcompeted by cave-roosting species near to major cave roosts. However, other models suggest that community dynamics are also determined by species dispersal abilities (Cottenie, 2005), which would also mean that populations of some species could potentially be rescued by immigration from outside of a fragment (Brown and Kodric-Brown, 1977; Menendez and Thomas, 2000; Stevens et al., 2007). In our study system, unless caves are also available within fragments, cave-roosting bats are unlikely to be permanent immigrants, but will use fragments as temporary foraging habitat. Moreover, they might persist over a fragmented landscape by combining foraging resources from a number of fragments and matrix habitats (see Tschamtko et al., 2002), and so karst outcrops that host large populations likely serve as an important spatial subsidy for fragment assemblages. Over the long-term, the number and quality of these subsidies in a landscape will have an important influence on the rescue effects available for fragment assemblages and hence the species richness they support (Anderson and Wait, 2001).

4.1. Conservation implications

The uneven distribution of major roosting resources has important consequences for both bat assemblage structure and its conservation. Our study highlights the influence that even isolated karst outcrops can have on shaping bat assemblages over a fragmented landscape. One implication of this is that biodiversity inventories that survey bats need to account for the fact that sampling is likely skewed to abundant cave-roosting species in karst areas. As a result more individuals should be captured near karst sites to detect rare species that are otherwise common at distant sites, thus allowing meaningful comparisons of species richness. Therefore, bat diversity assessments should report the distance of sampling sites to known roosting areas, and acknowledge the influence this may have on the implications of their data.

This study also has important implications for landscape management strategies seeking to maintain bat diversity. As relatively rare landscape features, limestone karst outcrops can serve as vital shelter for cave-roosting bats and, as we propose, are likely to be important population reservoirs for forest fragments. In the tropics, bats likely use caves as permanent roosts (Lewis, 1995) and, therefore, the loss or disturbance to these sites may not only have detrimental consequences for the bat populations they support, but may also have knock on effects elsewhere in a landscape if no other roosts are available. While karst protection in some Southeast Asian countries is still limited, Malaysia has made considerable progress in formalising protection at some sites

(Clements et al., 2006). However, small and isolated karst outcrops are under pressure from mining companies as a source of cement, basement minerals and marble. Even protected sites are under increasing pressure for development in order to meet the heavy demands of urbanisation. Such developments require a comprehensive environmental impact assessment (EIA), but there is no evidence to suggest that these are thorough enough to incorporate threats posed to biodiversity from karst mining. While we support previous suggestions that conservation measures in karst areas should consider endemic taxa (Gillieson, 2005; Clements et al., 2008), we emphasize that terms of reference for karst development projects need to consider impacts of activities both locally and on the wider landscape. As a minimum requirement, an experienced bat expert should estimate bat species presence and population sizes at all caves prior to development, and determine whether these sites may serve as important hibernacula. Such assessments should also identify the number of potential alternative roost sites within the vicinity, and document their occupancy and any threats they face. Bat researchers could inform this process by quantifying the flexibility of various Palaeotropical species to disturbance, the factors that influence colonisation of an alternative roost, and the amount of habitat needed around roosts to buffer these structures from extreme fluctuations in temperature and humidity. Moreover, national inventories of important bat caves and their conservation status, perhaps based on existing procedures (e.g. Mitchell-Jones et al., 2008; Niu et al., 2007), would facilitate EIA and help guide karst developments.

In the Krau landscape, cave-roosting species comprise a large proportion of bats captured at fragments within 11 km of Gunung Senyum; 39–100% of bat species at a site and 82–99% of the individuals (Appendix A). Hence, the loss of the cave complex as a roosting resource could lead to massive bat declines in the immediate surroundings. Insectivorous bats have an ecosystem value in agricultural areas, because as nocturnal predators they have considerable impacts on arthropod pest populations (Leelapaibul et al., 2005; Cleveland et al., 2006). Thus, while the conservation focus for tree cavity/foilage-roosting bats should be on retaining large areas of forest and maintaining connectivity (Struebig et al., 2008), landscape management needs to ensure protection of cave roosts as point resources for cave-roosting species.

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Appendix A

See Table A1.

Table A1

Number of individuals captured of 30 bat species sampled at nine sites in the Krau landscape, peninsular Malaysia.

| Family/taxon | Species code | Ensemble ^a | Forest site (with Euclidean distance from karst in km) | | | | | | | | |
|---|--------------|-----------------------|--|--------------|--------------|--------------|---------------|---------------|---------------|---------------|---------------|
| | | | F07 (0.5) | F20 (3.3) | F15 (7.2) | F10 (7.7) | F24 (11.6) | F04 (16.3) | S05 (17.9) | S01 (18.6) | S02 (24.4) |
| Nycteridae | | | | | | | | | | | |
| <i>Nycteris tragata</i> ^b | Ntr | T | 3 | 0 | 1 | 0 | 2 | 0 | 0 | 0 | 0 |
| Emballonuridae | | | | | | | | | | | |
| <i>Emballonura monticola</i> | Emo | E | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| Rhinolophidae | | | | | | | | | | | |
| <i>Rhinolophus affinis</i> ^b | Raf | C | 372 | 73 | 45 | 18 | 21 | 1 | 1 | 0 | 0 |
| <i>Rhinolophus lepidus</i> ^{b,e} | Rle | C | 210 | 43 | 16 | 13 | 40 | 1 | 0 | 8 | 12 |
| <i>Rhinolophus luctus</i> | Rlu | T | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Rhinolophus robinsoni</i> | Rro | C | 4 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| <i>Rhinolophus sedulus</i> ^c | Rse | T | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 2 | 0 |
| <i>Rhinolophus steno</i> ^b | Rst | C | 74 | 6 | 10 | 3 | 4 | 0 | 0 | 11 | 3 |
| <i>Rhinolophus trifoliatius</i> ^c | Rtr | T | 0 | 0 | 2 | 2 | 4 | 6 | 3 | 8 | 5 |
| Hipposideridae | | | | | | | | | | | |
| <i>Hipposideros bicolor</i> 131 kHz ^f | Hb31 | C | 15 | 1 | 1 | 0 | 1 | 23 | 21 | 1 | 3 |
| <i>Hipposideros bicolor</i> 142 kHz ^f | Hb42 | C | 193 | 32 | 5 | 0 | 5 | 1 | 13 | 2 | 9 |
| <i>Hipposideros cervinus</i> | Hce | C | 15 | 4 | 6 | 5 | 2 | 36 | 81 | 1 | 13 |
| <i>Hipposideros cineraceus</i> | Hci | C | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| <i>Hipposideros diadema</i> | Hdi | C | 77 | 2 | 28 | 20 | 11 | 3 | 0 | 4 | 0 |
| <i>Hipposideros doriae</i> ^e | Hdo | T | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 |
| <i>Hipposideros galeritus</i> | Hga | C | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Hipposideros larvatus</i> ^b | Hla | C | 22 | 5 | 13 | 0 | 0 | 0 | 0 | 0 | 1 |
| <i>Hipposideros lylei</i> | Hly | C | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Hipposideros ridleyi</i> | Hri | T | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 1 |
| Vespertilionidae | | | | | | | | | | | |
| <i>Kerivoula intermedia</i> ^c | Kin | T | 0 | 0 | 0 | 2 | 0 | 3 | 15 | 8 | 7 |
| <i>Kerivoula papillosa</i> ^c | Kpa | T | 2 | 0 | 1 | 1 | 6 | 4 | 11 | 8 | 7 |
| <i>Kerivoula pellucida</i> ^c | Kpe | T | 0 | 0 | 3 | 1 | 1 | 6 | 8 | 6 | 1 |
| <i>Miniopterus medius/schreibersii</i> ^{b,g} | Msc | E | 88 | 0 | 15 | 1 | 0 | 0 | 0 | 0 | 0 |
| <i>Murina cyclotis</i> | Mcy | T | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 3 |
| <i>Murina suilla</i> | Msu | T | 1 | 0 | 4 | 1 | 6 | 3 | 3 | 3 | 0 |
| <i>Myotis ater</i> | Mat | E | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 |
| <i>Myotis muricola</i> | Mmu | E | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| <i>Phoniscus atrox</i> | Pat | T | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 |
| <i>Phoniscus jagorii</i> | Pja | T | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| <i>Tylonycteris pachypus</i> | Tpa | E | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| Total bat abundance | | | 1080 | 166 | 157 | 71 | 104 | 89 | 162 | 67 | 66 |
| Proportional abundance of cave bats ^d | | | 0.99 | 1.00 | 0.80 | 0.83 | 0.82 | 0.74 | 0.71 | 0.40 | 0.62 |
| Total species richness | | | 15 | 8 | 19 | 14 | 13 | 13 | 12 | 16 | 13 |
| Proportional richness of cave bats ^d | | | 0.80 | 1.00 | 0.42 | 0.50 | 0.39 | 0.46 | 0.67 | 0.50 | 0.54 |

^a T, cavity/foilage-roosting narrow-space species; C, cave-roosting narrow-space species; E, edge/open-space species.^b Species associated with sites nearer the karst outcrop; abundance negatively correlated with assemblage dissimilarity (NMDS axis 1; see Fig. 2).^c Species associated with sites far from the karst outcrop; abundance positively correlated with assemblage dissimilarity (NMDS axis 1; see Fig. 2).^d Number of cave-roosting bats/species as a proportion of the whole assemblage at a site.^e Kingston et al. (2003) included *R. lepidus* as *R. refulgens* and *H. doriae* as *H. sabanus*. We follow the updated nomenclature in Simmons (2005).^f *Hipposideros 'bicolor'* comprises two phonic types with mean echolocation call frequencies of 131 kHz and 142 kHz. They differ genetically enough to warrant treatment as separate taxa and can be distinguished in the hand by subtle differences in noseleaf shape, forearm length and tibia length (Kingston et al., 2006).^g *Miniopterus* individuals captured could not be reliably identified by external measurements to *medius* or *schreibersii*. Both are obligate cave-roosting species classified as edge/open-space foragers according to their wing morphology.

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