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Diet, ecological role and potential ecosystem services of the fruit bat, *Cynopterus brachyotis*, in a tropical city

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Abstract

Urbanisation is happening at an unprecedented pace, affecting ecological interactions between frugivores and plants by altering the species composition of plant communities. *Cynopterus brachyotis*, a bat common in cities, is known to provide important ecosystem services, such as seed dispersal. Studying its diet offers insights into how ecological roles of bats in tropical landscapes could be affected by urbanisation. We documented the diet of *C. brachyotis* in Singapore, and tested the hypothesis that urbanisation decreases dietary breadth and proportion of native plants in its diet. We collected droppings of *C. brachyotis* at nine sites, and used morphological and molecular methods to identify plant species they contained. We evaluated whether species richness, proportion of native species and composition of plants in diet varied according to various urbanisation metrics. We recorded 33 plant species belonging to 25 genera and 21 families. Ten are native, 17 are exotic, and six are indeterminate. Twelve have never been reported in diets of *C. brachyotis* anywhere. Contrary to our hypotheses, urbanisation was not associated with reduced dietary breadth or declining reliance on native plants. Our results suggest urban *C. brachyotis* have a generalist approach to foraging and can readily exploit exotic plants as food. Because urbanisation does not affect dietary breadth or the proportion of native species they eat, these bats potentially continue to play important ecological roles by dispersing seeds of native plants even in the most urbanised sites, which is important in aiding succession in degraded landscapes. However, they may equally disperse exotic species they have exploited.

Keywords

Seed dispersal
DNA barcoding
Bat-plant interactions
Mutualisms
Pteropodidae

Electronic supplementary material

The online version of this article (<https://doi.org/10.1007/s11252-020-01034-x>) contains supplementary material, which is available to authorized users.

Introduction

Efforts to conserve biodiversity and ecosystem processes must include cities. As globally expanding habitats, urban areas are expected to house 68% of the world's human population by 2050 (United Nations [UN] 2018). Urbanisation is generally thought to be detrimental to biodiversity and is proceeding fastest in the world's most biodiverse regions (Seto et al. 2012). With most people living in cities, raising awareness of and appreciation for biodiversity is vital to public support for conservation (Kasada et al. 2017). Yet the importance of conserving biodiversity in cities is often overlooked in relation to other habitats.

Fruit bats, as seed dispersers and pollinators, provide key ecosystem services (Marshall 1985; Fujita and Tuttle 1991; Kunz et al. 2011). Although a global review found that bats generally respond negatively to urbanisation, the impacts on bats' ecological roles in tropical cities, especially in Asia, are poorly studied (Jung and Threlfall 2016). Preliminary evidence from South Africa and Malaysia suggests that while exotic plantings can help sustain urban fruit bat populations, this introduction of exotic species may also potentially disrupt natural ecological relationships (Jordaan et al. 2012; Voigt et al. 2011; Lim et al. 2018a, 2018b).

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Singapore is the only tropical nation whose population is 100% urbanised (United Nations [UN] 2018), and it has experienced more extreme deforestation than any other Southeast (SE) Asian nation – initially due to conversion to agriculture and more recently to urban development (Corlett 1992). In this context, dramatic land-use change has caused the extirpation of an estimated 33–72% of bat species (Lane et al. 2006). However, the lesser dog-faced fruit bat (*Cynopterus brachyotis*) has persisted (Chua and Lim 2011) and is common in Singapore (Chattopadhyay et al. 2019). It is found both in forests, such as nature reserves, that make up 23% of Singapore's land area (Yee et al. 2011) and urban environments (Leong and Chan 2011).

One key to *C. brachyotis*' success in Singapore is its behavioural flexibility. In natural habitat, *C. brachyotis* typically roosts in foliage, i.e., openly or in tents that it builds by chewing leaves (e.g., Kunz 1982). However, in cities like Singapore, it also uses commensal roosts, i.e., anthropogenic structures (Chai 2016). This has implications for roost fidelity – foliage roosts being more ephemeral, bats using them switch roosts more often than conspecifics in commensal roosts (Lewis 1995). Commensal roosting also has benefits, e.g., reduced predation risk and/or foraging effort and access to new habitats (Voigt et al. 2015), although those benefits may depend on proximity of the roost to and stability of food resources (Kunz 1982). Thus, high availability of fruiting plants in urbanised sites combined with flexible roosting behaviour may have contributed to *C. brachyotis*' persistence in Singapore.

With its ability to use both anthropogenic and natural resources (McKinney 2008), *C. brachyotis* is an urban adapter. Given its importance as a disperser of native plants (e.g., Tan et al. 1998; Corlett 2005), it may well provide ecosystem services even in cities. Yet because plants compete for the dispersal services of a limited number of frugivores (Carlo et al. 2003), the stereotypical, urban increase in relative abundance of exotic species (e.g., Williams et al. 2006) may reduce the dispersal success of native species. For example, by consuming exotic and cultivated plants in Malaysia, *C. brachyotis* potentially facilitated their invasion (Lim et al. 2018a). Any dispersal of invasive plants would be considered an ecosystem disservice (von Döhren and Haase 2015; Shackleton et al. 2016; Vaz et al. 2017).

When active greening efforts started in 1963, many exotic species were brought in as ornamentals (Corlett 1992) and now, they make up 44% of all vascular plants in Singapore – their species richness exceeds that of native species and their relative abundances likely do too, given their high densities (Chong et al. 2011). The planting of native and exotic species as a by-product of urbanisation can alter the availability of food for animals, e.g., by providing fruits year-round, thereby reducing natural patchiness owing to seasonal fruiting (Jung and Threlfall 2016). It can also facilitate novel species interactions and affect pollination and seed dispersal (Corlett 2005; Hobbs et al. 2006; Jordaan et al. 2012; Voigt et al. 2011; Sheherazade et al. 2017; Lim et al. 2018a; Lim et al. 2018b; Stewart et al. 2018).

In SE Asia bats are among the least-known vertebrates and, despite their key ecological roles and high rate of endangerment, receive little conservation support (Kingston 2010). In this context, understanding their roles in an urban environment could both increase support for their conservation and inform management strategies to minimise disservices (Haase et al. 2014), especially in

cities where they live near humans (Jung and Threlfall 2016). Therefore, we investigated:

1. The diet of *C. brachyotis* in Singapore.
2. The relationship between dietary breadth/composition and urbanisation.

We hypothesised that urbanisation narrows dietary breadth and alters dietary composition of urban *C. brachyotis*, and predicted that the overall species richness and proportion of native plant species in bat diets decline with increases in each of three landscape variables:

(1) Distance to primary and old-growth secondary forest. Singapore's primary and old-growth secondary forests are more speciose than other green spaces and are largely dominated by native species (Corlett 1997). Urbanisation also often favours the occurrence of exotic species over native species (McKinney 2006). Dietary breadth and consumption of native species could thus decline with distance to species-rich food patches dominated by native plants.

(2) Impervious cover. The availability of food sources for phytophagous animals could reasonably be expected to decline with decreasing green cover (i.e., increasing impervious cover).

(3) Managed proportion of vegetation. Actively managed vegetation (as in parks, gardens and streetscapes) might be less speciose given that landscapers usually prefer plants that tolerate drier, more exposed urban conditions (Corlett 2011b).

Materials and methods

Study area

Singapore is a tropical city-state south of Peninsular Malaysia (1.3521° N, 103.8198° E) with a land area of 724.2 km² (Singapore Land Authority [SLA] 2019). Compared to other big cities, Singapore has high canopy cover (> 29%; Ratti et al. 2016) but retains less than 1% of its original forests (Corlett 1992).

Selection of study sites and roosts

We selected nine sites across Singapore (Fig. 1; Online Resource 1) that represented varying levels of urbanisation and contained known anthropogenic *C. brachyotis* roosts as discovered by Chai (2016) and from public tips. A posteriori quantification of landscape variables suggested these sites represented varying degrees of urbanisation (Online Resource 1). At each site, we selected

roosts that had many droppings beneath them and were easily accessible, and where collecting droppings would cause the least nuisance to site users.

Fig. 1

Study area in Singapore. Markers show the location of nine sites where bat droppings from commensal roosts were sampled in this study

Data collection

Our sampling protocol follows Aziz et al. (2017b). We collected droppings at each site once a month (a sampling event) from September 2017 to January 2018 (except December) by placing one clear, 45 × 45 cm plastic sheet on the ground directly under each roost in the evening, removed between 0730 and 1200 the next day. We selected only droppings of unique colour and texture for analysis – we assumed this corresponded to the diversity of plants in the bats’ diets. Droppings consisted of fecal matter, ejecta (material that bats chew and spit out) and partially eaten plants. Because small fruit bats (such as *C. brachyotis*) usually have a maximum gut passage time of 60 min (Voigt et al. 2009), each dropping should normally contain only one plant species, though there is a chance it contains more than one.

We collected two subsamples of each dropping – one for morphological analysis and one for DNA barcoding. We swabbed individual droppings with cotton buds or picked them up using clean forceps, then placed them in 2 ml microcentrifuge tubes. We filled samples collected for DNA barcoding with 95% ethanol and kept them cool in an icebox in the field, before transferring them to a – 30 °C freezer.

More bats in a roost should produce more droppings. This could confound our results by inflating dietary breadth, so we counted all bats in a roost at each sampling event. Because we saw bats moving among roosts within a site (making it impossible to know how many individuals contributed to the previous night's droppings), we also counted all bats roosting within a continuous anthropogenic structure in a site.

Identification

We examined 704 individual droppings under a dissecting microscope to determine what type of plant material it contained, and recorded the type, colour, and consistency of each dropping. We cleaned and isolated all seeds in droppings and opportunistically collected fruits of known species near roosts to compare unknowns to known species.

We sowed 791 seeds on moistened paper towels in ventilated, covered containers, and recorded germination success, i.e., emergence of the radicle following Hodgkison et al. (2003). We then planted seedlings in commercial potting mix and compost and grew them in a sheltered, outdoor environment with ample sunlight and water. Finally, we identified seedlings to the lowest taxonomic level possible.

We selected 190 samples of droppings for DNA barcoding – a roughly equal number from each sampling event. We chose droppings that we subjectively determined to be unique from others within the same sampling event (based on morphological descriptions). We placed 0.5 cm² of each dried plant tissue sample in a sampling tube. The Canadian Centre for DNA Barcoding performed DNA extraction, PCR and sequencing, targeting the *rbcL* and *ITS2* gene regions, using standard protocols (details in Lim et al. 2018a). Because no universal barcode currently exists for identifying plant DNA, using multiple target sequences in combination can improve identification success (Clare 2014; Kress 2017). The *rbcL* region, being highly conserved, can provide robust assignment to a higher taxonomic level, i.e., genus (Kress and Erickson 2007), whereas *ITS2* should provide higher taxonomic resolution (Yao et al. 2010) but can be more

difficult to amplify and does not perform equally well for all species (Lim et al. 2018a).

We compared the recovered sequences to those in GenBank using the Basic Local Alignment Search Tool (BLAST). Adapting the assignment criteria of Lim et al. (2018a), we assigned taxonomic names to DNA barcodes by matching sequences using BLAST and then narrowing them down using geographical limitation whenever there were multiple species with equal matches (Online Resource 2), with reference to the most complete checklist of vascular plants in Singapore (Chong et al. 2009). We prioritised *ITS2* matches due to the higher taxonomic resolution of this region – where no *ITS2* barcodes were produced, we assigned genus names using *rbcL* matches.

Because DNA barcodes cannot differentiate among many closely-related plant species (Aziz et al. 2017b), it is impossible to assign specific epithets to rapidly-radiating taxa, i.e., *Ficus* (Lim et al. 2018a) and *Cecropia*, so we only assigned them to genus. For *Ficus* species, which are notoriously difficult to identify from seeds (Lim et al. 2018a), we used identified morphotypes (see also Ingle 2003) and assigned specific epithets only when we found fruits with identical seed morphology at the site.

Landscape variables and covariates for analyses

Using a base map of vegetation cover in Singapore (Yee et al. 2011) and a map of *C. brachyotis* roost sites (created in Google Maps), we extracted landscape variables for each site in ArcGIS Pro (ESRI 2017). For distance to primary and old-growth secondary forest, we calculated the shortest linear distance from roosts to the nearest primary or old-growth secondary forest. For impervious cover and managed proportion of vegetation, we first created a buffer (1-km radius) around each roost, based on the reported mean distance of 1.37 km between *C. brachyotis* roosts and foraging areas (Bumrungsri 2002) – we expected bats to largely forage within this area. We then calculated impervious cover by dividing the area of non-vegetated surface by the total area of buffer and managed proportion of vegetation by dividing the area of managed vegetation by the total area of all vegetation in the buffer.

To get a measure of the minimum distance bats may fly to forage, we located the nearest trees of the plant species with highest relative importance (defined below) in the diet of bats at one site (University) and noted their GPS coordinates. We then measured the linear distance between these trees and the roost using Google Maps – this is the presumed nearest source of fruits to the bats.

Data analysis

We named plants identified in the droppings and classified them by national status following Chong et al. (2009) and assumed that species not listed therein are exotic. To avoid overestimating the dietary importance of small-seeded fruits, we did not count seeds, but rather recorded occurrence of plant species in droppings (following Voigt et al. 2009). For each plant species, we calculated the frequency of occurrence (detections / total sampling events $\times$ 100) and relative importance (frequency of occurrence / total occurrences of all plant species $\times$ 100) – recommended variables for the dietary analysis of phytophagous bats (Voigt et al. 2009).

We tested for pairwise differences in species richness of plants and in proportions of native species between sites using an ANOVA with post-hoc Tukey's tests and Shapiro-Wilk tests to verify that residuals were normally distributed. To test our predictions, we fitted separate generalised linear mixed-effects models (GLMMs) with Poisson error distribution for species richness and binomial errors for proportions of native species (neither response variable was normally distributed). We verified the assumption of homogeneity of variance for all models (visual inspection of residual plots) and established that there was no overdispersion in GLMMs. Both GLMMs included distance to primary and old-growth secondary forest, impervious cover and managed proportion of vegetation as fixed effects and month as random effect. Number of bats was included as an additional fixed effect in the species richness model.

We constructed a non-metric multi-dimensional scaling (NMDS) plot with Jaccard similarity index using three dimensions to visualise dissimilarities in species composition between sites. We also conducted an ANOSIM test to test for differences in species composition between sites. Finally, we used distance-based redundancy analysis (db-RDA) to investigate the effect of landscape variables on species composition of plants in diet. We applied a rejection criterion of $\alpha = 0.05$ to all hypothesis tests. For all models, we used backward, stepwise selection to retain significant terms via likelihood-ratio test. We conducted analyses in R version 3.4.3 (R Core Team 2017), with packages *lme4* (Bates et al. 2015) for GLMMs, *vegan* (Oksanen et al. 2018) for NMDS, db-RDA and ANOSIM, and *bipartite* (Dormann et al. 2008) for bipartite plot.

Results

We collected a total of 704 droppings, of which 259 contained seeds. Of 791 seeds planted, 497 (62.8%) germinated. Six seedlings grew large enough within the study period to be identified – four to species and two to genus. We also managed to identify two plant species based on seed morphology (Table 1).

Table 1List of plant species found in the diet of *C. brachyotis* in Singapore

Family	Species	Native/Exotic?	National Status	f
Acanthaceae	<i>Avicennia</i> sp. *	Native	Cultivated	1
Anacardiaceae	<i>Mangifera indica</i>	Exotic	Casual/ Cultivated	1
Bignoniaceae	<i>Spathodea campanulata</i> *	Exotic	Naturalised/ Cultivated	1
Clusiaceae	<i>Garcinia subelliptica</i> *	Exotic	Cultivated only	1
Combretaceae	<i>Terminalia catappa</i> ¹	Native	Common/ Cultivated	1
Cucurbitaceae	<i>Coccinia grandis</i>	Exotic	Naturalised/ Cultivated	1
Fabaceae	<i>Saraca</i> sp. *	Exotic	Not assessed	1
	<i>Sindora coriacea</i> *	Native	Critically Endangered/Cultivated	1
Gentianaceae	<i>Fagraea crenulata</i> * ₂	Exotic	Cultivated only	1
	<i>Fagraea fragrans</i>	Native	Common/ Cultivated	1
Lamiaceae	<i>Clerodendrum laevifolium</i> *	Native	Common/ Cultivated	1
Loranthaceae**	<i>Dendrophthoe pentandra</i> *	Native	Common	1
Malvaceae	<i>Cola</i> sp. *	Exotic		1
	<i>Durio</i> sp.			1
Moraceae	<i>Ficus fistulosa</i> ²	Native	Common/ Cultivated	1

*Species not reported in diets of *C. brachyotis* before;**Family not reported in diets of *C. brachyotis* before;¹Morphological identification of seeds allowed for identification to species where DNA barcoding gave a genus name;²Morphological identification of seedlings allowed for identification to species where DNA barcoding gave a genus name;³Consensus between morphological identification of seedlings and DNA barcoding species identification;⁴Disagreement between morphological identification of seedlings (identified as *Macaranga bancana*) and DNA barcoding. Subsequent morphological comparison of seeds suggested likely to be *Cecropia pachystachya/peltata*

Family	Species	Native/Exotic?	National Status	f
	<i>Ficus grossularioides</i> ¹	Native	Common/ Cultivated	Y
	<i>Ficus</i> sp. 1			Y
	<i>Ficus</i> sp. 2			Y
	<i>Ficus</i> sp. 3			Y
	<i>Ficus</i> sp. 4			Y
Muntingiaceae	<i>Muntingia calabura</i>	Exotic	Naturalised/ Cultivated	Y
Musaceae	<i>Musa</i> sp.	Exotic	Cultivated only	N
Myrtaceae	<i>Syzygium jambos</i>	Exotic	Casual/ Cultivated	N
	<i>Syzygium nervosum</i> *	Exotic	Cultivated only	N
	<i>Syzygium polyanthum</i>	Native	Vulnerable/ Cultivated	N
	<i>Syzygium samarangense</i> *	Exotic	Cultivated only	N
Pentaphylacaceae	<i>Adinandra dumosa</i>	Native	Common/ Cultivated	Y
Piperaceae	<i>Piper aduncum</i> ³	Exotic	Naturalised	Y
Sapindaceae	<i>Dimocarpus longan</i> *	Exotic	Casual/ Cultivated	N
Sapotaceae	<i>Manilkara zapota</i>	Exotic	Cultivated only	N
Solanaceae	<i>Solanum</i> sp. ³	Exotic		N
Urticaceae	<i>Cecropia pachystachya/peltata</i> ₄	Exotic	Naturalised	Y

*Species not reported in diets of *C. brachyotis* before;

**Family not reported in diets of *C. brachyotis* before;

¹Morphological identification of seeds allowed for identification to species where DNA barcoding gave a genus name;

²Morphological identification of seedlings allowed for identification to species where DNA barcoding gave a genus name;

³Consensus between morphological identification of seedlings and DNA barcoding species identification;

⁴Disagreement between morphological identification of seedlings (identified as *Macaranga bancana*) and DNA barcoding. Subsequent morphological comparison of seeds suggested likely to be *Cecropia pachystachya/peltata*

Comparison of identification methods

Of 190 samples sequenced, 136 (71.6%) returned both *ITS2* and *rbcL* DNA barcodes; one (0.5%) returned only an *ITS2* barcode; 51 (26.8%) produced only *rbcL* barcodes and two (1.1%) failed to return sequence data. We discarded barcodes from two samples due to the high number of ambiguous bases or short usable sequence length. Only 16 samples (8.4%) returned different identities for the two barcodes, supporting the assumption that most droppings contain a single plant species.

There was consensus between results for morphological identification and DNA barcoding for two species and disagreement for one (Table 1). Using morphological identification of seeds and seedlings, we assigned specific epithets to four species that were only identified to genus via DNA barcoding (Table 1).

Diet of *C. brachyotis*

We detected a total of 33 plant species belonging to 21 families and 25 genera from 36 individual sampling events (Table 1). We identified 23 to species and 10 to genus. Of those, 10 are native and 17 are exotic. But the status of six plant taxa which we could not assign specific epithets to remain indeterminate. We found 12 species (identified by asterisks; Table 1) and one family that have never been reported in the diets of *C. brachyotis* anywhere (SA Aziz, unpublished database), and found seeds of 14 plant taxa. On average, we found 4.17 ± 1.46 species per sampling event (range = 2–7).

The most important species in the diet of *C. brachyotis* was the tembusu tree (*Fagraea fragrans*) – it occurred most often and at all sites (Fig. 2) and had the highest relative importance (15.3%; Fig. 3). All three species with the highest relative importance (tembusu, yellow stem-fig; *Ficus fistulosa* and sea almond; *Terminalia catappa*) are native species. There were 14 species that we only detected at one site and 10 that we only detected at one sampling event.

Fig. 2

Occurrence of plant species in the diet of *C. brachyotis* at each site. Box lengths indicate relative occurrence of each food item; thicknesses of interacting lines represent relative number of times a species was found at a site. Black = native species; white = exotic species; grey = status unknown

Fig. 3
Relative importance (%) of the top 10 plant species found in the diet of *C. brachyotis*

Dietary breadth

Although mean species richness of diet per sampling event was highest at Sg. Buloh (5.25 ± 0.50) and lowest at Changi (3.25 ± 1.26) (Fig. 4A), it did not differ significantly among sites ($F_{8,27} = 0.61, P = 0.77$). None of our three predictor variables significantly explained variation in dietary breadth (plant species richness), and the final GLMM retained no fixed effects ($P = 0.92$; Online Resource 3A).

Fig. 4

Boxplot showing (a) species richness of plants in diet and (b) proportion of native plant species in diet at different sites. Boxes represent first, median and third quartiles; whiskers indicate maximum and minimum value; crosses indicate means; points represent values at one sampling event

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Native species in diet

Representation by native species in the diet differed among sites ($F_{8,27} = 4.45$, $P < 0.01$), being higher at University than at Kallang, Kranji, Botanic Gdns. and Temple (Fig. 4B). However, none of our three predictor variables significantly explained variation in the proportion of native plants in the diet, and the final GLMM retained no fixed effects ($P = 0.30$; Online Resource 3B).

Species composition across sites

Bats at most sites were feeding on relatively unique sets of plants, with species composition being significantly different between sites ($R = 0.718$, $P = 0.001$; Fig. 5). Each of our three variables (distance to forest, impervious cover and managed proportion of vegetation) was a predictor of species composition

($R^2_{\text{adjusted}} = 0.274$, Pseudo $F = 4.03$, $P < 0.01$; Table 2). The nearest sources of the two most important species in the diet of bats at University, tiup tiup (*Adinandra dumosa*) and tembusu, were 125 m (in a young secondary forest patch) and 300 m from the roost, respectively.

Fig. 5

NMDS plot visualising distinctiveness of plant species composition of diet among sites. Each point represents one sampling event. Stress of the plot is 0.14

Table 2

Likelihood ratio table indicating degrees of freedom (df), χ^2 , Pseudo F-stat and p value of each term when performing backwards stepwise model selection for db-RDA

Term	df	χ^2	Pseudo F-stat	p value
Distance to primary and old secondary forest	1	−0.77	4.11	< 0.01
Impervious cover	1	−0.49	2.60	< 0.01
Managed proportion of vegetation	1	−0.59	3.16	< 0.01

Discussion

Our objective was to investigate the diet of urban *C. brachyotis* in Singapore and how urbanisation affects the dietary breadth and composition of native plants in its diet. We found no effect of urbanisation on dietary breadth and composition of native plants, allowing us to discuss some potential implications of urbanisation to the provision of ecosystem services and disservices.

Diet of urban *C. brachyotis*

Like its conspecifics elsewhere, *C. brachyotis* in Singapore has a wide-ranging diet and readily consumes exotic species (e.g., Phua and Corlett 1989; Hobbs et al. 2006; Lim et al. 2018a). Of the 33 species identified, 14 only occurred at one site. Many of these likely have limited occurrences in Singapore, given that half of them are casual (i.e., rely on repeated introductions to maintain populations in the wild) or cultivated plants. For instance, the only place we found *Cola* sp. was at Singapore Botanic Gardens, where it was planted as an exotic species at least a century ago (Mathieu 1918).

Despite our detection of novel dietary components, all three of the most frequently consumed plants (tembusu; *Fagraea fragrans*, yellow stem-fig; *Ficus fistulosa* and sea almond; *Terminalia catappa*) are native. Tembusu trees are common ornamentals along Singapore’s streets and in its parks and gardens (Tan 2011a), but it is interesting that this was the most important dietary item while elsewhere, *C. brachyotis* has been reported to consume *Ficus* spp. more than any other plants (e.g., Tan et al. 1998; Fletcher et al. 2012; Sheherazade et al. 2017; Lim et al. 2018a). This could just be a seasonal effect. Our study period (September to January) coincided with one of the tembusu’s fruiting seasons (Corner 1988). Perhaps this bat population exploits preferred food sources when they are available (see also Phua and Corlett 1989; Fletcher et al. 2012), and the species composition of its diet varies over the course of a year. Also, our methods only allow us to quantify frequency of occurrence (and not abundance), so we cannot control for the composition-by-mass of each plant in the diet.

These bats consumed several exotic plants, especially the calabur (*Muntingia calabura*) and spiked pepper (*Piper aduncum*). Both Neotropical species produce

small numbers of fruits for extended periods (Fleming 1982) – an attribute that can make plants vital in maintaining *C. brachyotis* populations even outside the plants' native range (Tan et al. 1998). For instance, the planting of ornamentals in Melbourne, Australia, by reducing temporal patchiness of food availability for *Pteropus poliocephalus*, has allowed these bats to expand their range (Williams et al. 2006). Indeed, high detection rates of exotic plants in diets of urban bats elsewhere (Corlett 2005; Lim et al. 2018a; Lim et al. 2018b) suggest their importance as a resource. Urbanisation, and the planting of many street trees and ornamental plants, may ensure a constant and nearby supply of food for the bats, allowing them to maintain their populations in the city (Williams et al. 2006). This can in turn benefit native plants, which are often dispersal-limited due to the loss of frugivores (Brook et al. 2003; Corlett 2011a, 2011b).

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Potential ecosystem services and disservices

We found seeds of 14 plant species in droppings under *C. brachyotis* roosts – clearly it had moved seeds away from parent plants, suggesting that it is a seed disperser in Singapore. Bats disperse seeds at feeding roosts throughout the night and across open spaces while in flight (Phua and Corlett 1989). Still, the quality of seed dispersal by *C. brachyotis* may depend on seed and fruit traits (Phua and Corlett 1989), such as fruit size and thus distance transported. Consequently, the generalisability of dispersal services provided by *C. brachyotis* requires further study.

Even in a highly urbanised, tropical landscape, *C. brachyotis* is eating and potentially dispersing native plants, such as the tembusu, a culturally-significant tree in Singapore (Tan 2011a), and thus likely providing an ecosystem service. Even if it mainly eats and disperses seeds in patches of managed vegetation, such urban populations of native plants can help buffer small, endangered populations in core nature areas such as nature reserves, reducing these plants' extinction risk (Corlett 2011a; Sheherazade et al. 2017). However, while this may represent a service to the plant, humans may view it as a disservice, i.e., weed propagation, if seeds are dispersed outside desired areas.

Urban *C. brachyotis* may also play a role in forest restoration. For example, at the University site, bats ate tiup tiup, a common secondary forest plant (Tan 2011b), and consumed other planted native species, such as tembusu, in a single night. This implies movement between forest and urban (i.e., degraded) patches – a process that can promote succession and forest regeneration (see also Corlett and Hau 2000; Sritongchuay et al. 2014; Sheherazade et al. 2017). In particular, the dispersal of tiup tiup, a pioneer (and often dominant) species in Singapore's

secondary forests (Tan 2011b), suggests these bats can help restore Singapore's degraded landscapes by facilitating succession (Corlett and Hau 2000).

Furthermore, although the bats we observed mainly seemed to forage near their roosts, we found *Avicennia* sp., a mangrove tree, in their droppings at sites about 6 km from the nearest mangroves. Therefore, they must be at least occasionally flying farther to forage and thus potentially providing long-distance dispersal of native plants (Shilton et al. 1999).

Our finding of high germination success proves that seeds remain viable even after being spit out or defecated by *C. brachyotis* – no surprise given evidence that passage through the gut of fruit bats does not reduce (and may even enhance) germination success (Utzurum 1995; Shilton et al. 1999; Hodgkison et al. 2003; Tang et al. 2007), and that fruit bats may even prefer fruits containing viable seeds (e.g., Utzurum and Hideman 1991; Dumont et al. 2004; Chen et al. 2017).

However, whether seed dispersal by bats is an ecosystem service depends on more than germination success. The conditions in which germination takes place matter too (Janzen 1981). Indeed, post-deposition seed fate and seedling establishment are better indicators of dispersal effectiveness (Tang et al. 2007; Schupp et al. 2010). Several of the roosts we sampled were over concrete, where deposited seeds are unlikely to germinate, in which case, *C. brachyotis* could be providing an ecosystem disservice by providing low-quality dispersal (see also Cheptou et al. 2008). Even if seedlings do manage to germinate in these most urbanised sites, seedling recruitment is surely reduced by the threat of being crushed by high human traffic (Vendan and Kaleeswaran 2011).

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Another potential ecosystem disservice by these bats is the dispersal of exotic species, including spiked pepper and *Cecropia pachystachya/palmata*, two plants that are invasive and spreading in Singapore (Nghiem et al. 2015). This bat is also dispersing plants that are only known to be under cultivation, such as *Fagraea crenulata* (Chong et al. 2009), possibly helping them to propagate naturally. The seeds of all the above species were viable even after mastication and/or gut passage.

Influence of urbanisation on dietary breadth and species composition

Our findings do not support our hypothesis that urbanisation restricts dietary breadth or the diversity of potential food sources for *C. brachyotis*. This is comparable to findings of similar dietary breadth of *C. brachyotis* between urban, agricultural and secondary forest sites in Peninsular Malaysia (Lim et al.

2018a, 2018b). The most obvious explanation is that because these bats can forage over wide distances (up to 14.5 km) each night (Bumrungsri 2002), they are not resource-limited, even in the most urbanised sites. However, the nearest sources of the most common plants bats were consuming at each site tended to be located near roosts, possibly indicating a preference for local foraging.

The diversity of plants (and thus potential food sources) may be just as high or even higher in managed urban landscapes as in natural forests (see also Cilliers and Siebert 2008). Indeed, plant species richness often increases with urbanisation (McKinney 2008). This is likely true in Singapore, where parks and roadsides have long been extensively cultivated with diverse ornamentals (Rao and Wee 1989). With the presumably higher proportion of exotic species in more urbanised sites, the diversity of potential food plants is not diminished for *C. brachyotis*, which so readily eats exotic species.

We did find evidence that which plants it eats varies among sites – this likely reflects the distinct species composition of floral assemblages at each level of urbanisation. In other words, the heterogeneous distribution of plant species across Singapore should produce variation in food options among sites. For example, *C. brachyotis* only consumed spiked pepper at Kranji, Sungei Buloh and Zoo, all in Singapore's north. This plant is a recent introduction, first recorded in Singapore in 2003 and thought to have spread southward from Malaysia (Tan et al. 2008), producing dense populations in northern Singapore (Nghiem et al. 2015). This correspondence between the spatial distribution of a plant and its occurrence in *C. brachyotis* diets corroborates our argument that these bats are mainly foraging within a limited geographical area.

There is no evidence that urbanisation in Singapore reduces the ability of *C. brachyotis* to forage on native plants, especially because our results did not support our hypothesis that this bat's consumption of native plants declines with increasing urbanisation. Perhaps a site's degree of urbanisation does not affect the occurrence of native species as potential food sources for *C. brachyotis*. In other words, with recent, growing emphasis on planting native trees in parks and along streets in Singapore (Corlett 2011b), perhaps native species remain readily available at all levels of urbanisation. Similarly, because the exotic species that *C. brachyotis* eats, e.g., *Cecropia pachystachya*, occur in edges and gaps of native forests (Lok et al. 2010), exotic species are available as food sources even in the least urbanised sites. However, without documenting what bats eat in relation to total plant diversity at each site, this conclusion remains speculative.

We did observe an apparent change in diet at one site (University). Three decades ago, researchers at the same site (Phua and Corlett 1989) found *C.*

brachyotis consuming only three species (*A. dumosa*, *Muntingia calabura* and tembusu), with *A. dumosa* the most important food item. They posited that *A. dumosa*, as the dominant pioneer plant on degraded land in Singapore, is key to maintaining dense *C. brachyotis* populations. We found six more species, and tembusu was just as important as *A. dumosa*. We suggest that with increased planting of ornamentals over time, this bat has adapted to the changing availability of food resources. Of course, the difference may simply speak to the fact that DNA barcoding is more powerful than identification methods available in 1989, or to differences in sampling times and durations, and even plant phenology.

Implications

Our results suggest that urban *C. brachyotis* opportunistically consumes plants near its roosts. Although elsewhere *C. brachyotis* is reported to fly an average total distance of 14.5 km per night and to forage up to 2.6 km from its roosts (Bumrungsri 2002), the context was different – a forest where food plants may be ephemerally available, and bats might therefore have to search further for food (Hodgkison et al. 2004). In cities, roosting near roadside trees and ornamental plants could provide *C. brachyotis* with easy access to a stable food supply, thereby reducing their energy expenditure and exposure to predators, among other costs of foraging. This knowledge can inform management strategies, e.g., by suggesting which native species to plant near known bat roosts to increase ecosystem services and minimise disservices.

Perhaps more importantly, we have shown that because urbanisation affects neither the dietary breadth nor proportional consumption of native plants, urban *C. brachyotis* can potentially provide ecosystem services. This seems especially important near forest patches, where they can disperse native plants and aid succession in degraded landscapes (Sritongchuay et al. 2014; Sheherazade et al. 2017). In Singapore, much of the urban matrix is interspersed with forest patches (Yee et al. 2011), raising the possibility that bats already play a role in forest restoration and maintaining gene flow among patches. By demonstrating the potential for fruit bats to provide ecosystem services in Singapore, our work stands to raise support for the conservation of these undeservedly maligned creatures.

Limitations and recommendations

The greater resolution afforded by DNA barcoding allowed us to identify many plants never before recorded in diets of *C. brachyotis*. It also allowed us to identify species that only occurred as pulp in droppings, e.g., *Musa* sp., and have large-seeded fruits, e.g., mango (*Mangifera indica*), whose seeds are not

swallowed and that we would have missed had we only used morphological methods.

However, there is a limitation of DNA barcoding. When it is unclear which plant part is eaten (i.e., *C. brachyotis* eats leaves and flowers in addition to fruits; Tan et al. 1998; Hodgkison et al. 2004), so too are bats' ecological roles – we could only conclude that it is a potential seed disperser when we found seeds.

Therefore, we suggest using camera-trapping to determine which plant parts bats are eating, an approach used, for example, to document *C. brachyotis* foraging in forests (Mohd-Azlan et al. 2010) and to show that *Pteropus hypomelanus* is an important pollinator (Aziz et al. 2017a).

For molecular identification of plants, we compared DNA barcodes to GenBank, which is useful, but only for species with representative sequences (Aziz et al. 2017b). Because Singapore has more than 4000 vascular plants (Chong et al. 2009), the reference DNA barcode database for its flora is incomplete (R. Meier, pers. comm.). For example, the genus *Syzygium* includes more than 1000 species, of which 66 occur in Singapore (Chong et al. 2009), but few of its species are in GenBank. This can produce misidentifications, i.e., when we only use best matches to plants with existing barcodes. Hence our caveat that the species names we assign using only DNA barcoding should be treated as tentative. Future molecular studies of bat diets should ideally include building their own barcode database by first sequencing known bat food plants from the study area (Aziz et al. 2017b).

Because of the short study duration, identifying plants by germinating seeds was challenging (it takes a long time before seedlings are large enough to identify), and without a complete local reference seed collection, so too was identifying them based on seed morphology. Both problems were exacerbated by the fact that it takes considerable taxonomic expertise to morphologically identify seeds and seedlings (Lim et al. 2018a). But morphological identification methods are hardly obsolete. For rapidly-radiating taxa, such as *Ficus*, or ambiguous matches from DNA barcoding, successful identification may hinge on growing plants from seeds (see also Hodgkison et al. 2004), as we have shown with *Ficus fistulosa* and *Fagraea crenulata*. Indeed, combining results from different methods can increase the certainty of identifications and number of plants identified (Aziz et al. 2017b; Nielsen et al. 2017), so we recommend continuing to combine methods in future studies.

A limitation of our study is that because droppings collected at day roosts should be biased toward the last meal, they may **only** represent only a subset of an individual's diet overall (Thomas 1988) or even over the course of the preceding

night (Elangovan et al. 2001). Reported gut passage times for *C. brachyotis* vary from 11 min (Phua and Corlett 1989) to over 12 h (Shilton et al. 1999) making the timeframe for detection uncertain. There is a small chance that the droppings we collected include items ingested earlier in the night – a possibility increased by the use of high-resolution molecular methods which may detect surface eDNA from the gut contaminating a seed or pulp.

Finally, without tracking bats, it is impossible to know for sure where they forage and produce droppings during the night – two aspects of their ecology that affect the ecosystem service of seed dispersal. Therefore, an appropriate next step is to use telemetry and observational studies to follow bats, document their feeding behaviour and find their seed rain, and thus determine the fate of these seeds, i.e., seedling recruitment.

Our findings demonstrate that *C. brachyotis* can play important ecological roles even in a city and these roles may translate to ecosystem services. A better understanding and quantification of ecosystem services they provide in urban settings can improve support for the conservation of these bats.

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Data availability

~~DNA sequence data generated during the current study will be made available upon acceptance.~~ All DNA sequence data associated with this project are archived in the BOLD public project 'JCSDB Seeds dispersed by Cynopterus in Singapore' and available at <http://www.boldsystems.org/>.

Electronic supplementary material

ESM 1

(DOCX 328 kb)

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