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Barn Swallows *Hirundo rustica* in Peninsular Malaysia: urban winter roost counts after 50 years, and dietary segregation from house-farmed swiftlets *Aerodramus* sp.

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Abstract. In Peninsular Malaysia, passage and wintering Barn Swallows often congregate at nocturnal roosts in towns, most conspicuously on utility wires and adjoining roofs and ledges. As a Holarctic migrant, the species is potentially susceptible to population crashes. The first objective of this study was to investigate half-centennial changes in the number of passage and wintering Barn Swallows utilising an urban roost at Bentong, Peninsular Malaysia, through monthly counts following equal procedures in 1966–68. The second objective was to assess evidence for competition in terms of dietary overlap with a recently established population of house-farmed swiftlets (*Aerodramus* sp.) using both morphological identifications and next-generation sequencing (NGS). Modern peak numbers in October 2015, at 63,290 swallows, were 72% of the November peak of 1967 (87,880). The negative trend may reflect a declining swallow population in the Palaearctic breeding area but may also be a consequence of diminished resources in this tropical wintering region. A notable change during the half-century interval has been the introduction of a large population of trophically similar house-farmed swiftlets *Aerodramus* sp. exceeding passage and wintering Barn Swallows at peak numbers. At an ordinal level, the diets of Barn Swallows and house-farmed swiftlets both include a high proportion of hymenopterans, but at the level of genus, there is dietary separation between them. Molecular NGS data based on lower taxonomic levels (i.e., family, genus, and species) showed only about 10% overlap. We conclude that, after an interval of half a century, dietary competition with the new resident population of house-farmed swiftlets is unlikely to account for the reduction in peak numbers of migratory Barn Swallows.

Key words. coexistence, dietary segregation, edible-nest swiftlets, next-generation sequencing, swallows

INTRODUCTION

Throughout the Southeast Asian biogeographical subregion, massed urban roosts of migratory Barn Swallow *Hirundo rustica* recur annually. As diurnal migrants, Barn Swallows form a component of the Eastern Palaearctic migration system (Nisbet, 1976), wintering from India through Southeast Asia and Indonesia, extending to the western Kimberley region of West Australia, but a scarce migrant or rare vagrant elsewhere in Australia (Turner & Rose, 1994). Barn Swallows on passage or wintering in the Thai-Malay Peninsula are mostly identified as *H. r. gutturalis* (see Wells, 2007). The breeding range of this subspecies extends from the eastern Himalayas, through northeast Russia (Siberia), China, the Korean peninsula, and Japan (Dor et al., 2010).

The Barn Swallow was included among 27,600 terrestrial vertebrate species potentially susceptible to the erosion of biodiversity that is affecting global populations (Ceballos et al., 2017). As Holarctic migrants, Barn Swallows are vulnerable in their northern breeding range, on passage, and also in their tropical wintering ranges. Decline in the quality of the wintering grounds is among factors contributing to the decreasing population of Barn Swallows in Europe (Møller & Vansteenwegen, 1997; Ambrosini et al., 2012; Sicurella et al., 2014). In Korea, an observed delay in spring arrival and, hence, decreased number of broods per season have been linked to population declines of Barn Swallows (Lee et al., 2011).

In Peninsular Malaysia, passage and wintering Barn Swallows forage widely over rural areas during daylight. In the evening, the birds congregate at nocturnal roosts, most conspicuously on utility wires and adjoining roofs and ledges in many towns, favouring sites well-lit by street lights (Medway & Wells, 1976). Resident Pacific Swallow *Hirundo tahitica*

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also participate in urban swallow roosts as, occasionally, do other migratory hirundines that reach Peninsular Malaysia in very small numbers (Wells, 2007). During 1966–69, urban nocturnal roosts of mixed swallows were counted at monthly intervals in the neighbouring towns of Bentong, Raub, and Karak in Pahang state, central Peninsular Malaysia. The fluctuation in numbers of roosting Barn Swallows in the three towns showed a consistent pattern, with peak counts in November and departure largely completed by April, leaving a few hundreds in May through July (Medway, 1973). ln 2015–16, monthly counts of roosting swallows were repeated in Bentong. The first objective of this study was to test for change in the numbers and seasonal fluctuation in the population of passage and wintering Barn Swallows.

Two major environmental changes were recognised as potential impacts on the number of passage and wintering Barn Swallows. First, during the half-century between 1966 and 2015, there was a general erosion of habitat diversity in rural Peninsular Malaysia (Hansen et al., 2013; Tan et al., 2017), including central Pahang State. This is largely attributable to logging and clearance of natural forests, coupled with wholesale adoption of oil palm *Elaeis guineensis* replacing rubber *Hevea brasiliensis* as the principal plantation crop. Consequential effects of these habitat changes on the aerial arthropod fauna have not been assessed but, considering that the food resources of aerial insectivores are heavily dependent on habitat diversity and structure (Grüebler et al., 2008; Orłowski et al., 2014), are potentially deleterious.

The second major change lay in potential interspecific competition between trophically similar avian species. Between Barn Swallows and Pacific Swallows in central Peninsular Malaysia, this is avoided by seasonal breeding of the latter during the period when minimum numbers of Barn Swallows are present: egg-laying from the first week of March to 10–23 July and successful fledging from the second or third week of May until 15–29 August (Hails, 1984). Dilution of the available aerial arthropod resource could still be caused by other trophically similar birds, notably swifts (Apodidae). In 1966–69, a small resident population of House Swifts *Apus nipalensis* nested on buildings in Bentong town centre, and a similar population was observed in 2015–16. However, during this half-century, through human-assisted practices termed 'house-farming', the population of another member of the swift family, the house-farmed swiftlets of genus *Aerodramus,* has expanded dramatically in range and numbers in towns throughout Southeast Asia, especially in Peninsular Malaysia (Thorburn, 2014, 2015; Connolly, 2016, 2017a, 2017b, 2017c; Leh, 2019). Before the 1990s, there were very few swiftlet house-farms in Peninsular Malaysia and none in or near Bentong. The promotion of swiftlet house-farming then became an objective of government policy (Nurshuhada et al., 2015). By 2013 it was estimated that over 60,000 active swiftlet house-farm units existed nationally (Malaysia Economic Transformation Programme, 2013) and this increase has not ceased. In 2012, the Bentong urban authority documented approximately 150 swiftlet house-farm units in the town and its vicinity, mostly located above shop lots (Majlis Perbandaran Bentong, 2012). Compared with 1966, this large new population of potential competitors for aerial arthropod prey could constitute a major impact on the available trophic resource for Barn Swallows in their wintering range around Bentong. Although the diet of European Barn Swallows is reasonably well known (see Waugh, 1978; Turner, 2006; Orłowski & Karg, 2011, 2013a, 2013b), there has been no comparable dietary study of East Asian Barn Swallows in the wintering region. Field observations in Malaysia have found that, while swallows and swiftlets cover large, overlapping daily ranges, they forage in different air layers (Bryant & Turner, 1982; Waugh & Hails, 1983). Among several Malaysian resident wild swiftlet species, analysis of food boluses has provided information on the prey composition (Lourie & Tompkins, 2000). Comparable data do not exist for house-farmed swiftlets, which appear to be phylogenetically distinct from their presumed wild progenitors (Cranbrook et al., 2013; Goh et al., 2018). Competition between swallows and swiftlets might be avoided by dietary segregation, that could be shown by differential selection of major prey types. The second objective of the present study was therefore to investigate the dietary differences between Barn Swallows and the house-farmed swiftlets now permanently resident in Bentong urban area.

MATERIAL AND METHODS

Determining swallow and swiftlet numbers. The study was conducted in the town area of Bentong, Pahang, central Peninsular Malaysia (Fig. 1). In this town swallows roosted mainly on utility wires along streets of the urban centre, spreading to ledges and roofs on adjoining buildings and the crowns of street trees. To ensure comparability with counts from half a century ago, counts were conducted for twelve months in 2015–16, using the methods previously employed. Routine mist-netting was not repeated. Monthly counts were made for two hours between midnight and 0230 hours, using the block-counting methods of Medway (1973), i.e., the average number of birds settled on 1 m length of utility wire multiplied by the total length and the number of parallel wires occupied. For non-linear roosting sites, on roofs, ledges of buildings, and street trees, as in 1966–68, the estimated block-size was adjusted according to circumstances including visibility, to 10, 20, 50, or 100 individuals. The 1966–68 counts of Barn Swallows were represented diagrammatically by Medway (1973) on a logarithmic scale. Fig. 3 shows numbers for Bentong only, retrieved from original notes, compared with counts from 2015–16 as logarithmic values. Pacific Swallows, recognisable from below by the grey belly (Fig. 2), present in low numbers, were omitted from count totals. Previously unpublished catches of Pacific Swallows in monthly mist-netting at nocturnal urban roosts in the three towns in Pahang State, 1966–68, show that the numbers became proportionally insignificant especially during the passage and wintering period (Table 1). Photographs were taken to confirm comparative representation of Pacific Swallows in the roost in 2015–16.

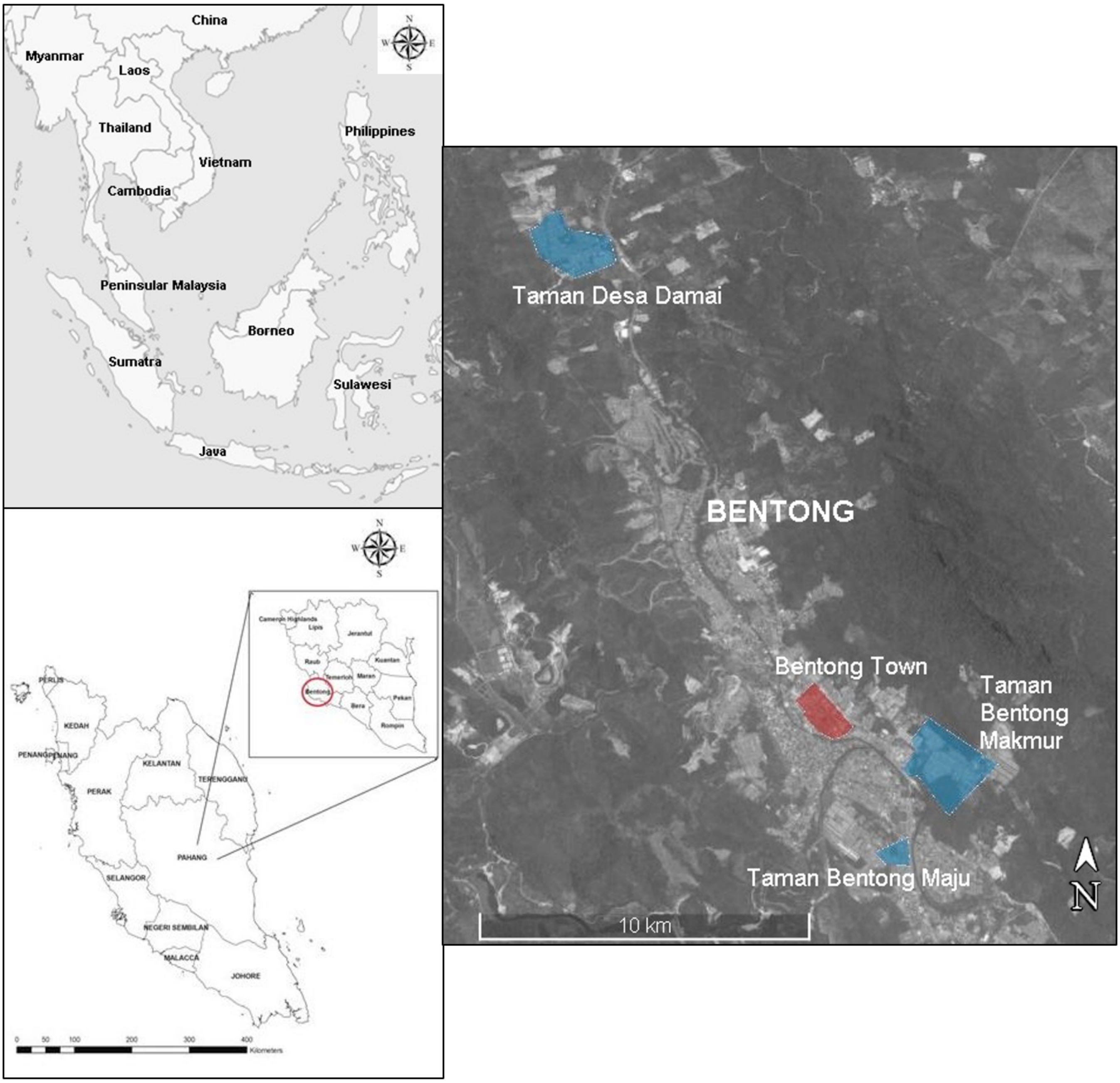

Fig. 1. (Left) Map of Peninsular Malaysia, with an enlarged plan of Pahang State; the circle indicates the study area, Bentong District. (Right) Google view of Bentong municipality, showing old town centre (red) and suburbs where house-farmed swiftlet colonies (blue) were counted.

Considering current uncertainty in the systematic relations of house-farmed swiftlets (Cranbrook et al., 2013; Rheindt et al., 2014; Goh et al., 2018), we identify these birds only to genus level, as *Aerodramus* sp. The Bentong Swiftlet House-farms Association and individual swiftlet farmers provided the total number of nests produced per harvest by house-farms in the town and vicinity. To estimate the number of swiftlets, this figure was multiplied by two (i.e., one male and one female), and 10% added to account for non-breeding fledglings (cf. Sankaran, 2001). At four representative house-farms, swiftlets numbers were estimated visually by M. S. Mansor and M. R. A. Halim as swiftlets swarmed back to roost at nightfall.

Diet sampling. In November 2015, to collect faecal samples, plastic sheets measuring 0.5 × 10 m were placed under occupied utility wires, 30 minutes after the swallows came to roost. Pacific Swallows were also present on utility wires in Bentong in winter 2015–16 but in very low numbers, as recorded in 1966–69 (Table 1, Fig. 2). The likelihood that the swallow droppings collected in November 2015 were contaminated by this species is negligible, and the sample can confidently be attributed to Barn Swallows. Fresh swiftlet droppings were also collected using plastic sheets on the floor of one house-farm, within the same month. Also in November 2015, ten Barn Swallows and ten house-farmed swiftlets were caught using mist-nets and sweep nets in the streets (for swallows) and a house-farm (for swiftlets). These birds

Table 1. Average monthly numbers of Pacific Swallows mist-netted in nocturnal roosts of predominantly Barn Swallows in Peninsular Malaysia (1964–69) and represented as per thousand of the average total swallow catch.

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Average	60	46	46	97	79	N/D	303	386	73	51	33	26
‰	0.88	0.62	0.92	4.60	84.95	N/D	295.32	23.11	1.51	0.69	0.38	0.34

Fig. 2. Swallows roosting on utility wires along streets of the Bentong town centre. Pacific Swallows, recognisable from below by the grey belly, were present in very low numbers during the passage and wintering period.

were administered tartar emetic, using a 1.33 mm diameter soft silicone tube attached to a 1 ml syringe which was inserted into the bird's oesophagus. The doses were 0.025 ml/g body weight of a 1% solution in water, administered at a rate of about 0.05 ml/sec (Poulin et al., 1994), based on the rate recommended for medical use (Diamond et al., 2007). Treated birds were immediately placed in a dark container lined with wax paper. Within 2–3 minutes, the birds regurgitated partially digested arthropods. Treated birds were released 15 minutes after regurgitation (Johnson et al., 2002). In addition, food boluses were collected from adult swiftlets returning to feed nestlings during the afternoon. These food boluses are readily regurgitated by swiftlets when handled upon capture (Langham, 1980; Lourie & Tompkins, 2000). All diet samples were preserved in 99.8% undenatured ethanol and stored at –20°C.

Morphological prey identification. Preserved diet samples were sorted with fine forceps on sterile petri dishes under a stereo microscope (Leica ZOOM 2000). Arthropod taxa were identified by the following appendages: elytra (e.g., Coleoptera, Hemiptera), wings (e.g., Hymenoptera, Isoptera), mouthparts including mandibles (most Orders), and other preserved fragments (e.g., heads, tibia, thorax, petiolus, abdomen), following Mansor et al. (2018a). Guidelines and identification keys from Chapman & Rosenberg (1991), Triplehorn & Johnson (2005), Whitaker et al. (2009), and Manhães et al. (2010) aided identification of prey fragments to Order, and sometimes to family and genus levels. The data from all samples of swallows and of swiftlets, respectively, were pooled to demonstrate the majority prey items in their diets.

Molecular diet analysis. Arthropod DNA was extracted from dietary samples using the NucleoSpin® Soil Kit (Macherey-Nagel GmbH & Co., Dueren) according to the manufacturer's protocol. PCR amplification of a 286 bp fragment of the mitochondrial DNA cytochrome c oxidase subunit I region (COI) was performed using forward primer LCO1490 (5'–GTCAACAAATCATAAAGATATTGG–3') and reverse primer HCO1777 (5'–ACTTATATTGTTTATACGAGGGAA–3') (Brown et al., 2012). Amplifications were performed in triplicate with 20 µL PCR mixture consisting of 4 µL of 5 × FastPfu Buffer, 2 µL of 2.5 mM dNTPs, 0.8 µL of each primer (5 µM), 0.4 µL of FastPfu Polymerase (TransGen Biotech, China), and 10 ng of template DNA. After an initial denaturing step at 94°C for 2 min 30 s, amplification proceeded for 35 cycles at 94°C for 30 s, 44°C for 30 s, 72°C for 45 s, and a final extension at 72°C for 10 min. Amplicons were extracted from 2% agarose gels and purified using the AxyPrep DNA Gel Extraction Kit (Axygen Biosciences, Union City, CA, U.S.A.), following the manufacturer's protocols and quantified using QuantiFluor™ -ST (Promega, U.S.A.). The primer set was modified using Nextera adaptors (Illumina, San Diego). The second PCR protocol was performed at 72°C for 3 min, 98°C for 30 s, followed by 12 cycles of 98°C for 10 s, 55°C for 30 s, 72°C for 30 s, and a final extension at 72°C for 5 min. Sample libraries were normalised, pooled in equimolar concentrations, and sequenced (2 × 250/300 bp) on the MiSeq Desktop Sequencer (Illumina, U.S.A.), following the standard protocols.

Data analysis. NGS amplicon sequences were filtered and collapsed into unique haplotypes (singleton removed), and then clustered into Operational Taxonomic Units (OTU) using the USEARCH v8.1.1861 (Edgar, 2013), with a specified 98% sequence similarity threshold. OTU sequences were edited using BioEdit version 7.0.9 (Hall, 1999), and queried through GenBank (http://www.ncbi.nlm.nih.gov/) or Biodiversity of Life Database (BOLD) (http:// www.boldsystems.org/; Ratnasingham & Hebert, 2007). A sequence that had at least 98% similarity to any other reference database was identified to species level (King et al., 2015; Wong et al., 2015). Following Lagkouvardos et al. (2016) and Mansor et al. (2018b), a sequence was assigned at a higher taxonomic level when it could not clearly be matched to a single species; at a genus level (>95% similarity) and at a family level (>90%).

Statistical analyses. Data were normally distributed (by inspection with quantile-quantile plots and Shapiro-Wilk tests). Monthly Barn Swallow counts in 2015–16 were compared with those of 1966–68 by paired *t*-test using the

Table 2. Counts of Barn Swallows at the urban roost in Bentong, used for Fig. 3.

Year	2015–2016			1966	1967	1968	Average 1966–68
	Utility wires	Other structures	Monthly total				
Feb	11,376	7,870	19,246		75,612	73,304	74,468
Mar	11,155	4,890	16,045	47,000	55,663	47,440	50,034
Apr	8,667	2,880	11,547		35,733	6465	21,099
May	1,827	350	2,177		795	1064	930
Jun	1,486	150	1,636		844		844
Jul	5,652	370	6,022		568	1484	1026
Aug	6,332	1,720	8,052	16,700			16,700
Sep	34,887	8,525	43,412		48,501		48,501
Oct	46,201	17,089	63,290		74,338		74,338
Nov	35,515	7,562	43,077		87,880		87,880
Dec	32,170	5,568	37,738	71,912	80,835		76,374
Jan	22,120	8,063	30,183			68,385	68,385

PAST software (Paleontological Statistics, 2.17) (Hammer et al., 2001). Dietary overlap between swallows and house-farmed swiftlets were computed using the 'bipartite' 2.05 package (Dormann et al., 2008) in R v.3.2.3 (R Core Team, 2015). Two indices were used in this study: (i) niche overlap, the mean similarity in interaction patterns among species reflecting resource preferences, following Horn's index (R_o) (Horn, 1966), in which values near 0 indicate no common use of dimensions, while a value of 1 indicates complete niche overlap; and (ii) Togetherness (T), describes the level of similarity in the use of resources across study species (i.e., occurrence of insect taxa) (Stone & Roberts, 1992).

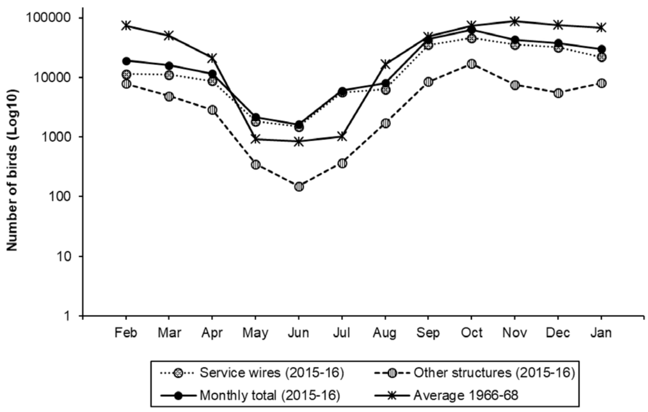

Fig. 3. Number of Barn Swallows in the urban roost in Bentong town, Pahang, in 2015–16 and averaged for 1966–68.

RESULTS

Counts of swallows and swiftlets. At the peak of the wintering season, almost all service wires in central old Bentong town were occupied by roosting swallows after nightfall, with birds spreading to roofs and ledges of buildings and street trees. The pattern of seasonal fluctuation in counts of Barn Swallows roosting in 2015–16 was broadly similar to that of 1966–68 (Table 2, Fig. 3). The population increased rapidly in August through September, but reached a peak in October, rather than November. Peak swallow numbers in 2015–16 were significantly smaller than those of 1966–68 (t = 4.407, df = 7, p = 0.02), with peak numbers in October 2015, at 63,290 swallows, were 72% of the November peak of 1967 (87,880). In both counts, the mid-winter peak was followed by a significant drop in numbers: 13% drop in 1966–68 and 32% in 2015–16 (see Table 2 attached to Fig. 3). The number of roosting swallows through February (19,246) and March (16,045) in 2015 remained lower than in 1966–68 (74,468 and 50,034, respectively), but was higher in months of the northern summer season, May (2,177), June (1,636), and July (6,022) (Fig. 3).

The population of house-farmed swiftlets in Bentong town and its neighbourhood increased from zero in 1966–68 to a high number in 2015–16, as shown by several indicators. The reported nest production from registered and active house-farms in Bentong town and suburban residential areas, in 2015, implied a population of about 82,500 breeding adults and non-breeding fledglings. Because of the scattered locations of house-farms in Bentong District, it was not possible to check this figure with a comprehensive count. Single counts of returning swiftlets in the evening observed minima of 2,600 swiftlets in one house-farm unit in Bentong town, and in the outskirts, minima of 2,400 in units at Taman Bentong Maju, 1,300 at Taman Desa Damai, and 4,000 at Taman Bentong Makmur, an average of 2,575 birds per house-farm (Fig. 1). One owner considered that, on average, 2,000 swiftlets occupied each of his three house-farms in Bentong (Mr. Sam K. F., personal communication). If these figures are typical, the swiftlet population of the 150 registered house-farms in Bentong and its vicinity is at least 82,500 and may approach 400,000. In short, in 2015–16 all indications of the population of house-farmed swiftlets, resident throughout the year, exceeded the number of passage and wintering Barn Swallow, even at peak time.

Table 3. Occurrence of arthropod taxa in diet of Barn Swallows and house-farm swiftlets using morphological analysis. Data are given as proportions (%).

	Barn Swallows		Swiftlets	
Prey taxa	**Occurrence**	**Percentage**	**Occurrence**	**Percentage**
Hymenoptera	+	49.49%	+	70.30%
Family: Formicidae				
Anochetus sp.	+	(1.02%)	–	
Camponotus sp.	+	(0.51%)	+	(7.27%)
Crematogaster sp.	–		+	(1.82%)
Odontomachus sp.	+	(1.02%)	–	
Pachycondyla sp.	+	(5.61%)	+	(0.61%)
Tetramorium sp.	+	(1.53%)	+	(0.61%)
Coleoptera	+	42.35%	+	20.00%
Isoptera	+	7.14%	+	0.61%
Hemiptera	+	0.51%	+	4.24%
Blattodea	–		+	0.61%
Orthoptera	–		+	4.24%
Araneae	+	0.51%	–	

Morphological identification of diet components. The impact of this gross increase in consumers of the aerial insect resource, and thus potentially on the local carrying capacity of swallows and swiftlets, can be evaluated by comparison of the diets of these two groups. In total, 361 prey fragments were morphologically identified from the November diet samples of Barn Swallow and house-farmed swiftlets. Hymenoptera emerged as the highest arthropod group in both. The food of swallows comprised four insect orders (Hymenoptera, 49.5%; Coleoptera, 42.3%; Isoptera, 7.1%; Hemiptera, 0.5%) and one Araneae (0.5%), while the swiftlets' diet included six insect orders (Hymenoptera, 70.3%; Coleoptera, 20%; Hemiptera, 4.2%; Orthoptera, 4.2%, Blattodea, 0.6%, and Isoptera, 0.6%). Most hymenopterans were ants, Formicidae, with *Anochetus* sp., *Camponotus* sp., *Odontomachus* sp., *Pachycondyla* sp., and *Tetramorium* sp. present in the diet of swallows, while *Camponotus* sp., *Crematogaster* sp., *Pachycondyla* sp., and *Tetramorium* sp. were in the diet of swiftlets (Table 3; Fig. 4).

Molecular analysis of diet components. The NGS run produced 100,810 paired-end reads from pooled dietary samples of swallows and house-farmed swiftlets. After bioinformatics processing, these reads were reduced to 27,872 unique haplotypes, which were then clustered into 58 OTUs (swallows, 16 OTUs; swiftlets, 42 OTUs). Most of the BLAST hits were assigned to class Insecta, with the similarity to the reference database ranging from 90% to 100%. Altogether, 50 distinct insect taxa belonging to 26 families from seven Orders were identified (Table 4). Orders identified were Hymenoptera (30%), Diptera (30%), Lepidoptera (16%), Coleoptera (12%), Hemiptera (8%), Isoptera (2%), and Ephemeroptera (2%). Fig. 5 illustrates diet distributions between swallows and swiftlets identified by molecular analysis. Low dietary overlap and togetherness values (R_o = 0.59; T = 0.17) were found between swallows and swiftlets, with overlap about 10%, indicating low overlap in resource use (in November). Alate ants (Hymenoptera: Formicidae)

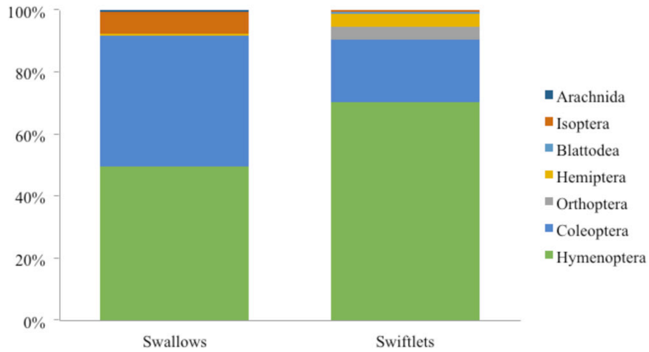

Fig. 4. Comparative diets of swallows and house-farmed swiftlets in Bentong, identified by morphological analysis.

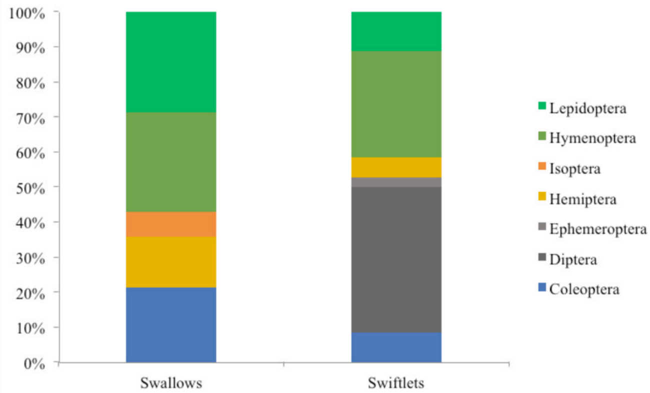

Fig. 5. Diet distribution of swallows and house-farmed swiftlets at Bentong identified by NGS molecular analysis.

Table 4. Occurrence of 50 distinct insect taxa based on OTU found in diet of Barn Swallows and house-farm swiftlets by NGS molecular technique. Sequence similarity is based on either GenBank or BOLD reference databases.

Prey taxa	Swallows	Similarity (%)	Swiftlets	Similarity (%)
ORDER: Coleoptera				
FAMILY: Curculionidae				
Curculionidae sp.	–		+	92.67
Xyleborus volvulus	+	100	–	
FAMILY: Nitidulidae				
Carpophilus mutilatus	+	100	–	
FAMILY: Scarabaeidae				
Scarabaeidae sp.	+	91.23	+	91.23
FAMILY: Elateridae				
Elateridae sp.	–		+	96.57
ORDER: Diptera				
FAMILY: Ceratopogonidae				
Ceratopogonidae sp. 1	–		+	100
Ceratopogonidae sp. 2	–		+	96.1
Ceratopogonidae sp. 3	–		+	90.08
FAMILY: Chironomidae				
Chironomus sp.	–		+	100
Chironomus incertipenis	–		+	99.57
Chironomus circumdatus	–		+	100
FAMILY: Muscidae				
Musca sp.	–		+	96.08
FAMILY: Mycetophilidae				
Mycetophilidae sp.	–		+	100
FAMILY: Sciaridae				
Sciaridae sp. 1	–		+	100
Sciaridae sp. 2	–		+	100
Sciaridae sp. 3	–		+	97.22
Sciaridae sp. 4	–		+	100
FAMILY: Stratiomyidae				
Stratiomyidae sp.	–		+	100
FAMILY: Syrphidae				
Toxomerus sp.	–		+	97.83
FAMILY: Tachinidae				
Phasia sp.	–		+	96.9
ORDER: Ephemeroptera				
FAMILY: Baetidae				
Cloeon sp.	–		+	100
ORDER: Hemiptera				
FAMILY: Aradidae				
Aradidae sp.	+	94.37	+	94.37
FAMILY: Cicadellidae				
Empoasca sp.	–		+	97.53
FAMILY: Pentatomidae				
Pentatomidae sp.	+	92.31	–	

Prey taxa	Swallows	Similarity (%)	Swiftlets	Similarity (%)
ORDER: Hymenoptera				
FAMILY: Braconidae				
Braconidae sp.	+	91.95	–	
FAMILY: Formicidae				
Formicidae sp. 1	–		+	94.81
Formicidae sp. 2	–		+	92.22
Formicidae sp. 3	–		+	93.07
Formicidae sp. 4	–		+	92.86
Formicidae sp. 5	–		+	92.22
Formicidae sp. 6	–		+	91.3
Camponotus reticulatus	–		+	100
Odontomachus simillimus	+	100	+	100
Pheidole parva	+	100	–	
Tetramorium sp.	+	96.54	+	96.54
FAMILY: Ichneumonidae				
Acrodactyla sp.	–		+	96.9
Ichneumonidae sp.	–		+	99.56
ORDER: Blattodea				
FAMILY: Termitidae				
Hospitalitermes medioflavus	+	99.13	–	
ORDER: Lepidoptera				
FAMILY: Erebidae				
Corgatha pleuroplaca	–		+	98.92
FAMILY: Hesperiidae				
Hesperiidae sp.	–		+	94.44
FAMILY: Geometridae				
Calluga sp.	–		+	96.39
Geometridae sp.	+	90.48	+	94.25
FAMILY: Oecophoridae				
Oecophoridae sp.	+	94.05	–	
FAMILY: Tortricidae				
Tortricidae sp.	+	92.31	–	
FAMILY: Xyloryctidae				
Plectophila sp.	+	96.4	–	

including *Odontomachus simillimus* and *Tetramorium* sp., chafers and dung beetles (Coleoptera: Scarabaeidae), flat bugs (Hemiptera: Aradidae), and geometrid moths (Lepidoptera: Geometridae), were among insect taxa found in the diets of both swallows and swiftlets. The remaining 45 prey taxa were found to be distinct between swallows and swiftlets.

DISCUSSION

The interval of half a century from 1966–68 to 2015–16 has been marked by progressively intensified environmental change in East and Southeast Asia, as elsewhere in the world. As aerial insectivores, East Asian Barn Swallows serve as biological monitors of one sector of habitat quality. The fluctuating numbers of Barn Swallows roosting in Bentong town as passage migrants and winter visitors provide a basis for local comparison between 1966–68 and 2015–16. Besides service wires, roofs, ledges of buildings, and street trees, there was no indication of other roosts elsewhere within the expanded urban area of Bentong, enlarged since 1960s, or its suburban fringe. The peak roosting population was reached in October in 2015–16, earlier than November in 1966–68. Peak numbers in 2015 were also smaller than that in 1966–68. This negative trend may reflect declining populations in the Palaearctic breeding area, as observed in Korea (Lee, 2009; Lee et al., 2011) and in Europe (Møller, 1989; Robinson et al., 2003; Saino et al., 2004; Crowe et al., 2010; Teglhøj, 2018). Declining numbers of passage and wintering swallows could also be attributed to the reduced holding capacity of the central Peninsular Malaysian wintering area as a result of local deterioration in biodiversity. This region has experienced extreme and rapid forest loss from 90% forest coverage in the 19th century to only 38–45% remaining by 2012, largely by clearance for agriculture, plantation forest, or settlements (Miettinen et al., 2011; Hansen et al., 2013; Tan et al., 2017). Loss and degradation of stopover habitat along migration routes has further contributed to declining trends of East Asian migratory birds (Yong et al., 2015).

Both in 1966–68 and in 2015–16, the midwinter peak was followed by a significant fall in numbers. In both cases, this is likely to reflect onward movement of Barn Swallows to Indonesia and Australia. It is notable that average counts in 1966–68 subsequently held up into February, while in 2015–16 there was a continuing decline in monthly counts through November to February, again suggesting enhanced onward movement by swallows on passage, probably attributable to proven deteriorating habitat quality in a traditional wintering area.

The falling counts in April, resulting from the departure for northern breeding grounds, were as distinctive in 2015 as in 1966–88; but in 2015 the counts of Barn Swallows remaining in the Bentong roost in May, June, and July were higher than in 1966–68. Since no individuals were marked, it is equally possible in both instances that these few birds were late departures, early arrivals, or possible non-migrating individuals. If a higher number failed to migrate in 2015, it can be conjectured that diminished biodiversity resources prevented the birds from fattening to departure weight in March and April.

Morphological analysis showed that the diets of Barn Swallows and house-farmed swiftlets both included a high proportion of hymenopterans. An abundance of alate ants, with small beetles, was found in the diet of swallows in the breeding grounds by Orłowski & Karg (2011, 2013a, 2013b), Turner (1994), and Kopij (2000) in wintering grounds. Specialisation on flying ants by swiftlets was also observed by Lourie & Tompkins (2000). The high proportion of micronutrients in Hymenoptera and Coleoptera (Razeng & Watson, 2015) may encourage the selection of these components in the diet of both avian groups.

The representation of hymenopterans at the level of genus, however, suggests dietary separation between passage and wintering Barn Swallows and house-farmed swiftlets in central Peninsular Malaysia. The NGS data provide greater taxonomic detail, strengthening the conclusion from morphological identifications that there was little overlap in resource use by these populations of Barn Swallows and house-farmed swiftlets. NGS analysis of their prey expands the morphological identifications to show that Barn Swallows took a lower number of insect taxa than house-farmed swiftlets, which utilised a wider variety of prey, thereby reducing dietary competition. The NGS run identified 31 distinct insect taxa consumed by swiftlets that were absent from Barn Swallows' diet (Table 4). Such diet variability allows house-farmed swiftlets to adapt successfully to prey availability in urban areas (Lourie & Tompkins, 2000). Furthermore, the presence of flies in the diet of house-farmed swiftlets indicates the success of these resident birds to exploit local urban resources, thus contributing to their high density and reproductive success in this environment. High consumption of flies was found in the diet of swallows in the breeding ground in Scotland (Waugh, 1978) and Poland (Orłowski et al., 2014), and the reduction of fly populations is believed to be a reason for the decrease of reproductive success and the offspring quality of swallows (Møller, 2001; Ambrosini et al., 2002).

In conclusion, these observations confirm that the number of Barn Swallows now (2015–16) wintering at Bentong town in central Peninsular Malaysia has declined significantly by comparison with the population in 1966–69. If this trend is general throughout central Peninsular Malaysia, a decline of this extent may reflect a diminished breeding population in Palaearctic East Asia as much as a consequence of deterioration in habitat quality in this tropical wintering area (Lee et al., 2011; Gordo & Doi, 2012; Bonisoli-Alquati et al., 2015).

There are no comparative data to test for change in available food resources in the wintering grounds in Peninsular Malaysia. The identification of diet items presented here may therefore be useful for future comparisons. However, the dietary evidence reported here is sufficient to show that one significant change in local biodiversity, i.e., the enormous increase in a resident population of house-farmed swiftlets, has probably impacted less on the availability of aerial arthropod prey for Barn Swallows than habitat degradation. Dietary competition with the novel, large population of house-farmed swiftlets is unlikely to be a factor contributing to the observed reduction in numbers of wintering Barn Swallows, nor to the increased proportion of swallows on passage to further wintering grounds, identified in central Peninsular Malaysia by this comparison over a half century, 1966 to 2016.

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