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ROOSTING AND NEST-BUILDING BEHAVIOUR OF THE WHITE-NEST SWIFTLET *AERODRAMUS FUCIPHAGUS* (THUNBERG) (AVES: APODIDAE) IN FARMED COLONIES

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ABSTRACT. — The edible-nest swiftlets of the genus *Aerodramus* are amongst the most unusual of birds, being able to navigate in total darkness aided by echolocation and using their own saliva to construct the nest. They are a valuable economic resource, the edible nests being much sought after. Knowledge of nesting and breeding ecology of this species has so far been limited to cave colonies whilst studies focusing on the house-farmed population are lacking. We studied the roosting and nest building behaviour of the white-nest swiftlet *Aerodramus fuciphagus* (Thunberg) in two separate house-farmed colonies of different age in Miri Division, Sarawak, from Jun.2010 to Jan.2011 (Site-I) and Feb.2012 to Oct.2012 (Site-II). Two types of infra-red (IR) cameras were used, namely (i) fixed focal-lens IR to monitor large colony and (ii) Pan-Tilt-Zoom camera for close-up observation. This paper reports new discovery in which three basic activity sessions are described; first emergence period (0600–0700 hours), post-emergence period (0700–1000 hours) and returning period (1800–1900 hours). During the post-emergence period, approximately half of the sampled colony was observed re-entering the swiftlet house to resume nest construction. Ten ethogram categories were developed to describe the roosting behaviours of the white-nest swiftlets: proximity fluttering, random roosting flight, pair switching, parallel shifting, mounting, preening, defaecating, resting, territorial display, and nest building. Our results also revealed that there is a disparity in sexual contribution in nest building, where one partner is twice more hardworking and return more frequently during the post-emergence period to build nest. We hypothesized that it is the male (i.e., Individual-A) that contributes more to nest building, reasons being (i) Individual-A is the one that mounted Individual-B and not the other way around, (ii) Individual-A is nearly twice as hardworking in nest building, correlating with the fact that spermatogenesis is less energy demanding than oogenesis, and (iii) more protective over its partner when their nest reaches full size, a point of time when copulation is expected.

KEY WORDS. — *Aerodramus fuciphagus*, swiftlet, edible nests, roosting, nest building, colony, sexual contribution

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INTRODUCTION

The white-nest swiftlet *Aerodramus fuciphagus* (Thunberg) is one of several small cavernicolous, echolocating and insectivorous swifts from the Family Apodidae (Chantler & Driessens, 1995). Swiftlets are arguably the most accomplished flyers among all bird species, spending most of their lives on the wing, catching and feeding on insects in flight (Cranbrook & Lim, 1999). When at roost, these species are able to construct nests using salivary nest cement secreted from a pair of sub-lingual glands (Lim & Cranbrook, 2002) mixed, in most species of swiftlets, with material such as feathers and plant fibres. The nest of the white-nest swiftlet is comprised primarily of pure saliva (Cranbrook & Lim, 1999). This edible nest cement is the main ingredient of the highly-prized and renowned “bird’s nest soup” which is of significant commercial and reputed pharmaceutical value (Ismail, 1999; Tompkins, 1999; Lim, 2000). Because of their valuable nests, edible-nest swiftlets have a long historical affiliation with humans from the early exploitation of natural cave colonies to the more enterprising undertaking of swiftlet farming in recent years.

Making use of the propensity of wild swiftlets to nest within disused buildings, swiftlet farmers now build empty house structures to attract new nesting colonies (Lim & Cranbrook, 2002). These can be built in towns where their valuable contents are easily guarded and the swiftlets are able to forage over the surrounding countryside. Inside the dark, empty, cave-like environments, members of the house colonies can be found roosting, clinging side by side in pairs on the parallel planks and beams that have been purposely set up to entice them to nest. Swiftlet pairs have been reported to roost and build their nest at their permanent roosting site, therefore implying high nest-site fidelity and pair kinship in colonial swiftlets (Lim, 1999). Large numbers of individuals tend to congregate and nest within close proximity of each other, while those roosting far away from any nest are believed to be sexually immature juveniles or non-reproductive individuals (Medway 1962a; Lim & Cranbrook, 2002). In general, nest building behaviour is commonly associated with courtship display and pair formation in birds (Soler et al., 1998a). With regard to the white-nest swiftlet, it was believed that both sexes contribute to nest building that normally takes place at night while at roost (Kang & Lee, 1991).

Over the years, the edible-bird nest industry has seen an influx in international market revenues that has prompted the establishment of more and more “swiftlet houses” in Borneo (Mardiastuti et al, 1997; Lim & Cranbrook, 2002). In Sarawak, the conventional management of swiftlet houses is largely manipulated by local entrepreneurs or farm managers, most of whose practices lack a scientific basis. Present knowledge on the biology and ecology of Bornean swiftlets (*Aerodramus* spp.), in particular the cave populations, is reasonably well documented (e.g., Medway, 1962a, 1962b, 1967; Lim, 1999, 2000; Lourie & Tomkins, 2000; Thomassen, 2005). However, important ecological information such as roosting and nesting behaviour, either in caves or farmed colonies, is scarce and not clearly understood. Information such as how the swiftlets interact with each other at roost, whether they pair for life or are they polygamous, and where sexually immature fledglings roost within the colony are not only scientifically interesting, but are very useful to swiftlet farmers. Therefore, systematic ethological study using continuous digital video recording system was used in this study to find some insights to these questions.

The study of animal behaviour describes ways in which animals interact with their environment and the survival value of that behaviour (Drickamer & Vessey, 1992). Ethology can be defined as the systematic biological approach to the study of animal behaviour, while an ethogram describes an inventory of the behaviour patterns performed by the species under investigation (Prakash et al., 1994). In the case of modern ethological studies, there has been significant enhancement of quantitative observations using recent data collection techniques such as remote photography and highly complex digital equipment such as multichannel event recorders. In contrast to conventional direct observation, video images provide objective study materials and are highly repeatable for intermittent or rigorous analysis (Reif & Tornberg, 2006). In addition, remote video monitoring is highly manageable with only minimal disturbance to the nesting colony (Johnston et al., 2003).

Given the rapid developments in this field, the use of continuous video recording has become commonly applicable in avian behavioural studies (Reif & Tornberg, 2006). Monitoring of nesting and roosting behaviour using non-stop video surveillance systems and time-lapse digital video has built up mounting interest in recent ornithological research (e.g., Pechacek, 2005; Smithers et al., 2005; Pierce & Pobprasert, 2007). In the past, the behavioural patterns of white-nest swiftlets in farmed colonies were rather subject to theoretical interpretation based on observations made on their natural cave-dwelling counterparts. Unlike the wild colonies, the swiftlets living in swiftlet-houses are highly adaptive towards habitat modifications in cave-like mimicry or limited roosting space on parallel wooden beams installed in close proximity. The advantages of using digital video recording technique confer an excellent opportunity to unravel the potentially complex behavioural mechanisms among colonial swiftlets. In this study, we present the nightly ethogram of the white-nest swiftlet colony at roost with emphasis on the division of labour in nest building.

MATERIAL AND METHODS

Study area and video recordings. — The swiftlet colonies used in this study were located in two swiftlet houses (4°23'39"N, 113°59'12"E) in Miri Division, Sarawak. They were identified as *A. fuciphagus* (Thunberg) by C. K. Lim and the Earl of Cranbrook based on the point that although the rump feathers were paler than the back, these swiftlets were distinctly different from *A. germani* in which the rump feathers are greyish-white with a black shaft. Further, white-nest swiftlet populations found in inland caves have rump colouration that is the same as the back (i.e., currently accepted as subspecies *A. fuciphagus vestitus*). Therefore we identified the swiftlet populations in house farms in this study as *A. fuciphagus fuciphagus*. Two types of infra-red CCTV recording equipment were used in this behavioural study; (i) fixed focal-lens Infra Red (IR) camera (1/3 Sony Super HAD CCD-NIR-6036) and (ii) Pan-Tilt-Zoom camera (Sony DN-PTZ Camera High Resolution IR-corrected aspherical power lens) with PTZ Key3 Joystick Controller. Site-I is an eight-year old colony with more than 4,000 pairs, while Site-II in the adjacent building is only four years old with roughly 700 pairs of swiftlets. Two IR cameras were installed in each swiftlet houses, wired via video cables to a four-channelled digital video recorder (H.264 4CH DVR) connected to a 15” inch flat screen monitor. To acquire sufficient viewing coverage of the sampled colony, the fixed-lens static IR camera scope was positioned perpendicularly facing the targeted nesting compartments. The PTZ camera was wall-mounted adjacent to the IR camera in site-II. All recordings were automatically stored into the DVR hard disk as video files that were periodically retrieved for later viewings or analysis. Site-I was studied from Jun.2010 to Jan.2011, while recording at Site-II began from Feb.2012 to Oct.2012. In the first site, a small colony of 20–30 (out of 150) breeding pairs within four central compartments was left unharvested while monthly harvesting was conducted in the second site. At Site-II, a pair was targeted among a small breeding cluster of five pairs for close-up observation. We tested the hypothesis of equal sexual contributions to nest building activity by marking one of the individuals in the targeted pair. Markings were done on the wing tips and tail feathers with fluorescent green marker (MARK HER™ livestock marking paint) on 20 Feb.2012. The marked individual was designated as Individual-A and its unmarked partner as Individual-B. After a one-month trial of video monitoring, the nest of this targeted pair was removed on 31 Mar.2012 in an attempt to dissect the specific nesting behaviours within a full cycle of nest building.

Data analysis. — To compare the daily activity pattern and population size at both sites, data for Site-I was pooled from the maximum number of recording hours available from Jun.2010 to Jan.2011. Likewise, data for Site-II ranged from Feb.2012 to Oct.2012. Each roosting area (within the viewing scope of the fixed focal lens IR camera) was monitored to calculate the total number of roosting individuals and periodic intervals of nest attendance (Chazarreta et al., 2011). All video footage was viewed on fast-forward mode. However, comprehensive screening was done occasionally at normal speed to characterise miscellaneous activities that might be potentially overlooked (Pechacek, 2005). Subsequently, all prescribed activities were transcribed onto activity log sheets according to the 24:00 hours timeline with numbers of bird counted per observation hour. Following Martin & Bateson (1993) and Pechacek (2005), a simple method of instantaneous sampling (fix-interval time point) was chosen to organise and screen the data systematically. For consistency and comparison, recording time was fragmented and analysed from four quarter-hour sampling intervals (Q1, Q2, Q3 and Q4) per observation hour. Sample points were derived from each quarter-hour to infer the general roosting behaviours and their associated movements displayed by the targeted individuals. Using the multifocal PTZ camera, we confirmed the stated behaviours by capturing still photos of the targeted pair. Total number of individuals, mean and standard error (SE) for each hour were used to plot the graph for daily emergence and returning pattern. Finally, cumulative graphs describing the corresponding monthly pattern for both sites were generated from the mean numbers of nest attendance counted for every month.

For focal observation on the targeted pair, the nest building rate was measured by calculating the duration and total frequency of periodic intervals during deposition of salivary layers. Time of nest building commence from the first indicative point of the bill movements extruding saliva until break between any deposition of layers. The close-up view using multifocal PTZ lens enabled clear and detailed verification of specific time and duration of saliva deposition by each individual (marked-A and unmarked-B). Similarly, total duration was calculated in minutes by screening every quarter-hour over 24 hours. Observational notes were made on specific behaviours, roosting positions and nest building technique displayed by the pair in response to different phase of nest completion. Comparison of nest building duration between the two was tested via 2-sample independent t-test. Mean daily frequency of all classified roosting behaviours of the pair was tabulated and divided into four weeks observation. All statistical tests were carried out using Microsoft Office Excel 2007 and MINITAB 13.2 (MINITAB Inc. 2000).

RESULTS

Daily patterns of emergence and return. — Overall, 2,688 hours of observations were analysed by tallying 10,752 quarter-hourly counts from the two colonies. Three basic activity sessions can be described, namely the first emergence period (0600–0700 hours), post-emergence period (0700–1000 hours) and returning period (1800–1900 hours). In general, the white-nest swiftlets spent between 12–17 hours roosting inside the swiftlet house. The earliest sign of flight movements commenced between 0600–0615 hours. Subsequently, the number of individuals present decreased abruptly as the swiftlets exited their roosting site, but roughly half of the estimated population would return shortly after 0700 hours. A unimodal curve was observed within the period 0700–1000 hours, peaking between 0800–0900 hours. From 1000 hours onwards, the numbers began to decline again and reverted to its initial empty state leaving just the young fledglings at the nests (Fig. 1). Later in the afternoon, a few individuals may gradually enter the house as early as 1700 hours. By 1840 hours, large swarm of swiftlets would typically rush back to their roosting sites. The frantic condition normally lasted for 15 to 20 minutes. Such daily outrush and return was similar from month to month for both sites. Based on the numbers of returning individuals during the post-emergence period, the percentage of return for Site-I and Site-II ranged from 48–87% (Dec.2010 to Jan.2011) and 29–66% (Feb. to Oct.2012) respectively (Table 1).

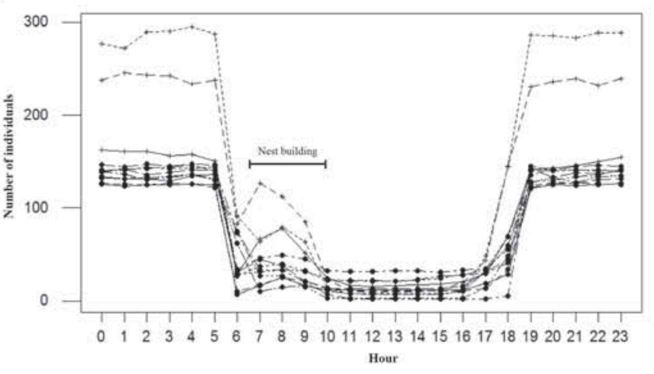

Fig. 1. Cumulative graph showing average numbers of roosting individuals per observation hour between Site-I (cross markers) and Site-II (solid circles).

Table 1. Maximum number of returning individuals (n), estimated population size (N) and percentage of return (%) during the post-emergence period (0700–1000 hours) for swiftlet colony in Site-I and Site-II.

Site	Date	Maximum number of returning individuals (n)	Estimated population size (N)	Percentage of post-emergence return (%)
I	Jun.2010	143	163	87
I	Dec.2010	189	246	77
I	Jan.2011	143	295	48
II	Feb.2012	94	142	66
II	Mar.2012	49	142	35
II	Apr.2012	43	136	32
II	May 2012	56	136	39
II	Jun.2012	38	127	30
II	Jul.2012	34	128	27
II	Aug.2012	50	145	34
II	Sep.2012	59	148	40
II	Oct.2012	42	146	29

Classification and description of ethogram. — We developed ten terminologies to describe the roosting behaviours of the white-nest swiftlets (Fig. 2). Each behaviour pattern is mutually exclusive. The mean daily frequency ± SE of the listed behaviours is presented in Table 2 with corresponding diagrams illustrating each movement (Fig. 3). Detail descriptions are as follows:

Proximity fluttering. — Fluttering in proximity to another individual is among the common roosting behavioural displays by both single and paired individuals. Within each nesting compartment, swiftlet at roost will either move by fluttering at one point or circling for a short while around their nest before returning to the exact roosting area. In general, proximity fluttering and random roosting flights activities

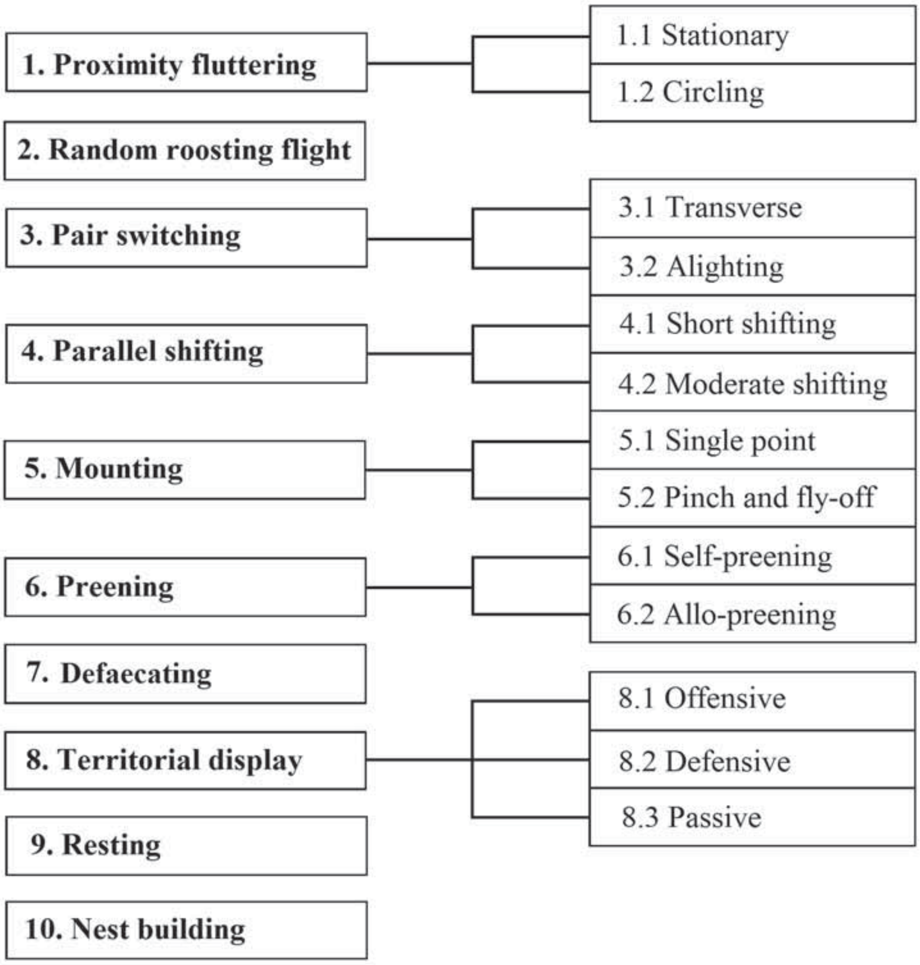

Fig. 2. An ethogram chart of the white-nest swiftlet (*A. fuciphagus*) showing roosting behaviour classifications with their associated movements.

Table 2. Mean daily frequency performed by both Individual-A and Individual-B for proximity fluttering (PF), random roosting flights (RRF), pair switching (PSw), parallel shifting (PSh), mounting (Mo), preening (Pr) defaecating (Def) and territorial display (TD). Resting (Res) is measured in minutes. Values are presented as mean ± SE.

Ethogram	**First week**		**Second week**		**Third week**		**Fourth week**		**Total**		**Daily average**	
classification	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**
PF	3.3±0.9	3.3±1.6	3.4±1.1	0.6±0.2	3.6±0.8	1.1±0.6	3.3±0.9	1±0.6	13.5	6	3.4±0.5	1.6±0.6
RRF	5.3±1.3	4.9±1.4	1.3±0.4	0	1.1±0.6	0.1±0.1	1.8±0.6	1.3±0.5	13.5	10.1	2.5±0.6	1.7±0.6
PSw	8.9±1.9	1.9±0.6	6±1.3	4±1.2	7.7±1.7	2.4±0.4	7.3±1.9	1.3±0.5	29.8	9.6	7.5±0.9	2.5±0.4
PSh	5±0.9	3.5±1.2	4.3±0.6	6.4±1.2	3.4±0.8	6.9±0.5	4.8±1.3	11.3±1.4	17.5	28	4.3±0.4	6.4±0.7
Mo	0.8±0.5	0	0.4±0.2	0	0.1±0.1	0	0	0	1.3	0	0.4±0.2	0
Pr	24.8±2.4	24.9±2.9	27.9±2	27.3±2	24.3±2.1	24.1±1.8	20±2.4	20±2.4	96.9	96.3	24.7±1.2	24.6±1.2
Def	3.3±0.9	3±0.9	4.7±0.4	5.9±0.7	3±0.8	4.6±0.6	1.8±0.5	0.8±0.5	12.7	14.2	3.3±0.4	3.8±0.5
TD	1.3±0.3	1.3±0.4	3.9±0.9	0.7±0.3	2.1±0.3	1±0.4	0.8±0.3	0	8	3	2.1±0.3	0.8±0.2

typically build up during the final hours (0500–0600 hours) before the first emergence from the swiftlet house. Of the observed pair, Individual-A and Individual-B displayed this behaviour 3.4 ± 0.5 and 1.6 ± 0.6 times nightly respectively.

Random roosting flight. — This behaviour consists of a continuous series of proximity fluttering or random directional flights with one to four stops. Intense random flights usually occurred during the first hour after returning to the colony (1830–1930 hours) and gradually decreased throughout the night. Just before dawn, the activities increased and during this frantic period, a nesting individual may occasionally failed to locate their own nest but eventually managed to return to it after a few attempts. The nightly mean frequency for both Individual-A and Individual-B was 2.5 ± 0.6 and 1.7 ± 0.6 respectively.

Pair switching. — Pair switching behaviour is much more apparent and frequently displayed by nesting pairs compared to non-nesting pairs. This swapping action requires an individual to switch its roosting position with that of its partner by a transverse or alighting movement. In detail, a pair is described as switching transversely by mounting promptly over the partner to the other side of the nest. Likewise, alighting is performed in the same manner through brief fluttering but this is less commonly displayed. Nesting swiftlets probably exhibit this behaviour to accommodate space for each other and their nestlings (if present) inside the small cup-shaped nest. During nest building, this movement was frequently observed in the nesting pair when taking turns secreting fresh salivary layers onto nest. From our observations, one individual is apparently much more active than the other through repetitive switching over time (A = 7.5 ± 0.9, B = 2.5 ± 0.4).

Parallel shifting. — Parallel shifting is a non-flight movement in which the individual moves horizontally along the plank from its roosting position to another temporary point. The shifting movement is almost inquisitive by drifting sideways using their clingy tarsi coupled with few wing beats on the vertical beam. The distance may range from very short to moderate (depending on the available gaps between nests). With reference to the observed pair, Individual-B was observed to move away frequently from the nest via this movement (A = 4.3 ± 0.4, B = 6.4 ± 0.7), although at very short distances. Apparently, this behaviour can be an indicative of breaks between nest building sessions and to give room for the partner to resume building.

Mounting. — Mounting-like contacts are less frequent compared to other roosting behaviours. Due to the relatively short duration of copulation in birds (a few seconds), the movement resembles false copulation display during frequent body contacts inside the cramped nest. It can also be seemingly aggressive at times with multiple attempts at mounting and pinning down the roosting partner. More common is a single attempt at mounting immediately followed by alighting beside its partner. Another scenario is the mount-and-fly-off sequence, mostly outside the scope of view, but returning to the site a few seconds to several minutes later.

Preening. — Preening activity can be classified into two types; self-preening and allo-preening. In general, this activity can be considered one of the commonest behaviour performed by roosting pairs. These include almost every reachable part of their body (nape, back, vent, crown, underparts) which mainly consist of their flight feathers (wing and tail feathers). Roosting pairs typically spent several minutes (about one to five minutes) in one continuous preening session. On average, they spent about 25 min nightly, most frequently during nest building intervals and immediately after returning to nest in the evening.

Defaecating. — Observations on this particular behaviour were not possible using the fixed IR camera, hence data were collected only from the PTZ recordings on the marked pair. Both Individual-A and Individual-B showed almost similar patterns of defaecating. One individual might not necessarily defaecate during the night but the mean frequencies suggest that both tend to defaecate at least three to four times while at roost. The numbers (or frequency) were relatively constant. Mean nightly frequencies of both Individual-A and Individual-B were recorded at 4.7 ± 0.4 and 5.9 ± 0.7 times respectively.

Territorial display. — This behavioural display can be divided into three categories; offensive, defensive and passive. An offensive territorial display is described when one individual initiated a move towards another neighbouring individual or pair at roost, while showing some degree of aggressiveness. In most observations, the offender was from nearby nesting compartments. For defensive display, an instant reaction from this would naturally lead to retaliation from the harassed individual (or pair) by chasing away the offender via shrugging and lifting both wings coupled with threatening jabs from the bill. This behaviour is characterised by combination of rigorous pecking, wing lifting, intense fluttering and occasionally strong quarrel-like contacts which eventually forced the intruder away. Defensive actions were commonly displayed by Individual-A in which it seemingly played a more protective role over its partner (A = 2.1 ± 0.3, B = 0.8 ± 0.2). Such activity showed an increasing trend during the second and third week of nest building. For the third category, passive territorial display is considered being more sedentary towards external disturbance such as intentional or accidental approach by other swiftlet.

Resting. — Resting or inactive period is calculated by total of quarter-hours spent resting throughout the night and during the post-emergence return. During this period, swiftlet pairs may appear stationary (occasional head movements/ wing lifting only) and comfortable at their roosting sites or inside their nest. Between the pair, the mean nightly frequency suggests that Individual-A rested longer for an average of 174.8 ± 21.6 min while Individual-B for 140.8 ± 16.5 min. This was also attributed with more time spent by Individual-A resting during the post-emergence period. As the nest reached its completion, the pair was observed to spend significantly more time resting during the final week (A = 303.8 ± 29 min, B = 232.5 ± 41.3 min).

Nest building. — This particular behaviour occupied substantial hours of the overall time spent inside the swiftlet house during the breeding period. Nightly observational records indicated that nest building may occur at any time of the night but two peak activity sessions were apparent before the pre-emergence period (0500–0600 hours) and immediately after the returning period (1800–2000 hours). This activity was also observed during the post-emergence period (0700–1000 hours), although at a lower rate and with irregular involvement between the swiftlet pair. The pair would start the initial building by clinging firmly on the nesting spot while the head is stretched far and held low. The bill is then open and shut repeatedly while regurgitating the fresh thin saliva and the process continues as the upward attachments expanded into a proper but shallow cup-shaped nest. The building process consists of chewing, retching and sweeping motion from the open bill with repetitive jabs on newly added layers (see Fig. 3).

For close-up observation using the PTZ camera, a total of 600 hours during the nest building period was comprehensively analysed. In this study, the marked nest was completed in 32 days. Initial base construction begins from the first day since nest removal until day-14. Mean total time spent during the first week for both individuals was 80.3 ± 13.7 min. From that point, the nest building rate increased substantially during the second (140.2 ± 6.2 min) and third week (108.5 ± 6.1 min), subsequently slower on the fourth week (60.6 ± 6.6 min) and levelled off on the final remaining days (Table 3). From the cumulative data of the first week, both individuals showed corresponding pattern with a gradual hike before reaching the peak during the second and third week (Fig. 4). Both Individual-A and Individual-B started depositing saliva during the first two days at relatively shorter duration (33.6–34.4 min). The duration extended sharply by the third day onwards, ranging from 41.5–165.7 minutes, until the nadir in the fourth week (day-25).

During the post-emergence period, Individual-A spent a total of 104.8 min of nest building compared to just 30.5 min by Individual-B (Table 3). This accounts to13 visits by the marked Individual-A compared to only six visits by the unmarked partner-B. Between them, Individual-A was observed building nest alone for seven sessions while Individual-B contributed for only a single session. Both partners were observed building together for five sessions. Overall, Individual-A showed significant effort and endurance with 61.7 ± 4.3 min of mean nest-building time compared to just 40.1 ± 3.4 min by Individual-B (t_{45} = 3.94, P = 0.001). During nest building, Individual-A will normally alternate and take turn with its partner after three to five minutes of adding multiple salivary layers. We have observed that the shortest duration of saliva deposition is slightly over 10 seconds and the longest recorded without any break is about 7 min.

DISCUSSION

Swiftlets are free-flying birds that have a regular daily flight routine even if nesting in artificial houses. They typically emerge from their nesting colony to forage for insects at daybreak and return shortly before dark (Kang & Lee, 1991). Earlier studies have confirmed that this pattern is exhibited by most cave swiftlets (Lee & Kang, 1994; Lim, 1999). Thus a common understanding has developed that swiftlets will only return at dusk or approaching nightfall once they have left their roosting site at dawn (Lim & Cranbrook, 2002). At Lubang Salai, a natural white-nest swiftlet cave in middle Baram, Sarawak, adult swiftlets have been reported to return occasionally throughout the day to feed their nestlings (Lim, 1999). However, previously unconfirmed observations by local birds' nest harvesters in limestone caves at Bau-Jambusan in western Sarawak have claimed that adult black-nest swiftlets *Aerodramus maximus* return in the early morning to build the nest (Lim, pers. comm., 2000). Such a claim is now proven, albeit for a different species, in house colonies of white-nest swiftlets using advanced video monitoring technology. Here, the full-daily activity patterns of the house-farmed swiftlets were expectedly similar to that of the wild colony, only with a significant time frame

Fig. 3. Ten terminologies for ethogram description of the white-nest swiftlet (*A. fuciphagus*). Pictorial boxes are numbered as: 1 = proximity fluttering; 2 = random roosting flights; 3 = pair switching; 4 = parallel shifting; 5 = preening; 6 = mounting; 7 = territorial display; 8 = defaecating; 9 = resting; 10 = nest building. (i) Individual-A was observed secreting fresh salivary layers on the hinge of nest and subsequently continued by Individual-B on day-nine. (ii) Note the head direction and bill movements in sweeping motion from side to side. (iii) An almost complete small half-cup shaped nest observed on day-20.

Table 3. Nest building duration by Individual-A and Individual-B during the post-emergence period (0700–1000 hours) and the total time spent within 25 days. Values are presented in minutes. Dash (–) indicates absent of nesting individual.

Day	Post-emergence period (min)		Total nest building (min)			Weekly Mean (A+B) ± SE
	A	B	A	B	Total (A+B)	
1	3.5	0.8	21.9	11.7	33.6	First week = 80.3 ± 13.7
2	–	–	21.9	12.5	34.4	
3	–	–	65.5	21.1	86.6	
4	–	–	51.9	19.8	71.8	
5	–	–	68.4	30.9	99.4	
6	–	–	82.4	46.8	129.2	
7	7.7	–	63.0	43.8	106.9	
8	–	–	94.5	48.9	143.4	Second week = 140.2 ± 6.2
9	7.6	7.8	91.1	74.6	165.7	
10	–	–	76.4	46.4	122.7	
11	5.5	–	73.1	53.3	126.4	
12	0	–	81.5	74.7	156.2	
13	4.1	–	94.4	45.8	140.2	
14	–	–	67.5	59.3	126.9	
15	–	–	72.9	43.6	116.5	Third week = 108.5 ± 6.1
16	7.1	–	68.8	52.0	120.7	
17	16.8	10.9	69.7	49.0	118.7	
18	17.8	–	75.8	51.7	127.5	
19	16.0	4.9	58.0	37.4	95.4	
20	–	–	46.5	40.3	86.8	
21	7.2	–	55.0	38.8	93.8	
22	8.3	3.3	44.5	27.6	72.1	Fourth week = 60.6 ± 6.6
23	–	2.8	39.7	24.1	63.8	
24	3.2	–	33.5	31.6	65.1	
25	–	–	25.6	15.9	41.5	
Total	104.8	30.5	1543.4	1001.5	2544.9	
Mean ± SE	4.6 ± 1.2	1.2 ± 0.6	61.7 ± 4.3	40.1 ± 3.4	101.8 ± 7.3	

addition termed as the ‘post-emergence period’ (0700–1000 hours) in between the first emergence (0600–0700 hours) and returning period (1800–1900 hours).

Our findings highlight a new discovery with reference to the irregular and asynchronous visits by one partner of the breeding pairs to the colony during the post-emergence period. Within this period, we found that significant number of swiftlets returned to build the nest. This behaviour has been overlooked in past studies (i.e., without using CCTV constant monitoring method) where it was assumed that once the swiftlets leave their roosting place, they will spend the entire day foraging outside except for those having a young brood to feed. Furthermore, the absence of reliable 24-hour power supply would not have permitted the kind of observation undertaken in this study. Outside the caves, large foraging flocks of swiftlets were normally most active during early morning and late afternoon (Manchi & Sankaran, 2010). At this time, it is not uncommon that they will disperse and maximize aerial hunting by following airborne insects with rising thermal up-currents until midday (Lim & Cranbrook, 2002). In another study on chimney swift *Chaetura pelagica*, Zammuto & Franks (1981) suggested that swifts may re-enter their roosting site due to decline of aerial prey after sunrise compared to high abundance of insects during the early hours. Nonetheless, the post-emergence return pattern observed in this study does not seem to be linked to the availability of food source or they taking refuge from heavy rain, but rather explicitly associated to nest building by one assiduous partner. Unlike the black-nest swiftlet, the diet of white nest swiftlet is relative diverse, hence are much adaptable with the food available in the area (Lourie & Tompkins, 2000).

Between the two swiftlet colonies, a higher returning percentage was observed in Site-I as compared to Site-II. This was probably due to the experimental manipulations in which selected colonies in Site-I was left for breeding while nests in Site-II were continuously harvested. As a result, the high total numbers of roosting individuals counted here can be attributed to the nestlings raised in each nest as opposed to breeding pairs without nestlings in Site-II. Nonetheless, the similarity of the patterns exhibited by both colonies is the key point of interest. In addition, the numbers of returning individuals during the post emergence period (i.e., to build the nest) is also correlated with the swiftlet annual breeding cycle. Lower returning percentage (27–39%) was observed in Site-II from Apr. to Jul.2012, which coincided with the lowest breeding activities and hence less nest building activity. During this period, the swiftlets undergo an intense annual moult cycle, whereby energy is shifted for production of new feathers at the expense of reproduction (Lim, 1999).

In the present investigation, some plausible explanations that might have influenced this scenario are the high energy demands and extra investments required to build and complete the nest before the egg-laying period (Soler et al., 1998b). In addition, Lim & Cranbrook (2002) suggested that the combination of intrinsic physiological vigour and availability of food source played an important role in determining the onset of the breeding cycle in swiftlets. At the peak of the breeding season, the salivary glands of swiftlets undergo huge production of saliva before the egg-laying period (Medway, 1962b; Lim & Cranbrook, 2002). With much enlarged and hyperthrophied salivary glands, an impromptu response might be logical in which the swiftlets would re-enter the swiftlet house after a quick feeding after dawn and "emptied" their fresh glutinous saliva load to build nest before embarking on another long foraging journey. By late morning, the natural foraging rhythm during daylight continued as they replenished their energy in preparation for the subsequent prolonged nest building activity at night. For comparison, in broiler chicken *Gallus domesticus*, the salivary glands contain numerous mucous cells which can alternate between accumulation and discharge of mucous within a cycle (Newman, 2000). Studies on glycoprotein synthesis and secretion pathways have shown that intracellular retention half times of different mammalian glycoproteins vary from 30–120 min (Yeo et al., 1985; Bostrom et al., 1986). This is within the interval from the last nest deposition in the wee hours before dawn until the 'post-emergence' return. By inference, swiftlets seem able to maximise their salivary secretion capability by continuous production and intermittent usage of salivary nest cement until the nest is fully completed.

This was further corroborated by the close-up observation made on the marked pair. Although nest building is habitually carried out at night, about 6.8% (Individual-A) and 3% (Individual-B) from the overall nest building minutes was essentially spent during the post-emergence period (see Table 3). At daytime, the nest building ratio for Individual-A is three times greater than Individual-B. Hence, it is most likely that asynchrony in post emergence return between the nesting pair is probably associated with the breeding strategy or post-mating sexual selection process (Soler et al., 1998a). Here, the male's reproductive success is determined through its willingness, toleration and commitment towards nest building as pair-bond insurance on future parental investment with the female partner (Szentirmai et al., 2005; Alvarez & Barba, 2011). In other bird species, these male quality traits in nest building behaviour were also observed in great bowerbirds *Ptilonorhynchus nuchalis* (Doerr, 2009), barn swallows *Hirundo rustica* (Soler et al., 1998a) and penduline tits *Remiz pendulinus* (Szentirmai et al., 2005).

On average, nest building duration for the white-nest swiftlet is 30 days (Lim & Cranbrook, 2002). Our results revealed that the nest growth rate accelerated the most during the first and second week, then gradually waned in the third to fourth week and finally levelled off beyond the fourth week. Lim (1999) reported that nest growth curve calculated from the rate of extension of the nest-cup as sigmoidal or reaching plateau as it entered the egg-laying phase. The general nest building profiles for house-farmed swiftlets is also similar to that of black-nest swiftlets. In accordance with Kang & Lee (1991), a single black-nest swiftlet may spend about 25–60 min daily for nest construction and each

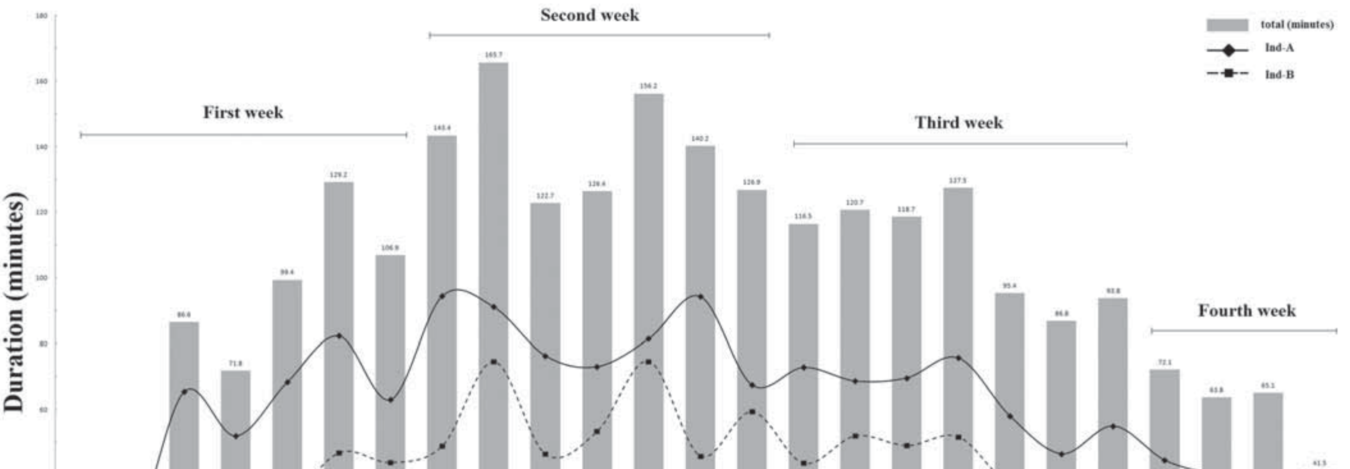

Fig. 4. Cumulative graph showing nest building duration (minutes) for the observed pair. Diamond-solid and square-dashed lines indicate Individual-A and Individual-B respectively. Histogram bars denote the total minutes spent by both individuals.

building bout may last up to 4 min. Generally, both sexes are known to contribute in nest construction but evidence on the comparative assiduity of labour between male and female is not well understood then. Based on the nest building cumulative graph (Fig. 4), the marked Individual-A was observed spending almost double nest building minutes compared to its partner. It seems that one of the sexes is much more active, laborious and diligent than the other. The unequal contribution from each pair member is significant, which suggests that male and female swiftlets play different roles in nest building. This may be an adaptive response to sustain their multi-brooded reproductive strategy in terms of energetic. Many studies have shown that female birds predominantly require enormous amount of energy for egg production (e.g., Hails & Amirrudin, 1981; Hails & Turner, 1985; Marvelde et al., 2012). De Neve & Soler (2002) added that females may also be flexible in their own reproductive effort by adjusting their laying date and clutch size prior to assessing their mate's qualities. With this observation, it can be hypothesised that it is the male (i.e., Individual-A) that is more active in nest building because female (i.e., Individual-B) swiftlets need to channel substantial energy for egg production. Furthermore, testimonies from swiftlet farmers confirmed that newly established breeding pairs readily used an artificial nest nailed onto the plank for laying, thus suggesting that female swiftlet is comfortable to use any structure deemed sufficiently large to hold her clutch without undergoing the laborious nest building process herself.

Of the observed behaviour patterns, many seem to be related to finding, recognising and retaining a roosting and nesting position within the crowded colony (e.g., proximity fluttering, random roosting flight, pair switching, parallel shifting and territorial display). Others relate to self-maintenance (e.g., preening, defaecating and resting) and maintenance of the pair bond (e.g., allo-preening and mounting). This study also revealed that some roosting behaviours are considerably more evident during the nest building period than at other times. Proximity fluttering, pair switching, parallel shifting and territorial display are clearly dynamic behavioural modes which are useful for flight mobility, space usage and protection in cramped and tight nesting sites. For instance, higher frequencies for both proximity fluttering and random roosting flight behaviours during the first week was evidently caused by frantic movements from panic reaction of the marked pair when their nest was experimentally removed. As for parallel shifting, this particular behaviour probably designate how roosting individuals locate neighbouring nests and perhaps aid newly breeding pairs to find suitable or vacant spot to build their nest. This may also be a form of territorial claim as thin semi-circular salivary smears had been observed along both sides of an established nest. These overlapping smears may thicken overtime but never developed into another nest, suggesting this was not done by a different breeding pair. Likewise for territorial display, high frequency of defensive actions was commonly displayed by the marked pair in the later stages of nest building, perhaps signalling the onset of female ovulation period. Hence in this case, the more prominent Individual-A is more active and protective over its partner by showing natural aggressiveness towards other swiftlets. Another equally important activity is resting for nesting pairs. At the peak of nest building (i.e., second and third week), high energy expenditures are presumably in favour of long and sufficient resting period.

Although the definite sexes of the marked pair were unconfirmed due to wear and fading of the markings over a 10-month period, we have strong justification that division of labour is essential between nesting pair in order to suit their annual breeding strategy. On a final note, we postulate that Individual-A is most likely to be the male because (i) consistently mounting Individual-B and not the other way round, (ii) twice more hardworking in nest building because comparatively less energy is needed for spermatogenesis as compared to oogenesis (i.e., each egg is 20 × 14 mm, ≈ 2g), (iii) showing more protective behaviour over its partner as their nest reaches full size, at a time when the female is known to ovulate and become receptive, and (iv) the usage of unoccupied artificial nest in swiftlet house indicates the female is perfectly comfortable to use any structure that was not constructed by her for laying.

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Research on swiftlet in Sarawak was pioneered by the Earl of Cranbrook nearly half a century ago at Niah Cave, Sarawak in 1956. The momentum started then has never ceased, and two generations of Sarawakian researchers have continued Lord Cranbrook's footsteps and endeavours—further dissecting the secrets of the edible-nest swiftlets.

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