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First record of the nesting biology of the red-vented barbet, *Megalaima lagrandieri* (Aves: Piciformes: Megalaimidae), an Indochinese endemic

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Abstract. We report on the nesting biology of the red-vented barbet (*Megalaima lagrandieri*) in its natural habitat in Loc Bac forest (southern Vietnam, Lam Dong Province). Two active nests containing nestlings and one nest in the process of excavation were observed during 2012 and 2013. Both parents participated in the provisioning of their brood throughout the day, making a maximum of 52 daily visits with food. The nestlings' diets consisted of fleshy fruits, insects and spiders as well as vertebrates. Plant matter was added to the nestlings' diet from the initial days of feeding, and its proportion increased over time. We provide a first description of the red-vented barbet nesting hole and comment on the hardness of the wood. A description of the two-week-old nestlings is also provided.

Key words. Asian barbets, cavity nesting, Brinell's test, frugivory, nestling period

INTRODUCTION

Asian barbets are a characteristic component of the avifauna of forested landscapes in South and Southeast Asia. According to recent systematic revisions based on morphological and molecular evidence (Moyle, 2004; Feinstein et al., 2008; Tex & Leonard, 2013), apart from the genus *Calorhamphus* (two species), the family Megalaimidae embeds the genera *Psilopogon* (one species) and *Megalaima* (31 species), which are now placed by certain authors within the genus *Psilopogon* (Dickinson & Remsen, 2013). In Indochina, these small to relatively large barbets inhabit lowland and mountain forests as well as disturbed or secondary woodlands, plantations and gardens. Certain wide-ranging species such as the lineated barbet *M. lineata* or, especially, the coppersmith barbet *M. haemacephala* may inhabit parks and boulevards in large cities.

Asian barbets are primarily frugivorous, feeding on a variety of tree fruits and playing an important role in seed dispersal (Lambert, 1989; Yahya, 2000, 2001; Trounov & Nguyen, 2009; Chang et al., 2012; Trounov, 2012). Additionally, they nest in self-excavated tree cavities. Hence, along with forest-dwelling African and South American barbets (Short & Horne, 2001, 2002), they are unique among birds because they combine a specialised frugivorous diet with the ability to bore nest holes. The morphology of the jaw apparatus in *Megalaima* barbets reflects a peculiar combination of adaptations to physically prepare fruit for consumption and to excavate hard substrates (Trounov et al., 1996).

However, the biology of Asian barbets has been studied unevenly. To date, the most comprehensive data concerning reproductive biology are available for a few *Megalaima* species, which include the white-cheeked barbet *M. viridis* and the crimson-fronted barbet *M. rubricapilla* in India (Yahya, 1988, 2001), the widely distributed coppersmith barbet (Baker, 1934; Short & Horne, 2001, 2002; Lok & Lee, 2009) and the endemic Taiwan barbet *M. nuchalis* (Koh & Lu, 2009; Lin et al., 2010).

In Southeast Asia, knowledge of the reproduction of barbets is based mostly on fragmentary observations (Stepanyan, 1995; Wells, 1999; Lok et al., 2009a, b; Lok & Lee, 2009), and data on the reproductive ecology of species that inhabit forests are especially scarce. Field studies of the reproductive biology of barbets that live in southern Vietnam are still in their early stages. To date, the data available are for the blue-eared barbet *M. australis* (Trounov & Vasilieva, 2012).

The red-vented barbet *M. lagrandieri* Verreaux, 1868 is one of the largest representatives of the genus. Its length is 29.5–34 cm, and it weighs 175–214 g (Stepanyan, 1995; Robson, 2008). This Indochinese endemic is recorded in Vietnam, Laos and Cambodia, where it inhabits lowland and mountain evergreen and semi-evergreen forests at elevations of up to 2000 m a.s.l. This bird is rather common in certain regions, but it is difficult to observe because it is not numerous and is rather retiring. The ecology and biology of this species are poorly studied, making the red-vented barbet one of the most enigmatic birds of Indochina. Importantly, the nest of this species has not been described previously, and no reliable data exist on the breeding period, brood size or nestlings' diet in this barbet.

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In this paper, we present new data on the nests, nestlings and their provisioning, facilitating a greater understanding of this enigmatic species.

MATERIAL AND METHODS

Study area. All field observations were conducted during two research expeditions in April 2012 and April 2013 in the territory of Loc Bac Forestry Enterprise (Bao Lam District, Lam Dong Province, Vietnam) in two locations within 15 km of each other; the approximate coordinates are 11°50′N, 107°38′E, at nearly 600 m a.s.l., for the 2012 observations and 11°44′N, 107°42′E, at nearly 800 m a.s.l., for the 2013 observations. The area consists of a hilly landscape with an elevation difference of 600–1100 m a.s.l. and a developed river and brook system. The 2012 observations were conducted on hill slopes covered with lowland, high, polydominant evergreen tropical forest consisting of the tree families Magnoliaceae, Euphorbiaceae, Guttiferae, Theaceae, Fagaceae, Meliaceae, Moraceae, Anacardiaceae, Dipterocarpaceae, Apocynaceae, Burseraceae and Lauraceae. The 2013 observations were conducted on hill slopes covered with mountain, high, polydominant evergreen tropical forest consisting of the tree families Magnoliaceae, Sapindaceae, Podocarpaceae, Euphorbiaceae, Fagaceae, Theaceae, Sapotaceae, Leguminosae, Anacardiaceae, Altingiaceae, Rhodoleiaceae, Elaeocarpaceae, Lauraceae, Sterculiaceae and Dipterocarpaceae. In the areas in which the study was conducted, the forest has been severely damaged by selective cutting and other deforestation activity. The area has a monsoon climate, with the rainy season beginning between April and May and ending between October and November. During the study periods, heavy but relatively short-term rains were common during the afternoon and at night. The temperature varied from 24–25°C at night to 31–32°C during the day.

Nest search and description. The search for the nests was conducted by following adult birds using acoustic cues and visual observations. For each nesting hole located, the height above ground and the trunk diameter at the hole level were measured with the help of trigonometric calculations and photographs, based on comparisons with the directly measured hole aperture diameter. In total, we found three nests: two nests containing nestlings and one nest in the process of excavation. With the permission of the local authorities, the dead treetop containing the nest was obtained for examination and measurement at the end of the expedition in 2013.

Wood hardness was evaluated by applying the Brinell's hardness test method (Tabor, 2000: 155) to a radial section of the portion of the trunk adjacent to the nesting cavity. A carbide ball with a diameter of 14 mm and a test load of 100 kg were used. Measurements of deformations were performed with a digital caliper. The test was applied three times for each of the two wood samples collected. Wood density was calculated after weighing the sample to the nearest 0.1 g. All tests were performed under laboratory conditions at a relative humidity of 40%.

Parental behavior and provisioning of nestlings. Observations of parental behavior near the nests were conducted from dawn until twilight (05:15 to 18:30) from natural shelters (bushes) or a hide tent with the use of binoculars and Nikon D4 camera with a 500 mm lens at a distance of approximately 20 m. We recorded the timing of each parental visit and photographed birds with food items in the bill. Nest No. 1 was observed for three days: 28–30 April 2012. Nest No. 2 was observed for nine days during the period 6–19 April 2013; this period included the day before the nestlings hatched and the first to fourth, seventh, ninth, eleventh and thirteenth days after hatching. Nest No.3 was observed for three days: 11, 12 and 16 April 2013.

We recorded the type of food (fruit, invertebrate or vertebrate) and the frequency at which it was delivered. Food items were identified either by direct observation or from photographs; if the food could not be reliably identified, it was noted as undetermined. The approximate size of food items was evaluated in relation to the barbet's bill length and calculated afterwards from photographs via comparison to a directly measured hole aperture diameter.

Nestling description. Two nestlings taken from the nest were sacrificed for ornithological research and are currently held in the Zoological Museum of Moscow State University (ZMMU R-3447, R-3448). Before preservation, the nestlings were photographed, weighed and measured; standard morphometric parameters were taken using a digital caliper.

RESULTS

Nest descriptions and nest construction. The principal parameters of the studied nests are given in Table 1 and in Fig. 1. All observed nesting holes were excavated in dead wood in tree trunks of broadleaved trees of unidentified species, with relatively open exposure (on steep hill slope, near clearing in the forest or beside stream). In all cases, the hole aperture was oriented toward the open space (Fig. 4A).

The apparently single nestling in Nest No. 1 died for an unknown reason on the third day of observation. The parents were observed to have made repeated and unsuccessful attempts to remove the dead body, sometimes tearing feathers from its tail. The quill feathers were well formed and greenish in color, indicating that the deceased nestling was close to the fledging stage. Both nestlings of Nest No. 2 were sacrificed for research purposes.

In vertical section, the nest hollow was bottle-shaped with a curved entrance tunnel (Fig. 1). The nesting cavity did not contain any filling, and its walls were dry, smooth and clean. The approximate total volume of the nest hollow was 2783 cm^3, and the volume of the nesting cavity was 2395 cm^3. The hardness of the wood adjacent to the nesting cavity averaged 0.4 kgF mm^{-2}, and the wood density averaged 31.2 kg m^{-3}.

Nest No. 3 was located at a distance of approximately 2.5 km from Nest No. 2. Over the course of three days, one adult was observed regularly pecking at the hole three times a day,

Table 1. Main parameters of the nesting holes of the red-vented barbet found in southern Vietnam.

Nest No.	Year of observation	Status	Tree trunk diameter (mm)	Hole height above ground (m)	Hole aperture diameter (mm)	Brood size
1	2012	active	540	15	64	1 nestling
2	2013	active	310	9.5	63	2 nestlings
3	2013	under excavation	310	16	60	–

between 10:00 and 10:25 (9 min average), between 13:00 and 13:35 (9 min average) and between 14:45 and 15:30 (14 min average). The bird did not completely enter the hole, but rather plunged into it to the shoulder level; therefore, the nest excavation was only in its initial stage. The excavation progressed slowly, and the nest was abandoned for the rest of the observation period after 16 April.

Mating and parental behavior. Because the red-vented barbet is sexually monomorphic, it was impossible to define the sex of either of the parents in most cases, except for the act of copulation.

Copulation by the pair taking care of Nest No. 1 was observed three times: at 06:53–07:07 on 25 April 2012 and at 14:42–14:52 and 17:20 on 28 April. In all cases, the couple spent approximately 10–20 min close to each other on the same tree near the nesting site before the act. The partners were sitting calmly, preening themselves or moving through the crown with short jumps and making short harsh calls while cocking the tail. The male was once observed to preen the feathers on the female's back. The female seemed to be the initiator of the coupling. She flew up to the male with soft chirring calls, swinging her tail horizontally, fluffing out her feathers and pulling down her wings slightly, whereupon the male mounted her. Two mounts occurred for approximately 5–6 seconds during the first coupling. One mount was recorded during each of the other two couplings. The male was not observed to feed his mate prior to copulation; however, we once observed the partners of this same couple touching bills and passing a small berry or fruit stone from one to another without mating.

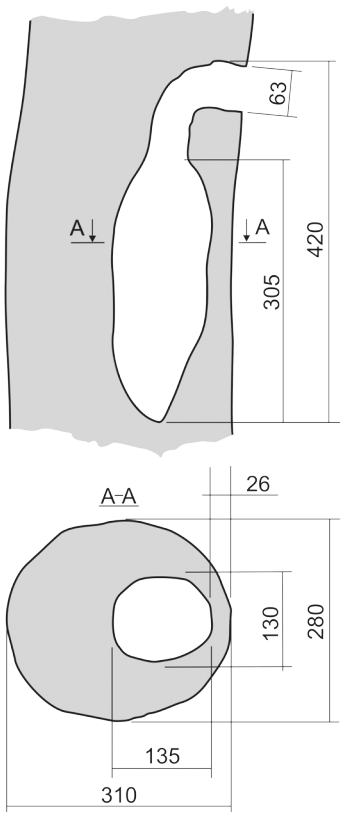

Fig. 1. Longitudinal and transversal sections of the nest of the red-vented barbet. All distances are given in millimetres (mm). "A" stands for the level of the transversal section.

Communication between the mates was relatively extensive. Both the couple caring for Nest No. 1 and the couple caring for Nest No. 2 were regularly observed to spend approximately 30–40 min near each other, especially in the afternoon, before going to the roost. Mates were typically observed to sit calmly side-by-side or to move for short distances in the same tree crown until one of the birds left its partner to spend the night in the nesting hole. This departure occurred from 17:40 to 18:25, depending on weather and lighting conditions.

Upon entering the nest, the parent remained seated near the entrance with its head out, surveying the surroundings for 5–15 min before disappearing inside the hole. In the morning, the parent left the nest at 05:20–05:25.

We were unable to differentiate the contribution of the male and the female to the nestlings' provisioning, but both parents reliably participated in the feeding of their brood in Nests No. 1 and 2. Occasionally, the two mates met at the hole entrance, or one of them had to wait in the vicinity until the second mate left the nest.

Upon bringing the food, the parents typically sat for 5–7 seconds in the crown of the nesting tree or a nearby tree to look around and sometimes manipulated the food by mashing it. Only rarely did they fly directly to the hole without delay. The parents went completely inside the hole to feed the nestlings.

At midday, from 12:00 to 14:00, several of the parents' arrivals with food (no more than three times in one day) resulted in a prolonged (up to 10 minutes and more) period of surveillance from the usual observation site, with the food in its beak. Often, the bird then swallowed the food and flew away without visiting the nest.

We did not have the opportunity to observe any cases of nest defense or any territorial contacts between the parental couple and other birds.

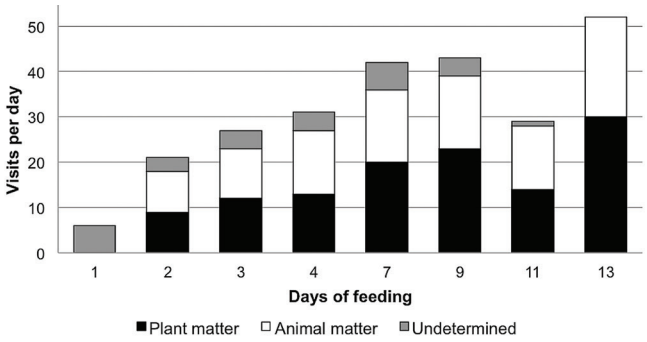

Fig. 2. Proportions of plant and animal food in the diet of the red-vented barbet nestlings during the early nestling period.

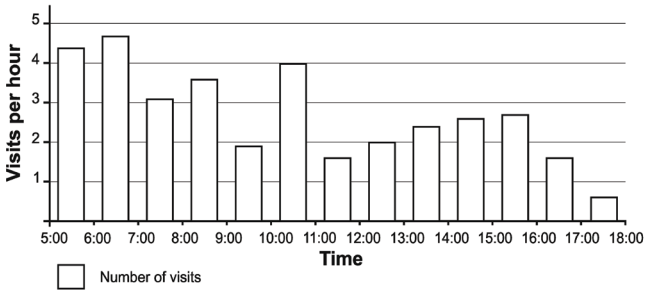

Fig. 3. Frequency of parental feeding visits during the early nestling period (average for seven days of observation, from 2nd to 13th day of feeding) in the red-vented barbet.

Nestling provisioning and nest sanitation. Data on the parental provisioning of the brood during the early stage of the nestling period were obtained from Nest No. 2. The first visits with food were observed on 7 April (presumably the day of hatching of at least one nestling) in the afternoon between 15:00 and 17:20. During this period, the parents returned a few times with very small, unidentified food items held in their bill tips. Prior to this time on both this day and the day before, both mates were regularly observed near the nest and periodically entered the hole without food, with clean and dry bills. Beginning from the second day of feeding, the nestlings reliably received fruit, among other food items, and the proportion of plant matter in the food increased gradually as the nestlings grew (Fig. 2). During the following days, the parents brought food more frequently and in greater quantities, passing on larger insects and fruit or carrying 3–4 medium-sized fruit at once or up to 10 small berries. During the first four days of feeding, the parents mashed the food intensively, so that it was sometimes hardly identifiable by the observer. Starting from the seventh day, however, the fruit and insects were fed whole to the nestlings. Larger insects were killed by squeezing them in the bill or by striking them against tree branches. On the eleventh day of feeding, the parents twice brought vertebrates (medium-sized lizards) to the nest.

The frequency of brood provisioning increased as the nestlings developed, reaching a value of 52 visits per day (on the thirteenth day of feeding). The nestlings were fed throughout the day, with two intensity peaks (when parents brought food every 4–7 minutes) in the early morning and in the afternoon at approximately 15:00–16:00, in addition to a short increase in intensity at approximately 11:00 (Fig. 3).

Plant food included fleshy fruits (Fig. 4C, D), primarily figs; at least five varieties of *Ficus* spp. (Moraceae) fruits with an approximate diameter of 10 to 25 mm were recognised on photographs. Other fruits identified belonged to *Litsea cubeba* (Lauraceae), diameter 8–10 mm; *Campylospermum serratum* (Ochnaceae), diameter 14×18 mm; *Cinnamomum* sp. (Lauraceae), diameter 12×25 mm; and *Knema* sp. (Myristicaceae), diameter 23×38 mm. The inflorescences of the liana *Wrightia* sp. (Apocynaceae) were also brought occasionally.

The animal food brought to the nest consisted of diverse arthropods (Fig. 4E, F): beetles (Coleoptera: Scarabaeidae: Lucanidae: Elateridae – *Campsosternus* sp.) up to 40 mm in length; large flying termites (Isoptera: Termitidae) up to 25 mm; large cicadas (Hemiptera: Cicadidae) up to 30–40 mm; a carpenter bee *Xylocopa* sp. (Hymenoptera: Apidae) 40–45 mm in length; large wasps (Hymenoptera: Vespidae) up to 30 mm in length; a robber fly (Diptera: Asilidae) 35 mm in length; bush cricket *Zabalius* sp. (Orthoptera: Tettigoniidae) 50 mm in length; and large spiders (Aranei: Heteropodidae) up to 30 mm in length.

Vertebrate prey consisted of lizards of the family Agamidae: the spotted flying dragon *Draco maculatus* (head-body length approximately 80 mm) and the Gunther's bloodsucker *Bronchocela smaragdina* (head-body length approximately 130 mm) (Fig. 4B). We once observed a parent's unsuccessful attempt to catch a striped tree skink *Lipinia vittigera* climbing the tree bark above the nest hole.

The data on nestling provisioning in Nest No. 1 were less substantial. The food brought to the nest also consisted of fleshy fruits (figs, *Litsea cubeba* and *Campylospermum serratum* berries); large insects such as a mantis (Mantodea: Mantidae) and a stick-bug (Phasmatodea); and a gecko *Cyrtodactylus irregularis* (Sauria: Gekkonidae) with a head-body length of approximately 90 mm.

The removal of fecal masses from Nest No. 2 was observed for the first time on the fourth day after the beginning of feeding; the parents carried excrement away twice per day, dropping it some distance from the nest. Waste removal occurred three times on the seventh day of feeding, nine times on the ninth day and eight times on the eleventh day. On the thirteenth day, the parents made 17 flights with waste and 52 flights with food, so the ratio of feeding to sanitation visits was approximately 3:1. The parents sometimes discarded fruit stones or uneaten fruit. The waste was typically removed during departure after feeding, but the parents periodically made special sanitation visits.

Nestling description. Two nestlings from Nest No. 2 were examined on the fourteenth day after the start of feeding. They were similar in size and developmental stage, indicating that they had hatched more or less simultaneously.

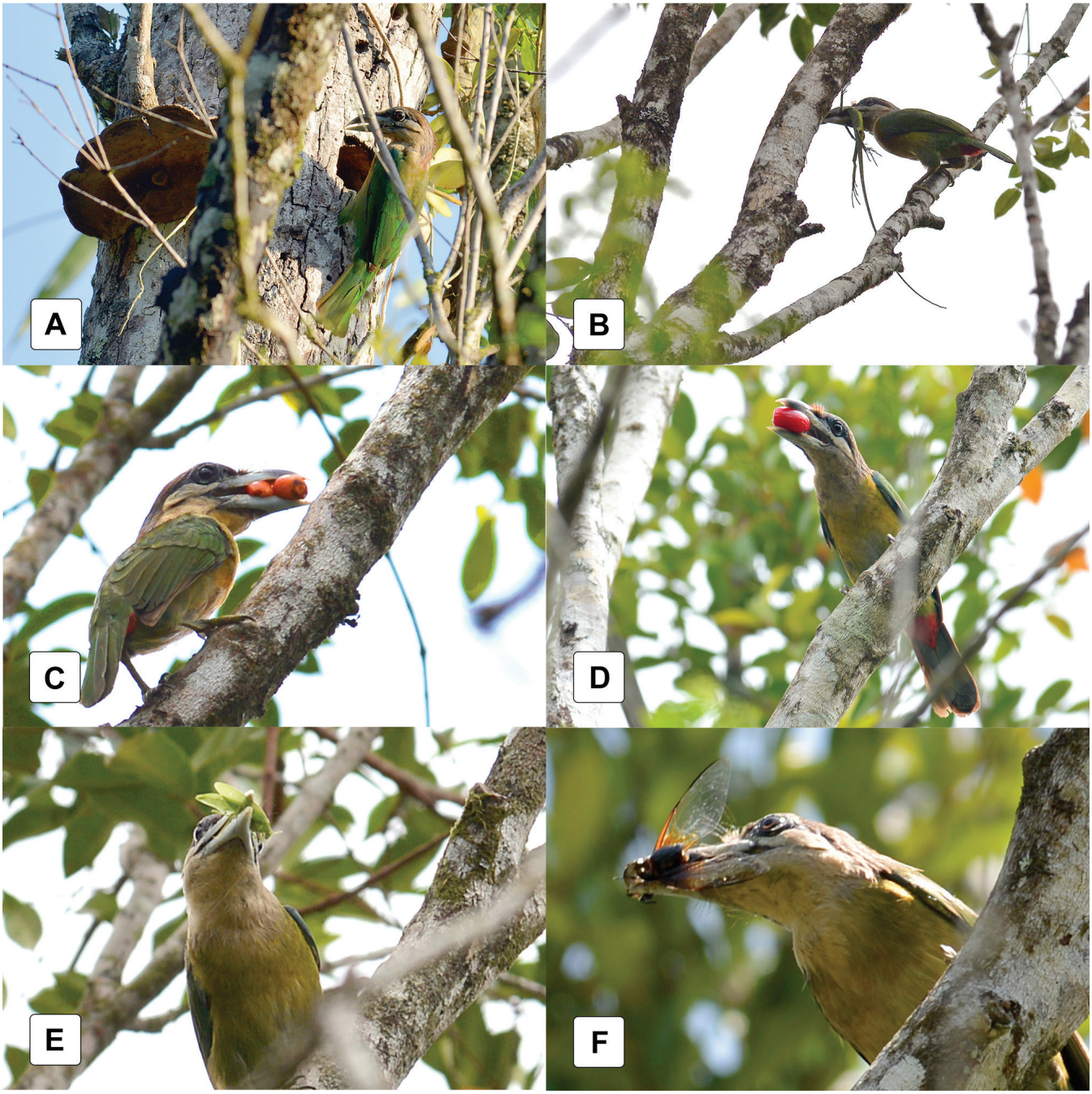

Fig. 4. A, Parent red-vented barbet on the nesting hole. B–F, with different food items: B, lizard *Bronchocela smaragdina*; C, figs; D, fruit of *Knema* sp.; E, bush cricket *Zabalius* sp.; and F, cicada.

The nestlings (Fig. 5) were mostly naked with a well-developed hypodermic fat layer. The acoustic meatuses were opened, and the eyes were slightly opened forming narrow slits in the slightly larger nestling (ABV-00217) and were closed in the smaller nestling. The average length of the primary flight pin feathers was 9.1 mm, that of the secondary flight pin feathers was 6.9 mm and that of the tail pin feathers was 3.5 mm. The maximal pin feather length for the dorsal, flank, head and neck pterylae was 1.5 mm each. The maximal length of bristles on the bill base was 4.0 mm. The principal nestling measurements were the following for the first/second nestling, respectively: total length 157.0/157.0 mm, weight 106.0/93.0 g, wing length 44.0/37.2 mm, wingspread 165.0/160.0 mm, tarsus length 36.9/34.8 mm, head length 55.9/49.9 mm, bill length 22.0/21.8 mm, bill height 11.6/11.4 mm, and bill width 16.5/15.1 mm.

At this stage, the nestlings were unable to hold their heads up and could crawl slowly on a flat surface. The first vocalisation (quiet cheeping) was heard near the nest beginning from the seventh day after the start of parental provisioning.

Several parasitic or commensal arthropods were discovered in the nesting cavity and on the nestlings' skin: tiny mites (Acari, Mesostigmata), imagoes and puparia of unidentified flies (Diptera) and booklice (Psocoptera).

Fig. 5. Fourteen-day-old nestling of the red-vented barbet.

DISCUSSION

The principal traits of the reproductive biology and parental behavior of the red-vented barbet appear to be similar to those of other studied *Megalaima* species.

Nesting period. Stepanyan (1995) noted that in southern Vietnam, the testes of the male red-vented barbet begin to enlarge in January and reached their maximal size between March and May. He reported on one female with a brood patch at the end of April and noticed that adults carrying food were regularly observed in May and June. According to our year-round observations in Bu Gia Map National Park (Binh Phuoc Province), parents carrying food were recorded starting from the beginning of April. In Loc Bac region in April 2012 and 2013, we recorded two other Asian barbets provisioning nestlings at the same time as the red-vented barbet: the blue-eared barbet (three nests) and the Indochinese barbet *M. annamensis* (two nests).

Nest construction and nest site selection. Like other *Megalaima* species, the red-vented barbet is a primary cavity nester: our observations are the first to confirm that this species is able to bore the holes by itself in dead wood. Previously, the form of the nesting cavity has been described in detail only for the white-cheeked barbet, crimson-fronted barbet (Yahya, 1988, 2001) and blue-eared barbet (Trounov & Vasilieva, 2012). The nest of the red-vented barbet closely resembles the nests of these species because of its deep bottle-shaped cavity with a narrow, bent access tunnel.

Several factors appear to be of great importance for nest site selection in this species. Given the location of all observed nesting trees, their relatively open exposure seems to be crucial. The diameter of the trunk of the nesting trees of Asian barbets is apparently correlated with the size of the bird (Yahya, 2001; Trounov & Vasilieva, 2012). According to our data, the mean diameter of nesting trees in southern Vietnam is 162 mm (n=9) for the small-sized blue-eared barbet (Trounov & Vasilieva, 2012) and 375 mm (n=6) and 360 mm (n=4) for the larger green-eared barbet and lineated barbet, respectively (Trounov, pers. obs.). The relatively large red-vented barbet nests in trees with a mean diameter of 387 mm (n=3). The mechanical properties of the substrate are also most likely important. The wood hardness of the red-vented barbet's nesting tree was approximately three or four times lower than the hardness of balsa wood (maximal value 1.6 kgF mm^{-2}), the lightest and softest wood known. Because barbets are known to be less specialised for pecking than woodpeckers (Trounov et al., 1996), it is probable that they are only able to bore holes in a relatively soft substrate.

Brood size, brood number and nestling development. Limited data do not allow us to estimate the typical brood size of the red-vented barbet and the brood number in one reproductive season; for other *Megalaima* species studied, clutches numbering 1–4 eggs have been recorded, and broods of one or two nestlings are rather common (Yahya, 2001; Short & Horne, 2002; Lin et al., 2010; Trounov & Vasilieva, 2012). Data on the brood number per season for Asian barbets are very scarce; however, Yahya (2001) reports a second brood for several observed pairs of crimson-fronted and white-cheeked barbets. The data of Lin et al. (2010) on the Taiwan barbet and our observations on blue-eared barbet (Trounov & Vasilieva, 2012) also indicate that these species may nest more than once per year. The repeated copulation observed in the red-vented barbet couple caring for Nest No. 1 plausibly indicates that the mates were ready to start a new nesting cycle after the expected fledging of their single nestling, which was in a rather advanced developmental stage at the time of its death.

Among Asian barbets, a brief description of the nestlings and their development is available only for the white-cheeked and crimson-fronted barbets (Yahya, 2001). The 14-day-old nestlings of the red-vented barbet are rather similar in developmental state to the 12 to 15-day-old nestlings of both these Indian species with regard to eye opening, vocalisation and bristle growth, but are slightly behind in plumage development: the feathers on the head, wings, shoulders and tail are well developed, and their brownish or greenish coloration is already clearly discernible, in the 12-day-old white-cheeked barbet, but only pin feathers are present on the head and body in the 14-day-old red-vented barbet. This delay in development plausibly indicates that the red-vented barbet has a somewhat longer nestling period. According to the existing data, the larger species of Asian barbets tend to have a more prolonged nestling period than the smaller ones, e.g., 23–29 days in the Taiwan barbet (Lin et al., 2010), 33–36 days in the blue-eared barbet (Trounov & Vasilieva, 2012), 35–37 days in the crimson-fronted barbet, 36–38 days in white-cheeked barbet (Yahya, 2001) and the green-eared barbet (Trounov, unpublished observations), and more than 38 days in the largest Asian barbet species, the great barbet *M. virens* (Short & Horne, 2002). As the red-vented barbet is one of the largest *Megalaima* species, its nestling period may also be relatively long.

Brood provisioning. The feeding of the brood in frugivorous birds is of particular interest. If the low energy value of fleshy fruit may be compensated by the abundance of this resource

and the ease of access to it, the low protein content of the food is considered to be the principal limiting factor for fruit-eating birds (Morton, 1973; Bosque & Pacheco, 2000; Levey & del Rio, 2001). The resulting protein deficiency may substantially affect the growth and development rate of the nestlings, especially in early stages of feeding (Morton, 1973). Even highly specialised frugivorous species often feed their brood with animal food. For example, the Neotropical barbets *Eubucco* spp., with a mixed diet that consists of fruit and arthropods (Remsen et al., 1993), feed their broods exclusively with insects, at least during certain developmental stages (Worth, 1938), and the strictly frugivorous toucan-barbets *Semnornis* spp. (Remsen et al., 1993) begin feeding their brood with insects and then gradually add fruit to the nestlings' diet (Skutch, 1944). The same tendency has been shown for toucans, which are highly specialised fruit-eaters closely related to Neotropical barbets: the Aracaris *Pteroglossus* spp. also begin to feed their nestlings only with insects, and the proportion of fruit fed increases over the fledging period (Skutch, 1958). In contrast, the diet of the nestlings of the white-cheeked barbet, crimson-fronted barbet and blue-eared barbet includes plant matter from the initial stage of feeding, although the proportion of animal matter is relatively higher during the early nestling period and decreases gradually during later stages (Yahya, 2001; Trounov & Vasilieva, 2012). Similarly, the red-vented barbet nestlings reliably consumed fruit from at least the second day of feeding, and the proportion of plant matter in the food increased stably from the early to middle feeding stages (Fig. 2) except for the eleventh day, when the provision of large vertebrate prey changed the habitual feeding routine. In the red-vented barbet, the proportion of animal matter in the nestlings' diet is relatively high (approximately 40–45%, not including undetermined food) if compared with other studied *Megalaima* species: approximately 25% in the white-cheeked barbet and 2% in the crimson-fronted barbet (Yahya, 2001), 27% in the Taiwan barbet (Lin et al., 2010) and 15% in the blue-eared barbet (Trounov & Vasilieva, 2012) in the middle of the nestling period. Insects and spiders are common food items in the barbets' brood diet (Lin et al., 2010; Trounov & Vasilieva, 2012), but the feeding of 11-day-old nestlings with relatively large reptiles was rather surprising. Apparently, reptiles represent a regular part of the red-vented barbet nestlings' diet because two pairs were observed to bring lizards to the nest.

It is agreed that the high proportion of protein-poor plant matter in the nestlings' diet causes the retardation of brood development and the prolongation of the nestling period in frugivorous birds (Morton, 1973). Moreover, development tends to be longer in cavity-nesting birds (especially excavators) than in open-nesting species (Snow, 1962; Morton, 1973; Martin & Li, 1992). However, in woodpeckers, which feed their brood with animal food, the nestling period rarely exceeds 24–27 days (Martin & Li, 1992; Winkler & Christie, 2002), whereas it usually lasts more than 30 days in Asian barbets. Hence, the extremely long development of barbets, especially in large species, is presumably caused not only by the general evolutionary trend in cavity-nesters associated with a lower risk of nest failure (Martin & Li, 1992), but also with the mixed diet of the nestlings.

In the Asian barbets whose nesting biology has been studied, activities associated with brood care are normally performed by both mates (Yahya, 2001; Short & Horne, 2002; Lin et al., 2010; Trounov & Vasilieva, 2012). The participation of both mates is apparently crucial for a successful nesting cycle, especially because of the high frequency of parental provisioning visits (up to >4 times per hour, on average, during the middle nesting period) and frequent nest sanitation. Our limited observations of the red-vented barbet also showed that both parents participated in brood care, at least in feeding the nestlings.

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