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BREEDING BIOLOGY OF THE HILL SWALLOW *HIRUNDO DOMICOLA* IN WESTERN GHATS, INDIA

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The breeding biology of Hill Swallow *Hirundo domicola* – which has been previously considered as a subspecies of Pacific Swallow *Hirundo tahitica* – was studied from 2002 to 2005 in Silent Valley National Park and Muthikkulam Reserve Forests, Western Ghats, India. Nesting of the species was observed from November to April with peak egg-laying during February-March. Nests were placed in the walls of tunnels/culverts and on the roofs of buildings. The clutch size averaged 2.44 eggs, and was found to be low in nests placed in buildings (2.07 eggs) compared to those in tunnels/culverts (2.71 eggs). Average incubation period was 15.78 days and nestling period was 19.1 days. Nest attentiveness and duration of the on- and off-bouts increased with the progress of incubation. Nesting success rate was higher than the average of tropical species but lower than the temperate hirundines. The main known causes of nest failure were predation and nest falling. In general, many life history traits (including clutch size, developmental periods and parental care) of *H. domicola* varied from its conspecific House Swallow *H. tahitica*, and thus support the recent separation of it as a distinct species.

Keywords: breeding biology, Hirundinidae, *Hirundo domicola, Hirundo tahitica*, life history, parental care, tropics

INTRODUCTION

The Family Hirundinidae includes *c*. 84 species of passerines widely distributed in both temperate and tropical habitats (Turner and Rose 1989; Turner 2004). These birds are highly aerial and exclusive insectivores (Turner 2004). Little is known of the biology and ecology of many hirundines, especially tropical species. But several temperate species like Barn Swallow *Hirundo rustica*, Cliff Swallow *Petrochelidon pyrrhonota* and Tree Swallow *Tachycineta bicolor* are well-known and used as models in a large number of ecological studies (see reviews in Turner 2004). Available information on the reproductive traits of hirundines that breed in the tropics shows significant variation from the typical traits of tropical birds (Hails 1984; Ali and Ripley 1987; Turner 2004). Many of them have large a clutch size and longer developmental periods compared to that of temperate birds (Ali and Ripley 1987; Turner 2004).

Pacific Swallow *Hirundo tahitica* (Ali and Ripley 1987; Grimmett *et al.* 1999) is one of the 17 hirundines occurring in South Asia (Rasmussen and Anderton 2005) and constitute two disjunctly distributed subspecies (*Hirundo tahitica javanica* and *Hirundo tahitica domicola*). Based on the morphological, vocal and ecological differences, these subspecies were recently recognised (Rasmussen and Anderton 2005) as two distinct species, namely House Swallow *Hirundo tahitica* and Hill Swallow *Hirundo domicola*. The House Swallow is a common bird known from Andamans, Myanmar, Malay Peninsula and Indonesia (Ali and Ripley 1987; Turner 2004). Hill Swallows are sedentary residents distributed in the grassy slopes around plantations and human habitation in southern Western Ghats (from south Karnataka through Nilgiris and Kerala) and Sri Lanka from 700-2,400 m (Ali and Ripley 1987; Turner 2004; Rasmussen and Anderton 2005). Jathar and Rahmani (2006) also listed Hill Swallow as one of the birds endemic to the South Asian mainland and Sri Lanka. The breeding biology of House Swallow has been well-studied in Malaysia (Hails 1984). However, relatively little is known about Hill Swallows except for the descriptions of breeding seasonality, nests and clutch size (Ali and Ripley 1987; Turner 2004).

This paper describes the breeding biology and life history of Hill Swallow and compares this information with the available data for House Swallow and other hirundines. Aspects considered include timing of breeding, nest-site characteristics, nest measurements, clutch size, developmental periods, growth rates, parental care strategies, nesting success and causes of nest failures.

STUDY AREA

Data were collected from two study areas: in Silent Valley National Park (11º 00'-11º 15' N; 76º 15'-76º 35' E; area: 89.52 sq. km, hereafter: Silent Valley) during January 2003 to May 2005, and Muthikkulam Reserve Forest (10º 56'-10º 59' N; 76º 41'-76º 45' E; area: 63.83 sq. km, hereafter: Muthikkulam) during September 2002 to April 2004. Both the sites are located in the south-western corner of the Nilgiri Biosphere Reserve in the Western Ghats of India. In both the areas, the terrain is undulating and hilly, with elevation ranging from 658 to 2,383 m above msl at Silent Valley, and 610 to 2,065 m above msl at Muthikkulam. Both sites are similar in vegetation types, dominated by the west coast tropical evergreen forest followed by the southern montane wet temperate forest, and grasslands restricted mainly to the higher slopes and hill tops (Nair and Balasubramanyan 1985; Basha 1999; Balakrishnan 2007). Both sites experience similar and typical tropical climate, with mean annual temperature below 27°C and mean annual rainfall above 4,500 mm. However, the north-east monsoon is slightly heavier in Muthikkulam compared to that of Silent Valley. In Silent Valley, the breeding sites were found in the remnants of the abandoned hydro-electric project (tunnels and buildings) at Sairandhri. The study site at Muthikkulam included the surroundings (about 5 sq. km) of the Siruvani dam with several abandoned and partially occupied (by officials of forest and irrigation departments) buildings, tunnels and culverts.

METHODS

Nests were located by following the activities of adult birds (regular to and fro movement to probable breeding sites, carrying food or nest materials, etc.) or by searching potentially suitable habitats (building, culverts, tunnels, etc.). Once found, contents of the nests were checked using a mirror and torch on a pole. Nests were inspected every 1-2 days or everyday during the transition of nesting stages with the help of field assistants to determine the breeding phenology and nest fate. Clutch initiation dates were determined either by direct observation of egg laying or by calculations made using known hatching dates and mean developmental periods. Clutch size was measured as the final number of eggs laid and duration of developmental period was calculated based on visual inspection of nests. Seven chicks from three nests were weighed on alternate days (from day 1 to 19) using Pesola spring balances to determine the growth rates. After nest success or failure, height of the nest above ground, nest measurements such as nest diameter, cup diameter, outer nest depth and cup depth were recorded, and nest thickness based on standard methods was calculated (Soler *et al.* 1998).

To assess parental care patterns and nest attentiveness, the birds' incubation behaviour during early (1-8 days) and late incubation (9-16 days) period by hourly watches at nests following standard methods (Nolan 1978; Halupka 1994; Norment 1995) was measured. Day-light hours (6:00 to 18:00 hrs) were divided into four sections (06:00-09:00, 09:00-12:00, 12:00-15:00 and 15:00-18:00 hrs) and observations were made in each section to control for variation in incubation behaviour during the day (Nolan 1978; Smith and Montgomerie 1992; Conway and Martin 2000a). The parameters measured or calculated were nest attentiveness (per cent time spent on the nest incubating eggs), on-bout duration (mean incubation bout duration in minutes) and off-bout duration (mean time spent away between two incubation visits in minutes) based on standard methods (Kendeigh 1952; Conway and Martin 2000a). Similarly, provisioning rates (number of feeding visits/hr) during early (1-6 days), mid (7-13days) and late (14-19 days) nestling periods were also recorded by hourly watches at nests. The total observation period was 133 hrs, which include 114 hrs during incubation and 19 hrs during nestling period. As the birds were not colour-marked or sexed, data presented are combined parental investment of both males and females.

Nests that produced at least one fledgling were considered as successful nests. Hatching, nestling and breeding success were defined as: the probability that eggs laid would hatch, the probability that hatchlings would fledge, and the probability that eggs laid would survive from laying to fledging, respectively. Daily nest survival and nest success rates were calculated based on Mayfield method (Mayfield 1975). Daily nest survival and nest success rates were calculated separately for the reproductive phases, study sites and substrate types. Standard errors for survival rates were calculated based on the methods described in Johnson (1979). All tests were two tailed, and differences were considered significant at $p < 0.05$. Mean ±SD values are reported throughout. All statistical analyses were performed by using SPSS 10.0 (SPSS Inc.).

RESULTS

Timing of breeding

A total of 36 Hill Swallow nests during 2002 to 2005 were located and monitored; 21 nests in Silent Valley and 15 nests in Muthikkulam. In Muthikkulam, the earliest first egg-laying date was November 23 (November 23 and February 06 for 2002-03 and 2003-04 breeding seasons, respectively), while it was February 09 (February 12, February 18, and February 09 for 2003, 2004 and 2005 breeding seasons, respectively) in Silent Valley. Except for three nests observed at Muthikkulam during November-December 2002, all the nesting attempts were during February-April and peak egg-laying occurred during February-March at both sites (Fig. 1).

Nests and nest sites

All the breeding sites were located within an elevation

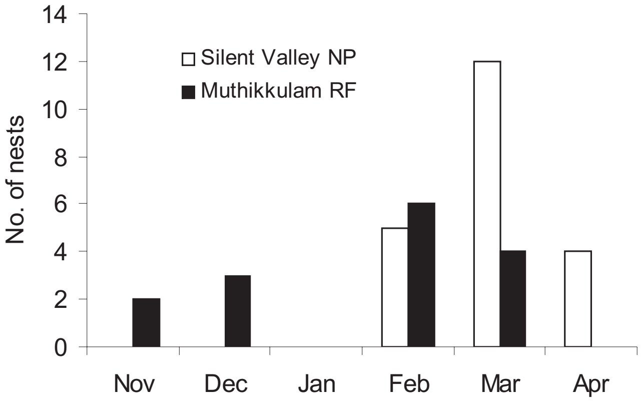

Fig. 1: Timing of monthly clutch initiation (n = 36) from early November to late May 2002-2005, for Hill Swallows at Silent Valley National Park and Muthikkulam Reserve Forest

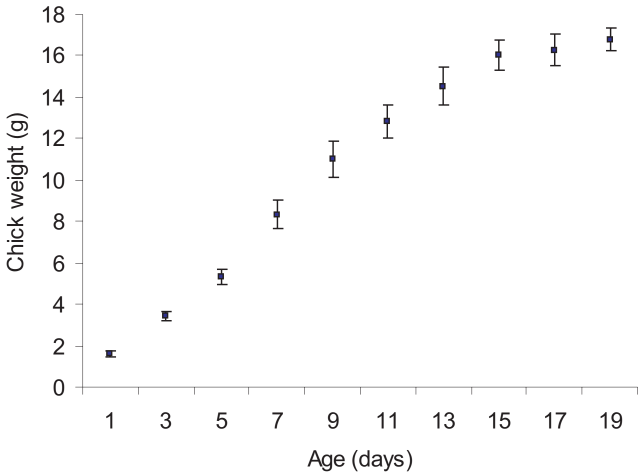

Fig. 2: Growth rate (mass) of Hill Swallow nestlings as a function of age

range of 800 to 1,200 m above msl. Of the 36 nests examined in this study, 17 were built on rock surfaces (under overhangs) in man-made tunnels, four on the wall of culverts and 15 on roofs of abandoned buildings. All the nests placed on buildings were single nests, but the nest sites in tunnels and culverts also comprised of small colonies of 3-5 nests. All the nests were cup-shaped (nest diameter: 11.43 ±0.72 cm, cup diameter: 8.59 ±0.71 cm, outer nest depth: 7.84 ±0.71 cm, cup depth: 5.2 ±0.72 cm, nest thickness: 1.42 ±0.32 cm) made with mud pellets as major structural constituent. Dried grasses, moss, pteridophyte roots and lichens were also used in the structural layer, mostly in nests placed in tunnel/culvert sites. The amount of these materials was considerably minimal in the nests placed in buildings. However, in the building sites, the mud cups were supported by a mud foundation built in the lower portion of the ceiling beams. These foundations were made with powdery mud (different from the material of the cup) which has terracotta-like hardness upon drying. Feathers were used as the inner lining layer in all nests. Addition of feather was also observed during the early incubation stage. Both sexes participated in the nest construction and birds often reused old nest sites with certain amount of repair. Time required for nest construction was not estimated because majority of the nests were found during the late construction period or other reproductive stages. We observed a pair take seven days to repair an old nest at a building site.

Nest morphometry significantly varied between the nesting substrates (building vs. tunnel/culvert nests) and between nests with different clutch sizes (Table 1). The nests were placed 2.06 ±0.39 m above ground (range: 1.58-2.7 m). Nest heights significantly varied between the building sites (2.49 ±0.20 m, range: 1.9-2.7 m, n = 15) and tunnel/culvert sites (1.76 ±0.09 m, range: 1.58-1.9 m, n = 21) (t = -14.64, p < 0.001). All the nest sites were in the vicinity of water (<15 m).

Clutch size, developmental periods and growth rates

The mean clutch size was 2.52 ±0.51 in Silent Valley (n = 21) and 2.33 ±0.49 in Muthikkulam (n = 15), while for all clutches together it was 2.44 ±0.5 (20 nests with 2 eggs and 16 nests with 3 eggs). Clutch size was significantly smaller in building nests (2.07 ±0.26 eggs, n = 15) than in tunnel/culvert nests (2.71 ±0.46 eggs, n = 21; t = 4.89, p < 0.001).

Table 1: Measurements of Hill Swallow nests

Nest size variables	Tunnel/culvert nests N = 13	Building nests N = 9	*F*	*P*	Nest with two eggs N = 11	Nest with three eggs N = 11	*F*	*P*
Nest diameter (cm)	11.78 ±0.59	10.92 ±0.58	11.544	0.003	10.90 ±0.53	11.96 ±0.42	27.139	0.001
Cup diameter (cm)	8.79 ±0.75	8.30 ±0.57	2.763	0.112	8.23 ±0.67	8.95 ±0.57	7.547	0.012
Outer depth (cm)	8.25 ±0.39	7.24 ±0.66	20.546	0.001	7.34 ±0.63	8.35 ±0.33	21.994	0.001
Cup depth (cm)	5.73 ±0.34	4.43 ±0.23	99.047	0.001	4.61 ±0.44	5.79 ±0.33	49.911	0.001
Nest thickness (cm)	1.50 ±0.34	1.31 ±0.28	1.793	0.196	1.34 ±0.36	1.50 ±0.28	1.512	0.233

Table 2: Breeding parameters of Hill Swallows at Silent Valley National Park and Muthikkulam Reserve Forest

Parameter	Silent Valley	Muthikkulam	Pooled
No. of eggs	53 (21)	35 (15)	88 (36)
No. of hatchlings	36 (15)	17 (8)	53 (23)
No. of fledglings	26 (10)	13 (6)	39 (16)
Hatching success (%)	67.92	48.57	60.23
Fledging success (%)	72.22	37.14	73.58
Breeding success (%)	49.06	37.14	44.32
% of successful nests	47.62	40.00	44.44

Values in parentheses are number of nests

The average length of incubation period from laying the last egg to hatching was 15.78 ±0.97 days (range: 14-17 days, n = 9 nests). The mean duration of on- and off-bouts in early incubation (1-8 days) was 11.89 ±5.88 min (range: 2-28 min, n = 60 hrs) and 16.89 ±7.95 min (range: 2-41, n = 60 hrs), and during late incubation (9-16 days) was 18.46 ±7.74 min (range: 5-43 min, n = 54 hrs) and 21.07 ±9.32 min (range: 2-58 min, n = 54 hrs), respectively. Nest attentiveness averaged 39.64% (n = 60 hrs) on early incubation and 55.77% (n = 54 hrs) during late incubation.

Hatching was synchronous in all nests monitored. The number of nestlings in a brood averaged 2.3 ±0.47 (n = 23 nests) and they reached a peak mass of 16.79 ±0.57 gm (n = 7 nestlings) on day 19 (Fig. 2). The average nestling period from the hatching to first leaving of the fledglings from the nest was 19.1 ±0.88 days (range: 18-21 days, n = 10 nests). Both male and female birds fed the young ones simultaneously. Provisioning rates during early (1-6 days), mid (7-13 days) and late (14-19 days) nestling days were 7.67 ±2.73 (n = 6 hrs), 14.33 ±2.16 (n = 6 hrs), 20.19 ±2.87 (n = 7 hrs) trips/hr, respectively. The total nesting period (incubation and nestling periods together) was 34.75 ±1.67 days (range: 33-38, n = 8 nests). The juveniles returned to the nests with parents for roosting for about 6.5 ±1.29 days (range: 5-8 days, n = 4 nestlings) after first leaving of the nest.

Nesting success and causes of mortality

Of the 36 nests monitored during this study, 16 (44.44%) successfully fledged young, on average, 2.44 ±0.51 young per successful nest. Hatching (% eggs hatched), fledging (% hatched chicks fledging) and breeding success (% eggs fledged) for all nests monitored were 60.23%, 73.58% and 44.32%, respectively. Hatching and fledging success rates considerably varied between study sites (Table 2). Daily survival rates significantly varied between the different reproductive stages and between the nesting sites (Table 3). Chick survival rates were slightly higher than the egg survival rates (Table 3), and breeding failures during chick-rearing occurred when the chick was, on average, 4.33 ±1.86 days old (range: 3-8 days). The overall Mayfield nest success rate for all nests monitored was 26.07%. There was not much variation in the Mayfield nest success rates between study sites: 27.66% in the Silent Valley and 24.05% in the Muthikkulam. However, Mayfield success rates varied significantly between nesting sites: from 18.7% in the tunnel/culvert nests to 37.42% in the building nests (Table 3).

Fourteen (70%) of the 20 nest failures were due to the predation of eggs (10 nests) and nestlings (4 nests). The identity of predators could be recognized in only one nest, in which the Indian Garden Lizard *Calotes versicolor* consumed the entire contents of the nest during incubation stage. Four nests failed due to the nest falling during the early incubation stage. Nestlings of two nests were also lost due to the attack of red ants. No infanticide, egg or nestling desertion, starvation, partial egg or brood loss and brood parasitism were observed during the study.

Table 3: Daily nest survival rates and nest success of Hill Swallows for different reproductive phases, study locations and nesting sites in Western Ghats

	Exposure days	No. of nests	No. of nests failed	Daily nest survival (±SE)	% nest success
Reproductive phases (all data pooled)					
Incubation	273	36	13	0.952 ±0.013	46.31
Nestling	254	23	7	0.972 ±0.010	58.64
Overall nesting	527	36	20	0.962 ±0.008	26.07
Study locations					
Silent Valley	303	21	11	0.964 ±0.011	27.66
Muthikkulam	224	15	9	0.960 ±0.013	24.05
Nesting sites					
Tunnel/culvert	276	21	13	0.953 ±0.013	18.70
Building	251	15	7	0.972 ±0.010	37.42

DISCUSSION

Hirundines show significant geographic variation in the timing of breeding. In subtropics and tropics nesting is limited to the wet season when insects are most abundant or can occur almost throughout the year, sometimes with peaks during rains (Turner 2004). Majority of the species in India breed chiefly during March-July (Ali and Ripley 1987). In Silent Valley, breeding of Hill Swallows is restricted to the dry season (February-April) which is consistent with the records (March-May) of Ali and Ripley (1987) from southern India. In Muthikkulam, a few nests were recorded in November-December and this indicates the start of early breeding in this site as reported (December-June) for Sri Lanka (Ali and Ripley 1987). It is not clear whether the heavy north-east monsoon in Muthikkulam compared to Silent Valley is associated with the early breeding of Hill Swallows at this site. Due to the preference of elusive sites for nest placement, it is likely that a few nests went undiscovered during this study. However, no recently used nests were found in the tunnels/culverts or buildings examined. Significant regional variation in the timing of breeding was also reported for conspecific *H. tahitica* (Andamans: May-June, Myanmar: March-May, Malaysia: January-August, Philippines: July-October) (Hails 1984; Ali and Ripley 1987; Turner 2004). Thus, further studies are required to understand the factors (including abundance of insects, rainfall, etc.) resulting in the geographic variation in the timing of breeding of Hill Swallows.

Most species of swallows are known to use artificial structures for roosting and nesting, and this feature has given new opportunities for population expansion and range expansion in many species (Hails 1984; Ali and Ripley 1987; Oatley 2002; Jackson and Spottiswoode 2004; Turner 2004). Hill Swallows are also known to attach their nests to a variety of structures including wall or rock-face, under road culverts or in tunnels, and most commonly under eaves or against ceiling beams and rafters in houses (Ali and Ripley 1987). All the nests recorded during this study were also placed in man-made structures (tunnels, culverts and buildings). Nest structure of Hill Swallows is typical to that of other species (see Hails 1984; Ali and Ripley 1987; Turner 2004). The nests built in tunnels/culverts are often larger than the nests in buildings and these nests had larger clutch size compared to the latter. However, this advantage was not reflected in the breeding productivity (Table 3).

Hirundines in the temperate habitats normally lay 3-6 eggs and sometimes up to 8 eggs (Turner 2004), however, the normal clutch size in the tropics is 2-5 eggs (Ali and Ripley 1987; Turner and Rose 1989; Turner 2004). The average clutch size (2.44 ±0.5, mode = 2 eggs) of Hill Swallow is the smallest reported for the swallows breeding in mainland India (*Hirundo rustica*: 4-6 eggs, *H. smithii*: 3-5 eggs, *H. flavicola*: 3-4 eggs, *H. daurica*: 3-5 eggs, *H. striolata*: 3-5 eggs; Ali and Ripley 1987). The mean clutch size of Hill Swallows is also significantly lower than that of the conspecific House Swallow *Hirundo tahitica* in Malaysia (mean = 2.98 ±80 eggs, mode = 3 eggs, range = 2-5 eggs; Hails 1984) and the median clutch size (3.5 eggs) reported for the passerines in India (Ali and Ripley 1987; Pramod and Yom-Tov 2000). In many hirundines seasonal decline of clutch size is reported (Hails 1984; Sakraoui *et al*. 2005; Turner 2004), however, this could be attributed to the late breeding of young inexperienced birds which normally lay small clutches (Turner 2004). Although such seasonal declines are not identified, variation in the clutch sizes between the nesting substrates (tunnel/culverts v/s buildings) is prominent in Hill Swallows.

Estimates of incubation (15.78 ±0.97 days) and nestling periods (19.1 ±0.88 days) obtained in this study are slightly lower than that of *H. tahitica* (Hails 1984), but within the range of general patterns reported for hirundines (Turner 2004). Hirundines are known to grow slowly compared to other passerines (Turner 2004). The growth rate of *H. domicola* was similar to that of *H. tahitica* (Hails 1984) and typical of other hirundines (Turner 2004).

There are some conspicuous differences in the parental care between *H. domicola* and conspecific *H. tahitica*. In the case of latter, only female incubated the eggs (Hails 1984), whereas both sexes of *H. domicola* actively participated in all the breeding activities including nest construction, incubation and feeding young (see also Ali and Ripley 1987). Nest attentiveness (per cent time spent on the nest incubating eggs) was also significantly higher in *H. domicola* (39.64% and 55.77% for early and late incubation periods, respectively) compared to that of *H. tahitica* (36.9%, Hails 1984). High nest attentiveness and male's participation in the incubation could be due the low ambient temperature at the study sites (<27 °C) compared to that of *H. tahitica* nest sites (>30 °C). The length of on- and off-bouts increased by the progress of incubation, which indicates that, the nest trips decreased in the late incubation stage and the longer on-bouts were preceded by long off-bouts and vice-versa. For the entire incubation period, on- and off-bout durations ranged between 2-43 min and 2-58 min, respectively. Similar intra- and inter-specific variations in parental effort are reported for several species (Conway and Martin 2000a) which is attributed by a number of factors such as temperature needs of the developing embryos, nutritional requirements of parents and predation pressure (Conway and Martin 2000a,b; Deeming 2002; Fontaine and Martin 2006). However, it is difficult to decipher the reasons for these variations in Hill Swallow due to low sample sizes, failure to control for the clutch sizes and lack of data on the temporal variations in micro-climate.

As reported for the conspecific *H. tahitica* (Hails 1984), the hatching and fledgling success rates were significantly higher in *H. domicola* compared to other tropical birds (Stutchbury and Morton 2001). However, high hatching (90% or more) and fledgling success (38-80%) rates are commonly reported for most species of hirundines (Turner 2004) and the species build nests in caves and man-made structures (Lack 1954). The overall nesting success (Table 3) calculated based on the Mayfield method was also slightly higher than the average success rates (<23%) reported for tropical species but lower than the temperate (27-60%) species (Robinson *et al*. 2000; Stutchbury and Morton 2001). Nests placed in tunnel/culvert sites experienced more failures compared to the nests in building and this may be due to the apparently high inaccessibility of the nests placed in latter.

Predation at the nests was reported minimal in majority of the hirundine species studied (Earlé 1989; Jackson and Spottiswoode 2004; Turner 2004). However, fourteen of the 20 nest failures of Hill Swallows were characterised by the disappearance of eggs or nestlings. Eggs disappeared from 10 nests (in one instance the broken eggs were found on ground below the nest) and nestling from four nests. The only predation event observed was by the Garden Lizard *Calotes versicolor*, which consumed the eggs from nest placed in a building site. In two nests, the nestlings were found dead due to the attack of red ants. Other potential predators/destructors observed at the breeding sites include snakes (e.g., Indian Rat Snake *Ptyas mucosa*), owls (unidentified species) and several species of bats. Bats (Indian False Vampire Bat *Megaderma lyra*) and lizards (*Gekko gecko* or G*ekko stentor*) are reported as important predators of *H. tahitica* (see Hails 1984). However, further intensive studies using advanced methods (e.g., video surveillance monitoring) are required to identify the nest predators of *H. domicola*. Another major cause of nest failure was the nest falling during incubation, which is commonly reported for several species of hirundines (Hails 1984; Oatley 2002; Jackson and Spottiswoode 2004). Oatley (2002) also noted that the durability of the nests may depend on the quality and composition of the mud used for nest construction. This indicates that the availability of suitable wet mud may be an important factor determining the outcome of breeding in hirundines.

In conclusion, the results of the present study provide further evidence that members of the Family Hirundinidae show substantial variation in the reproductive traits which are apparently atypical of tropical birds (e.g., longer developmental periods). However, the clutch size recorded in this study is the lowest record for the genus. The many differences in the life history traits (clutch size, developmental periods and parental care) enumerated herein also support the recent erection (Rasmussen and Anderton 2005) of *H. domicola* as a distinct species from *H. tahitica*.

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