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Habitat selection theory and cave-dwelling birds: The corollary

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Abstract. Habitat selection, a crucial process of animal life, follows a hierarchical structure of orders ranging from broader (macro) to smaller (micro) scales. It is a multi-scale process that involves both innate and learned behavioural decisions. Different animals, including birds in various habitats, are described in/for the hierarchical orders of habitat selection. The cave-dwelling birds, on the other hand, were never subjected to this. We studied the edible-nest swiftlet (*Aerodramus fuciphagus*) (ENS), as a model species from 79 limestone caves in two ecologically heterogeneous karst areas to test the hypothesis that order-level habitat selection theory applies to cave-dwelling birds, and we found that the ENS follows the hierarchical habitat selection process. The habitat selection at microscales of cave morphology (R^2=0.13, p>0.05) and colony-site is random (R^2=0.42, p>0.05). The birds display strong avoidance of long, wide, and large caves (E=-1). This study is the first to highlight cave-dwelling birds' hierarchical framework of habitat selection. It also provides inputs for sustainable commercial farming of the edible-nest swiftlet.

Key words. cave-dwelling birds, cave morphology, habitat selection theory, order-level selection, conservation implementation

INTRODUCTION

Habitat refers to the physical environment where an organism lives (Hildén, 1965; Krausman, 1999). It encompasses distinct environmental factors, resources, and conditions essential for survival, reproduction, and inhabitation (Block & Brennan, 1993). Selecting a habitat is a critical process in an animal's life (Danchin et al., 1998), involving active decision-making (Krausman, 1999) across multiple spatial scales (Mayor et al., 2009). The habitat selection process has a hierarchical framework, ranging from broad (macroscale) to narrow (microscale) levels, requiring behavioural choices such as selecting a home range or feeding site (Johnson, 1980; Orians & Wittenburger, 1991; Jones, 2001). Until now, a maximum of six levels of habitat selection have been identified. The first-order selection defines a species' broad geographical range (distribution), while second-order selection refers to the home ranges chosen within the distribution. The use of specific sites within home ranges constitutes third-order selection, and the final, fourth-order selection involves microscale decisions, such as locating food or nest sites (Johnson, 1980). This multiscale approach to habitat selection has been studied across several mammals such as the pygmy rabbit (*Brachylagus idahoensis*) (McMahon et al., 2017), boreal woodland caribou (*Rangifer tarandus caribou*) (Rettie & Messier, 2000), and tundra wolf (*Canis lupus*) (McLoughlin et al., 2004). Similar frameworks have been applied even to birds such as the crested serpent eagle (*Spilornis cheela*) (Walther et al., 2014) and Eurasian eagle-owl (*Bubo bubo*) (Martínez et al., 2003). The examples indicate that hierarchical habitat selection has been studied in various habitats. However, we did not find any similar example of this approach in relation to cave dwelling animals.

Ecologists classify caves as oligotrophic ecosystems due to their minimal input of light energy (Bay et al., 2024), and organic material (Kováč, 2018), along with a simplified trophic structure often truncated at the base (Fernandes et al., 2016). They are often described as natural laboratories (Mammola et al., 2020) because of their stable microclimatic conditions in comparison to surface ecosystems (Kováč, 2018). However, the challenges posed by perpetual darkness and nutrient scarcity limit the diversity of organisms that inhabit these environments, making caves ideal to study habitat specialisation and selection. Even though many animals are known to use these subterranean (hypogean) habitats, most research has focused on surface ecosystems. The study of birds that use caves remains significantly underexplored, despite there being 119 avian species belonging to 11 orders that have been documented utilising caves for roosting, nesting, and breeding (Betts, 1916; Hyem, 1932; Coles, 1944; Chapin, 1948; Pearson, 1953; Skead, 1971; Bilney et al., 2006; Holland et al., 2009; Manchi & Sankaran, 2009; Mohammad et al., 2017; Collar & Sharpe, 2020; Strickler & West, 2020; Zampaulo et al., 2023). Most existing research has concentrated on economically valuable cave-dwelling swiftlets (*Aerodramus* sp.) (Table S1). Species

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Fig. 1. The cave-dwelling edible-nest swiftlet (*Aerodramus fuciphagus*).

such as the swiftlets of Southeast Asia and the oilbirds of South America play a major role as primary producers and energy providers (guano, prey, and nest). Their specialised ability to echolocate allows them to breed deep within caves, utilising the darkness for safety and ecological benefits (Griffin, 1958; Price et al., 2004; Medway, 2008).

Of the 28 cave-dwelling *Aerodramus* species, only nine have been studied for macroscale habitat use, and research on their habitat selection within caves remains limited (Table S1). In the Andaman and Nicobar Islands, the edible-nest swiftlet (ENS) (*Aerodramus fuciphagus inexpectatus*; Fig. 1) has been studied for its nest-site selection (Manchi & Sankaran, 2011). Our study hypothesises that habitat selection in these birds is influenced by cave morphology, colony-site characteristics, and microclimatic parameters. We used the ENS as a model species to identify the orders of habitat selection within cave-dwelling birds and explore how environmental and structural cave features shape their habitat selection decisions.

MATERIAL AND METHODS

Study area. The Andaman and Nicobar Islands, flanked by the Andaman Sea, comprise 572 islands harbouring 394 known limestone caves, of which 324 are in the Andaman Islands (Manchi & Sankaran, 2014). Our study was at two significant North & Middle Andaman district cave complexes (Fig. 2). Baratang Island has the Andaman and Nicobar Archipelago's largest and most significant cave complex of more than 175 caves spread over 0.77 km^2 in a protected Reserve Forest between Wraffter's Creek and Naya Dera (12°05′N, 92°45′E). Chalis-Ek (13° 2.9′N, 92°59.2′E), on North Andaman Island (Fig. 3), is a limestone hillock, believed to have 41 caves, and one of the five most significant cave complexes in the island groups with 30 known caves (Sankaran, 2001; Manchi & Sankaran, 2014; Bandopadhyay, 2017).

Data collection and analyses. We define the cave habitat selection orders for birds in accordance with Johnson (1980) and Owen (1972). The first, second, fifth, and sixth orders of habitat selection are well-defined based on the secondary data available. However, as the third and fourth orders are poorly defined in the literature, we collected primary data in order to properly define them. Based on accessibility and feasibility, we chose to sample 79 caves: 55 from Baratang and 24 from Chalis-Ek. We used a standard survey protocol (Ford & Cullingford, 1976; Kawalkar & Manchi, 2020; Gurjarpadhye et al., 2021) to record each study cave's (Fig. 4) morphometric measurements (for third-order selection) and colony-site characteristics (for fourth-order selection) using a Distometer (Leica S910). We fixed survey stations from the entrance to exit, keeping a one m distance between each survey station. At each survey station, we measured vertical angle (ϴ), bearing from true north and the distances (m) to the left wall (L), right wall (R), cave ceiling (U), and cave floor (D). We also used the Compass Project Manager (Ver. 5.23.3.8.223) to derive the cave statistics/map-derived morphometric variables (n=12) for further analysis (Table 1).

Following Burger & Gochfeld (1990), we defined the aggregation of more than one breeding pair of study species as a nesting colony (Fig. 5). For the colony-site morphometry, we sampled 67 nesting colonies from 55 caves (39 nesting colonies in 31 caves at Baratang and 28 nesting colonies in 24 caves at Chalis-Ek). Some caves had more than one swiftlet colony. We used a Leica S910 Distometer to collect data concerning the following colony-site characters: (i) the distance of the nesting location from the nearest cave opening, (ii) the distance of the nesting location from a bat colony, (iii) the height of the colony, (iv) vertical angle (wall angle), (v) length of the colony, (vi) the perimeter of the colony, and (vii) direction of the colony; and a handheld environment meter (Kestrel 5000) to collect the micro-climatic data (temperature, humidity, atmospheric pressure, and wind speed). The breeding populations of the ENS in the study caves at Baratang and Chalis-Ek were monitored using the nest count method (Sankaran, 2001; Manchi & Sankaran, 2014). Nests were searched and counted monthly during the breeding season (January to June 2019). As these birds are known to be monogamous (Koon & Cranbrook, 2002), each nest corresponds to a pair of swiftlets (Gurjarpadhye et al., 2021).

The maximum count of active nests during the season was considered the cave's breeding population. Multiple-regression modelling (Mac Nally, 2000) was used to investigate the breeding habitat and colony-site selection by the ENS, which was influenced by cave morphology and colony-site characteristics. The analysis considered 12 cave-morphometry variables, 7 colony-site morphometry variables, and 4 microclimatic variables. To reduce multi-collinearity effects, the habitat variables (Table 2) were tested using Spearman's rank correlation test, and variables with r>0.60 were selected for further analysis. The remaining non-collinear variables were used for modelling to avoid potential errors. Residual plots were used to check the assumptions of the linear and multiple regression models. Habitat-use patterns (Jones, 2001) result from habitat-selection processes, so Ivlev's Electivity Index (E) was also used to understand habitat availability and usage by the ENS.

Table 1. Morphological diversity in the caves (alpha= 0.05; *p value>0.05)

Sr. no.	Morphometric parameters	All caves (p-value)	ENS caves (p-value)	Non-ENS caves (p-value)
1	Included Length	*	0.03	*
2	Horizontal Length	*	0.02	*
3	Cave Bearing from true North (degrees)	*	*	*
4	Inclination (degrees)	*	*	*
5	Cave depth	0.02	*	*
6	Surface length	0.00	0.03	*
7	Surface width	*	*	*
8	Surface Area	0.00	0.00	0.04
9	Cave Volume	0.00	0.00	0.02
10	Average diameter	*	*	*
11	Wall Area	0.00	0.00	0.01
12	Average Inclination	0.02	0.01	*

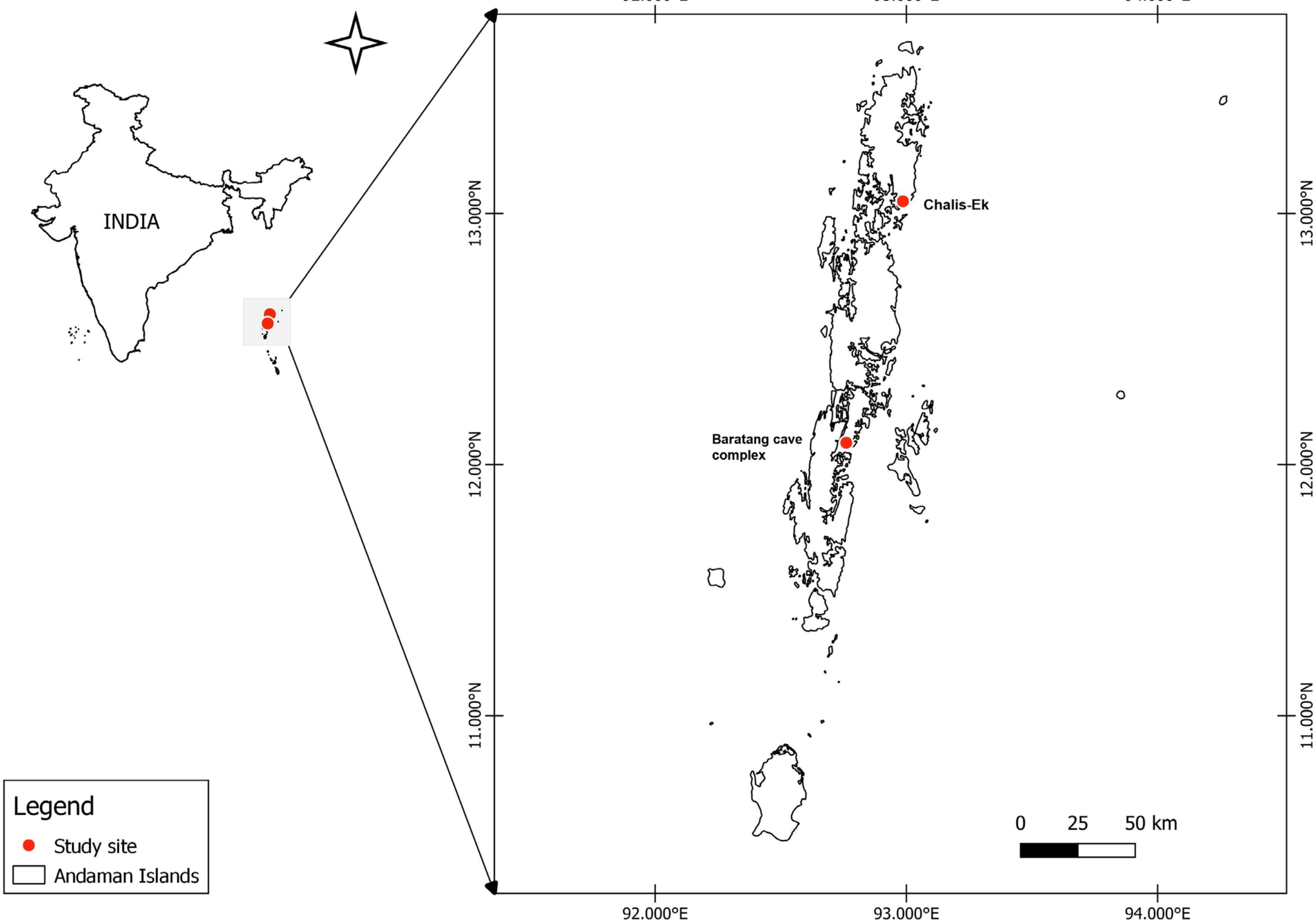

Fig. 2. The geographical location of Baratang and Chalis-Ek in the Andaman Islands.

Fig. 3. A limestone hillock believed to have 41 caves, known as Chalis-Ek.

Fig. 5. The breeding colony-site of the edible-nest swiftlet in the caves of Chalis-Ek.

Fig. 4. Limestone caves are breeding habitats of the edible-nest swiftlet in the Andaman Islands.

RESULTS

Following Johnson (1980) and Owen (1972), we identified six orders of habitat selection. Geographical distribution in the islands is the ENS's first order of habitat selection. The second order comprises the choice of habitat (caves) within the islands. Limestone caves are the only known nesting and roosting habitats of ENS in the Andaman and Nicobar Islands, though recently the populations were also observed using cave-like urban habitats (Sankaran, 2001; Chantler & Boesman, 2019; Gurjarpadhye et al., 2021). As a third order, while selecting among the available caves, the ENS occupied 62 (78.48 %) of the 79 structurally diverse and morphologically varying caves (Table S2). However, the caves with (n=62) and without (n=17) the ENS breeding population do not have significant morphological differences (Table 1; $p>0.05$), which indicates that the ENS does not select nesting and roosting caves based on cave morphometry.

We surveyed 67 accessible ENS breeding colonies from 55 caves to understand the colony-site characters as a fourth-order of the habitat selection. We estimated that there are 3,024 birds (44.37 % of the 6,976 birds in both the study areas) breeding in the study caves (n=55), ranged between 2 and 232 breeding individuals, i.e., 1–116 breeding pairs in each cave. In both Baratang and Chalis-Ek, there were significant differences in the colony-site characters between the colonies ($p<0.05$). In Baratang, there was no difference in the micro-climatic parameters ($p>0.05$), but in Chalis-Ek ($p<0.05$), there were significant changes within the caves. Upon comparison, we found that no notable difference in the colony-site characters ($p>0.05$) was detected between Baratang and Chalis-Ek. Nevertheless, the microclimate parameters, such as temperature, humidity, and atmospheric pressure at both study locations varied significantly ($p<0.05$). The wind speed and light intensity were similar (W/S=0 and Lux=0) in all the caves on both study sites (Table S3).

The fifth order of habitat selection goes further to the micro level to select the specific site in a colony to build an individual nest. As the ENS is known to attach its nest to cave walls in the dark zones, the site characters are crucial in selecting specific places for nest-building. The significance of nest-site characteristics, their selection, and their contribution toward nest success were noted by Manchi & Sankaran (2011) who showed that the ENS in the Andaman and Nicobar Islands prefer nesting locations with a combination of rough surfaces on inwardly inclined walls (wall making an acute angle with the ground; Manchi, 2009), with or without support (usually an accumulation of rocky material at the base of the nests; Manchi, 2009). Further, a slightly rough rock surface and the nest height were significant predictors of nesting success in ENS (Manchi

Table 2. Correlation matrix obtained from the multi-collinearity statistics of the cave morphometric variables obtained from the multi-collinearity statistics of the cave morphometric variables

Variables	Included Length	Horizontal Length	Cave Bearing from true North	Inclination	Cave Depth	Surface Length	Surface Width	Surface Area	Cave Volume	Average Diameter	Wall Area	Average Inclination
Included Length	**1**											
Horizontal Length	0.98	**1**										
Cave Bearing from true North	-0.02	-0.04	**1**									
Inclination	0.36	0.26	-0.13	**1**								
Cave Depth	0.96	0.92	-0.04	0.38	**1**							
Surface Length	0.81	0.85	-0.12	0.03	0.79	**1**						
Surface Width	0.76	0.80	0.00	0.00	0.74	0.63	**1**					
Surface Area	0.81	0.81	-0.07	0.13	0.81	0.77	0.68	**1**				
Cave Volume	0.25	0.37	-0.10	-0.16	0.13	0.47	0.22	-0.00	**1**			
Average Diameter	0.15	0.27	-0.14	-0.25	0.08	0.45	0.19	-0.03	0.95	**1**		
Wall Area	0.51	0.49	0.06	0.29	0.32	0.28	0.30	0.24	0.20	-0.04	**1**	
Average Inclination	0.11	0.01	0.03	0.41	0.17	-0.10	0.01	0.13	-0.51	-0.55	0.10	**1**

& Sankaran, 2011), which indicates the direct implications of the specific nest-site selection.

The spatio-temporal foraging habitat selection in ENS and plume-toed swiftlets (*Collocalia affinis*, previously known as glossy swiftlets, hereafter PTS) during the breeding season is defined by Manchi & Sankaran (2010). Both swiftlets shared all microhabitats except inside the forest and stream bank canopy. The ENS were more active in forested areas, whereas PTS were more active in open paddy lands in the Andaman Islands. There is a niche separation of the foraging niches for both species; the ENS forage high above the canopy, while PTS forage at the canopy level and near the ground (Manchi & Sankaran, 2010).

Multi-collinearity statistics allowed the selection of six non-collinear variables from 12 cave morphometric variables for the multi-regression modelling. No cave morphometric character seemed to influence the breeding cave selection by the ENS (R^2=0.13, $p>0.05$) (Table 3a). Furthermore, with 42% of the variability (R^2=0.42, $p>0.05$) (Table 3b), no colony-site character was seen to strongly influence the ENS's colony-site selection. Nevertheless, the atmospheric pressure emerged as a significant parameter ($p<0.05$) influencing the fifth order of habitat selection by ENS (Table 3c). The Ivlev's Electivity Index (E) suggested that lengths between 80–90 m and 140–150 m, surface areas of 1,000–1,100 m^2, wall areas of 2,001–3,000 m^2, and volumes of 800–900 m^3 and 3,900–4,000 m^3 are avoided by ENS. However, while selecting its habitat, ENS does not show preference for any factors: cave morphology, colony-site character, or microclimatic parameters (Table S4).

DISCUSSION

This study examined habitat selection in cave-dwelling birds, using the ENS as a model species. Based on the existing habitat selection theories, we identified six orders of hierarchical habitat selection for cave-dwelling birds. We hypothesised that cave morphometry, colony-site characteristics, and microclimate influence habitat selection in ENS. However, the results of this study showed that the cave-dwelling ENS randomly selects its breeding habitat, suggesting that these factors do not significantly affect habitat selection in this species.

The distribution of all 8 sub-species of ENS (*Aerodramus fuciphagus*) throughout Southeast Asia's islands (Chantler & Boesman, 2019) confirms their preference for islands as their first order of habitat selection. It further affirms that the geographical distribution of the ENS in the Andaman and Nicobar Islands is its first order of habitat selection. In the case of ENS, the second-order habitat selection is the macro-habitat that the species uses throughout its geographic range, which is a cave or a subterranean habitat. In the Andaman and Nicobar Islands, ENS naturally inhabits limestone caves (Sankaran, 1995, 1998; Manchi & Sankaran, 2014; Table 1). However, it has started using cave-like structures, abandoned old buildings, and houses because of

Table 3. Multiple regression modelling for the (a) cave morphometric variables, (b) nest-site characters, and (c) micro-climate

(a)

Source	Value	Standard error	t	Pr > |t|	Lower bound (95%)	Upper bound (95%)
Intercept	-68.73	38.91	-1.76	0.08	-146.70	9.24
Included Length	0.14	0.13	1.05	0.29	-0.12	0.40
Cave Bearing from true North	0.02	0.03	0.75	0.45	-0.04	0.09
Inclination	0.39	0.50	0.77	0.44	-0.62	1.41
Cave Volume	0.00	0.00	1.41	0.16	0.00	0.00
Wall Area	-0.00	0.00	-1.49	0.14	-0.02	0.00
Average Inclination	1.28	0.86	1.47	0.14	-0.45	3.02

(b)

Source	Value	Standard error	t	Pr > |t|	Lower bound (95%)	Upper bound (95%)
Intercept	2.30	18.39	0.12	0.90	-34.51	39.12
Distance from mouth	-0.09	0.14	-0.63	0.52	-0.37	0.19
Distance from bat colony	0.08	0.15	0.52	0.60	-0.23	0.40
Wall angle	0.33	0.24	1.35	0.18	-0.16	0.82
Height of the colony	0.06	0.22	0.29	0.76	-0.37	0.50
Length of the colony	-3.87	2.51	-1.54	0.12	-8.89	1.15
Width of the colony	4.26	2.61	1.63	0.10	-0.96	9.49
Perimeter of the colony	0.93	1.15	0.81	0.42	-1.37	3.24
Direction of the colony	-0.02	0.02	-0.82	0.41	-0.06	0.02

(c)

Source	Value	Standard error	t	Pr > |t|	Lower bound (95%)	Upper bound (95%)
Intercept	2545.60	860.24	2.95	0.00	826.54	4264.65
Temperature	-0.95	2.44	-0.39	0.69	-5.83	3.91
Humidity	0.28	0.36	0.76	0.45	-0.45	1.01
Atmospheric pressure	-84.95	28.93	-2.93	0.00	-142.76	-27.14

human ranching efforts (Thorburn, 2015; Chua & Zukefli, 2016; Manchi et al., 2022), as seen in other swiftlets. The selection of specific caves for breeding/roosting by ENS in the Andaman and Nicobar Islands is considered third-order selection. ENS does not depict selection of any specific cave morphometric parameter, but the ENS exhibits a strong avoidance of certain cave morphometric parameters during breeding. However, research has suggested that the caves with greater structural heterogeneity offer more nesting sites like avons, cracks, crevices, and cavities that are inaccessible to predators (Arita, 1996; Brunet & Mendellin, 2001). The cave-dwelling oilbirds in South America, which breed and roost exclusively inside such caves or deep gorges, exemplify the preference for long caves (Holland et al., 2009; del Risco et al., 2020; Winkler et al., 2020). In contrast, the Mariana swiftlet was observed using much shorter tunnels, less than 5 km (Wiles & Woodside, 1999). Selecting a colony site with specific features in a cave represents the fourth-order habitat selection. None of the 12 studied colony-site characteristics in the Andaman and Nicobar Islands significantly influenced colony-site selection, though some are known to affect the process (Manchi & Sankaran, 2011). Swifts and swiftlets, with poorly developed legs but strong claws, prefer nesting on vertical surfaces (Lovette & Fitzpatrick, 2016). Their stringent breeding site preferences depend on suitable areas like cave walls and ceilings (Nguyên et al., 2002). Nest density can reach up to ~100 nests/m², depending on the availability of these spaces. In marine caves in Vietnam, suitable nesting areas extend up to 3 m above high tide, while in dry caves, they reach 1 m above the ground (Nguyên & Voisin, 1998). In Thailand's Si-hi Islands, the height of these areas ranges between 2.5 m and >10 m. In the Baratang and Chalis-Ek caves, ENS colonies occupy heights between 1.83–9.39 m and 1.69–15.97 m, respectively, though this height variation does not affect colony-site selection or nesting success (Manchi & Sankaran, 2011). Though wall height and angle can reduce predator pressure (Viruhpintu et al., 2002) and a study noted differences in nests on inwardly inclined walls (<90°) in the Andaman and Nicobar Islands (Manchi, 2009; Manchi & Sankaran, 2011), the vertical angle of the walls was not observed influencing nest site selection in the present study. It may be due to low predation pressure inside the caves in the Andaman and Nicobar Islands.

The presence of bats (Chiroptera) significantly influences colony-site selection for swiftlets. Bats, being nocturnal, and swiftlets, being diurnal, often avoid competition through niche separation, with molossid bats leaving caves as swiftlets return (Medway, 2008). Some studies suggest that swiftlets thrive in areas with fewer bats, potentially due to competitive exclusion (Fenton, 1975). Field observations in Baratang and Chalis-Ek caves found fewer swiftlets in caves with more bats, although bats and swiftlets co-exist on Nicobar Island (Sankaran, 1996). The impact of bat species varies: intermediate roundleaf bats (*Hipposideros larvatus*) roost in less competitive areas like cave entrances (Nguyên et al., 2002), while greater bent-winged bats (*Miniopterus schreibersi*) often roost near or on swiftlet nests, increasing competition. More research is needed in order to gain a deeper understanding of the niche separation and feeding dynamics between bats and swiftlets.

According to Nguyên et al. (2002), the microclimate is crucial for the breeding of ENS. While Baratang and Chalis-Ek caves show significant differences in temperature and humidity ($p<0.05$). Both sites have zero wind speed and light intensity (0.00 km/h, 0 lux). Nguyên & Voisin (1998) found that when relative humidity in dry caves drops below 70%–80%, swiftlet nests fall off the walls. In the closed caves of Baratang and Chalis-Ek, with high relative humidity (92.43 ± 4.69% and 81.34 ± 10.34%), nests remain intact. Environmental stability and humidity support species diversity, though temperature limits some bat species (de Sousa Barros et al., 2020). Insectivorous bats predict aerial insect abundance using atmospheric pressure, and fewer bats leave the roost as pressure rises (Paige, 1995). Tracking atmospheric pressure may serve as an evolutionary strategy in bats, reducing the need for torpor. Since swiftlets are also aerial insectivores, atmospheric pressure could similarly influence their roosting behaviour. This aspect needs further confirmation.

The findings highlight a hierarchical habitat selection process in cave-dwelling swiftlets. The Andaman and Nicobar Islands represent the first-order selection. Since the aerodynamic swiftlets can travel long ranges for food, their breeding caves may not be near suitable foraging areas, making it inappropriate to define their home range as a second-order selection. Instead, the second-order selection pertains to breeding or roosting locations such as caves, cliffs, gorges, waterfalls, or similar natural or man-made structures. The third-order selection involves choosing specific caves with particular characteristics for nesting and roosting. The fourth order focuses on selecting colony-site features within the cave; the fifth order addresses nest-site choices within different parts of the cave; and the sixth order involves selecting microclimate variables within each cave. The present study put forth the hypothesis that the characteristics of the cave, colony site, and the microclimate have an impact on how the ENS that live in caves choose their habitat. By disproving this theory, we conclude that, at least in the Andaman Islands, the ENS's habitat selection procedure is arbitrary. It will be intriguing to comprehend the selection procedure through long-term research. Additionally, since the study indicates avoiding a certain range of cave structures, regular population monitoring and dispersal studies can address these findings. Finally, it will be interesting to test their behaviour in ex-situ conditions after understanding the nature of the selection process in the in-situ conditions.

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APPENDIX

Table S1. The documentation of habitat specifications of *Aerodramus* sp. in previous studies.

Sr. no.	Swiftlet species	Habitat order	Habitat details	Key references
1	Edible-nest swiftlet (*Aerodramus fuciphagus*)	1,2,5,6	• Nesting in caves and cave-like habitats • Nesting/ Roosting locations inside the cave, • Nest-site characters and preference and their influence on the breeding success, • Micro-climate of the ENS caves • Classification of the ENS caves based on visual size categorisation • The shape of the cave entrances, wall textures • Breeding success and cave morphometry • Forages through bushes to catch arachnids and do not fly above 800m • Forested habitat and microhabitats above forest canopy level	Langham, 1980; Sankaran, 1998; Sankaran, 2001; Manchi, 2009; Mane, 2017; Manchi & Sankaran, 2011 Nguyên et al., 2002; Gurjarpadhye et al., 2021; Manchi et al., 2022; Manchi & Sankaran, 2010
2	Mariana swiftlet (*Aerodramus bartschi*)	1,2,4	• Occupy cave walls or ceilings in the natural caves and tunnels	Pratt et al., 1987; Jenkins, 1983; Morton & Amidon, 1996; Reichel et al., 2007; Johnson, 2015
3	Australian swiftlet (*Aerodramus terraereginae*)	1,2	• Nests in dark and twilight cave zones • Nests 2–20 m above cave floor on smoothly concave walls, • Extrusions or cracks readily utilised	Tarburton, 1988
4	White-rumped swiftlet (*Aerodramus spodiopygius*)	1,2,4	• Roosts and breeds in lava tube caves • Occupy dark and twilight zones, particularly in caves near mature forests, • The average height of nests above the cave floor was 5.1±5.98 and 1.5 to 30m • Caves that have formed in the tower-like outcrops of a belt of grey limestone • Nests in the twilight cave zone or on the underside of large boulders also share caves with bats	Tarburton, 1986; Tarburton, 1988; Tarburton, 2009; Tarburton, 2011
5	Volcano swiftlet (*Aerodramus vulcanorum*)	1,2	• Nests in volcanic rock crevices	Thomassen & Povel, 2006
6	Germain's swiftlet (*Aerodramus germani*)	1,2	• Uses dry and marine caves, micro-climate (temperature and humidity) affects breeding success. • Forages over water bodies, forests, and open paddy land	Nguyên & Voisin, 1998; Nguyên et al., 2002; Petkliang et al., 2017
7	Black-nest swiftlet (*Aerodramus maximus*)	1,2,5	• Uses caves • Nest high (≥15 m) on the cave walls and ceiling	Tompkins, 1999
8	Tahiti swiftlet (*Aerodramus leucophaeus*)	1,2	• Wide variety of nest sites: caves, deep or shallow, depressions under rocks or coastal cliffs.	Kirwan et al., 2023
9	Atiu swiftlet (*Aerodramus sawtelli*)	1,2	• Roosting location is mostly dark zones of the cave • The nests are both in twilight and dark zones • Nests are on flowstones and stalactites • The distance of the nests from ground ranges from 3.2±0.2m and 4.8±0.01m	Fullard et al., 1993; 2010 Tarburton, 1990
10	Mountain swiftlet (*Aerodramus hirundinaceus*)	1,2,5	• The nests are placed in the twilight zone • The height of the nests from the cave floor ranges from 1.2-3m	Tarburton, 2003

Table S2. The definition of the cave morphological parameters and the cave statistics of the edible-nest swiftlet and non-edible-nest swiftlet caves in the Andaman and Nicobar Islands.

Sr no.	Morphometric variables	ENS caves (Mean±SD)	Non-ENS caves (Mean±SD)	p-value (alpha=0.05)
1	Included Length (m): It is the measurement or extent of the cave from end to end along the survey passage, including all the inaccessible areas.	37.58 ± 35.18	25.68 ± 27.78	0.27
2	Horizontal Length (m): The map-derived parameter tells us the length of the cave covered horizontally on the earth's surface.	24.24 ± 22.43	16.11 ± 16.57	0.17
3	Cave Bearing from true North (°): It is the horizontal space (usually measured in degrees) between two intersecting lines or surfaces at or close to the point where they meet	193.84 ± 114.70	210.05 ± 113.40	0.61
4	Inclination (°): It tells at which angle, vertically or horizontally, the cave is inclined in the three-dimensional space	57.27 ± 10.90	55 ± 10.52	0.45
5	Cave depth (m): It is the distance down of a cave from its opening at the earth's surface	27.21 ± 26.23	19.66 ± 22.18	0.28
6	Surface length (m): It is the measurement or extent of the cave ceiling from end to end	10.62 ± 11.49	6.57 ± 7.17	0.17
7	Surface width (m): It is the horizontal length of the cave surface	12.54 ± 8.71	10.99 ± 11.70	0.55
8	Surface area (m^2): It is a map-derived parameter that gives the area of the cave surface, mostly the ceiling	178.15 ± 423.76	134.57 ± 265.59	0.69
9	Cave Volume (m^3): It is a three-dimensional space enclosed by the cave.	538.92 ± 1665.16	602.56 ± 1251.92	0.88
10	Average diameter (m): An expression of the average size of a cave, obtained graphically by locating the diameter associated with the midpoint of the cave-size distribution; the middlemost diameter that is larger than 50% of the diameters in the distribution and smaller than the other 50%.	2.66 ± 1.94	2.58 ± 1.92	0.88
11	Wall area (m^2): It is a two-dimensional parameter that is usually map derived, which is the multiplication length of the cave walls by its breadth	472.50 ± 824.14	454.6 ± 760.62	0.93
12	Average Inclination (°): This considers the average of all the vertical angles recorded at every survey station	48.30 ± 8.14	52.36 ± 6.45	0.07

Table S3. The edible-nest swiftlet colony-site characteristics at Baratang and Chalis-Ek, Andaman Islands.

Sr. no.	Characters	Baratang Island	Chalis-Ek	p-value (alpha=0.05)
1	Distance from the cave entrance/ nearest opening from the colony (m)	30.63 ± 20.43	24.75 ± 26.65	0.31
2	Distance of the bird colony from the bat colony (m)	7.35 ± 7.28	7.31 ± 6.87	0.97
3	Height of the colony (m) — distance from the ground to the colony	4.98 ± 2.44	5.25 ± 3.20	0.12
4	The vertical angle — the angle at the nesting location (°) from the ground	74.19 ± 10.8	70.21 ± 9.47	0.69
5	Length of the colony (m) — the longest distance between the nests within the colony	1.07 ± 1.03	0.97 ± 1.90	0.79
6	Width of the colony (m) — lateral extent of nests, measuring the distance between the farthest nests across the width of the occupied area	1.02 ± 1.31	1.55 ± 2.98	0.32
7	The perimeter of the colony (m) — boundary around the colony's occupied area	3.83 ± 3.59	6.02 ± 7.97	0.14
8	The direction of the colony (°) — orientation of the swiftlet colony	192.45 ± 106.92	195.27 ± 93.14	0.91
9	Temperature (°C) — Temperature near the colony	28.0 ± 0.93	28.74 ± 1.38	0.01
10	Relative Humidity (Rh%) — Humidity near the colony	92.43 ± 4.69	81.34 ± 10.34	0.00
11	Atmospheric pressure (Pa) — Pressure at the colony	29.80 ± 0.05	29.59 ± 0.09	0.00
12	Wind speed (km/hr) — the rate at which air moves past the swiftlet colony's location	0.00 ± 0.00	0.00 ± 0.00	NA
13	Light intensity (lux) — amount of light energy received per unit area at the colony's location	0.00 ± 0.00	0.00 ± 0.00	NA

Table S4. Habitat preference and avoidance by the edible-nest swiftlet.

Sr. no.	Predictor variables	Number of classes, Class interval	Preference		Avoidance	
			Class	E	Class	E
1	Cave length	13, 10	30–40	0.23	10–20	-0.22
			50–60	0.12	80–90	-1
			60–70	0.12	140–150	-1
2	Surface Area	9, 100	200–300	0.13	1000–1100	-1
			500–600	0.13		
			3200–3300	0.14		
3	Average Diameter	5, 2	2–4	0.02	6–8	-0.22
			12–14	0.12		
4	Horizontal Length	16, 10	50–60	0.12	40–50	-0.32
			60–70	0.12	0–10	-0.07
5	Surface Length	5, 10	50–60	0.12	0–10	-0.04
			60–70	0.12		
6	Cave Depth	8, 10	30–40	0.12	50–60	-0.40
			40–50			
7	Wall Area	13, 100	201–300	0.19	2001–3000	-1.00
			301–400	0.19	0–100	-0.23
			401–500	0.19	701–800	-0.16
8	Surface Width	5, 10	40–50	0.12	20–30	-0.02
			10–20	0.03	30-40	-0.40
9	Cave Bearing	4, 90	180–270 (SW)	0.06	270–360 (NW)	-0.05
			0–90 (NE)	0.002	90–180 (SE)	-0.01
10	Cave Inclination	5, 10	61–70	0.12	30–40	-0.16
			41–50	0.07	51–60	0.09
			71–80	0.04		
11	Average Inclination	8, 5	35–40	0.12	0–5	-0.22
			45–50	0.12	55–60	0.07
					31–40	0.31
					0–100	0.14
12	Cave Volume	17, 100	100–200	0.12	800–900	-1.00
			200–300	0.12	3900–4000	-1.00
			400–500	0.12		
			500–600	0.12		
			600–700	0.12		