POPULATION DYNAMICS OF THE EDIBLE-NEST SWIFTLET *AERODRAMUS FUCIPHAGUS INEXPECTATUS* IN THE ANDAMAN ISLANDS

Thesis Submitted to Bharathiar University in Partial Fulfillment
of the Requirements for the Award of the Degree of

DOCTOR OF PHILOSOPHY IN ZOOLOGY

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I, **Prathamesh Hemant Gurjarpadhye,** hereby declare that the thesis, entitled **"Population Dynamics of the Edible-nest Swiftlet *Aerodramus fuciphagus inexpectatus* in the Andaman Islands"** submitted to the Bharathiar University for the award of the Degree of **Doctor of Philosophy in Zoology,** is a record of original and independent research work done by me during November 2017- October 2023 under the supervision and guidance of Dr Manchi Shirish S., Principal Scientist (SACON), Department of Conservation Ecology & Head, Sálim Ali Centre for Ornithology and Natural History (SACON), South India Centre of Wildlife Institute of India, MOEFCC, Govt. of India and the Co-supervision of Dr Ram Pratap Singh, Ex-Senior Scientist (SACON) Associate Professor and HoD Department of Life Science, Central University of South Bihar, Gaya-824236, Bihar, India. It has not previously formed the basis for awarding any Degree / Diploma / Associateship / Fellowship or other similar titles to any candidate of any University.

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(PRATHAMESH HEMANT GURJARPADHYE)

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SUMMARY

Population dynamics play a fundamental role in ecological research and have important implications. It refers to the study of how the size and composition of populations of organisms change over time and in response to various factors such as birth and death rates, immigration and emigration, environmental conditions, resource availability, and interactions with other species. Many researchers have long studied terrestrial avian population dynamics; however, birds in hypogean environments, such as the Edible-nest Swiftlet, did not receive much attention.

The Edible-nest Swiftlet (*Aerodramus fuciphagus inexpectatus*) is a cave-dwelling bird studied primarily in ex-situ habitats due to its economic importance. The studies in wild or urban areas majorly focus on breeding biology, ecology, habitat, and population trends. However, many aspects of population dynamics are never attempted due to a lack of resources and practical difficulties, such as in the Andaman Islands. Therefore, this study aims to investigate the population dynamics of the Edible-nest Swiftlet in the Andaman Islands. The study aims to investigate the various aspects of population dynamics: site-fidelity, colonial sex ratio, and inter-colonial dispersal patterns, considering the biotic and abiotic factors influencing these traits. The study overall intends to provide valuable insights into the swiftlet's research and conservation.

The study was conducted on the Andaman and Nicobar Islands, home to the important cave complexes at Baratang Island, Chalis Ek, and Interview Island. These cave complexes have been under legal protection for the *in-situ* conservation of the Edible-nest Swiftlet and were considered for the study due to their significance in the species' conservation in the archipelago.

As part of the first objective, the study aimed to understand the breeding site-fidelity and biotic and abiotic factors affecting the Edible-Nest Swiftlet in caves from 2017 to 2019. Caves were selected using stratified random sampling and divided into classes based on breeding population sizes. In 2017, 117 nests were counted from 12 caves, and in 2018, 212 nests were found. The breeding population varied between 75.9% and 91.5% of the total, with each nest representing a pair of birds. The Edible-nest Swiftlets' nesting site fidelity was assessed using the Capture-Mark-Recapture technique. 207 adult birds, or

88.4% of the 234 total, were caught and marked in 2017. Most adult birds (66.18%) remain faithful to their breeding caves, as evidenced by the recapture of 137 adult birds in 2018. The study also discovered that regardless of prior years' success, in 2018, the species' total breeding success was much higher (91.5±7.1%) than in 2017. Regardless of past breeding success or failure, the species chooses to "always stay", i.e., remain at the same breeding site.

Simultaneously, the study also aimed to understand the relationship between breeding success, habitat morphology, and micro-climatic variables in a cave. A standard survey method was used to map the breeding habitat. The multi-collinearity test removed correlated parameters, and non-collinear variables (cave length, cave inclination, surface length, wall area, and cave bearing) were chosen for their logical relevance to the bird's ecology. The results suggest that 11 accessible caves had a varied range of morphometric measurements. A linear multiple regression model with five non-collinear variables revealed an insignificant relationship between breeding success and cave structure ($R^2=0.57$, $p>0.05$).

The microclimate data collected from the Edible-nest Swiftlet breeding season caves using HTC-Easy Log data loggers placed at cave entrances and nesting locations. The average mean temperature and relative humidity were used for analysis. The goodness of fit statistics, Spearman's correlation test, and linear and multiple regression modelling were performed using XLSTAT software Ver. 2020.2.1. Non-collinear variables were chosen for further analysis, and multiple regression modelling was used to predict influential factors and develop inferences about the determinants of patterns affecting breeding success. The study found that the Edible-nest Swiftlet individuals returned to the same caves for breeding despite the previous year's lower success. The average rate of breeding success of the Edible-nest Swiftlet was higher than most members of the genus *Aerodramus*, except for Germain's Swiftlet *Aerodramus germani*, Mountain Swiftlet *Aerodramus hirundinaceus*, and Mascarene Swiftlet *Aerodramus francicus*. This study revealed that the Edible-nest Swiftlet has fidelity towards their breeding caves, as documented in other Apodidae species. Overall it is now evident that no significant relationship between the cave structure and the breeding success of the Edible-nest Swiftlet. Non-collinear variables explained 57% of the variability in breeding success. Cave length and surface length had slight effects on breeding success. Microclimate variables, the temperature and relative humidity, did not affect breeding success. The study found that the Edible-nest Swiftlet is faithful to its breeding caves, rejecting the prior-experience hypothesis. The findings suggest improving conservation strategies to enhance the species' population in the Andaman and Nicobar Islands. Long-term capture-mark-recapture studies are needed for a deeper understanding of site-fidelity behavior.

To understand the inter-colonial dispersal patterns, the results of the data from the recaptured individuals showed that the recapture in the Edible-nest Swiftlet was high (66.2%), compared to earlier studies on various Apodids. The present two-year study indicated that the return rates of Edible-nest Swiftlet did not directly depend on the breeding success or failure of the previous year. Further research is needed to determine if individuals are always site faithful and understand the impact of other factors like sex and age on their return rates.

As part of the second objective, the study examined the colonial sex ratio of Edible-Nest Swiftlet in 47 caves in Baratang Island, Chalis Ek, and Interview Island, collecting data from 2017 to 2019 using capture-mark-recapture method. The Edible-nest Swiftlet, a traditionally known monomorphic bird in the Andaman and Nicobar Islands, was identified using a molecular method. Blood samples were collected from the birds' brachial veins and used to isolate genomic DNA. Multiplex PCR methods were used to amplify the region of CHD1 gene using P8/P2 and 2550F/2718R pair of primers. The results were visualized and stained using Hi-SYBr Safe Gel Stain. This study used morphometric measurements of 1111 Edible-nest Swiftlet birds to identify their sex. Descriptive statistical analyses were performed to derive indicators for each morphometric measurement, and differences between sexes were analyzed using t-tests and stepwise Discriminant function analysis. Factors with r values below 0.6 were discarded from the final analysis. The study involved 1545 adults and 253 offspring from 48 caves at three study sites.

Sex identification was accomplished using the primer pair P8/P2 was used to amplify the CHD1 gene of the Edible-nest Swiftlet. Furthermore, after PCR amplification, P8/P2 alone resulted in a single band of ~380bp on 2% Agarose gel in males and females. Sex identification is impossible based on these results. Another set of primers, 2550F/2718R, was used to resolve this problem. The PCR products run on 2% Agarose gel after PCR amplification. Female samples revealed a band of ~ 550bp, whereas male samples revealed no amplification.

However, Polyacrylamide gel electrophoresis (PAGE) was used to differentiate sex in Edible-nest Swiftlet, showing successful male and female sex differentiation. However, PAGE is expensive, time-consuming, and labour-intensive, and Polyacrylamide is a known carcinogen. To overcome this problem, A multiplex PCR method was used to amplify the CHD1 gene in Edible-nest Swiftlet (ENS) and Chicken (CH). The method identified two bands (380 bp and 550 bp) in female Edible-nest Swiftlet and Plume-toed Swiftlet (PTS), while only a single thick band of 380 bp was observed in male Edible-nest Swiftlet and Plume-toed Swiftlet. The method was used to process 1798 Edible-nest Swiftlet samples, identified 942 male and 856 female. The study found that Edible-nest Swiftlet colonies maintain a 1.11:1 sex ratio, with most (72.91%) maintaining a 1:1 ratio. Nine colonies are male-biased, while three have a female-biased sex ratio with very low presence of males. Additionally, 253 offspring from Baratang Island showed a 1:1 sex ratio, confirming the balanced offspring sex ratio.

The morphometric characters of the Edible-nest Swiftlet individuals were used to unveil the sexual dimorphism in the species, if exists. The study found that among the nine morphological characters, only two factors (body length and weight) contribute to cryptic dimorphism discovered in the Edible-nest Swiftlet. The discriminant function coefficient showed that body length and weight were the most significant differences between sexes. The sexual dimorphism index (SDI) suggests culmen width differentiates both sexes, but it is not considered a discriminating factor. The mean discriminant score of the females is 0.17, and for males is -0.15. The confusion matrix for the cross-validation results correctly classified 100% of 527 females and 30.82% of the 584 males. This implies that the females (Body Length between 12 -15.2cm) can be differentiated from the males based on body length. This study explored the Edible-nest Swiftlet, colony sex ratios and structures of the cave-dwelling Apodid species. It suggests further research questioning the monogamy in swiftlets. The study also revealed cryptic Sexual Size Dimorphism (SSD) in the Swiftlet, a unique feature not found in other Apodids. This research contributes to our understanding of swifts and swiftlets.

As part of the third objective, the study aimed to understand inter-colonial dispersal patterns and factors affecting the Edible-nest Swiftlet population in three Andaman and Nicobar Archipelago cave complexes: Baratang Island, Challis-Ek, and Interview Island. Twelve caves from four different population classes were selected using stratified random sampling. Adult birds were captured using the capture-mark-recapture method, and offspring were captured on the nests and removed before fledging. The study used a molecular method for individual sex identification. Cave locations were recorded using a Handheld Global Positioning System (GPS) and distance analysis using QGIS. Data on seven colony-site characteristics of Edible-nest Swiftlet nesting locations was collected from all sites using a Distometer. Micro-climatic data was collected at every nesting site using a Handheld Environment Meter. The study aimed to provide insights into the inter-colonial dispersal patterns and factors affecting the species.

The study used capture-recapture data to estimate the Edible-nest Swiftlet populations using the Lincoln Index and goodness of fit tests. The software MARK was used for survival estimates and capture probability and four predefined models were used to check the dependence of survival and capture probabilities as a function of time. Based on the lowest Akaike's Information Criterion (AICc), Delta AICc >2, and superiority of the Akaike's Information Criterion Weight (AICc weight) the best fit model was selected. The Likelihood Ratio Test (LRT) was used to assess the goodness of fit of two competing statistical models. The longevity of the Edible-nest Swiftlet was calculated using capture-mark-recapture data, and the nesting area was calculated using the Distometer. Linear regression modelling used SPSS to determine the association between population size and density, population size, and sex ratio. The study found that no adult birds dispersed between colonies, indicating breeding site fidelity in the species. 253 offspring were captured in 12 caves on Baratang Island between 2017 and 2018 and attempted to be recaptured in 48 caves. 34 Edible-nest Swiftlet individuals were recaptured, with 38.23% from the same caves showing philopatry and 61.77% showing natal dispersal by first breeding away from the birth cave. Natal dispersal was female-biased, with females showing a longer dispersal distance than males. A female's maximum distance was 4.07km on Interview Island and 0.75km on Baratang Island.

The study also points at the non-significant correlation between colony-site selection and the nest site selection for the Edible-nest Swiftlet. The cave wall's vertical angle did not significantly influence the relative humidity and temperature in Baratang and Chalis-Ek. The birds chose nest sites where it was not windy and completely dark. Out of the estimated population of 501 birds, 75.64% were captured between December 2017 and June 2019. The overall recapture rate was 42.22%. The CMR model and LRT showed that the two analyses competed statistically based on the goodness of fit. The species' predicted Mean life span is 2.85 years, with one female bird showing the highest longevity at 17 years and six months. The study also found no correlation between population size, density, sex ratio, and reproductive success.

Overall, the study provides important information on the species' dispersal pattern, colony sex ratio, and how biotic and abiotic factors influence population dynamics. The findings of this study provide an opportunity to better understand the monogamous or polygamous sexual mating behaviour of the Edible-nest Swiftlet. This research provides a baseline for population monitoring and the habitat needs of the species on the islands. It is the first attempt to comprehend the cave-dwelling swiftlet population dynamics. The research also investigates the features of colony locations, the structure of the surroundings, and the importance of microclimate for breeding success. These findings will help to improve the design of ex-situ swiftlet houses used to manage this commercially important species. This work lays the groundwork for future research and opportunities to get a better understanding of dispersal in ex-situ situations.

Chapter I

CHAPTER I

INTRODUCTION

1.1. BACKGROUND

The “dynamics” of bird populations, how their numbers increase and decrease as time goes by, are controlled by birth (natality), death (mortality), immigration, and emigration (Ehrlich et al., 1988). The population will grow if birth (natality) and immigration are higher than death (mortality) and emigration, and vice-versa. The population or density remains constant if growth and decline are harmonious (Ehrlich et al., 1988). A fundamental goal in population ecology is understanding how species’ populations are regulated. The changes in the species’ population over time are termed population dynamics (Newton, 1998; Schaub & Abadi, 2011).

Population dynamics research and theory can be divided into two main categories: quantitative and qualitative. The descriptions of changes in population size and the nature of population growth or decline for a specific organism and research into the forces and biological and physical processes underlying those changes are qualitative (Juliano, 2007). Modern population dynamics research is necessarily quantitative, and many statistical methods exist to describe and explain demographic processes in populations (Schaub & Abadi, 2011).

These demographic processes can be well explained using parameter estimations, a crucial tool in investigating the species’ population dynamics in ecology and its applications, such as conservation biology or wildlife management (Schaub & Abadi, 2011). The parameters used are population density, sex ratio, dispersal, birth rate (natality), death rate (mortality), longevity, and survival rate (Ferris & Wilson, 1987). All the parameters have been studied in greater detail, for instance, by Austin (1951), who investigated site fidelity in colonial birds and continued Werth’s (1947) early work on bird dispersal studies. After that, Allee et al. (1949) described how colonial birds’ fitness depended on density. These parameters are, however, affected by dispersal (Natal and breeding dispersal), which all living creatures experience at some point in their evolutionary process (Comins et al., 1980; Figure 1.1). It is the process by which a species maintains its current range (Greenwood, 1980), takes over abandoned habitats (Howard, 1960), and expands its range (Comins et al., 1980; Paradis et al., 1998). Animal dispersal involves two main types of movements: natal dispersal, or movement from birth to the first breeding site, and breeding dispersal, or movement between subsequent breeding sites. The population of a species is further governed by the number of individuals that disperse or get added to the population (Caiafa et al., 2021).

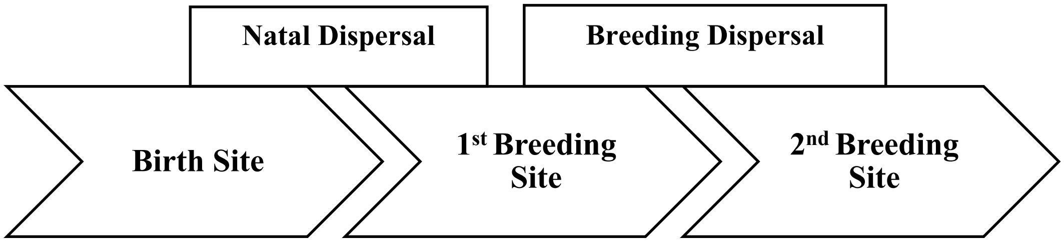


Figure 1.1: Types of dispersal experienced by the birds (Greenwood, 1980)

Dispersal is a critical factor in population synchronization (Paradis et al., 1998; Greenwood, 1980) and is responsible for decreasing the likelihood of extinction (Comins et al., 1980). Additionally, it supports discontinuous ranges for species (Howard, 1960), sometimes leading to broad distributions. Dispersal also affects population genetics by influencing gene flow, inbreeding, and outbreeding (Howard, 1960; Greenwood, 1980; Dobson & Jones, 1985; Tonkyn & Plissner, 1991; Paradis et al., 1998). Understanding the population dynamics of the species, particularly in fragmented settings, depends on dispersal, a major demographic mechanism (Lahaye, 2001). These two types of movement are of utmost importance in population and evolutionary ecology (Greenwood, 1980; Johnson & Gaines, 1990). The makeup of a species' life history is likely to be significantly influenced by variations in death rates (Ricklefs, 1977; Michod, 1979; Charlesworth, 1980). However, nothing is known about how death rates differ amongst bird species. It has been demonstrated that variation in several reproductive traits of birds is strongly correlated with differences in body weight (Blueweiss et al., 1978; Western & Ssemakula, 1982; Peters, 1983; Calder, 1984; Sæther, 1985; Sæther, 1987; Sæther, 1989). One important trait that correlates with body weight is longevity or aging in birds, which is observed to increase with body weight (Lindstedt & Calder, 1976; Lindstedt & Calder, 1981; Sæther, 1989). Due to several biochemical and biological features, birds should be more susceptible to reactive oxygen species (ROS) damage to their mtDNA than mammals. These traits include higher metabolic rates (1.5–2.5 times greater than similar-sized mammals) (Holmes & Ottinger, 2003; Skujina et al., 2005). Higher body temperatures (3°C higher mean body temperature), higher blood glucose levels (2–5fold higher mean blood glucose levels), seasonally elevated blood lipid levels, and enormously high total lifetime energy expenditures (5–10 times greater). As per the mitochondrial theory of aging, the cumulative influence of these features should have a detrimental effect on their longevity (Skujina et al., 2005).

Sex ratio in the population is another critical factor that can affect bird population dynamics. The adult sex ratio is an essential part of population demography. The adult sex ratio is crucial to social behaviour, mating patterns, and parental care (Donald, 2007; Liker et al., 2014). It is hypothesized that imbalanced adult sex ratios will affect pair bonds and mating behaviour because the less frequent sex in the population has more potential mates to mate with than the more common sex (Donald, 2007; Liker et al., 2014). Skewed adult sex ratios result from biased sex ratios at birth, sex-specific mortality (Székely et al., 2014), or permanent emigration (Morrison et al., 2016). Adult sex ratios are commonly male-biased in bird populations (Donald, 2007), most often driven by female-biased mortality in juveniles and adults (Liker et al., 2005; Székely et al., 2014; Gownaris et al., 2020). In a study on population dynamics, in Temminck's Stint (Callidris temminck), hatching and fledging success were recorded at 52% and 50-60%, respectively. After one year, half of the chicks were still alive. Males mature sexually at the age of 1.8 years, and females at the age of one year. The average annual death rate for adults was 19%, which increased steadily over time, from 7% in the first year to 33% after four years. The average lifetime of breeding adults was estimated to be seven years (Hildén, 1978).

One of the factors affecting bird breeding dispersal, according to the studies, is nesting success. It has been observed that birds whose previous movements were successful have a higher return rate and display remarkable site persistence compared to birds whose movements were unsuccessful (Haas, 1998; Flynn et al., 1999; Hoover, 2003; Porneluzi, 2003; Sedgwick, 2004). This occurrence is known as the "decision rule" in the theory of prior experience (Haas, 1998; Hoover, 2003). It is possible to see a similar trend in Mountain Plovers *Charadrius montanus*, where birds that mated the year before tend to disperse for shorter distances than those that did not (Skrade & Dinsmore, 2010). Estimating the population size is crucial to elucidate bird dispersal study dynamics (Figure 1.2).

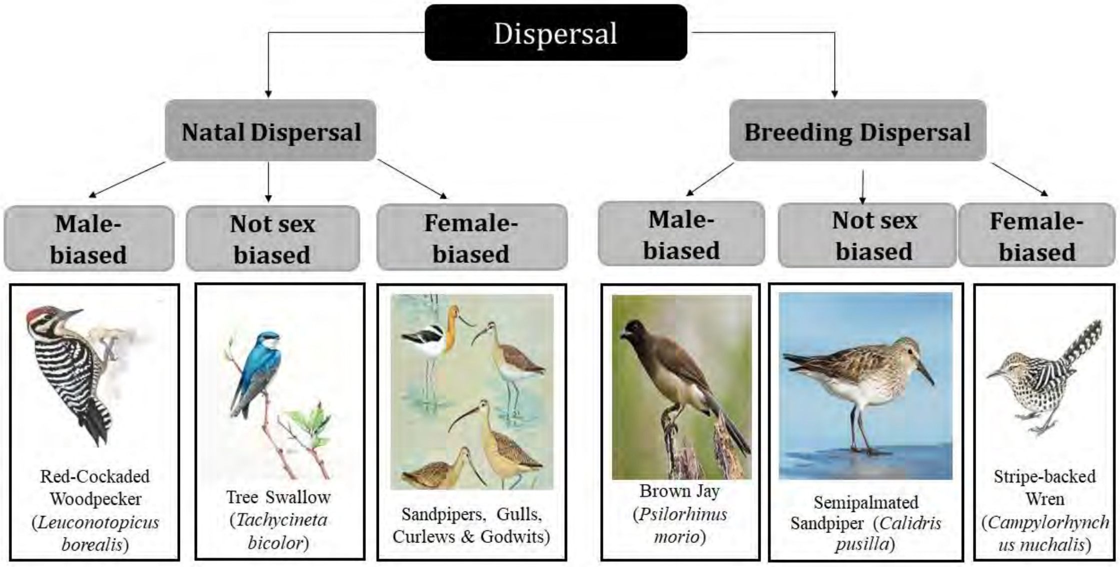


Figure 1.2: Examples of the types of breeding dispersal and natal dispersal in various species of birds (Dobson & Jones, 1985; Winkler et al., 2004; Clarke et al., 1997; Gratto, 1988; Yaber, 2002)

Because of the significant fluctuations in animal populations that trigger and influence conservation action and planning (Gregory et al., 2004), population estimation and monitoring are vital to population dynamics and are regarded as essential components of species prioritization, research design, policy making, conservation practice, and management (Sankaran, 1998; Brouwer et al., 2003; Taylor & Pollard, 2008; Moussy et al., 2022). Animal population monitoring is intermittent, frequently poorly organized, and sporadic globally (Pereira & Cooper, 2006). It also contains many taxonomic, geographical, and methodological biases (Schmeller et al., 2012), even within the most commonly studied groups, such as birds (Garnett & Geyle, 2018). Furthermore, monitoring methods and programmes may fall short of consistency, fundamental objectivity, standardization, replication, and longevity (Lindenmayer et al., 2012; Buckland & Johnston, 2017). Moreover, when the population monitoring methods for the birds in the understudied habitat are not yet standardized, the prioritization and conservation of the species are challenging.

Cave/subterranean habitats may be the most underlooked and lack scientific attention compared to other terrestrial habitats. These habitats remain vulnerable (Slay, 2019) due to various threats, including anthropogenic pressures (Wynne et al., 2021; Ferreira et al., 2020). As the essential energy providers for the oligotrophic subterranean habitat, robust population monitoring for conserving cave-dwelling birds is necessary (Johnson et al., 2017). Numerous survey methods have developed over time to estimate the population of terrestrial birds (Sutherland et al., 2004; Bibby et al., 2000). However, few techniques (Figure 1.3) have been established to estimate the cave-dwelling bird populations due to the undulating terrain, inaccessibility, and limited knowledge of the subterranean habitat, including caves. The twilight (dawn and dusk) and night-time hours are when echolocating cave-dwelling birds are known to enter and leave their roosting caves (Manchi, 2009; Mane & Manchi, 2019). Since birds' roosting and nesting places in caves are inaccessible or usually unknown, it is challenging to estimate their population. The accessibility to the breeding sites is crucial for population estimation because reaching all the nesting sites in a cave is challenging (Johnson et al., 2018).

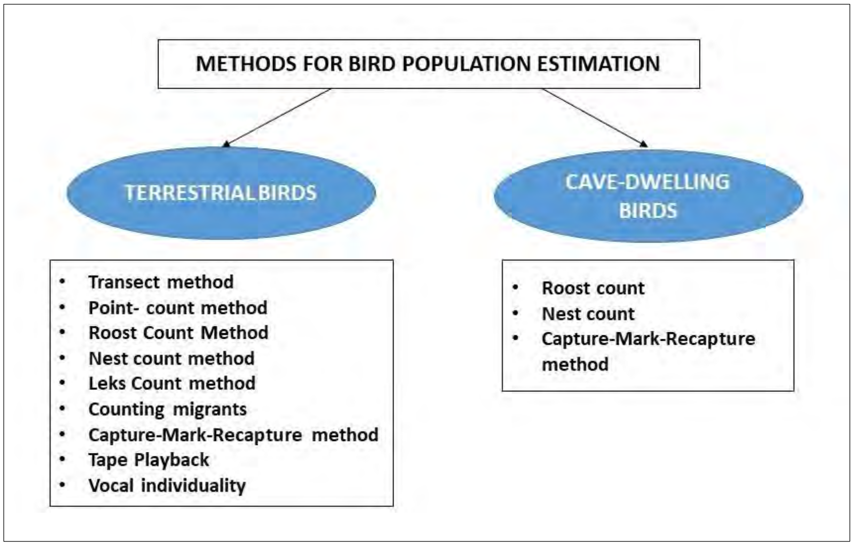


Figure 1.3: Examples of known methods for estimating populations of Terrestrial and cave-dwelling birds (Medway, 1962; Otis et al., 1978; Bosque & Ramirez, 1987; Tarburton, 1987; Pollack, 1991; Pollack, 2000; Gibbons et al., 1996; Bibby et al., 2000; Sankaran, 2001; Newton et al., 2002, Urfi et al., 2003; Sutherland et al., 2004, Manchi & Sankaran, 2008; Manchi & Sankaran, 2014; McFarlane et al., 2015; Idrees et al., 2016; Mane, 2017, Mane & Manchi, 2017; Johnson et al., 2018)

The Apodids are the most known colonial birds living in caves, and their population dynamics have not received much attention (Figure 1.7). Further, it is critical to understand the species' population dynamics towards managing this natural resource, the edible nest, and the conservation of its producer. Present study aims to investigate the characteristics and population dynamics of the cave-dwelling Edible-nest Swiftlet *Aerodramus fuciphagus inexpectatus* of the Andaman and Nicobar Islands. The scientific outputs of the study might provide insights to improve *in-situ* management of the cave-dwelling swiftlets and other similar cave-dwelling birds.

1.2. SYSTEMATICS OF SWIFTLETS

The swiftlets belong to the order Caprimulgiformes, the family Apodidae. The family name, Apodidae, is derived from the Greek ἄπους (*ápous*), meaning "footless", a reference to the small, weak legs of these most aerial of birds (Camfield, 2004). The swiftlets cling to vertical surfaces of cave walls or nesting planks with the help of feeble feet, often feathered tarsi, and four strong and well-clawed heterodactyl toes, the hallux is reversible (Davis, 2001; Chua & Zukefli, 2016).

There has been controversy about phylogeny and taxonomy because of the lack of distinctive morphological characteristics between swiftlet species (Mayr, 1937; Chantler & Driessens, 1995; Thomassen et al., 2003; Mane, 2017). The DNA-DNA hybridization analysis broadly considered the owls (Strigiformes), the nightjars (Caprimulgiforms), the swifts, and hummingbirds (Apodiformes) to form a monophyletic congregation (Sibley & Ahlquist, 1990; Mane, 2017). The family Apodidae (Swifts and swiftlets) and Hemiprocnidae (Treeswifts) have normally been grouped along with their most closely allied Trochilidae (Hummingbirds) (Chantler & Driessens, 1995; Mane, 2017). Brooke (1970) divided Collocalia into three different sub-genera: *Aerodramus* (Echolocating Swiftlets), *Collocalia* (Non-echolocating Swiftlets), *Hydrochous* (Non-echolocating Giant Swiftlets), which is well-supported by recent phylogenetic studies within the Collocaliini (Chantler, 2017; Mane, 2017). However, it is proposed to either combine these three genera into a single genus, *Collocalia* (Salmonsen, 1983; Chantler & Driessens, 1995), or incorporate new sister groups, *Chaeturini* and *Apodini,* into the pre-existing genus based on various morphological and behavioural characteristics (Sibley & Ahlquist, 1990; Mane, 2017).

Because of the restrictions of morphological identification, Lee et al. (1996) used molecular techniques to sequence the cytochrome-b mitochondria DNA of swiftlets to reposition the taxonomy. However, a restricted portion (406 bp) of the complete cytochrome-b DNA was sequenced, leaving many questions unanswered. Further, Thomassen et al. (2003) sequenced the complete cytochrome-b gene, and the result strongly supported swiftlet monophyly. However, due to high variation in the cytochrome-b gene in *Hydrochous* species, the placement of *Hydrochous* within the swiftlet phylogenetic tree was deficiently explained (Looi & Omar, 2016). In another study, Jordan et al. (2004) incorporated more swifts and swiftlet species using an additional NADH dehydrogenase subunit-2 gene (ND2) in the analysis for generating better and more comprehensive taxonomic results. The result supported the Swiftlet monophyly and separated the swiftlets into *Aerodramus* and *Collocalia*. Further, as the author proposed for not attributing the echolocation ability to a single genus because the pygmy swiftlet (*Collocalia troglodytes*) is an echolocating swiftlet species that was previously grouped under non-echolocating *Collocalia*, which shows echolocation is not an accurate parameter for the swiftlet taxonomical classification. Thomassen et al. (2005) incorporated two additional sequences, nuclear non-coding b-fibrinogen intron 7 (Fib7) and 2S rRNA (12S) into the pre-established cytochrome-b sequence data set to investigate the phylogenetic relationships of *Hydrochous gigas* with other members of the swiftlets which shows Waterfall Swift *Hydrochous gigas* as *Aerodramus*'s sister group and classified the swiftlets into a single genus *Collocalia* (Gray, 1841; Looi & Omar, 2016).

Based on recent phylogenetic studies, swifts and hummingbirds (Order: Apodiformes) were included within Order: Caprimulgiformes. Study shows that the order Caprimulgiformes is not monophyletic: The Aegothelidae (Owlet & Nightjars) was the sister group of the Apodiformes (Swifts & Hummingbirds). Although some of the divisions within this group remain controversial, there is broad consensus that the swifts are most closely related to the Treeswifts (Barrowclough et al., 2006; Mayr, 2009). Currently, Order Caprimulgiformes consists of 18 genera containing 112 species (Figure 1.4).

1.3. CHARACTERS OF SWIFTLETS

The swiftlets are small cavernicolous echolocating birds from the Family Apodidae, which feed on aerial insects during light hours (Chantler & Driessens, 1995). The adaptation to aerial life and insectivorous feeding habits is reflected in the aerodynamic body. Body bullet-shaped, with a short neck and long-tapered and bow-shaped wings. Wings narrow, back-swept, and down-swept, with shallow camber; adapted for high-speed rather than manoeuvrable flight. The long primaries and short secondaries produce a strong downward force and forward propulsion; swiftlets sweep through the air with flickering wing beats and protracted scything glides (Thomas, 1997; Davis, 2001). Deeply forked tails are found in many species of swifts (Apodidae) and swallows (Hirundinidae) may reflect selection for both aerodynamic and display functions. Deeply forked tails in aerial foraging aves may be an adaptation for pursuing and capturing the agile prey or foraging close to vegetation and low to the ground (Waugh & Hails, 1983; Davis, 2001). Fanning of the wing and tail feathers is a frequently observed behavior associated with rapid flight changes during prey captures by swiftlets (Thomas, 1997; Davis, 2001; Manchi & Sankaran, 2010; Collins & Thomas, 2012). Bill is very short, wide, and without bristles, with a broadened gape extending below eyes to increase sweep. bills dusky, or lower mandible flesh-toned; nostrils inoperculate oblique holes opening vertically at the base of the maxilla. Tongue short, triangular, bifurcate at the tip, and not extendable. A wide-gaped mouth can accumulate insects in a saliva-cemented bolus, carried in a pouch under the tongue when feeding young (Davis, 2001).

Echolocation is the capability to orient while flying in dim light or complete darkness. The ability to echolocate by producing audible clicks has evolved in only two groups of birds: The Neotropical Oilbird (Steatornithidae) and members of the Paleotropical Swiftlets (Apodidae) (Griffin, 1958; Medway, 1959; Price et al., 2004). Echolocation provides a unique advantage for these birds by allowing them to roost and nest in the dark crevices of caves, free from visually orienting predators or competitors (Fenton, 1975; Medway & Pye, 1977).

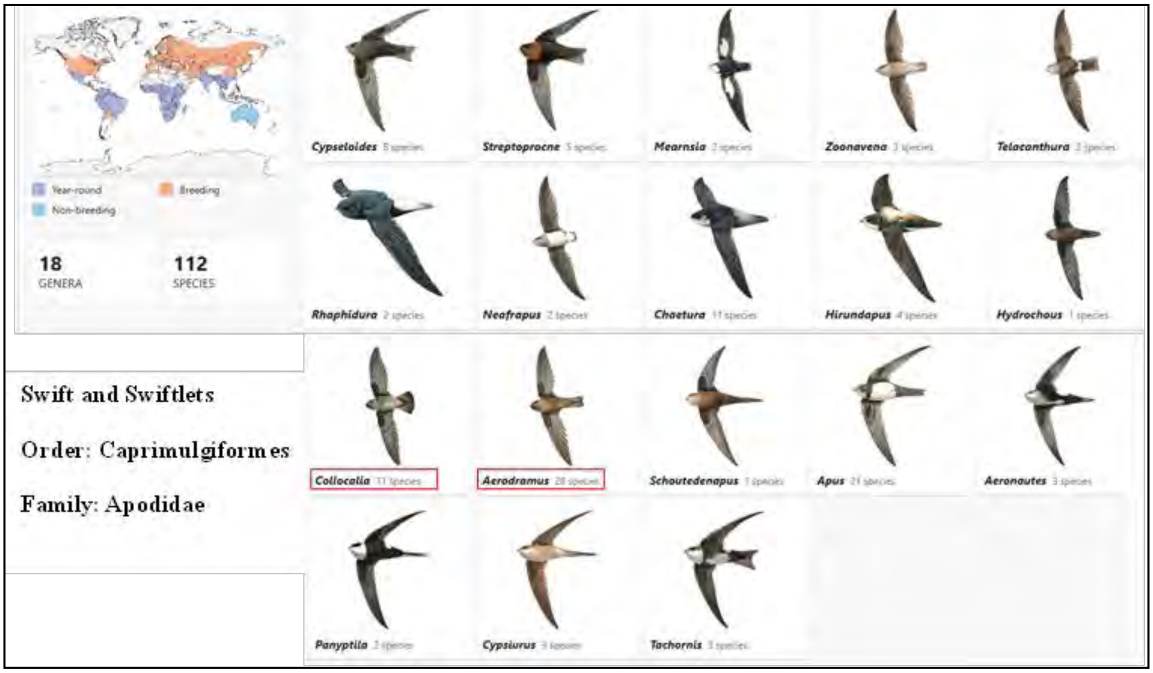


Figure 1.4: The Swift and Swiftlet species in the world (Winkler et al., 2020)

Studies show that these birds, unlike bats (Chiroptera), use the echo clicks primarily for avoiding obstacles while flying rather than for capturing its prey (Medway, 1962; Cranbrook & Medway, 1965; Medway, 1967; Fenton, 1975; Price et al., 2004). While most echolocating swiftlets emit double clicks "*tik, tik, tik*" during echolocation, each of which consists of two broadband pulses separated by a brief pause (Griffin & Suthers, 1970; Medway & Pye, 1977; Suthers & Hector, 1982; Price et al., 2004), oilbirds emit a single discrete pulse sound for orientation (Griffin, 1953; Konishi & Knudsen, 1979; Price et al., 2004). The intra-click delay can differ slightly between species and even between individuals. The second click of a doublet is often louder than the first, with most of its acoustic energy occurring between 2 and 8 kHz (Suthers & Hector, 1982). As exception, the Atiu Swiftlet *Aerodramus sawtelli* and the Black-nest Swiftlet *Aerodramus maximus* (Medway, 1959; Medway & Pye, 1977; Price et al., 2004) produce single clicks in contrast to doublets (Price et al., 2004).

Swiftlets are known to be monogamous and show nest site fidelity, are faithful to their nesting sites, and rebuild their nests in the same site even after their nests are removed (Viruhpintu et al., 2002; Manchi, 2009; Mane, 2017). They start breeding at one-year-old

(Nguyen et al., 2002; Looi & Omar, 2016). However, across different species and geological regions the breeding seasons and the period of various activities such as nest-building, egg laying, egg incubation, and young rearing vary. These variations are influenced by climatic factors such as rainfall, air humidity, and food availability (Langham, 1980). The breeding cycle of the swiftlets is approximately 92–120 days, usually with two eggs in a clutch (Langham, 1980; Lim et al., 2002; Viruhpintu et al., 2002; Mane, 2017; Looi & Omar, 2016). The incubation and fledging periods for swiftlet species vary from 21-28 days and 39-58 days, respectively (Medway, 1962; Langham, 1980; Lim et al., 2002; Looi & Omar, 2016). Some swiftlets breed year around (Tarburton 2009; Looi & Omar, 2016). During the breeding season, swiftlets take approximately 30-45 days to complete a single nest and about 60-80 days in the non-breeding season (Aowphol et al., 2008; Looi & Omar, 2016). Nests were initially believed to be built almost exclusively by male swiftlets within approximately 35 days (Marcone, 2005). However, it is reported that both sexes participate in the nest building (Lim et al., 2002; Manchi, 2009; Looi & Omar, 2016).

Swiftlets are one of the most accomplished flyers among all bird species, spending most of their lives on the wing, catching and feeding on insects in flight (Cranbrook & Lim, 1999). The unusually wide mouth opening and small beak make catching flying insects (Davis, 2001; Manchi, 2009). The wings of the Apodidae family have nine or ten primary and eight to eleven extremely short secondaries, which give the members of this family their remarkable speed and powerful lift (Davis, 2001). For instance, the Chimney Swift *Chaetura pelagica* (Linnaeus, 1758) was found to fly at a maximum speed of 110 km/h, and the White-throated Needletails, *Hirundapus caudacutus*, were seen flying at a maximum speed of 170 km/h (Latham, 1802). Along with being aerodynamic, the swiftlets can cling to steep surfaces because of their powerful paws, which feature sharp, curved claws (Davis, 2001; Manchi, 2009). By sensitizing hemoglobin for the best oxygen delivery in hypoxic circumstances at higher altitudes with lower atmospheric pressure, studies demonstrate the remarkable physiological adaptation of these birds to a high-altitude way of life (Josep et al., 1999; Manchi, 2009). Swiftlets breed naturally in limestone caves. They cling to the cave wall and ceiling surface (Ford & Cullingford, 1976; Langham, 1980; Lim et al., 2002; Looi & Omar, 2016). Many studies show the relationships between nesting success and environmental factors and the influence of various nest-site characters (Jehle et al., 2004; Phach & Voisin, 1998; Sankaran, 2001; Viruhpintu et al., 2002; Looi & Omar, 2016).

The roosting ecology studies on Oilbird *Steatornis caripensis* of South America, Cave Swallow *Petrochelidon fulva* of North America, and Swiftlets (*Aerodramus* and *Collocalia*) from the Eastern region show that these birds spend significant phases of their life roosting in caves or cave-like habitats (Mane, 2017). The only echolocating, nocturnal foragers echolocating swiftlets are distinctive among the Aves (Osmaston, 1906). The Black-nest Swiftlet *Aerodramus maximus* and the Mossy-nest Swiftlet *Aerodramus salangana* were described by Harrisson (1976) as foraging at night under a full moon. These local birds spend the night in their nesting locations. Common Swift *Apus apus* and other family members are known for roosting in the air (Tarburton & Kaiser, 2001); occasionally, breeding adults, non-breeders, and fledged individuals have been reported roosting to 2000–3000m elevations. The Common Swift *Apus apus*, Vaux's Swift *Chaetura vauxi*, Chimney Swift *Chaetura pelagica*, and Alpine Swift *Tachymarptis melba* have well-studied roosting habitats (Lack, 1951; Lack, 1956; Baldwin & Hunter, 1963). The length of the roosting phase is dependent on several factors, including the species' behavior, age, and climate (Spendelow, 1985; Watson, 1997), which are ultimately connected to the species' energetics and the diurnal pattern of its prey density (Zammuto & Franks, 1978; Rodgers, 1987). When at roost, these species construct nests using the nest cement, i.e., saliva secreted from a pair of sub-lingual glands (Lim & Cranbrook, 2002; Ramji et al., 2013) mixed in most species of swiftlets, with material such as feathers and plant fibers. The swiftlet species like Germain's Swiftlet *Aerodramus germani* (Oustalet, 1876) and Indian Swiftlet *Aerodramus unicolor* use comparatively more saliva to bind their feathers. These nests appear dark in color and are known as black nests, and the nest producers are recognized as Black-nest Swiftlet (Manchi, 2009).

Table 1.1: Plumage of various Swift and Swiftlet Species (Source: Handbook of the Birds of the World, 2022)

Species	**Plumage**
Satin Swiftlet *Collocalia uropygialis* (Gray, 1866)	Dark blue glossy plumage and possess a short beak with a wide gape.
White-collared Swift *Streptoprocne zonaris* (Shaw, 1796)	Black plumage with an utterly white collar
White-naped Swift *Streptoprocne semicollaris* (DeSaussure, 1859)	Dark plumage with a striking white hind collar
Biscutate Swift *Streptoprocne biscuits* (Sclater, 1866)	Blackish brown plumage with an incomplete white collar
Chestnut-collared Swift *Streptoprocne rutila* (Vieillot, 1817)	Bright reddish chestnut throat
Tepui Swift *Streptoprocne phelpsi* (Collins, 1972)	Bright reddish chestnut throat
Philippine Spinetailed Swift *Mearnsia picina* (Tweeddale, 1879)	Glossy plumage
Purple Needletail *Hirundapus celebensis* (Sclater, 1865)	Glossy plumage
White-throated Needletail *Hirundapus caudacutus* (Latham, 1802)	Glossy plumage
Glossy Swiftlet *Collocalia esculenta* (Beavan, 1867)	Glossy plumage

Biscutate Swift *Streptoprocne biscuits*

White-collared Swift *Streptoprocne zonaris*

White-naped Swift *Streptoprocne semicollaris*

Glossy Swiftlet *Collocalia esculenta*

Satin Swiftlet *Collocalia uropygialis*

White-throated Needletail *Hirundapus caudacutus*

Tepui Swift *Streptoprocne phelpsi*

Philippine Spinetailed Swift *Mearnsia picina*

Plate 1.1: Plumage of Various species of Swift and Swiftlets (Source: Handbook of the Birds of the World)

The nest of the Edible-nest Swiftlet or White-nest Swiftlet *Aerodramus fuciphagus* (Hume, 1873) comprises pure saliva. This salivary nest glue mainly comprises glycoproteins (Cranbrook & Lim, 1999; Manchi, 2009; Ramji et al., 2013). Further, due to significant commercial and reputed pharmaceutical value, Edible nest is used in renowned "bird's nest soup" as the main ingredient (Ismail, 1999; Tompkins, 1999; Lim, 2000; Ramji et al., 2013). Because of their valuable nests, Edible-nest Swiftlets have a long historical association with humans, from the early exploitation of natural cave colonies to the more enterprising undertaking of swiftlet farming in recent years (Ramji et al., 2013). Traditional Chinese Medicine describes the nest as highly medicinal and an aphrodisiac. Because of the over-exploitation of the nests around the world, the wild populations of the species are in decline (Dai et al., 2021; Yeo et al., 2021). Most swiftlet species show dull grey-brown plumage with some exceptions of dark blue glossy color plumage: a slight gloss in fresh plumage, and the function of this sheen is still unknown (Table 1.1, Plate 1.1). The increased albedo of glossy feathers is believed to be vital in protecting the plumage, or the gloss could affect thermoregulation and aerodynamics (Josep et al., 1999; Manchi, 2009).

1.4. GLOBAL DISTRIBUTION OF SWIFTLETS

Palaeotropical swiftlets (Genera *Aerodramus, Collocalia, and Hydrochous*) are typically small, dark, insectivorous birds with torpedo-shaped bodies and high aspect ratio wings that testify to a life spent on the wing. They are found in the Indo-Pacific region, i.e., from the Western Indian Ocean to Southern continental Asia, Indonesia, Northern Australia, and New Guinea to Islands of the West and South Pacific. In the Northern region of India, they extend to the Himalayas and China. The southern range reaches Mauritius in the Indian Ocean, Queensland, Australia, and East New Caledonia in the Southwestern Pacific region. The Edible-nest or White-nest swiftlets are found in Southeast Asian countries or regions within the geographical range including the Andaman and Nicobar Islands, Hainan Island in China, Palawan Island in the Philippines, the coasts and islands of Vietnam, Cambodia, Thailand, Myanmar, Malaysia and Singapore, and the Indonesian archipelago, including Sumatra, Java, the Lesser Sunda Islands, and Borneo (Nguyen et al., 2002; Koon & Cranbrook, 2002, Manchi, 2009; Mane, 2017; Figure 1.5).

Edible-nest Swiftlet *Aerodramus fuciphagus inexpectatus*

Indian Swiftlet *Aerodramus unicolor*

Plume-toed Swiftlet *Collocalia affinis affinis*

Himalayan Swiftlet *Aerodramus brevirostris*

Plate 1.2: Swiftlet Species found in India (Photo Credit: Himalayan Swiftlet; Ayuwat Jearwattanakanok)

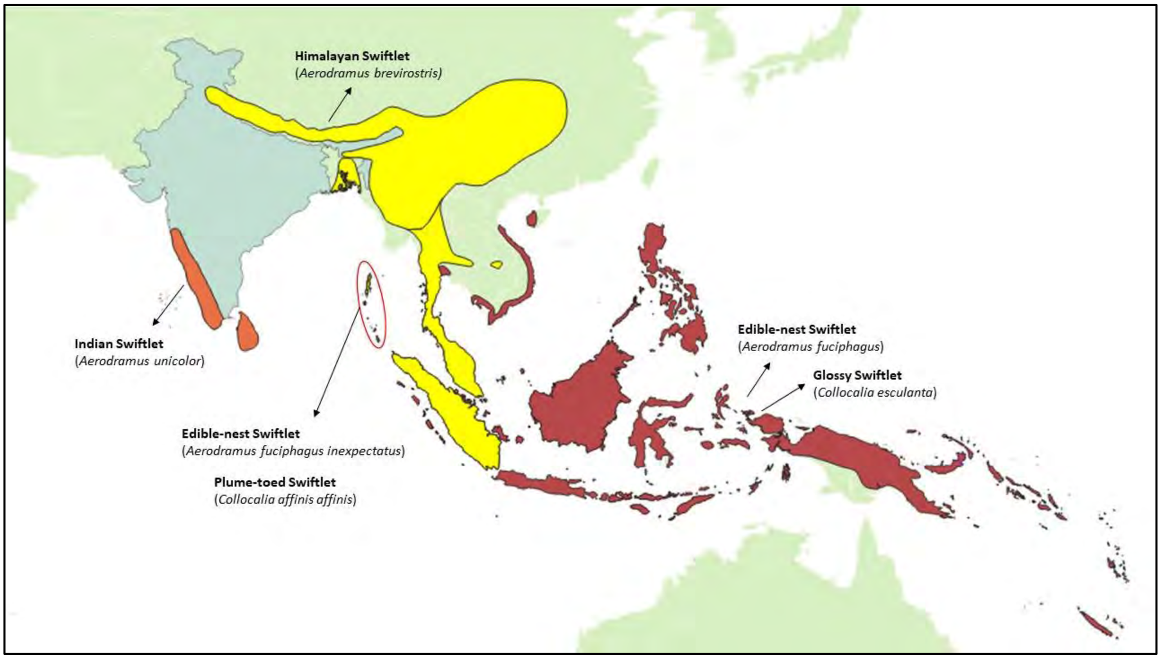


Figure 1.5: Global Distribution of Swiftlets (Data credits: Copyright Birdlife International and Handbook of the Birds of the World, 2022)

Currently, Order Caprimulgiformes consists of 18 genera containing 112 species. There are 39 species of swiftlets belonging to the genus *Collocalia* (11 Species) and *Aerodramus* (28 species) (Winkler et al., 2020; Figure 1.4). Further, Swiftlets are divided into five conservation status criteria according to the Global IUCN Red List (2022) as follows: two species are Vulnerable (VU): Seychelles Swiftlet *Aerodramus elaphrus* (Oberholser, 1906) and Atiu Swiftlet *Aerodramus sawtelli* (Holyoak, 1974), Two species are Near Threatened (NT): Mascarene Swiftlet *Aerodramus francicus* (Gmelin, 1789) and Volcano Swiftlet *Aerodramus vulcanorum,* one species is Endangered (EN): Mariana Swiftlet *Aerodramus bartschi* (Mearns, 1909), three species are Data Deficient (DD): Whitehead's Swiftlet *Aerodramus whiteheadi* (Ogilvie-Grant, 1895), Mayr's Swiftlet *Aerodramus orientalis* (Mayr, 1935) and Three-toed Swiftlet *Aerodramus papuensis* (Rand, 1941) and 31 species are Least Concerned (LC) (Winkler et al., 2020).

India has four species of Swiftlets distributed within its political boundaries (Plate 1.2). The Indian Swiftlet *Aerodramus unicolor* is endemic to the Western Ghats and Sri Lanka. The Himalayan Swiftlet *Aerodramus brevirostris* is found in the Northeastern region of India (Osmaston, 1906; Ali & Ripley, 1970; Sankaran, 1998). The Plum-toed Swiftlet

Collocalia affinis affinis, is a sub-species endemic found in the Andaman and Nicobar Islands. The bird uses moss, twigs, leaves, flowers, and others (Koon & Cranbrook, 2002), bound together with a small quantity of saliva. Saliva is also used to attach the nest to the rock surface. The Edible-nest Swiftlet *Aerodramus fuciphagus inexpectatus* is India's most economically important species. Locally, it is known as Hawabill and is widely distributed in the Andaman and Nicobar Islands.

1.5. STUDY SPECIES

EDIBLE NEST-SWIFTLET *AERODRAMUS FUCIPHAGUS INEXPECTATUS* (HUME, 1873)

The Edible-nest Swiftlet *Aerodramus fuciphagus inexpectatus* (Hume, 1873) are cave-dwelling gregarious birds living in the colonies and belonging to the Family Apodidae (Figure 1.6). The species is endemic to the islands in the Bay of Bengal of Indian territory. They are monogamous with high nest site fidelity and live in the limestone caves of the Andaman and Nicobar Islands. They roost and breed inside caves or in cavern-like places, hang to the surface of walls and ceilings, or on self-supporting bracket-shaped nests (Langham, 1980; Koon & Cranbrook, 2002). Edible-nest Swiftlets are aerial foragers and insectivores. They do not perch anywhere besides roosting and nesting sites in caves (Josep et al., 1999).

Echolocation provides a unique advantage for these birds by allowing them to roost and nest in the dark regions of caves, free from visually orienting predators or competitors (Medway, 1959; Fenton, 1975). Compared to Bats (Insectivorous Microchiroptera), this species has primitive echolocation. The *Aerodramus* swiftlets produce broadband clicks while flying, primarily for avoiding obstacles. These clicks are audible to humans, with peak frequencies (PFs) between 1 and 16 kHz. Swiftlets do not use echolocation to collect extensive information from the echoes of their clicks like bats do; they only use it for low-resolution target discrimination. Swiftlet signals have a disorganized, click-like sound, which shows that frequency structure is not a key component in these calls (Pye, 1980; Fullard et al., 1993).

The breeding season of Edible-nest Swiftlet is from December to August. The nest comprises saliva secreted by sub-lingual glands (Shah et al., 2014). The body length and tail length of this bird measure in the range of 115–125mm and 49-53mm, respectively. The Edible-nest Swiftlet is a medium-sized bird with a body weight of about 13–18gm. The plumage is black-brown under part and a slightly grey rump with a tail fork 10–19% of the tail length (Chantler, 2017; Mane, 2017).

Figure 1.6: Edible-nest Swiftlet *Aerodramus fuciphagus inexpectatus* (Hume, 1873)

While most species use saliva to bind the vegetative matter (leaf, moss, twigs, and others) or feathers into nests, the Edible-nest Swiftlet builds nests wholly of the saliva (mucilaginous secretion). They have a pair of sublingual glands (Marshall & Folley, 1956), which enlarge during the breeding season for the nest building (Medway, 1962). The edible nest of the swiftlet is considered an essential item in Traditional Chinese medicine and cuisine, making it a significant and expensive agricultural product in the global market (Sankaran, 2001; Ibrahim et al., 2009; Thorburn, 2015; Mardiastuti, 2016). This salivary glue mainly comprises glycoproteins, consisting of protein (61.0–66.9%) with 15.9–31.6 mg/g protein of essential amino acids and carbohydrates (25.4–31.4%). Sulphur-containing essential amino acids methionine, cysteine, and glutamine were the main amino acid constituents, and mineral elements like sodium (Na), calcium (Ca), magnesium (Mg), and potassium (K) are also constituents of the salivary secretion (Saengkrajang et al., 2013). In medicine, an edible bird's nest extract has been shown to increase epidermal growth factor and suppress influenza virus infection (Guo et al., 2006; Saengkrajang et al., 2013). Edible bird nest has reportedly been identified to contain estradiol hormones (Ma & Liu, 2012; Saengkrajang et al., 2013). These hormones benefit women since amenorrhea and irregular menstruation are more common when estrogen levels are low (Bergemann et al., 2005; Saengkrajang et al., 2013).

The edible nest trade dates back to the T'ang dynasty in the 16th century, when the edible bird nest became important in Chinese cuisine and pharmacy. The trade gained momentum after the Asian economic crisis of 1997-1998, leading to the loss of wild populations in Southeast Asia. Since then, the Edible-nest Swiftlet has been exploited throughout its distribution range (Medway, 1963; Lau & Melville, 1994; Sankaran, 2001). Presently reaching USD 2,521 per kilogram in the world export market (Lidyana, 2019; Mursidah et al., 2020), the price of edible birds' nests is perhaps one of the most valuable natural products per unit weight. Indonesia alone dominates 75% of the edible-nest exports in the international market (60% exported to China, 25.7% exported to the United States and while the rest is supplied by Malaysia, Thailand, Myanmar, Vietnam, Southern China, and the Philippines (Kuan & Lee, 2005; Nugroho & Budiman, 2013; Tan et al., 2014; Nurshuhada et al., 2015). According to Ya'acob et al. (2021), the production of swiftlet nests is expected to increase due to continued demand from China, where it is prevalent among the people besides measuring the status of individuals in China.

1.6. CONSERVATION OF THE EDIBLE-NEST SWIFTLET

Across the distributional range of the species, the cave (*in-situ*) populations of Edible-nest Swiftlets have drastically declined due to over-exploitation of their nests and is a result of the indiscriminate nest harvesting (Lau & Melville, 1994; Sankaran, 1995; Sankaran, 2001; Koon & Cranbrook, 2002; Nguyen et al., 2002; Gausset, 2004; Hobbs, 2004). Nugroho and Whendrato (1996), mentioned the reductions of swiftlet populations, particularly of *Aerodramus fuciphagus*, *Aerodramus germani*, *Aerodramus maximus*, and *Aerodramus unicolor* in many caves of the nest-producing countries. For instance, the uncontrolled harvesting of nests in China probably led to the local extinction of

Aerodramus fuciphagus and *Aerodramus maximus*. Aitken (1894) in the Western Ghats of India and Gunawardana (1997) in Sri Lanka documented a decline in *Aerodramus unicolor*'s population. Also, a drastic decline (>80%) in the *Aerodramus fuciphagus* was observed by Sankaran (1995; 1998; 2001) in the Andaman and Nicobar Islands, India. Good Wong (1989) recorded a 43% reduction in the wild population of *Aerodramus fuciphagus* and *Aerodramus maximus* in other countries such as Malaysia. Further, in Indonesia, few also attribute the population decline to the rapidly growing Edible-nest Swiftlet farming industry (Mardiastuti & Soehartono, 1996; Nugroho & Whendrato, 1996).

The production of white nests from natural caves has significantly decreased, and many caves do not bear swiftlet populations due to overharvesting. Thus, harvest management of cave swiftlets was considered unsustainable (Lau & Melville, 1994). It is understood that a high proportion of the nests coming to international trade are from swiftlet farms (Mardiastuti, 2016). Further, measures such as leasing and management of caves by local people have failed to protect the swiftlets in many locations (Koon & Cranbrook, 2002; Nguyen et al., 2002).

However, in India, according to Sankaran (2001), nest collection was common in 95% of caves in the Andaman and Nicobar Islands (n= 291). The percentage of nests from the Andaman and Nicobar Islands reaching the global market remains unknown (Lau & Melville, 1994). As a result, the Edible-nest Swiftlet was critically threatened (IUCN Criteria A1c) in the Andaman and Nicobar Islands, as > 80% of the Edible-nest Swiftlet population was lost between the late 1980s and early 1990s. Also, it was predicted by Sankaran (1998; 2001) that in the absence of regulation, the potential extinction of the white-nest swiftlet on the Andaman and Nicobar Islands by 2025. Considering the over-exploitation of the nests to be a threat to the Edible-nest Swiftlet populations in the islands, a systematic and pragmatic approach for in-situ and ex-situ conservation of the edible-nest swiftlet population was suggested by Sankaran (2001). Under the in-situ conservation program, the protection began from 2000 onwards in the 28 caves on Challis-Ek, North Andaman, and one in Interview Island. Further, a survey by Manchi and Sankaran (2014) from February–April 2008 concluded that the swiftlet population in protected caves of Challis-Ek and Interview Island increased by 39%, whereas it declined by 74% in unprotected caves (1,799 nests in 1997).

1.7. PAST STUDIES ON THE EDIBLE-NEST SWIFTLET IN THE ANDAMAN ISLANDS

Swiftlets are a species of ecological importance (Medway, 1963; Lau & Melville, 1994; Sankaran, 2001). Owing to the significance of the bird, many studies have been conducted on their breeding and foraging ecology (Medway, 1962a; Medway, 1962b; Tarburton, 1987a; Collins, 2000; Manchi & Sankaran, 2008; Manchi, 2009; Manchi & Sankaran, 2011; Manchi & Sankaran, 2014; Johnson, 2015; Johnson et al., 2017; Mane & Manchi, 2017; Petkliang et al., 2017; Mane, 2017; Tampus & Escasinas, 2019). Studies have also looked into swiftlet physiology (Hails & Turner, 1985; Nasir & Ibrahim, 2014; Ibrahim, 2016; Looi & Omar, 2016), echolocation (Suthers & Hector, 1982; Smyth & Roberts, 1983; Price et al., 2004; Thomassen et al., 2007; Brinkløv et al., 2013), behavior (Bryant & Tatner, 1990; Manchi & Sankaran, 2010; Mane & Manchi, 2017), flight dynamics (Tarburton, 1986; Davis, 2001).

A few swiftlet species produce edible-nest (Edible-nest Swiftlet, Germain Swiftlet, Black-nest Swiftlet, and a few others), which is amongst the most expensive agricultural products in the global market (Medway, 1963; Lau & Melville, 1994; Mardiastuti & Soehartono, 1996; Nugroho & Whendrato, 1996; Sankaran, 2001; Manchi, 2009). As the nest is harvested from both wild and farmed populations, the research interest has also grown in the swiftlet populations in *ex-situ* conditions (Ramji et al., 2013; Chua & Zukefli, 2016; Connolly, 2016; Burhanuddin & Noor, 2017; Mursidah et al., 2020).

The Andaman and Nicobar Islands are the westernmost limit of the Edible-nest Swiftlet and is considered a subspecies Andaman Edible-nest Swiftlet (*Aerodramus fuciphagus inexpectatus*) endemic to the islands (Abdulali, 1964; Abdulali, 1967; Ali & Ripley, 1983; Cranbrook et al., 2013). The initial surveys to understand the population status and distribution were done by Sankaran (1995, 1998). The first attempt at breeding population estimation was made in the Nicobar Islands, where the total number of birds was assessed to be 2500-3600 (Sankaran, 1995). During the survey, the surveys also pointed out that the decadal population decline in yields ranged from 40% to 90% in 24 out of 36 swiftlet caves (Sankaran, 1995). In 1998, a survey was done in the Andaman Islands (Sankaran, 1998); the population of breeding pairs of Edible-nest Swiftlet was estimated to be 4621 breeding pairs. It was the first attempt to assess the population, distribution, and threats in the Andaman and Nicobar Islands (Sankaran, 2001). During the years (2001-2014), different studies were carried out by Manchi and Sankaran (2009) to identify potential predators for the swiftlet populations, which include species of owls, snakes, ants, and others. One of the most comprehensive studies on the Edible-nest Swiftlet and Plume-toed Swiftlet (*Collocalia affinis affinis*) is by Manchi (2009), which focused on the breeding ecology, including the biology, chronology, success, and breeding habitat in Challis-Ek and Interview Island. Subsequently, researchers continued and reassessed the population at three sites in the North and Middle Andaman Islands: Chalis-ek, Interview Island, and Baratang Island (Manchi & Sankaran, 2014). After the population reassessment, these are also identified as the most critical priority sites for swiftlet protection and conservation (Manchi & Sankaran, 2014). Later, Mane (2018) looked into the holistic research, roosting ecology of the Edible-nest Swiftlet, vegetation composition of the karst areas, and detailed behavior of Owls as the principal predators of the swiftlets. Mane et al. (2019) conducted detailed studies on the karst vegetation to understand the composition at Baratang Island. The study found remarkable vegetation patterns in the karst forest present at the cave complex of Baratang.

Figure 1.7: Global research conducted on Edible-nest Swiftlet *Aerodramus fuciphagus inexpectatus*

Along with the habitat, Mane and Manchi (2017) also looked into the roosting behavior of the species and the effects of lunar phase and breeding chronology. Simultaneously, Mane and Manchi (2019) also studied the spatiotemporal roosting movements of the swiftlets. Further, the most recent study by Manchi et al. (2022) has extensively studied the caves as habitat, pointing out a significant outcome on the role of the cave morphology in the habitat selection of the swiftlet. The study also identified the foraging grounds of the swiftlet in the Andaman Islands and prioritized the locations for the swiftlet *ex-situ* house.

However, many aspects of the species' population dynamics have never been attempted to be understood in past research concerning the Edible-nest Swiftlet because of its practical difficulties and uncertainty (Figure 1.7). The species' population dynamics can contribute to the Edible-nest Swiftlet's conservation in various ways towards managing populations and prioritizing the habitats for conservation focus. Other crucial questions about their population structure, colonial dispersal, breeding co-variates, longevity, life span, and survival rate remain undiscovered. The present study was designed to contribute to the knowledge regarding the population dynamics of the Edible-nest Swiftlet in the Andaman Islands. This study is the first related to the abiotic and biotic parameters that affect the population dynamics of any swiftlet species in its natural habitat (Figure 1.7).

1.8. AIM AND OBJECTIVES

The study was planned to understand more about population dynamics and its characteristics: population structure, dispersal, longevity, life span, survival rate, and co-variates of breeding in Edible-nest Swiftlet from the Andaman Islands. This study provides the baseline for future studies and opportunities to manage the in-situ and ex-situ populations better. The study was initiated and conducted to accomplish the following primary objectives:

1. To investigate the site-fidelity and understand the biotic and abiotic factors influencing the breeding site-fidelity in the Edible-Nest Swiftlet
2. To investigate the colonial sex- ratio in Edible-Nest Swiftlet
3. To understand the inter-colonial dispersal patterns and factors affecting the dispersal of the Edible-nest Swiftlet

1.9. ORGANIZATION OF THESIS

This Ph.D. thesis is organized into six chapters. The thesis opens with a chapter on the introduction and discussion about the study species and existing knowledge. After the introduction, the study area chapters cover the details about the Andaman Islands, followed by the intensive study areas. There are three technical chapters based on the objectives of the study. These chapters are divided into the introduction, objectives, methodology, results, discussion, and conclusion. Similar methods used for bird capture and recapture, blood collection, genetic data analysis, and others are detailed in each respective technical chapter for the convenience of readers. Further, the thesis concludes with a synthesis chapter that summarizes the overall findings and provides the significance of the study to future research and development.

Chapter 1 briefly introduces the subject and study species, current research in the field, and the present study's aim and objective. The chapter further details the study species and the lack of scientific attention given to this group of birds and highlights the study's rationale.

Chapter 2 describes the study location, the Andaman and Nicobar Islands, its geography, climate, vegetation, and geology. It also introduces caves in Andaman and Nicobar Islands and the details of the caves selected for this study. Further, it describes the location, vegetation, climate, and number of swiftlets inhabited caves in intensive study areas.

Chapter 3 focuses on understanding the adult site fidelity and factors influencing site fidelity in the Edible-nest Swiftlet. Further, the decision rule phenomenon "Prior-experience hypothesis" is tested and explained in detail.

Chapter 4 investigates the colony sex ratio, adult sex ratio (ASR), and offspring sex ratio (OSR) in Edible-Nest Swiftlet. This chapter further describes the use of bird morphometrics to identify a sexual dimorphism in combination with discriminant function analysis (DFA) and molecular techniques in Edible-Nest Swiftlet.

Chapter 5 focuses mainly on understanding the inter-colonial dispersal patterns, biotic and abiotic factors affecting the dispersal, and the density-dependent "Allee effect" in Edible-nest Swiftlet. Further, population dynamics parameters, namely longevity, mortality, survival, and life expectancy in Edible-nest Swiftlet, are discussed.

Chapter 6 concludes the population dynamics of the Edible-nest Swiftlet in the wild and provides information about important parameters that drive population dynamics: dispersal pattern, colony sex ratio, longevity, breeding success, life span, survival rate, and how the abiotic and biotic factors play a role in the dispersal. Finally, the important outcomes of the present study are compiled and presented as the baseline for future studies and inputs for better management of the *in-situ* and *ex-situ* populations. This chapter concludes the thesis by compiling major findings of the study.

Chapter II

CHAPTER II

STUDY AREA

2.1. ANDAMAN AND NICOBAR ISLANDS

2.1.1. Geography

Since Darwin and Wallace, islands have been recognized as important in studies of organismic variety, biogeography, and evolution. They make excellent locations for studying evolution, speciation, and adaptive radiation (Takayama et al., 2018). These island groups have a diversity of biota with significant endemism due to geographic isolation (Naithani, 2008). Islands comprise 5.3% of Earth's land area and are home to about 19% of bird species, 17% of rodents, and 17% of flowering plants (Bernie et al. 2015).

India has two important island groups: (1) Lakshadweep Islands and (2) Andaman and Nicobar Islands. The Lakshadweep Islands are the atolls off India's southwestern coast, whereas the Andaman-Nicobar archipelago is a group of islands and submerged mountain range peaks off the eastern coast stretching from Banda Aceh in Indonesia and the Lesser Sundas through the Arakan Yoma (Manipur-Burma) mountains to the Coco and Preparis Islands of Burma (Lodrick, 2023). The Andaman and Nicobar Islands emerge as an arc into the Bay of Bengal. The Bay of Bengal borders the archipelago to the West, while the Andaman Sea borders it to the East (Andrews & Sankaran, 2002).

The Andaman group of islands comprises more than 572 islands. North, Middle, and South Andaman, known collectively as Great Andaman, are the main islands; others include Landfall Island, Interview Island, the Sentinel Islands, Ritchie's Archipelago, and Rutland Island. Little Andaman in the south is separated from the Nicobar Islands by the Ten Degree Channel, about 90 miles (145 km) wide (Naithani, 2008; Bandopadhyay & Carter, 2017). The Nicobar Islands consist of 19 islands. Among the most prominent are Car Nicobar in the North, Camorta, Katchall, and Nancowry in the center of the chain, and Great Nicobar in the South. About 90 miles southwest of Great Nicobar lies the north-western tip of Sumatra, Indonesia (Naithani, 2008; Bandopadhyay & Carter, 2017).

The Great Andaman comprises the Andaman Group's five major islands: Baratang, Rutland, North, Middle, and South Andaman. Between Little and Great Andaman is Duncan Passage. The Ritchie's Archipelago, located northeast of South Andaman Island, comprises of several tiny islands, including Havelock, Neil, and Henry Lawrence Islands. The largest islands are divided by east-west tidal channels (straits), surrounded by dense mangrove forests on both sides. These straits are the Macpherson Strait between the South Andaman and Rutland Islands, the Middle Strait between the Baratang and South Andaman Islands, the Humphrey Strait between the Middle and Baratang Islands, and the Austin Strait between the Middle and North Andaman Islands. The Barren and Narcondam islands, situated in the Andaman Sea NE and NNE of Port Blair and part of the Andaman Group, are two more volcanic islands (Naithani, 2008; Bandopadhyay & Carter, 2017).

The Nicobar Group is dispersed over a 259 km area. They span an area of 1841 km^2 and have a greatest width of around 58 km (Bandopadhyay & Carter, 2017). There are 22 islands in all, 13 of which are inhabited. The northern, central, and southern Nicobar Islands groups are separated. West of the Nicobar Group is the dormant Nicobar Fan (Bowles et al., 1978), a topographically isolated section of the Bengal Deep-Sea Fan. The Nicobar Group's administrative center is located on Car Nicobar Island. Important islands from the Nicobar Group of Islands include Katchal, Camorta, Nancowry, Till Angchong, Chowra, Little Nicobar, and Great Nicobar (1045 km^2) (Naithani, 2008; Bandopadhyay & Carter, 2017).

2.1.2. Climate and Vegetation

The climate of the Andaman and Nicobar Islands is tropical but moderated by sea breezes (Lodrick, 2023). Temperatures typically vary between tropical and subtropical climates, with 79–89% humidity and daily temperatures ranging from 27–33°C and 21–25°C in the summer and winter (Chakravarthy et al., 1987; Lodrick, 2023). The NE monsoon begins to arrive in November, while the SW monsoon follows at the end of May. Since the SW monsoon, which blows from May through September, and the tropical cyclones that follow in October and November, bring abundant amounts of rainfall to Port Blair on South Andaman, it receives an average of 300–350 cm yearly (Chakravarthy et al., 1987).

The Nicobar Islands see substantially less rainfall, with an annual average of 51 cm (www.imd.gov.in, Hydromet Division, IMD, New Delhi). During the dry months, maximum daily sunlight hours of 8 to 10 hours are often reported, but clouds limit this to 3 to 8 hours during the rainy season.

The Andaman and Nicobar Islands are known for their exceptional diversity of habitat types, from sandy beaches to coral reefs, mangroves, and mountains with thick forests. The majority of the islands in the Andaman Group are covered in tropical rainforests with towering trees that frequently reach heights of more than 30 m (Gupta, 2011; Champion & Seth, 2005). Parkinson (1923), while describing the vegetation of these islands, stated that "from the water's edge to tops of the highest hills, the islands are nearly everywhere densely wooded". The forests of the Andaman and Nicobar Islands are classified into 11 types (Champion & Seth 2005): Giant evergreen forests, Andaman tropical evergreen forests, Southern hilltop tropical forests, cane brakes, wet bamboo brakes, Andaman moist deciduous forests, littoral forests, tidal swamp forests, and submontane hill valley swamp forests (Champion & Seth, 2005; Naithani, 2008).

About 80% of the 8249 km^2 land area is still covered in woods, renowned for their ecological diversity, worldwide relevance, and high species endemism. The inner evergreen and deciduous tropical and subtropical wet broadleaf forests and the coastal mangrove forests comprise most of the Nicobar Islands' vegetation, respectively. Other coastal characteristics include tidal creeks, sizable mangrove swamps, and mud flats. The Andaman and Nicobar Islands are home to one of the largest mangrove ecosystems in the world, with a total area of 966 km^2 (Andrews & Sankaran, 2002).

Out of 572 islands in the archipelago, 94 islands in the Andaman-Nicobar Group have been recognized as sanctuaries because of their distinctive and exceptional flora and wildlife. Four national parks—Mahatma Gandhi Marine Park, Mount Harriet, Rani Jhansi Marine Park, and Saddle Peak National Park—and two—Campbell Bay and Galathea—are located in the Andaman Group and Great Nicobar Island, respectively (Andrews & Sankaran, 2002; Bandopadhyay & Carter, 2017).

2.1.3. Geology

The Java-Sumatra trench's North-eastern and Burma's southern strip are parts of the Andaman-Nicobar arc. These islands are believed to have originated from a single eruption in the late Pliocene to early Pleistocene. Highly seismic, seismic, and aseismic zones with earthquake segments with shallow to intermediate foci in the Earth's crust are present throughout the region of the Burmese arc from Arakan to the Andaman Nicobar Islands to Sumatra and beyond (Kumar, 1981; Kumar, 1990; Manchi, 2009). The Sunda-Andaman subduction zone, where the Indian plate subducts obliquely beneath the Burmese (Myanmar) microplate, a sliver of the Eurasian plate, along the Andaman Trench, includes the archipelago of the Andaman and Nicobar Islands as part of an accretionary complex (Curray, 2005; McCaffrey, 2009; Awasthi & Ray, 2020). According to Chibber (1934), the single eruption that gave rise to these islands is thought to have occurred between the late Pliocene and the Pleistocene period. These islands are a part of a geosynclinal basin. Due to historical tectonic action, the rocks are heavily folded. The geological formations represent the sedimentation from the Cretaceous to the Sub-Recent period. Gravel beds and elevated soil coverings have surface deposits that are quite recent in development. The current arrangement took shape only 26 million years ago (Andrews & Sankaran, 2002).

The Ophiolite Group, the Mithakhari Group, the Andaman Flysch Group, the Archipelago Group, and the Nicobar Group are the five principal lithological groups that make up the sedimentary sequence revealed on the Andaman-Nicobar Islands (Curray, 2005; Figure 2.1). Aside from the Andaman Flysch, all groups are separated by substantial dissimilarities. Ocean-floor volcanic/plutonic rocks may be found in the Ophiolite Group at the base of the sequence, while pelagic sediments are found at the top. According to Sarma et al. (2010) and Pedersen et al. (2010), these plutonic rocks date back to the upper Cretaceous (*94 Ma). The Mithakhari Group of the Eocene epoch (40 Ma; Allen et al., 2007) lies on top of the Ophiolite Group and is composed of trench-slope deposits of conglomerate, sandstone, shale, and volcaniclastics. According to Bandopadhyay and Ghosh (2015), the Oligocene-Early Miocene Andaman Flysch Group (*30–20 Ma; Allen et al., 2007) comprises submarine fan deposits made up mostly of unfossiliferous siliciclastic turbidites that take the form of sandstone-shale rhythmites. According to Bandopadhyay and Ghosh (2015), the Mio-Pliocene Archipelago Group rocks are mostly carbonate with modest amounts of siliciclastics and volcaniclastic sediments. They are thought to have been deposited on a marine shelf environment. Limestones, beach deposits, unidentified volcanic rocks, and Pleistocene tuffs are all in the top Nicobar group. The Archipelago group is the earliest known sedimentary stratum in the Andaman-Nicobar Islands. These well-developed marine deposits are located close to Baratang, Middle Andaman, and are found atop the Late Cenozoic strata of the Andaman-Nicobar area (Manchi, 2009; Bandopadhyay & Ghosh 2015).

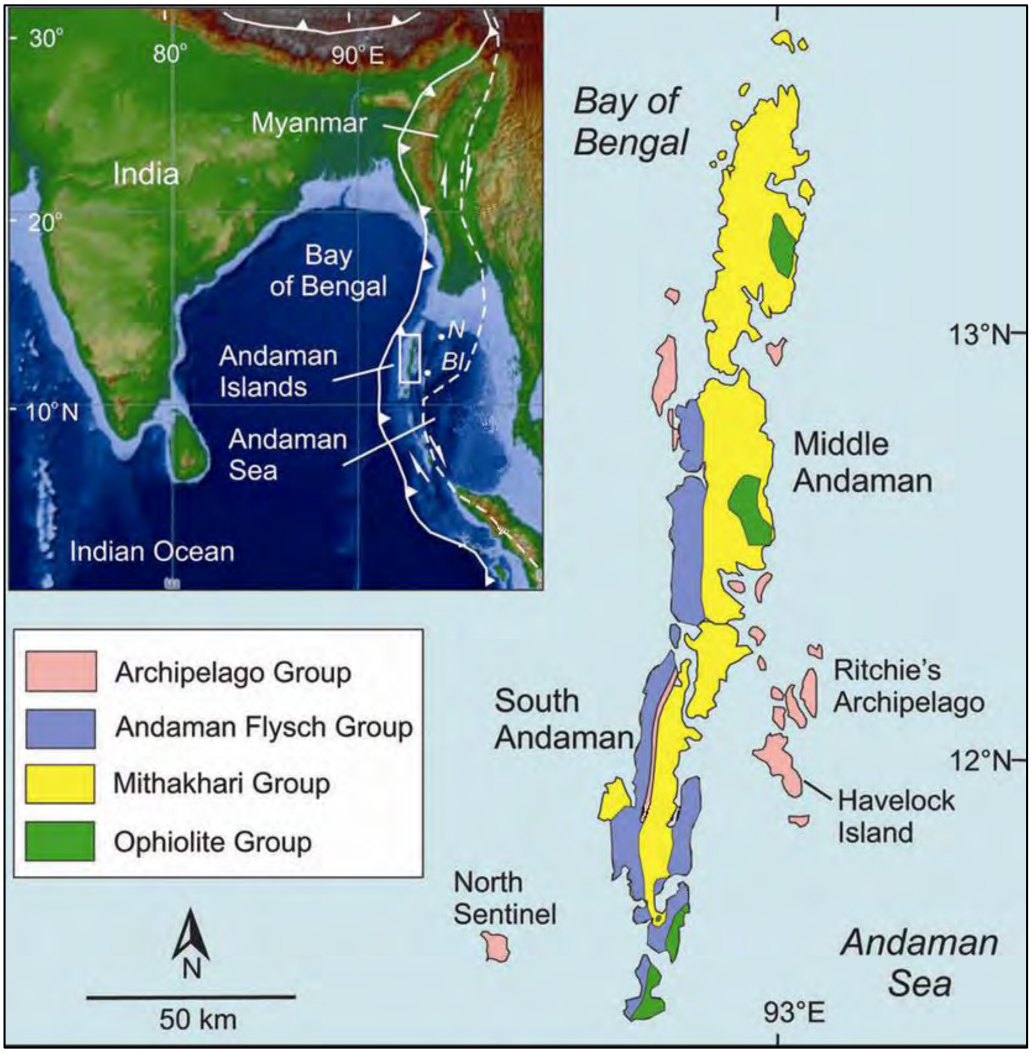


Figure 2.1: Geological map of the Andaman Islands showing the distribution of various lithological rock units (adopted from Pal et al., 2003)

2.1.4. Caves

Speleogenesis is the process of a cave system developing. Only lithified rocks: rocks made of particulate matter aggregates can form caves (Ford & Cullingford, 1976; Manchi, 2009). The characteristics of the original sediment and the diagenetic history changes brought about by the sedimentary processes during the transformation of the sediments into rock control the location of the caves. To explain why a certain cave or feature is where it is, it is crucial to thoroughly understand the surrounding limestone (Challinor, 1967; Ford & Cullingford, 1976; Manchi, 2009). Numerous caves may be found in the Andaman and Nicobar Islands. They can be divided into two main groups: (a) caves created by subsurface drainage and rock erosion in limestone formations and (b) caves created in sea cliffs by marine rock erosion (Challinor, 1986; Mane & Manchi, 2018). Subaerial erosion carves channels made by subsurface drainage, which are ultimately revealed. On the Andaman and Nicobar Islands, Sankaran (1998) documented 384 caverns, of which 325 are in the Andaman Islands and 59 are in the Nicobar Islands (Sankaran, 1998; Mane & Manchi, 2018). 86% of the 236 inland caves were subterranean, and 1% were at a stream's source. 14% of the caves visible from above were divided into those found on inland hills (97%), which made up the remaining 3%, and those found above ground on inland cliffs. Sankaran (1998; 2001) and Manchi (2009) found a total of 342 of the 384 caves that were surveyed to harbor swiftlet populations, including 291 caves with Edible-nest Swiftlet and 93 caves with Plume-toed Swiftlet. Of them, 249 caverns were home to populations of Edible-nest Swiftlet, 51 caves to Plume-toed Swiftlet alone, and 42 caves in which both species coexist (Sankaran, 2001).

2.2. INTENSIVE STUDY AREAS

2.2.1. Baratang Island, North and Middle Andaman Island

The southernmost portion of Middle Andaman is Baratang Island (12° 05′ N, 92° 45′ E, Figure 2.2 & 2.3) is the most significant known cave complex on the islands. Baratang cave complex is located between Wraffter's Creek and Naya Dera; the cave complex has 175 limestone caves and is 0.77 km^2 in size (Sankaran, 2001; Manchi & Sankaran, 2014; Mane et al., 2019; Plate 2.1).

Figure 2.2: Geographic location of Baratang, Chalis Ek, and Interview Island Cave Complex from Andaman and Nicobar Islands (Using ArcGIS 10.5, Esri, Redlands, California, USA).

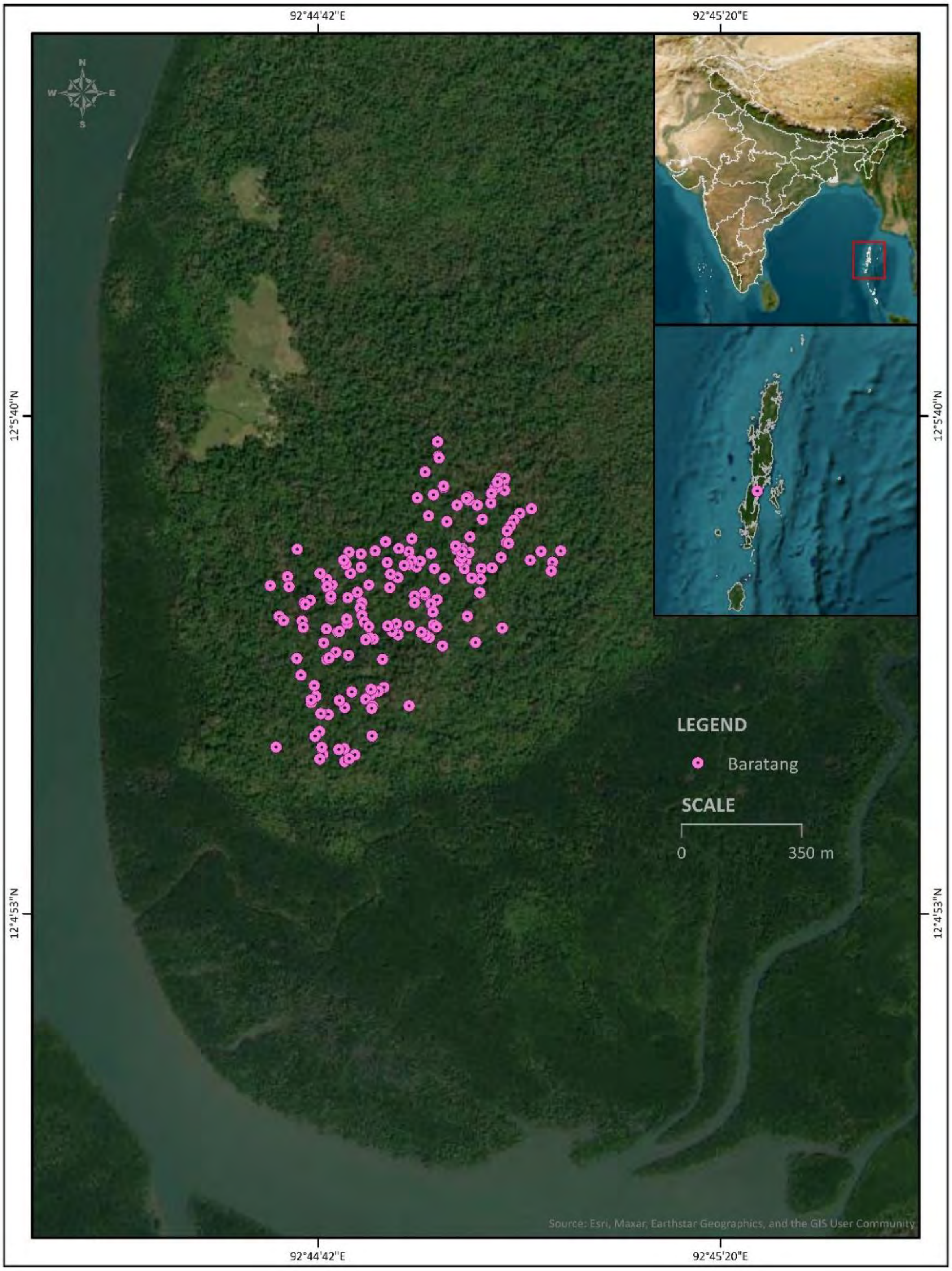


Figure 2.3: Geographic location of the cave complex in Baratang Island, Andaman, and Nicobar Islands (Using ArcGIS 10.5, Esri, Redlands, California, USA).

Plate 2.1: The limestone caves in the Baratang Island, Andaman and Nicobar Island

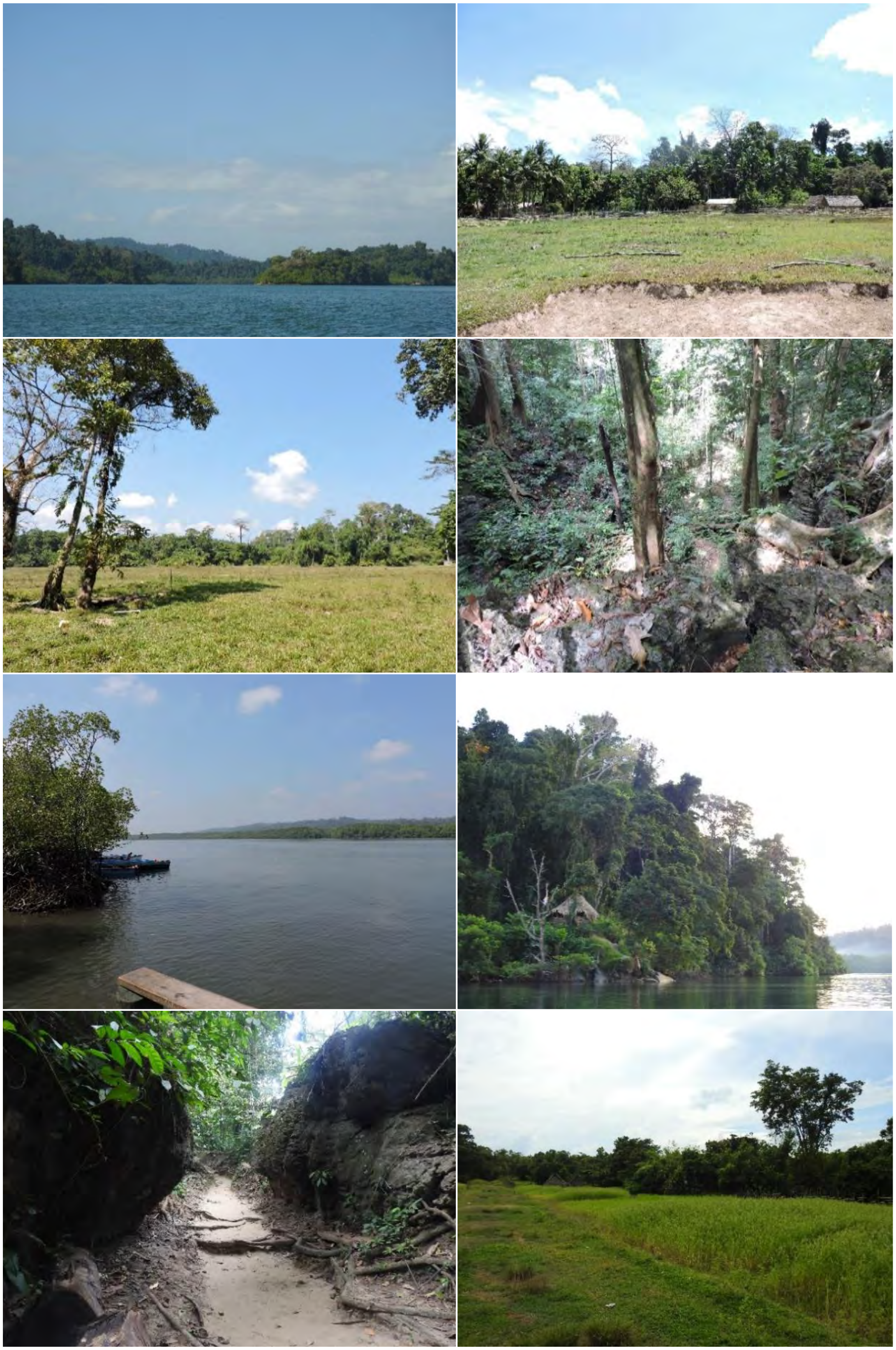


Plate 2.2: Habitat diversity in the Baratang Island, Andaman and Nicobar Islands

The Mithakhari Mélange's rocks almost completely encircle Baratang Island with Minor outcrops of earlier sedimentary rocks and limestone from the Mio-Pliocene Archipelago Group. There are hardly any significant thrusts or faults on this island (Bandopadhyay & Carter, 2017).

Baratang Island is also known for active mud volcanoes (Poddar, 1952; Bandopadhyay & Carter, 2017). Volcanic eruption flows often contain rock fragments of Mithakhari sandstones and rarely chert, chaotically embedded in a mud matrix (Bandopadhyay & Carter, 2017). On Baratang Island, the mean annual air temperature is 26.2 °C, and the average annual precipitation is 2870 mm (Kedzierski & Gargol, 2016). In 2004, the community of Wraffter's Creek was designated as an IBA (Rahmani & Islam, 2004). The area is a Reserve Forest and is protected under the Indian Forest Act 1927. The most dominant vegetation types in this karstland forest are Andaman tropical evergreen forest, Andaman semi-evergreen forest, littoral forest, and mangrove forest (Champion & Seth, 2005; Plate 2.2), with exclusive diversity patterns (Mane et al., 2019). These caves have been under legal protection since 2010 for the *in-situ* conservation of the Edible-nest Swiftlet (Manchi & Sankaran, 2014).

2.2.2. Chalis-Ek, North Andaman Island

Chalis-Ek is a group of inland limestone caves within a single hillock (Plate 2.3). It is located near Ramnagar, in the south-eastern part of North Andaman Island (13° 2.9' N, 92°59.2' E, Figure 2.2 & 2.4). As the vernacular name suggests, Chalis-Ek reportedly has 41 caves present in the hillock. The geology of the study site is not very well documented. However, Pal & Bhattacharya (2010) have described a detailed account of the metamorphic rocks belonging to the ophiolite series. Champion & Seth (2004) classified the vegetation of North Andaman into Andaman tropical evergreen, Andaman semi-evergreen, Andaman moist deciduous, Mangroves, and Littoral Forest (Champion & Seth 2004; Prasad et al. 2009; Plate 2.4). The communities living near the hillock are mostly dependent on the paddy cultivation which surrounds the forest.

Chalis-Ek in North Andaman was identified as one of the priority sites for swiftlet conservation by Sankaran (1998; 2001). Currently, only 35 caves are known in the hillock, of which 28 were reported to have a population of Edible-nest Swiftlet. Since 2001, the 28 caves have been under round–the–clock protection every year during the breeding season as part of the *in-situ* conservation program (Sankaran & Manchi, 2008).

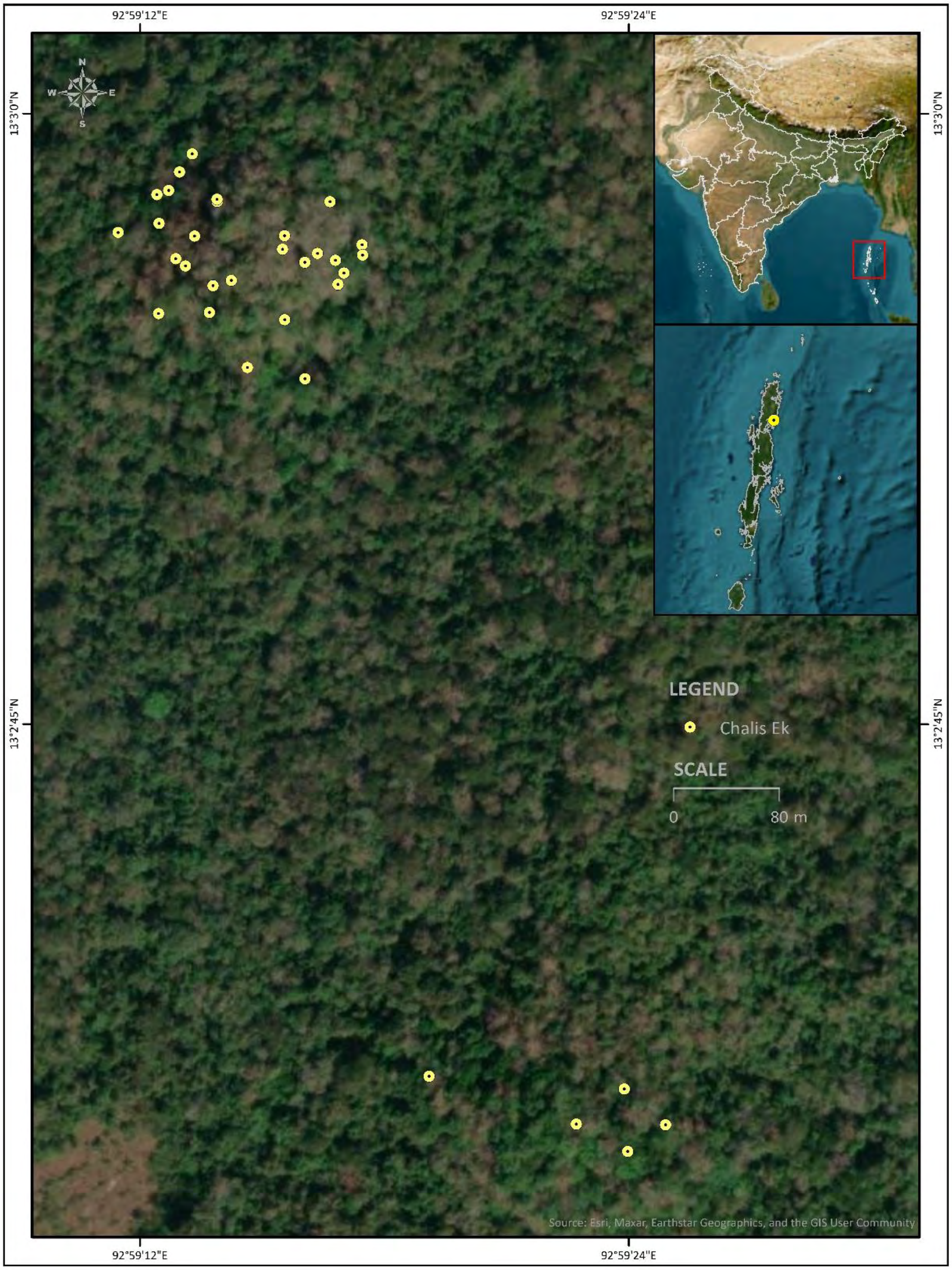


Figure 2.4: Geographic location of the cave complex in Chalis Ek, North Andaman, Andaman and Nicobar Islands (Using ArcGIS 10.5, Esri, Redlands, California, USA).

Plate 2.3: The limestone Caves in Chalis Ek, North Andaman, Andaman and Nicobar Island

Plate 2.4: Habitat diversity in the Chalis Ek, Andaman and Nicobar Islands

2.2.3. Interview Island, Middle Andaman

Interview Island (12°53' N, and 92°4' E, Figure 2.2 & 2.5), the westernmost island of the Middle Andaman group, is the largest Wildlife Sanctuary (133.40 km^2) in the archipelago (Murthy, 2007). This simple carbonate island (Kawalkar & Manchi, 2020) is known to have 35 limestone caves, of which 13 are coastal (Sankaran, 1998; Manchi & Mane, 2012; Plate 2.5). This uninhabited island of North and Middle Andaman has four major types of forests: Tropical Evergreen Forest, Andaman Semi-Evergreen Forest, Littoral Forest, and Mangrove Forest (Champion & Seth, 2005). It also has a rich faunal diversity (Pande et al., 1991; Manchi, 2009). There are more than 34 caves on the Interview Island, 13 of which are located on the shore and the rest in the interior. Of these, 18 inland caves are known to have Edible-nest Swiftlets, and two caves also have Plume-toed Swiftlet (Sankaran, 1998; Manchi, 2009). All caves with a population of Edible-nest Swiftlets are underground caves. Most of these caves are tunnels or cracks where nests can be plucked by hand. A cave with a significant population of the Edible-nest swiftlet has been secured under the Edible-nest Swiftlet conservation program from 1999 onwards.

Interview Island belongs to the Archipelago group of the geological series comprising soft limestone formed of coral and shell soft calcareous sandstones and soft white clays with occasional bands of conglomerates. In Quingely (1850), observed that the island comprises sedimentary formations, but the extreme West of the island is composed of igneous rocks described as 'granite–greenstone' (Murthy, 2007; Kawalkar & Manchi, 2020). Oldham (1885) distinguished the two sedimentary formation rocks beside the serpentine series. The Andaman Arc has a long history of tectonic events (Eguchi et al., 1979; Kawalkar & Manchi, 2020) because of its location in the proximity to a subduction zone West of the Indonesian Archipelago (Awasthi et al., 2013; Kunz et al., 2010; Rajendran et al., 2008; Kawalkar & Manchi, 2020). The most recent Tsunami of December 2004, following the mega-earthquake Mw 9.3 in the region, caused severe damage by creating around 2–3 m of land uplift in the northern part of the Andaman arc (Bandopadhyay & Carter, 2017; Rajendran et al., 2008).

Figure 2.5: Geographic location of the cave complex in Interview Island, Andaman and Nicobar Islands (Using ArcGIS 10.5, Esri, Redlands, California, USA).

Plate 2.5: Limestone Caves in the Interview Island, Andaman and Niocbar Islands

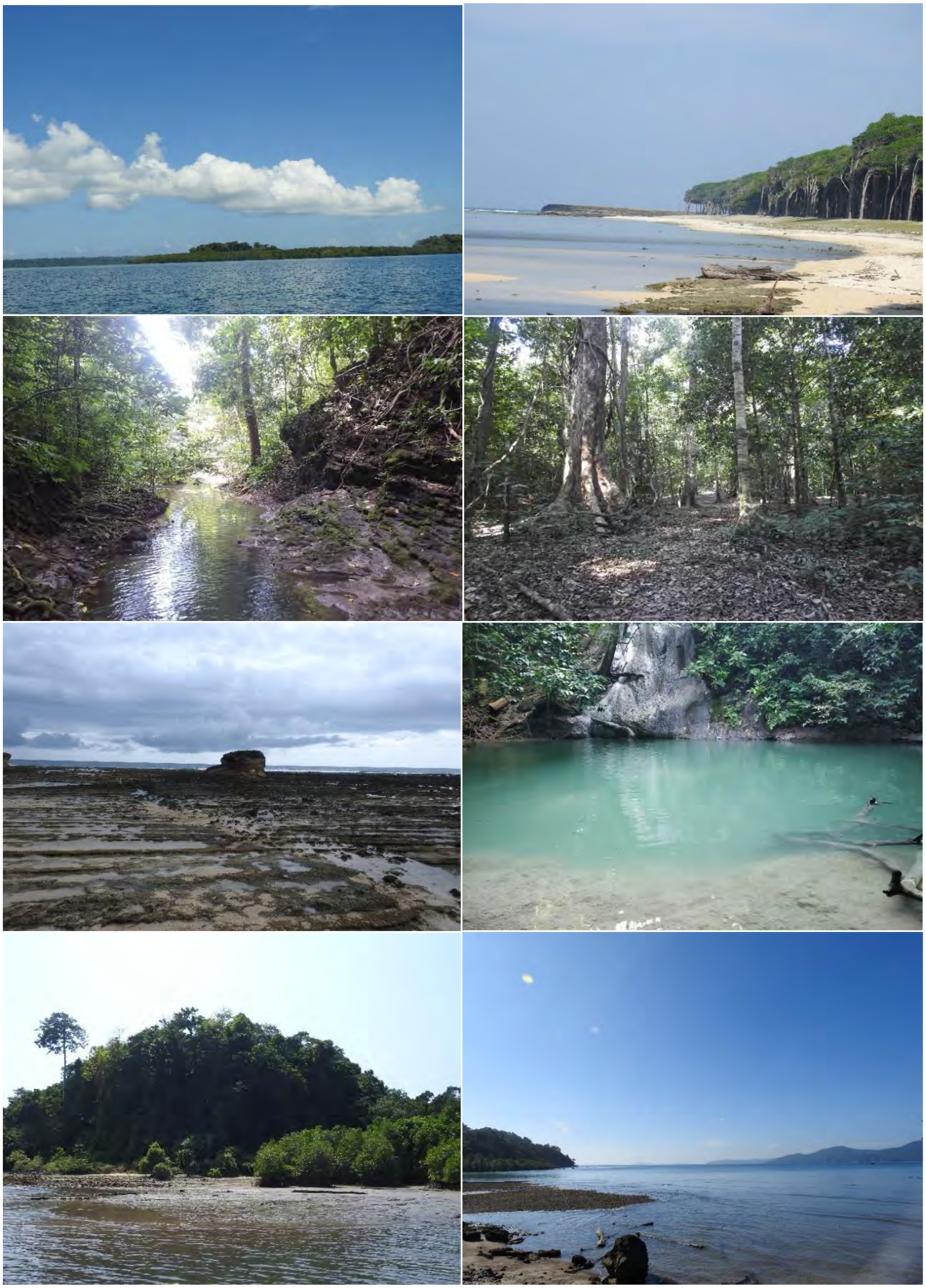


Plate 2.6: Habitat diversity in the Interview Island wildlife sanctuary, Andaman and Nicobar Islands

These tectonic movements further resulted in the development of terraces in the coastal zones, and Interview Island has the oldest and best-developed series of terraces (Awasthi et al., 2013; Rajendran et al., 2008). The 2004 earthquake caused around 2m upliftment along Interview Island's western and eastern coasts (Rajendran et al., 2008; Plate 2.6).

All of the intensive study sites have a wide range of geological and ecological features. The presence of the swiftlets in these locations was first scientifically documented by Sankaran (2001) and they were identified to be priority sites for the swiftlet conservation in the Andaman Islands. Because these sites have high swiftlet populations, they were chosen for the study.

Chapter III

CHAPTER III

BREEDING SITE-FIDELITY AND FACTORS INFLUENCING THE BREEDING SITE-FIDELITY IN THE EDIBLE-NEST SWIFTLET

3.1. INTRODUCTION

Breeding is among the most crucial phases of any animal life cycle and involves the decision to reproduce and contribute to reproduction (Pradel et al., 2012). Breeding in birds is highly specialized and occurs in diverse habitats, from high-elevation mountains to deep and dark subterranean habitats. Individuals can return to their known habitats, exhibiting site fidelity, or disperse to the available suitable areas between breeding attempts in a season or between the breeding seasons (Greenwood, 1980; Greenwood & Harvey, 1982). According to the decision rule, individuals assess their breeding success as prior experience and use the information to decide whether or not to return to the same breeding site during the subsequent season (Doligez et al., 1999). The win-stay or lose-shift strategy predicts an adult bird's preference for site fidelity (stay) when confident of producing offspring at the same site as the social mate or dispersal (shift) to other suitable locations for subsequent breeding attempts when unable to produce offspring at the same location. This strategy allows adults to produce the most broods in their lifetime (Campomizzi et al., 2012). Individuals experiencing high breeding success often have a higher probability of returning to the same breeding site in the following year (Kriŝtín et al., 2006). If the quality of a site (as determined by breeding success) is auto-correlated in time, this behaviour may increase individuals' fitness (Bergerud & Gratson, 1988; Hoover, 2003). Otherwise, individuals in a low-quality habitat may disperse in search of other, more suitable sites (Robinson, 1985). Site fidelity is directly influenced by fecundity and survival of the individuals and can affect population dynamics and demography (Hoover 2003). Adult birds tend not to return to the same site in the following years if they fail to produce young (Gavin & Bollinger, 1988; Haas, 1998) or produce fewer than two broods in cases of multiple-brooded species (Trine, 1996). For instance, in waders, such as the European Oystercatchers *Haematopus ostralegus*, stronger site fidelity was shown towards territories where chicks fledged successfully (Hazlitt & Butler, 2001). The Greater Flamingo *Phoenicopterus roseus*, Ovenbird *Seiurus aurocapilla*, and Bobolink *Dolichonyx* *oryzivorus* also signified the importance of prior experience (Gavin & Bollinger, 1989; Bernard et al., 2011; Pradel et al., 2012).

In Bobolinks *Dolichonyx oryzivorus,* breeding-site fidelity primarily results from experience-based choices by the birds and does not simply reflect patterns of mortality. Bobolinks appear to use their and others' breeding success at their site to influence their decision to return to a breeding site (Bollinger & Gavin, 1989). In Willow Flycatchers *Empidonax traillii*, male site fidelity was unrelated to site quality or previous breeding performance. In females, it was best explained by previous breeding performance but not by site quality. Previously successful females have more tendency to return to the same territory of the preceding season than unsuccessful birds. Site quality seemed to influence philopatry if no birds reared at a low-quality breeding site returned there to breed (Sedgwick, 2004). In the White Stork *Ciconia Ciconia* it was seen that pairs with higher fidelity rates have lower failure rates and that breeding failure and productivity in the previous season influenced the frequency of nest change in the following season. These results recommend that age is a significant factor related to nest fidelity; therefore, the individual experience could explain this behaviour in the White Stork. Changing the nest involves a reproductive cost for which nest fidelity can be considered an adaptive strategy to increase fitness (Vergara et al., 2006). A study on Spotted Sandpipers *Actitis macularia* observed male-biased philopatry. The return rate for males and females who successfully bred was 63%; for males and females who were unsuccessful, the return was 29% and 26%, respectively. Females often changed territories between clutches after nest failure (Reed & Oring, 1993).

Black Swifts *Cypseloides niger* are documented using the existing nest in subsequent years. One individual was recaptured nine years after the initial banding in the same nesting colony, showing nest site fidelity (Collins & Foerster, 1995). A study on swift species like Dobkin et al., 1986 on White-throated Swifts *Aeronautes saxatalis* also shows nest site fidelity.

All swiftlets are known to exhibit site fidelity (Medway, 1962a; Medway, 1962b). Swiftlet pairs have been reported to roost and build their nest at their permanent roosting site, therefore implying high nest-site fidelity, site tenacity, and pair kinship in the colony

(Lim, 1999; Koon & Cranbrook, 2002; Nguyên Quang et al., 2002). The birds also breed year-round, although depending on the weather conditions, particularly rainfall, the percentage of birds nesting varies (Koon & Cranbrook, 2002; Viruhpintu, 2002).

Moreover, the ex-situ conservation efforts of this species in the Andaman and Nicobar Islands have recently documented nesting in urban areas (Sankaran & Manchi, 2008; Manchi & Mane, 2012). As the basic understanding of the decision to stay or shift by the species is a critical component for conservation, management, and restoration efforts (Hoover, 2003), this study aims to understand the decision rule in the case of Edible-nest Swiftlets and testing the prior-experience hypothesis. Further, this study attempted to explore breeding success correlates using cave morphometrics and microclimate as variables.

3.2. OBJECTIVE

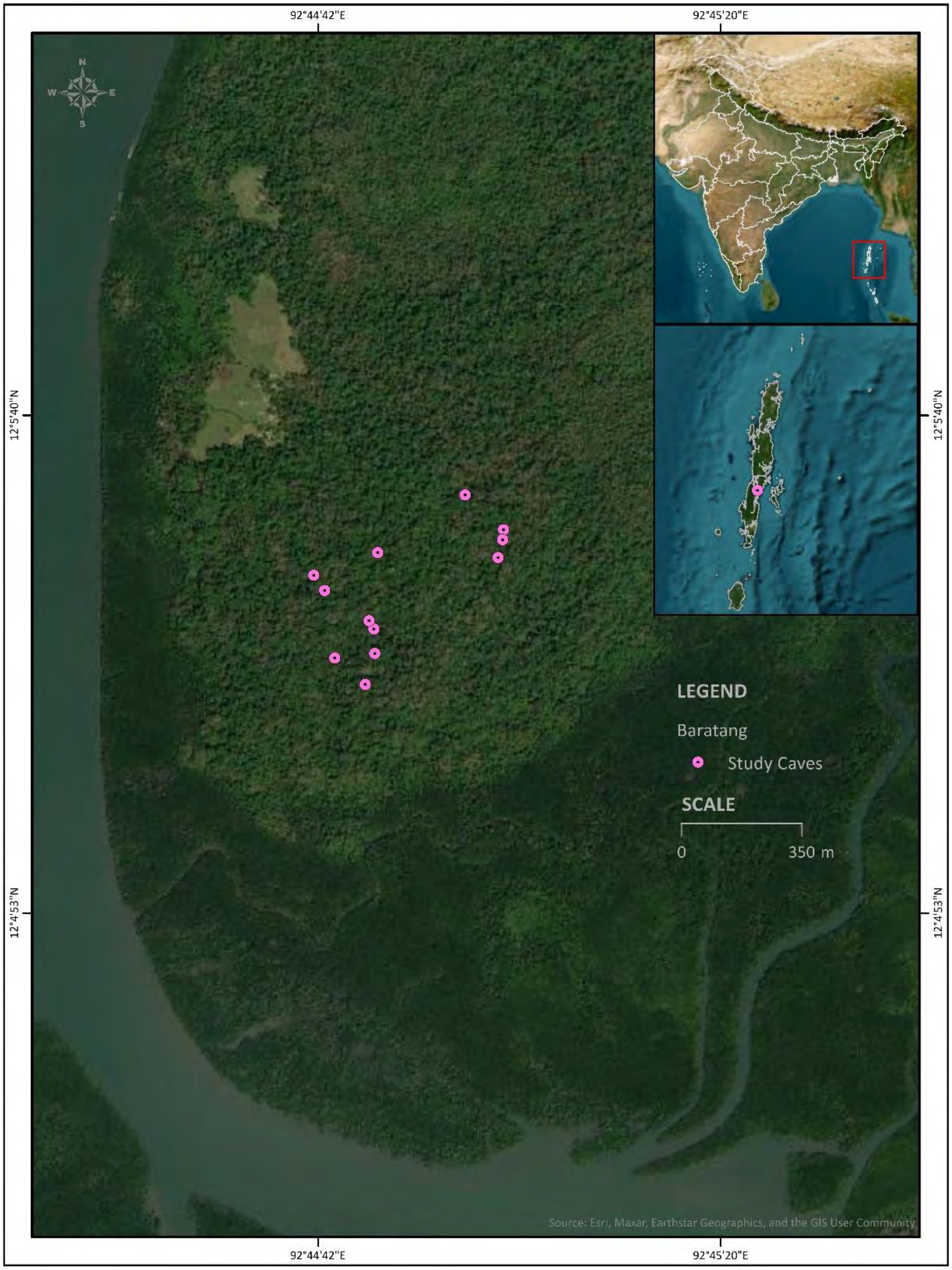
To investigate the breeding site fidelity and understand the biotic and abiotic factors influencing the breeding site fidelity in the Edible-Nest Swiftlet.

3.2.1 Research Questions

1. Does the Edible-Nest Swiftlet follow the decision rule phenomenon *"Prior-experience hypothesis"*?
2. Does the Edible-Nest Swiftlet show the Breeding site fidelity?
3. Is the breeding site fidelity in the Edible-Nest Swiftlet affected by the biotic and abiotic factors?

3.3. STUDY AREA

This study was conducted at the largest known cave complex on the islands, Baratang Island (12° 05′ N, 92° 45′ E, Figure 3.1). The area of the cave complex, containing 175 caves, is 0.77 km^2 and is situated between Wraffter's Creek and Naya Dera (Sankaran, 2001; Manchi & Sankaran, 2014; Mane et al., 2019). These caves have been under legal protection since 2010 for the in-situ conservation of the Edible-nest Swiftlet (Manchi & Sankaran, 2014) (for details, please refer to Chapter 2).



Source: Esri, Maxar, Earthstar Geographics, and the GIS User Community

Figure 3.1: Study caves (n=12) from Baratang Cave Complex, Baratang Island (Using ArcGIS 10.5, Esri, Redlands, California, USA)

3.4. METHODOLOGY AND DATA ANALYSIS

3.4.1 Selection of Study Caves

Initially, by visiting all the caves, the study confirmed that Edible-nest Swiftlet occupied 112 of the 175 caves known from the Baratang cave complex. The data concerning the breeding population in the 112 caves was collected using the nest count survey in the year 2017 to select the study caves. Further, using the Capture-Mark-Recapture method, 10% of the available caves (n=112) were selected to determine the Edible-nest Swiftlet population. Following the stratified random sampling method (Sutherland, 2006), caves were divided into various classes according to the breeding population sizes (0-10; 11-20; 21-30; 31-40 were pairs, Figure 3.2). Understanding the practical difficulties of using Capture-Mark-Recapture for caves with large swiftlet populations, the maximum class limit was retained at 31-40 pairs. In addition, the cave selection was greatly influenced by the accessibility of the cave and the feasibility of mist netting, considering the undulating terrain at the cave opening. In many places, setting up the mist net was difficult, and there was not enough place for a person to safely remove the birds from the mist net before they got badly entangled and injured.

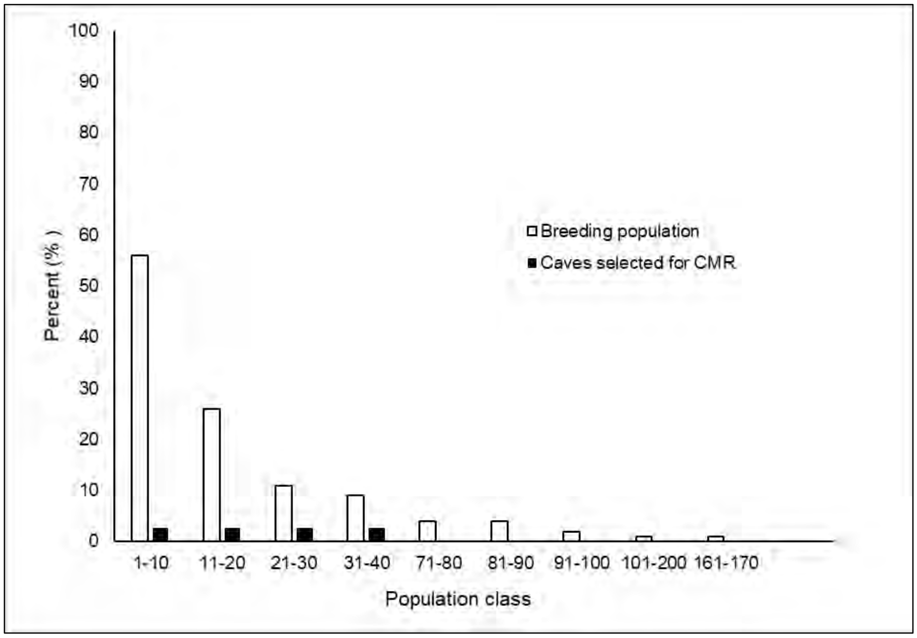


Figure 3.2: Caves selected (n=12) from various population classes (0-10; 11-20; 21-30; 31-40 pairs) for the Capture-Mark-Recapture method (CMR)

There was a risk of losing birds while capturing if a huge flock came at a time and got entangled in the mist net. The caves with large populations were avoided to prevent losing birds and causing errors in population estimation. Finally, to determine the population in various caves using the Capture-Mark-Recapture method, 12 caves from four different population classes were selected.

3.4.2. Monitoring Population and Breeding Success

The population size of Edible-nest Swiftlet inside each study cave was estimated using the nest count method (Sankaran, 2001; Manchi & Sankaran, 2014). Because Edible-nest Swiftlets are monogamous (Koon & Cranbrook, 2002), each nest was regarded as a breeding pair, i.e., two birds (Manchi, 2009). The Edible-nest Swiftlet begins nesting during December and continues until mid-February when the egg-laying begins. Eggs hatch from the second week of March until the end of April. By the end of April, the nestlings have begun to fledge. The Edible-nest Swiftlet lays its second bout of eggs between May and June, and the second batch of fledging takes place between July and mid-August (Manchi, 2009; Mane & Manchi, 2019). Nest count surveys were conducted in 2017 and 2018 between January and June. The presence of an incubating adult and nestlings made active nests more visible. During the breeding season, at the end of each month, all the nests from study caves were counted. Nest surveys were conducted with the assistance of experienced nest protectors, who carried out six surveys in 2017 and 2018. To minimize disturbance to the birds, all surveys were conducted during the daytime. Every day in the early morning (6:00–6:30 am), all the nests from selected caves were checked. The caves were physically surveyed from the beginning of the breeding season until the nestling to the fledgling stage to score the nest checks as an empty or occupied nest and to count the number of eggs and nestlings in the nests. As described by Jehle et al. (2004) and Manchi (2009), the breeding success of the Edible-nest Swiftlet was calculated using the following formula,

$$\text{Breeding success} = \frac{\text{Number of clutches that produce}}{\text{Total number of clutches}}$$

3.4.3. Determining Breeding Site Fidelity

The capture-mark-recapture method was used to determine breeding site fidelity. To ensure the safety of birds while being captured and handled, sterilized nitrile gloves and face masks were used as precautionary measures. After collecting the required data, birds were carefully released back near their breeding caves. During the nest-building season (December–January), adult birds were captured while returning to their breeding caves (between 5:00 and 8:00 pm) by placing the mist nets (6 m×2.6 m; 30 mm mesh) at the entrances of each study cave (Dunn & Ralph, 2004; Sankaran & Manchi, 2008; Manchi, 2009; Plate 3.1). Individuals apprehended for the first time were tagged with aluminium Z-rings with a unique identification number. The date of capture, ring number, and cave number were all recorded. The adult birds were recaptured at the end of the 2018 breeding season to see if they returned to the same cave for breeding regardless of breeding success. The first-time captured individuals were marked during the 2018 recapture, and the capture date, ring number, and cave number were noted. The capture date, ring number, and cave number where they were initially marked were all recorded once the birds were recaptured. Following data collection, all captured swiftlets were released safely near their respective breeding caves. All the necessary permissions for the bird handling were procured from the State Forest Department of the Andaman and Nicobar Islands.

3.4.4. Cave Morphometry and Microclimate Variables

The morphometry data of 11 caves of 12 selected study caves was gathered because the 12th cave was inaccessible. Between January and June 2018, a standard survey method was used for recording morphometric measurements of each study cave Using a Leica DISTO™ S910 P2P (https://leica-geosy stems.com/) (Ford & Cullingford, 1976; Kawalkar & Manchi, 2020). Several survey stations were fixed in each of the study caves, with a one-meter distance between them. Each cave mapping survey began at the cave entrance (e.g., survey station 1) and continued until the end of the cave (Figure 3.3).

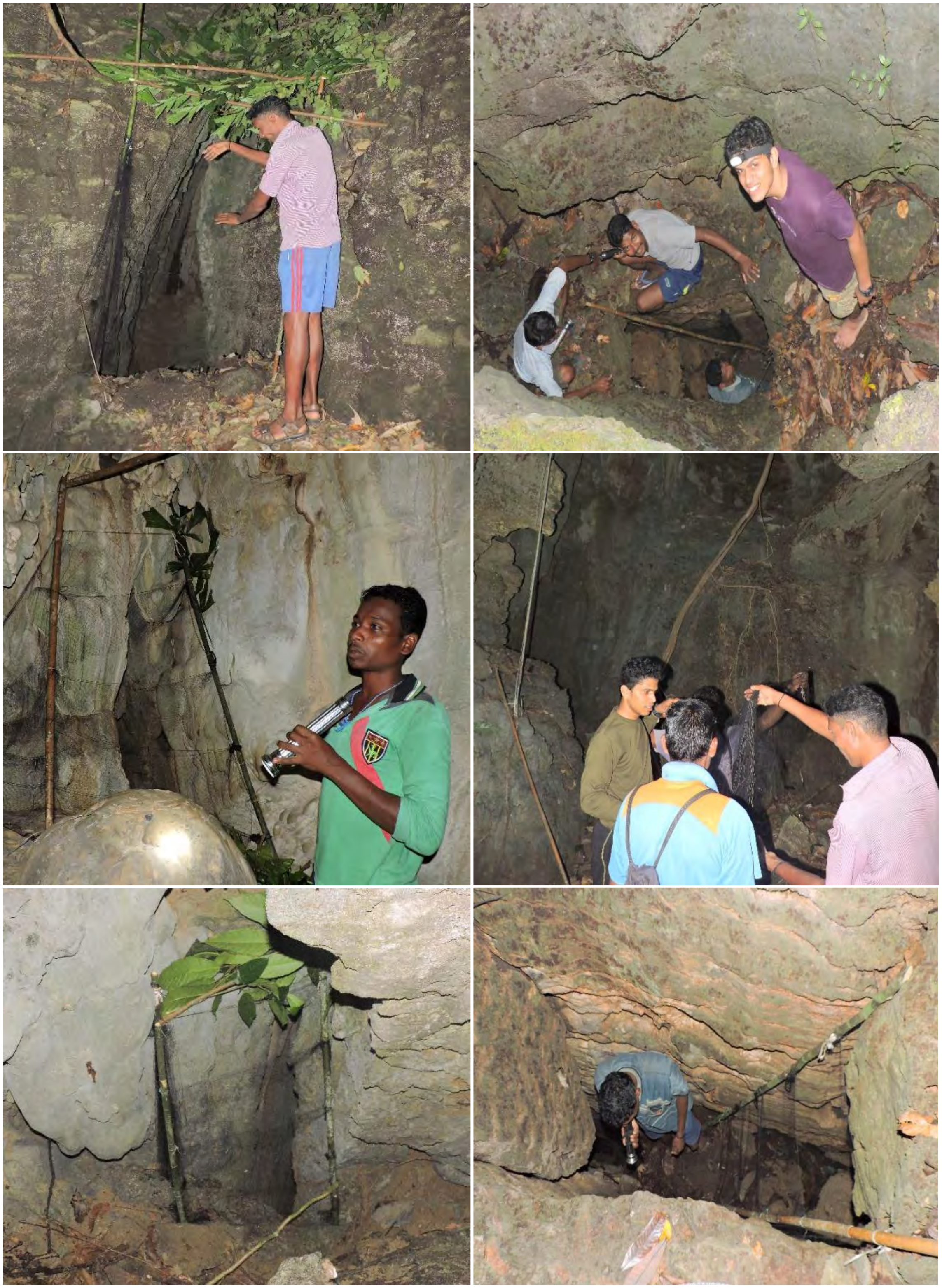


Plate 3.1: Capture of Edible-nest Swiftlet using Mist-nest at Cave entrance (Location: Baratang Island)

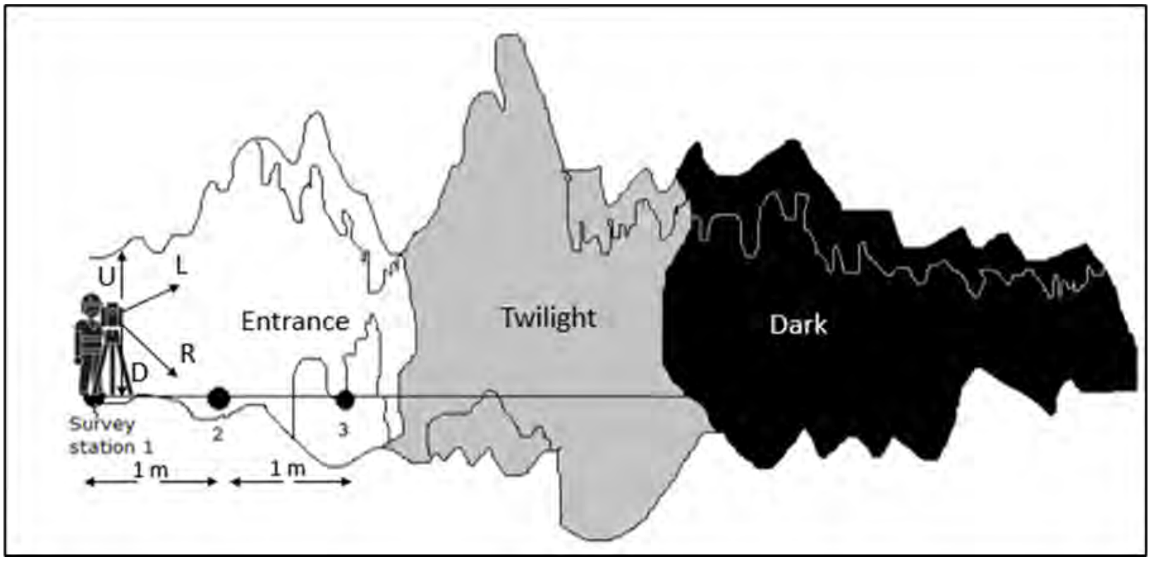


Figure 3.3: Illustration of the dummy cave with the survey stations at a one-meter distance across the caves, beginning from the cave entrance. L-left, R-right, U-up, D-down (Manchi et al., 2022)

The distance (meters) to the left wall (L), distance to the right wall (R), distance to the cave ceiling (U), distance to the cave floor (D), vertical angle (Θ), and bearing from true North were measured at each survey station. These measurements yielded 12 cave morphometric parameters derived from maps (Table 3.2). Cave measurements obtained were processed using WinKarst (Ver12.5, http://www.resurgentsoftwa re.com/winkarst.html) and Compass 32 Project Manager software (https://fountainware.com/compass/().

To collect microclimate data (Temperature and Humidity), HTC-Easy Log data loggers (http://htcin struments.com/humidity-temp-meter.html) were placed at the cave entrances and the nesting locations for several months (December, March, April, and May) during the ENS breeding season. The average mean temperature (°C) and relative humidity (%RH) were used for further analysis. Goodness of fit statistics, Spearman's correlation test, and linear and multiple regression modelling were performed using the XLSTAT software Ver. 2020.2.1 (Addinsoft, 2020). To reduce the effects of multi-collinearity, pairs of the habitat variables (Table 3.1) were tested for correlation using Spearman's rank correlation test (Golawski & Mroz, 2019). Only one data set was chosen for further analysis if two variables were positively correlated ($r>0.60$). To select among the correlating parameters, the ecological understanding of the cave morphometric parameters was used.

Further, only non-collinear variables (i.e., cave length, cave bearing, cave inclination, surface length, and wall area) were used for modelling to avoid the possibility of error. Multiple regression modelling was used to predict the influential factors and to develop inferences about the determinants of patterns (Mac Nally, 2002) affecting breeding success. The linear and multiple regression model assumptions were also tested using the normal distribution of residual plots.

3.5. RESULTS

3.5.1. Breeding Population and Success

In 2017, 117 Edible-nest Swiftlet nests were counted in 12 study caves using the nest count method. The breeding population of this monogamous species was estimated to be 234 individuals because each nest represents a pair of birds. Similarly, the detection of 106 nests in the same caves in 2018 revealed a breeding population of 212 individuals in the same 12 caves (Figure 3.3).

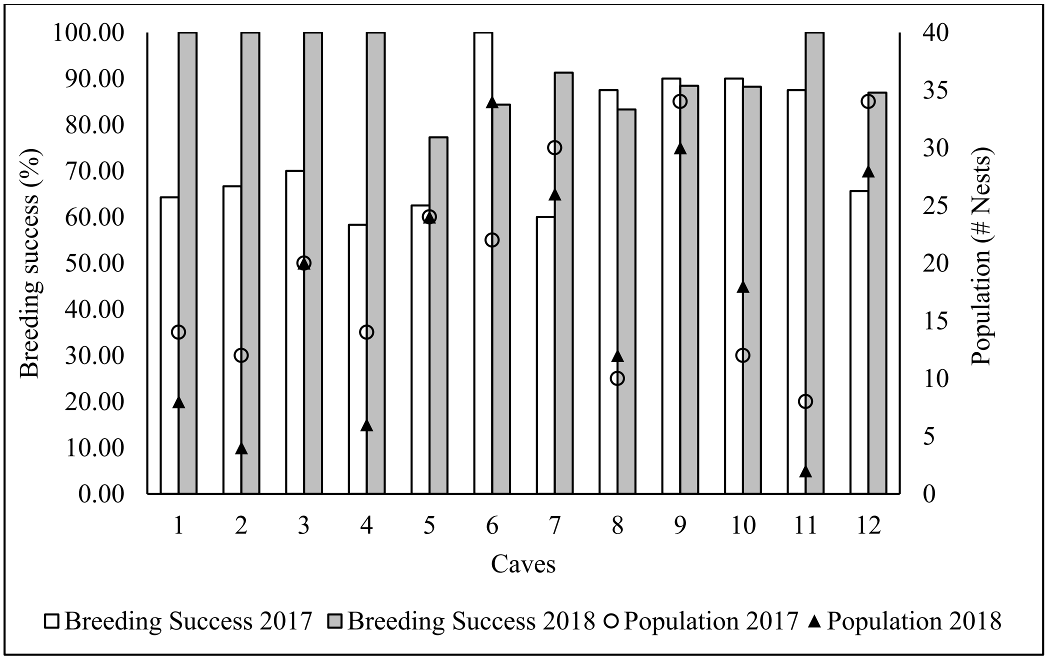


Figure 3.4: Breeding success of the Edible-nest Swiftlet in 2017 and 2018 in 12 study caves on Baratang Island, Andaman Islands

The Edible-nest Swiftlet individuals exhibited variation in the rates of their breeding success in 2017 was 75.9% (avg.) and in 2018, it was 91.5% (avg.). In two caves (4 and 7), the breeding success increased to 91.3% in 2018 from 60% in 2017. In 2017, one cave (Cave No 6) showed 100% breeding success, and in 2018, five caves (Cave No 1, 2, 3, 4, 11) showed 100% breeding success (Figure 3.4).

3.5.2. Decision Rule phenomenon and Prior-Experience Hypothesis

In 2017, 207 adult birds from the study caves were captured and marked, accounting for 88.4% of the 234 birds. Of which, in 2018, 137 adult birds were recaptured. These results from capture-mark-recapture experiments demonstrated that most (66.18%) adult Edible-nest Swiftlet individuals are faithful to their breeding caves, which supports presence of the breeding site fidelity in the species. None of the marked adult birds were recaptured in any cave other than where they were captured. It confirmed that the adults of the Edible-nest Swiftlet in the Andaman and Nicobar Islands do not disperse (n=207).

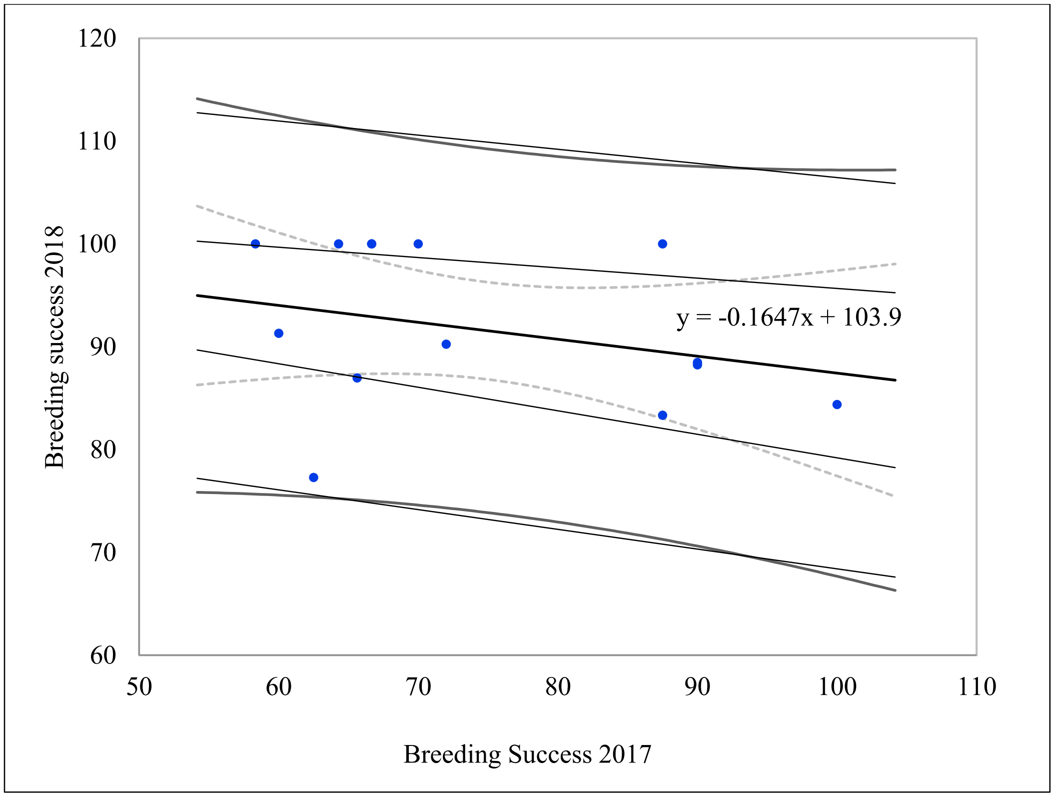


Figure 3.5: Regression of breeding success of 2018 by breeding success of 2017 ($R^2=0.08$, $p>0.05$)

Monitoring 207 Edible-nest Swiftlet individuals during the breeding seasons confirms that the species decides to stay at the same nest site regardless of prior experience of breeding success or failure (Figure 3.3). Comparative analysis showed that the overall breeding success of Edible-nest Swiftlet was significantly higher in 2018 ($p<0.05$, 91.5±7.1%) than in 2017 (74.9±12.9%). Linear regression ($R^2 = 0.08$, $p>0.05$) showed that the breeding success of the Edible-nest Swiftlet in 2018 was independent of the breeding success in 2017 (Figure 3.5).

3.5.3. Factors Influencing Breeding Success

Cave Morphometry

The 11 accessible caves had a varied range of morphometric measurements (Table 3.1). The multi-collinearity test for 12 morphometric variables resulted in the removal of correlated parameters (Table 3.2). The non-collinear variables (cave length, cave inclination, surface length, wall area, and cave bearing) were chosen for their logical relatedness to the bird's ecology. Further, a multiple regression model performed with five non-collinear variables (cave length, cave inclination, surface length, wall area, and cave bearing) revealed an insignificant relationship between breeding success and cave structure ($R^2=0.57$, $p>0.05$, Table 3.3).

Microclimate Variables

The study caves on Baratang Island maintained nearly stable temperatures throughout the study period, with a slight variation of 2 °C (23–25 °C, Figure 3.5). The relative humidity in the study caves varied considerably between 92% and 105% (Figure 3.6). As per the goodness of fit statistics, the temperature ($R^2=0.002$, $p>0.05$) and relative humidity ($R^2=0.008$, $p>0.05$) do not affect the breeding success of the bird.

Table 3.1: Morphometric parameters of the study caves on Baratang Island.

S. No.	Variables	Range	Mean ± SD
1	Cave Length (meters): An end-to-end measurement or extent of a cave along the survey passage, including all the inaccessible areas.	12.10-41.50 m	21.80±7.85m
2	Horizontal Length (meters): A horizontal length on the earth's surface covered by a cave.	8.30-27.00m	14.88±4.92m
3	Cave Bearing from True North (meters): It is the horizontal space (in degrees) between two intersecting lines / surfaces at / close to the point where they meet.	23°-357°	227.54±122.89°
4	Cave Inclination (degrees): It is an angle at which a cave is shaped vertically or horizontally in the three-dimensional space	44°-79°	53.54±10.18°
5	Cave Depth (meters): It is the distance between the opening of the Cave and the deepest end of the Cave in the earth's crest	8.70-31.50m	15.58±6.48m
6	Surface Length (meters): It is the measurement or extent of the cave ceiling from end to end	0.70 -8.00m	4.52±2.30m
7	Surface Width (meters): It is the horizontal Length of the cave surface	6.40 -22.30m	11.56 ± 4.83m
8	Surface Area (meter^2): It is a map-derived parameter that gives the area of the cave surface, mostly the ceiling	4.90 -179.60m^2	56.27 ±47.04 m^2
9	Cave Volume (meter^3): It is a three-dimensional space enclosed by the Cave.	14.20-367.20m^3	157.61 ± 132.15m^3
10	Average Diameter (meters): An expression of the average size of a cave obtained graphically by locating the diameter associated with the midpoint of the cave-size distribution	0.90-4.50 m	2.45 ± 1.20 m
11	Wall area (meter^2): It is a two-dimensional area obtained by multiplying the Length and Breadth of the cave walls.	74.50-567.60 m^2	241.77 ±140.72 m^2
12	Average inclination (degrees): It is an average of all the vertical angles recorded at every survey station	31.90-51.20°	45.782± 5.63°

Table 3.2: Multi-collinearity between morphometric variables of the study caves on Baratang Island

Variables	Cave length	Horizontal Length	Cave Bearing	Cave Inclination	Cave Depth	Surface Length	Surface Width	Surface Area	Cave Volume	Avg. Diameter	Wall Area	Avg. Inclination
Cave length (CL)	**1**	**0.834**	-0.136	-0.005	**0.945**	0.200	**0.873**	0.591	0.145	-0.068	0.445	0.319
Horizontal Length (HL)		**1**	-0.228	-0.018	**0.702**	0.364	**0.638**	**0.615**	0.401	0.183	**0.615**	0.126
Cave Bearing (CB)			**1**	-0.018	-0.127	-0.491	-0.027	-0.264	-0.173	-0.191	-0.109	0.196
Cave Inclination (CI)				**1**	0.237	-0.374	-0.241	-0.533	-0.355	-0.416	-0.237	**0.689**
Cave Depth					**1**	0.145	**0.800**	0.482	-0.027	-0.237	0.291	0.528
Surface Length						**1**	0.155	**0.800**	0.564	0.515	0.491	-0.305
Surface Width							**1**	**0.627**	0.136	-0.055	0.418	0.241
Surface Area								**1**	0.400	0.278	0.491	-0.109
Cave Volume									**1**	**0.961**	**0.927**	-0.369
Avg. Diameter										**1**	**0.802**	-0.491
Wall Area											**1**	-0.087
Avg. Inclination												**1**

* Values in bold show that variables are collinear to each other

Table 3.3: Multiple regression fit of Edible-nest Swiftlet breeding success and morphometric variables of the study caves on Baratang Island, Andaman Islands

Source	**Value**	**Standard error**	**t**	**Pr > |t|**	**Lower bound (95%)**	**Upper bound (95%)**
Intercept	124.486	24.808	5.018	0.004	60.716	188.256
Cave Length	0.565	0.547	1.033	0.349	-0.841	1.971
Cave Bearing from True North	-0.026	0.023	-1.135	0.308	-0.086	0.033
Cave Inclination	-0.366	0.352	-1.040	0.346	-1.270	0.539
Surface Length	-0.946	1.819	-0.520	0.625	-5.623	3.731
Wall Area	-0.061	0.031	-1.962	0.107	-0.141	0.019

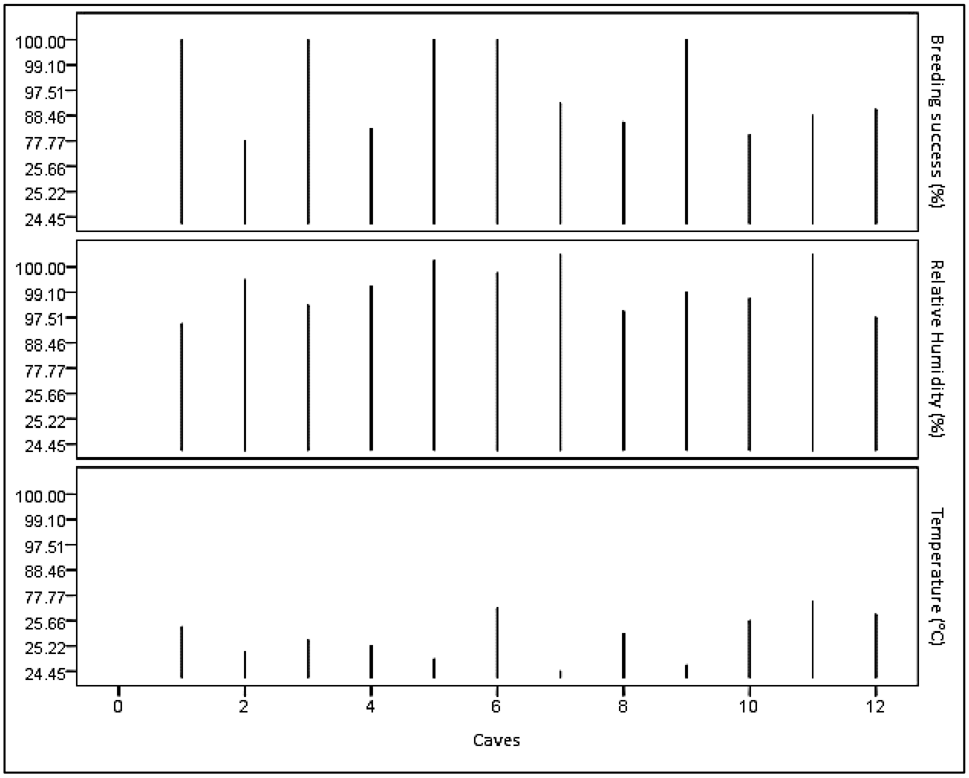


Figure 3.6: Breeding success of the Edible-nest Swiftlet, average temperature and relative humidity in the study caves on Baratang Island

3.6. DISCUSSION

Rejecting the prior-experience hypothesis, the Edible-nest Swiftlet individuals returned to the same caves for breeding despite the previous year's lower success. The average rate of breeding success of Edible-nest Swiftlet in the present study was higher as compared to most members of the genus *Aerodramus* except Germain's swiftlet (*Aerodramus germani*; 77%), Mountain Swiftlet (*Aerodramus hirundinaceus*; 77%) and Mascarene Swiftlet (*Aerodramus francicus*; 81%).

The Edible-nest Swiftlet individuals exhibited variation in breeding success rates in 2017 (74.9%) and 2018 (91.5%). In two caves (4 & 7), the breeding success increased to 91.3% in 2018 from 60% in 2017. Despite the lower overall breeding success in 2017, the Edible-nest Swiftlet individuals chose to stay and use the same caves for breeding in 2018. This finding supports Switzer (1993), as caves are unpredictable habitats with semi-(stable) microclimatic conditions. Moreover, the Edible-nest Swiftlet breeding success in 2018 was independent of the breeding success in the previous year. Langham (1980) recorded the decline in breeding success in Edible-nest Swiftlet in Malaysia with successive clutches, being highest in November (53.6%) and February (55.6%).

This study revealed that the Edible-nest Swiftlet has fidelity towards their breeding caves, as documented in other Apodidae species (Dexter, 1969; Medway, 1962a, b; Tarburton, 1987; Koon & Cranbrook, 2002; Nguyên Quang et al., 2002). The recapture rate of the marked adult individuals in the present study was high (66.2%), as observed in Common Swifts (*Apus apus*) by Lebreton et al. (1992). As both the swiftlets (Medway, 1962a; Medway, 1962b; Tarburton, 1987; Koon & Cranbrook, 2002; Nguyên Quang et al., 2002) and swifts (Dexter, 1969) are faithful to the colonies where they breed, it is apparent that they have high return rates. However, Johnson et al. (2018) could recapture only one Mariana Swiftlet (*Aerodramus bartschi*) from the roosting/nesting tunnel on Mariana Island, USA. Also, based on numerous studies involving marked individuals, return rates to breeding sites by birds are known to be highly variable and influenced by various factors, including previous breeding success, sex, and age of the returning individual (Newton & Marquiss, 1982; Shields, 1984; Warkenton et al., 1996). However, the present two-year study indicates that the return rates of Edible-nest Swiftlet do not directly depend on the breeding success or failure of the previous year. Nonetheless, further studies are required to finally answer the question of whether Edible-nest Swiftlet individuals are ’always’ site faithful and understand the effect of other factors (sex, age) on the return rates of the individuals.

This study result shows an insignificant relationship between cave structure and the breeding success of the Edible-nest Swiftlet. Overall, the R^2 value of the multiple regression model indicates that the selected non-collinear variables explain 57% of the variability in the breeding success. None of these variables significantly affect the species’ breeding success ($p>0.05$). Nevertheless, from the greater values of cave length and surface length (Table 3.2), these two variables somehow affect the breeding success of the study species. However, this needs further confirmation through a detailed study. Furthermore, several studies have highlighted the significance of the cave structure for individuals’s safety, as the presence of predators in caves is influenced by cave morphometry (Tarburton, 2009; Johnson et al., 2018). The effect of cave morphometry on the presence of predators, such as feral cats and crabs, is well documented (Tarburton, 1990, 2009). For example, cave length seems to be affecting the presence of one of the most well-known predators, like rats (Johnson et al., 2017). While collecting data, rats were encountered in the study caves during various visits. However, I did not find any predation of swiftlets by the rats in the study caves. Also, Manchi and Sankaran (2009) described the rats as the predators of the edible nests fallen on the cave floor. The echolocation developed in the Paleotropical swiftlets enables these cave-dwelling birds to explore the darker regions for safer breeding (Griffin, 1958; Brinkløv et al., 2013; Fenton, 1975).

The caves are known to be natural laboratories as they maintain an almost constant temperature throughout the year (Mammola, 2018). However, the study caves’ microclimate variables (temperature and relative humidity) indicated slight variations. These microclimate variations did not affect the breeding success of the Edible-nest Swiftlet, unlike the findings of Manchi and Sankaran (2011) from the caves in the Northern part of the Andaman Islands. Further, this difference in output might result from various aspects like variations in local climate and the type of caves. The Chalis-ek caves are mostly above-ground, unlike our study caves on the Baratang Islands (Manchi, 2009; Manchi, 2014; Manchi & Sankaran, 2009). Though the microclimate inside a cave does not directly influence the breeding success of the Edible-nest Swiftlet in the caves on Baratang Island, we agree with Manchi (2009) and Manchi and Sankaran (2011) that the high relative humidity during peak summer maintains the rigidity of the edible nest and might contribute in hatching success. The nests are also known to become stiff in dry conditions, resulting in cracks and breakage or nests falling from the cave wall or ceiling, subsequently hindering breeding success (Koon & Cranbrook, 2002; Nguyên Quang et al., 2002; Manchi & Sankaran, 2011).

This study found that Edible-nest Swiftlet is faithful to its breeding caves, irrespective of breeding success. Therefore, following the decision rule phenomenon, the birds chose to "always stay" and reject the prior-experience hypothesis. These findings imply improving the conservation strategies to enhance the Edible-nest Swiftlet population in the Andaman and Nicobar Islands. However, long-term capture-mark-recapture studies are necessary for a detailed understanding of the site-fidelity behaviour of swiftlets.

Chapter IV

CHAPTER IV

COLONIAL SEX RATIO IN EDIBLE-NEST SWIFTLET

4.1. INTRODUCTION

Many aspects of avian biology, such as behavioral studies, population dynamics, conservation genetics, migration, and evolutionary ecology, rely on sex determination. It is impossible to identify sex in many cryptically monomorphic species without detailed morphometrics, molecular techniques, laparoscopy, or dissection. Molecular sexing is appealing because it uses non-invasive techniques for accurate and rapid sex identification (Lessells & Mateman, 1996; Ellegren & Sheldon, 1997; Sheldon, 1998). Unlike mammals, birds have a ZW reproductive system in which females are heterogametic (ZW), and males are homogametic (ZZ). Sequences from alleles Z and W can differ slightly in females. This property is shared by the chromodomain helicase DNA binding 1 (CHD1) gene, which is highly conserved (Griffiths et al., 1996). The intronic sequences of CHD-Z and CHD-W are slightly different in size. Because it is present only in females (ZW), this size difference allows for sex determination in several bird species using appropriate molecular techniques (Fridolfsson et al., 1999). The CHD1W and CHD1Z genes exhibit extremely high sequence conservation, both among themselves and their mammalian homologs (Ellegren, 1996; Ellegren & Fridolfsson, 1997). As a result, the genes should be able to be used for general molecular sexing of birds.

Many bird's species benefit from plumage dichromatism or size dimorphism for sex determination. However, some species are monomorphic in plumage and differ only subtly in skeletal size. These differences can be so subtle that they are missed in the field by casual observation. Individual birds can be assigned sex using sex-specific behaviors (e.g., courtship feeding, begging, copulatory position) (Sandercock, 1998; Jodice et al., 2000; Shealer & Cleary, 2007), but this method requires that the birds be individually marked and recognizable from a distance. Dimorphism in birds can take many forms, including sex differences in size, plumage color, social and sexual behavior, and parental care (Owens & Hartley, 1998). Each type of sexual dimorphism has different ecological and evolutionary implications. Sexual dimorphism in plumage color (dichromatism) has been used as an index of a species' strength of sexual selection and thus linked to clade diversification (Barraclough et al., 1995; Phillimore et al., 2006; Marcaigh et al., 2021) and extinction risk following island introductions (McLain et al., 1999; Marcaigh et al., 2021).

Most passerine birds (69%) are monochromatic, with no differences in plumage color between the sexes (Barraclough et al., 1995; Marcaigh et al., 2021). However, differences in human and bird color perception abilities suggest that many examples of dichromatism may have been overlooked (Eaton, 2005; Marcaigh et al., 2021). Size sexual dimorphism is linked to sexual selection via territory size and mate acquisition, as well as natural selection via ecological divergence (Krüger et al., 2007; Marcaigh et al., 2021). Male and female morphological differences allow them to use niches differently (Selander, 1966; Marcaigh et al., 2021) and reduce intersexual competition (González-Sols et al., 2000; Marcaigh et al., 2021). It is critical in island systems, where birds can sometimes occur at higher densities due to reduced interspecific competition (MacArthur et al., 1972; Marcaigh et al., 2021), resulting in stronger intraspecific competition than on larger landmasses (Robinson-Wolrath & Owens, 2003). At the same time, island populations may be free of the interspecies competition that they face on the mainland, allowing them to expand into vacant niches (Diamond, 1970; Marcaigh et al., 2021). Furthermore, morphometric sexing is frequently a reasonable choice for quick and inexpensive efficient sex identification in cryptically monomorphic bird species because small and significant differences in biometric measurements usually exist between females and males, allowing for sex discrimination (Murphy, 2007; Cardoni et al., 2009; Dechaume-Moncharmont et al., 2011). The sexual dimorphism of birds is well known. Sexual size dimorphism results from current sexual and natural selection patterns that are sex-specific (Darwin, 1871; Fairbairn, 1997).

Various statistical analyses have been used to discriminate sexes over the years, including linear models (Jeffrey et al., 1993; Iko et al., 2004; Ura et al., 2005; Gill & Vonhof, 2006; Hallgrimsson et al., 2008, Dechaume-Moncharmont et al., 2011) and multivariate methods, such as principal component analysis (Rubega, 1996; McCrack DFA based on morphological measurements is a quick, inexpensive, and efficient method for determining sex in field studies on cryptically monomorphic bird species (Dechaume-Moncharmont et al., 2011). The DFA principle is to provide equations based on morphological measurements to predict bird sex. This equation is primarily calibrated on individuals of known gender. Each discriminant equation includes an estimate of the proportion of correctly sexed individuals. The use of PCR with chromo helicase-DNA (CHD) binding protein genes to determine the sex of birds has become a familiar and widely accepted method for confirming the individual's sex with 100 percent accuracy (Griffiths et al., 1998; Fridolfsson & Ellegren, 1999). Variations in morphometric measurements in Swifts such as the Biscutate Swift Streptoprocne biscutata and the Pallid Swift *Apus pallidus* have been studied (Pichorim, 2010; Boano et al., 2015). However, there is less information on morphometrics and discriminant function analysis (DFA) in swiftlets to identify the sexes. The Apodidae morphology is conservative and remarkably uniform in many morphological aspects; minor differences in the shape of the bill, tail, wing, and tarsus are visible, but they are subtle and may even be undetectable. Even when observed in hand, some species of the genera *Cypseloides, Aerodramus, Chaetur*a, and *Apus* are difficult to distinguish (Wetmore, 1957; Sims, 1961; Medway, 1966; Chantler & Driessens, 1995; Chantler, 1995; Chantler, 1999; Pichorim, 2010).

The fluctuation of the sex ratio in wild populations has a significant impact on population dynamics and, as a result, biodiversity preservation. Both males and females are required for reproduction in sexual creatures. As a result, a lack of either sex could endanger the population's viability. An overabundance of males, on the other hand, may increase conflict and hostility, reducing both male and female survivability. A reduction in the number of breeding females immediately reduces birth rates and population productivity. Although a few males can fertilize many females, females in male-biased populations may have to compete for breeding opportunities with superior males, which can result in extra mortality. If each individual's sex is determined solely by random chromosomal (Mendelian) sex determination, primary and secondary sex ratios in birds, which Mayr (1939) defined as the proportion of male to female eggs and chicks, can deviate significantly from the 1:1 expectation (Donald, 2007). Adult sex ratio (ASR) fluctuation patterns, which are strictly the sex ratio of breeding adults but are typically estimated as the sex ratio of all autonomous non-juvenile individuals, are poorly understood (Mayr, 1939). ASR is one of the fundamental concepts in population demography, and new research indicates that it is important in social behavior, mating systems, and parental care (Liker et al., 2014). The causes of ASR variation and their various effects on future populations are poorly understood (Donald, 2007). This information gap could have serious consequences for understanding population dynamics and conserving endangered species.

Recent research has discovered that globally threatened species appear to have highly skewed ASR, implying a smaller adequate population size and a higher risk of extinction (Clout et al., 2002). According to allee effect modeling, the risk of extinction increases with increasing male skew (Bessa-Gomes et al., 2004). The risk was demonstrated through viability analysis in Spanish populations of the Little Bustard (*Tetrax tetrax*), where population persistence was sensitive to a female shortage (Kearvell & Farley, 2016). Fisher (1930) proposed that a population's sex ratio is frequency-dependent. Deviations from an equal sex ratio would benefit individuals of the rarer sex because they would have a better chance of finding a mate. As a result, parents would benefit from producing a surplus of the rarer sex, and the population sex ratio would eventually return to equality. This scenario is altered if one sex is more expensive to produce. Parental expenditure for male and female offspring should be equal, resulting in a population sex ratio biased towards the sex that costs less (Fisher, 1930). Because females are the dispersing sex in Great Tit (Parus major), parents may overproduce daughters (Gowaty, 1993). The Little Grassbird, *Megalurus gramineus*, is a small, sexually monomorphic cooperative breeder passerine with a heavily skewed sex ratio toward males. However, the primary sex ratio initially favored females during the breeding season before shifting increasingly favoring men as the breeding season progressed (McIntosh et al., 2003).

There have been no studies on the colonial sex ratio, adult sex ratio (ASR), and offspring sex ratio (OSR) in species from the family Apodidae. The present study is the first to discuss the sex ratio in Edible-nest Swiftlet colonies.

4.2. OBJECTIVE

This chapter was designed to investigate the colony sex ratio, Adult Sex Ratio, and Offspring Sex Ratio. Further, the use of bird morphometrics to identify sexual dimorphism in cryptically dimorphic Edible-Nest Swiftlet is explained.

4.2.1. Research Questions

1. Does the Edible-nest Swiftlet show a 1:1 (M: F) colony sex ratio?
2. What is the Adult Sex Ratio (ASR) in Edible-nest Swiftlet?
3. What is the Offspring Sex Ratio (OSR) in Edible-nest Swiftlet?

4.3. STUDY AREA

The study was conducted at the Andaman and Nicobar Islands (06° 45'9 N and 13° 41'9 N, and 92° 12'9 E and 93° 57'9 E), which harbours the archipelago's important cave complexes at Baratang Island (12°'05' N, 92° 45'E; Figure 4.1), Chalis-Ek (13° 2.9" N, 92°59.2" E; Figure 4.2) and Interview Island (12° 56'17″ N and 92° 42'31″ E; Figure 4.3). These cave complexes have been under legal protection since 2010 for the *in-situ* conservation of the Edible-nest Swiftlet (Manchi & Sankaran, 2014). The study was undertaken in overall 47 caves (Baratang = 28, Chalis Ek = 16, and Interview Island= 3, for further details refer to Chapter 2).

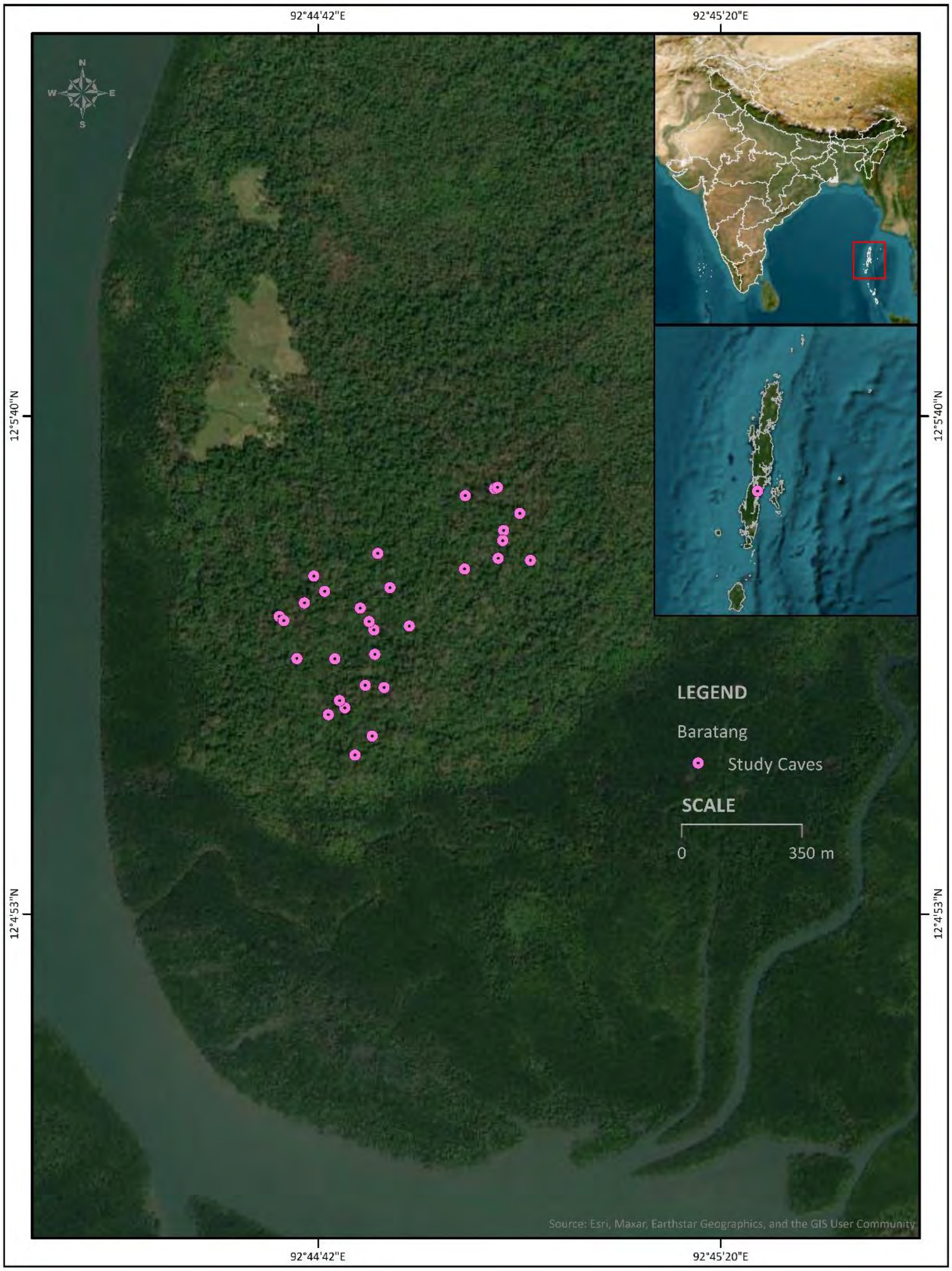


Figure 4.1: Geographic locations of the study caves (n=28) from cave complex in the Baratang Island (Using ArcGIS 10.5, Esri, Redlands, California, USA)

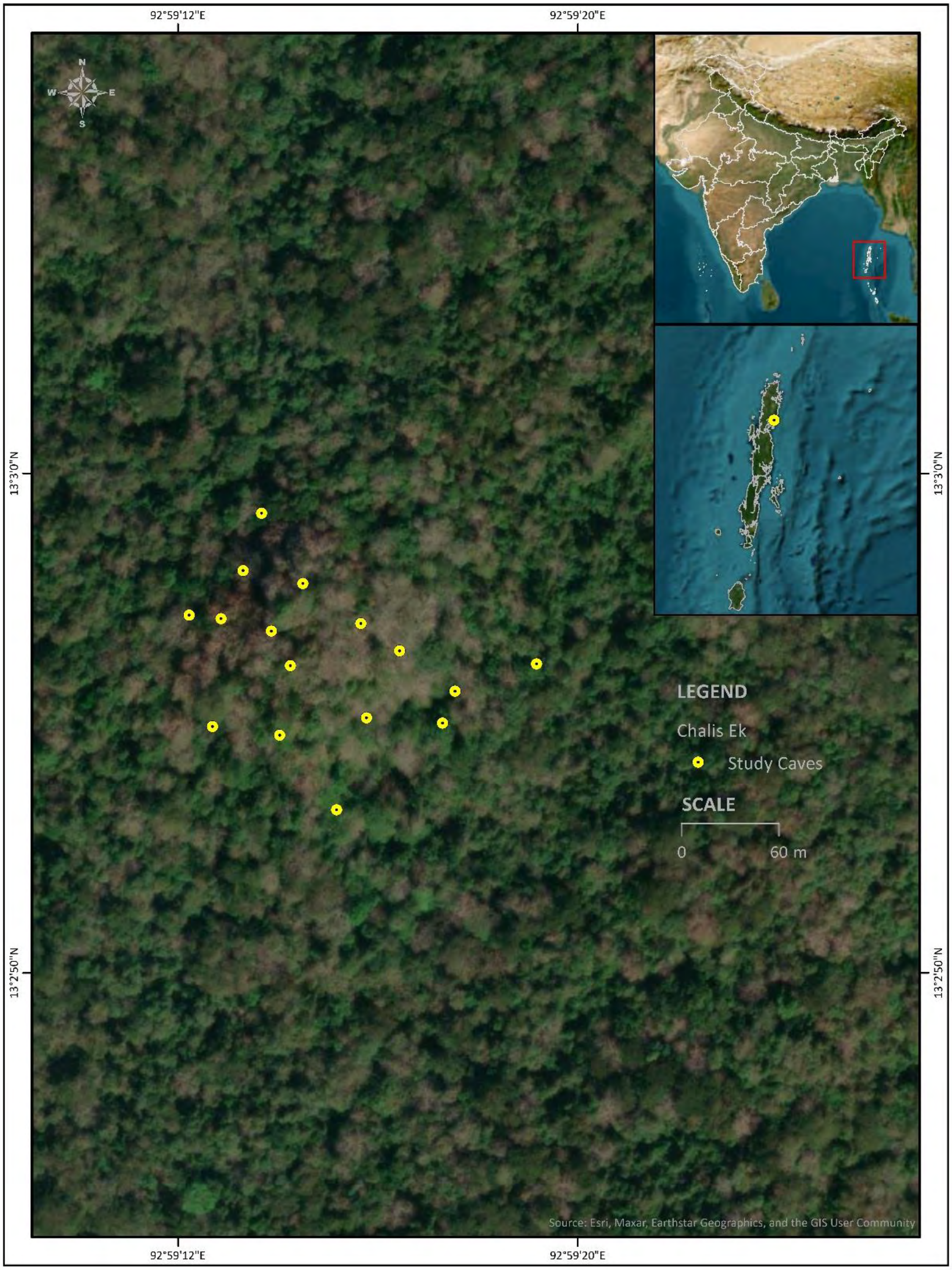


Figure 4.2: Geographic locations of the study caves (n=16) from Chalis Ek cave complex, North Andaman (Using ArcGIS 10.5, Esri, Redlands, California, USA)

Source: Esri, Maxar, Earthstar Geographics, and the GIS User Community

Figure 4.3: Geographic locations of the study caves (n=3) from Interview Island, North Andaman (Using ArcGIS 10.5, Esri, Redlands, California, USA)

4.4. METHODOLOGY AND DATA ANALYSIS

4.4.1. Bird Capture and Marking

Adult

This study was conducted between the years 2017 to 2019. Adult birds were caught using the capture-mark-recapture method (Sutherland, 2006). Sterilized nitrile gloves and face masks were worn during bird capture and handling as safety precautions to guarantee the birds' welfare. During the nest-building season (December-January), the adult birds were caught as they returned to their breeding caves (Between 5:00 and 8:00 pm) by placing mist nets (6 m x 2.6 m; 30 mm mesh) at the entrances of each study cave (Ralph & Dunn, 2004; Sankaran & Manchi, 2008; Manchi, 2009). First-time captures were marked with aluminum Z-rings bearing a special identification number. The cave number, ring number, and capture date were noted. All swiftlets that had been captured were released safely close to their respective breeding caves after data collection.

Offspring

The offspring of the Edible-nest Swiftlet were captured on the nests and carefully removed from the nest before fledging. The average age of the Edible-nest Swiftlets' chicks is 35 days in the Andaman Islands (Manchi, 2009). The chicks attend to a body size almost equal to adult birds by 30 days after hatching, i.e., just before fledging. Before that, the tarsus of the individuals was found thicker. Therefore, the chicks above the period of 30 days were selected for ringing (Manchi & Sankaran 2008). All the nests from selected caves were checked every day in the early morning (6:00–6:30 am). The caves were surveyed physically from the start of the breeding season till the fledging of the nestlings to score the nest checks as an empty or occupied nest and to count the number of eggs and nestlings in the nests. The fledglings of the Edible-nest Swiftlet were marked using the aluminum Z-ring. The capture date, ring number, Nest number, and cave number were recorded. Blood samples (approximately 30μL) from the wing veins (brachial or ulnar) using a sterile 1 ml disposable syringe were collected from each bird and stored in saline-saturated DMSO-EDTA buffer for sex determination before replacing the individuals safely in the same nest. Each recaptured individual was observed for the ring and its unique code number. The other individuals captured for the first time were marked using the aluminium Z-rings.

4.4.2. Sex Determination

Similar to the other members of the Apodidae, the Edible-nest Swiftlet (*A. f. inexpectatus*) in the Andaman and Nicobar Islands is known as sexually monomorphic, where the male and female do not depict any morphological variations. Therefore, the molecular method was adopted for individual sex identification of the birds (adults and offspring) captured from the study area. Prior permission was obtained to capture and collect blood samples from the Edible-nest Swiftlet (Permission No: CWLW/WL/134/480, Dated 20/03/2015) from the Andaman and Nicobar Forest Department.

Blood Collection and DNA Extraction

The blood samples (approximately 50μL) were collected from the wing veins (Brachial or Ulnar) using a sterile 1ml disposable syringe and stored in saline-saturated DMSO-EDTA buffer at Room Temperature for sex determination (Plate 4.1). The classical Phenol: Chloroform: Isoamyl alcohol method, with minor modifications, was used to isolate Genomic DNA from the blood sample using the following Protocol (Sambrook & Russell, 2006; Figure 4.4):

- 50 μL of blood sample was taken in a sterilized tube.
- Added 330 μL of Lysis Buffer 10mM Tris (pH 8.0) + 10mM EDTA) + 10 μL 10% SDS + 3 μL Proteinase K. Vortex the sample using Vortex Shaker.
- The samples were kept at 50^{0}C in a Dry Bath Overnight.
- After Overnight Digestion, 400 μL of Tris-saturated phenol was added to the Samples. Test tubes were gently mixed by inverting slowly. Test tubes were incubated at room temperature for 10min.
- After incubation, the test tubes were centrifuged at 14,000 rpm for 10 min. We took the upper aqueous layer from the sample in the new set of test tubes.

- Then 400 µL of Phenol: Chloroform: Isoamyl Alcohol (25:24:1) (Tris Saturated) was added. Test tubes were gently mixed by inverting slowly. Test tubes were incubated at room temperature for 10min.
- After incubation, the test tubes were centrifuged at 14,000 rpm for 10 min. The upper aqueous layer was taken from the sample in the new set of test tubes.
- Then 400 µL of Phenol: Chloroform (25:24) was added. Test tubes were gently mixed by inverting slowly. Test tubes were incubated at room temperature for 10min.
- After incubation, the test tubes were centrifuged at 14,000 rpm for 10 min. The upper aqueous layer was taken from the sample in the new set of test tubes.
- Add 250 µL of Chilled Isopropanol + 50 µL of 0.33M Sodium Acetate were added to the samples. Then, samples were Kept at -20^{0}C for 1 Hour.
- After 1 hour, the samples were centrifuged at 14,000 rpm for 10 min. The Supernatant was decanted from the test tubes.
- 1 mL 70% Ethanol was added to test tubes. Test tubes were gently mixed by inverting slowly. The test tubes were centrifuged at 14,000 rpm for 10 min. The Supernatant was Decanted from the test tubes. Repeat this step for 2 times.
- Further, The DNA pellet was dried at 45^{0}C until completely dry. Then, 50 µL of Nuclease-free water was added to it.
- Test tubes were incubated at 55^{0}C for 1 hour. Samples were kept at -20^{0}C for Further PCR Analysis.
- The concentration and purity of DNA were determined spectrophotometrically using Nano Drop™ 2000c Spectrophotometer at OD 260/280.

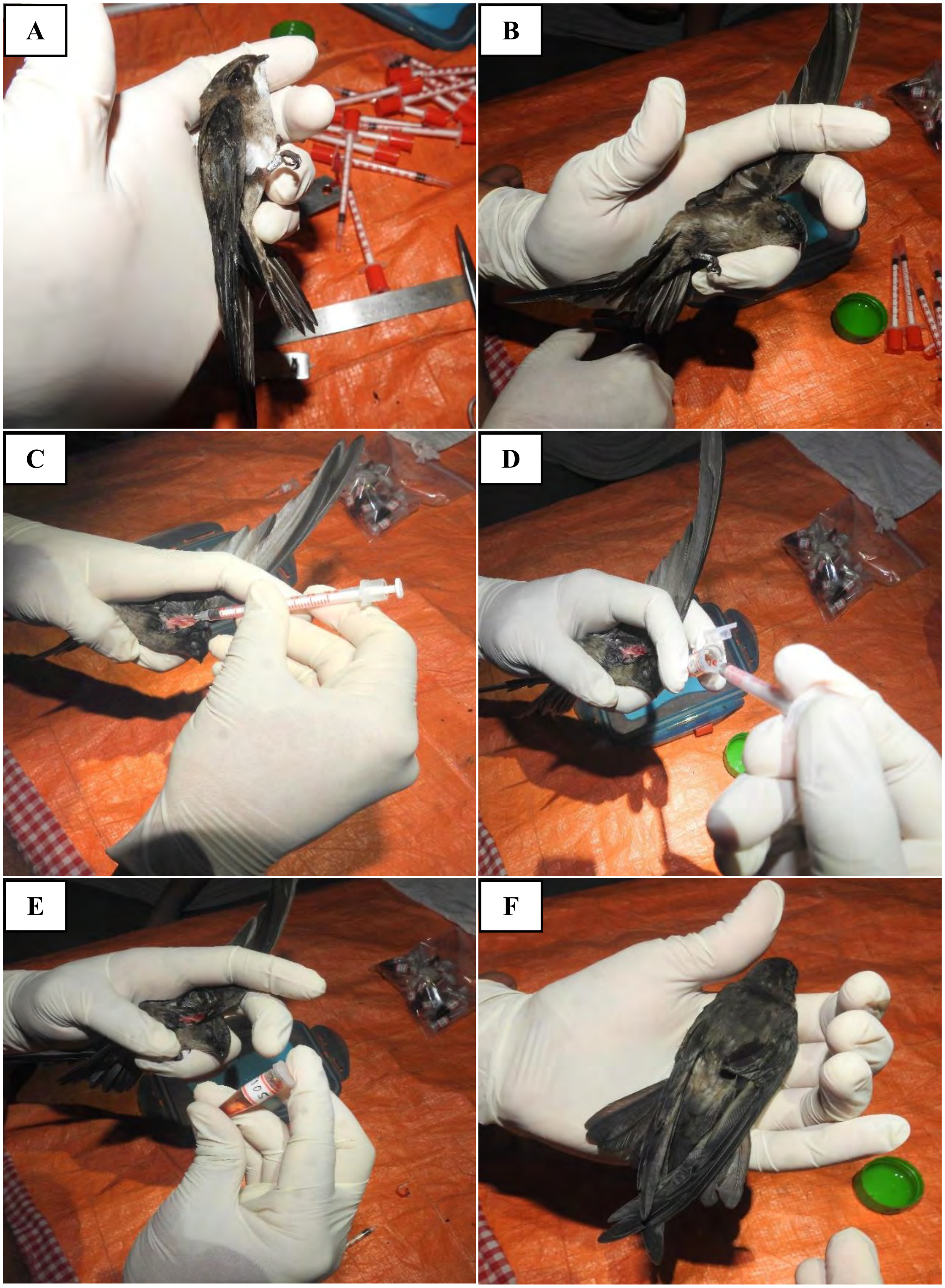


Plate 4.1: Blood sample collection- A: Holding a bird in the hand; B: Wings spread to located brachial vein; C: Collection of Blood using a syringe; D: Blood is preserved in buffer; E: Punctured area is cleaned with alcohol; F: Bird taking rest after blood collection

PCR Conditions and Analysis

The classical PCI method with minor modifications was used to isolate DNA from blood. Two sets of primers- P8(5′-CTCCCAAGGATGAGRAAYTG-3′) /P2(5′-TCTGCATCGCTAAATCCTTT-3′) described by Griffiths et al. (1998) and 2550F (5′-GTTACTGATTCG TCTACGAGA-3′) /2718R (5′-ATTGAAATGATCCAGTGC TTG-3′) by Fridolfsson and Ellegren (1999) were used in combination (for multiplex PCR) to amplify regions of CHD1 gene in Eppendorf thermal cycler. PCR amplification was performed in a 10 µL reaction using the 5 µL Taq PCR Master Mix (Qiagen, Hilden, Germany), 20 ng DNA, 1 µM 2550F/2718R primers, and 0.5 µM P8/P2 primers in a single reaction. The amplification protocol included initial denaturation at 95 °C for 5 min followed by 35 cycles of denaturation at 95 °C for 30 sec, annealing at 45.4 °C for 45 sec, and extension at 72 °C for 50 sec with a final extension of 72 °C for 10 min. The multiplex PCR products were visualized with UV light using 2% agarose and stained with Hi-SYBr Safe Gel Stain (Himedia Laboratories, Mumbai, India). A commercial 1 kb plus DNA Ladder (Qiagen) was used as size slandered (Sambrook & Russell, 2006; Figure 4.4).

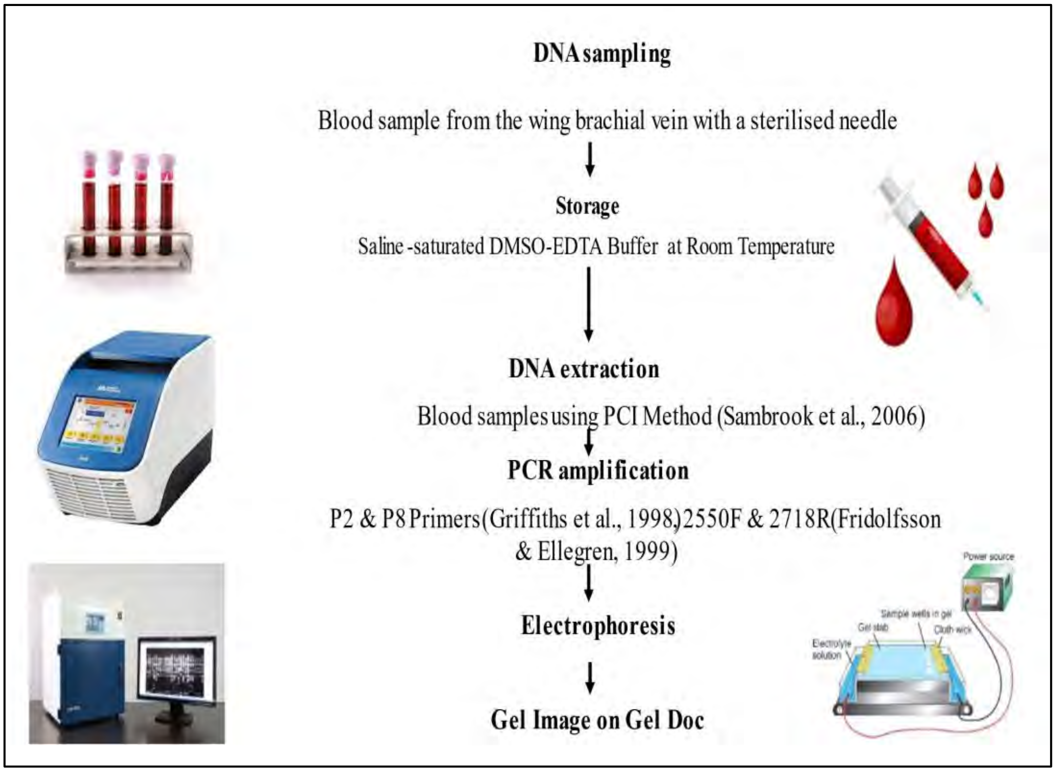


Figure 4.4: Illustration of Standard Protocol for Molecular sex identification

Gel Electrophoresis

- Gels are prepared as percentage weight/volume solutions. To prepare 2% gel, 2g agarose was added in 100ml 0.5x TBE buffer.
- The microwave oven was used to dissolve the Agarose. After the solution was clear, the flask was removed from the oven. Then, the flask was kept at room temperature to get cool.
- The gel-stained dye binds to DNA and fluoresces under ultraviolet light. Traditionally, ethidium bromide (EtBr) is used for this purpose. EtBr is mutagenic and must be handled as hazardous waste. Recently, nontoxic dyes like Hi-SYBr Safe DNA Gel Stain have been introduced. Then, 6 µL/100 mL Hi-SYBr Safe Gel Stain (Himedia Laboratories, Mumbai, India) was added to the gel. The gel was mixed correctly. All the bubbles were removed from the flask before pouring into the gel tray.
- Then, this solution was poured into the Gel tray. An appropriate size comb was inserted into the gel. The gel was allowed to solidify at room temperature.
- The comb was removed carefully without breaking the wells.
- Then, the gel was kept in an electrophoretic chamber containing 0.5x TBE buffer and attached electrodes. Remember: DNA is negatively charged and runs towards the positive electrode. The black electrode should be closest to your samples, and the red electrode should be farthest.
- 3-4 µL of Loading dye was added to the PCR product. Samples were mixed using a vortex shaker and spinner before loading in gel wells.
- Samples were loaded into wells carefully without breaking wells using a micropipette, and with the sample, one negative control and one DNA Ladder were added according to the requirement.
- The power pack was started, and the current/voltage was set according to requirement.

- The Gel was run up to 3/4th of its size. The gel was checked occasionally to ensure that the last tracking dye never got outside the gel.
- The power pack was switched off before removing the Gel. The gel was kept inside the Gel Documentation System, and images were captured under UV- light.
- The image captured by Gel doc was saved using the appropriate name and in a designated folder.
- A commercial 1 kb plus DNA Ladder (Qiagen) was used as size slandered (Sambrook & Russell, 2006; Figure 4.4).

4.4.3. Bird Morphometry

After capturing the adult or offspring Edible-nest Swiftlet, Morphometric measurements, Body length, Tail Length, Wingspan, Culmen length, Culmen depth, Tarsus length, Tarsus width, Hallux Length, and Body Weight were taken for morphometric sex identification (Table 4.1; Plate 4.2 & 4.3). The measurements were performed by the same person throughout. For this study, morphometric data of 1111 birds were used.

Table 4.1: Morphometric variable obtained from Edible-nest Swiftlet live captured in the Andaman Islands, India

S. No.	Morphometric Variable	Abbreviation	Method	Instrument Used	Accuracy
1	Body length (mm)	BL	Length of the stretched body, from the tip of the bill to the tip of the tail	Stopping Wing Ruler	1mm
2	Tail length (mm)	TL	The tail is measured from the base of the tail to the tip of the longest feathers.	Stopping Wing Ruler	1mm
3	Wingspan (mm)	WS	The measured distance between wingtips when the wings are held outstretched	Stopping Wing Ruler	1mm

S. No.	Morphometric Variable	Abbreviation	Method	Instrument Used	Accuracy
4	Culmen length (mm)	CL	Measured perpendicular to and including the lower mandible, just behind the nostrils	Vernier Calliper	0.1mm
5	Culmen depth (mm)	CD	Measured perpendicular to and including the lower mandible, just behind the nostrils	Vernier Calliper	0.1mm
6	Tarsus length (mm)	TL	The measured distance between the notch of the tarsal joint and the foot joint	Stopping Wing Ruler	1mm
7	Tarsus width (mm)	TW	Measured at the narrowest point on the right tibiotarsus anterio-posteriorly	Vernier Calliper	0.1mm
8	Hallux length (mm)	HL	Chord of right Hallux Talon	Vernier Calliper	0.1mm
9	Body weight (g)	BW	Measure using the formula, Body Weight = Weight of Cotton Bag (With bird) – Weight of Cotton Bag (Without bird)	Pesola®Spring Scale	Precision of ± 0.3 %

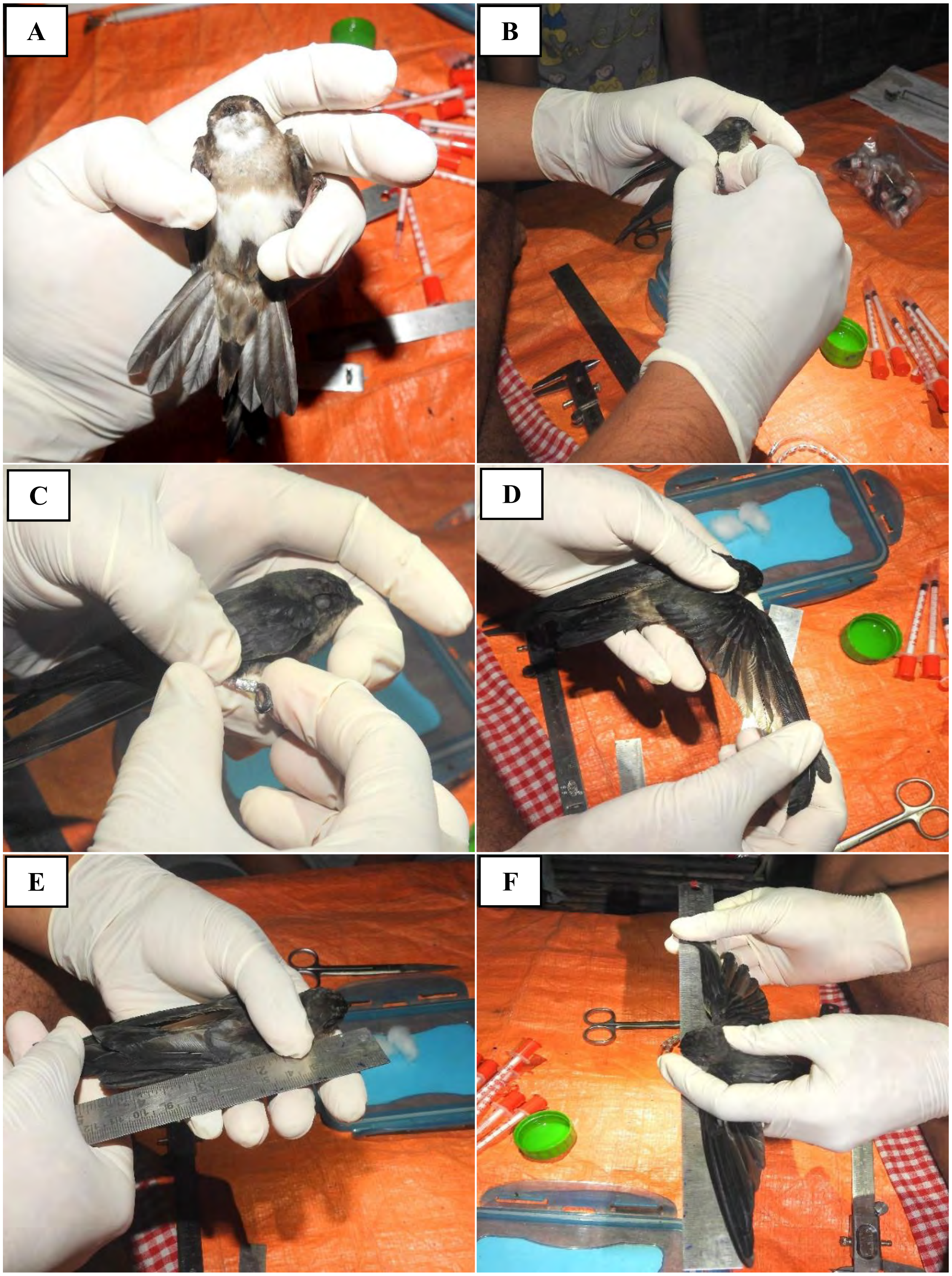


Plate 4.2: Ringing and Morphometric data collection of Edible-nest Swiftlet- A: Bird in hand; B: Putting Z-ring on leg; C: Bird with Aluminium Z-ring; D: Measuring Wing length; Measuring Body length; Measuring Wing span

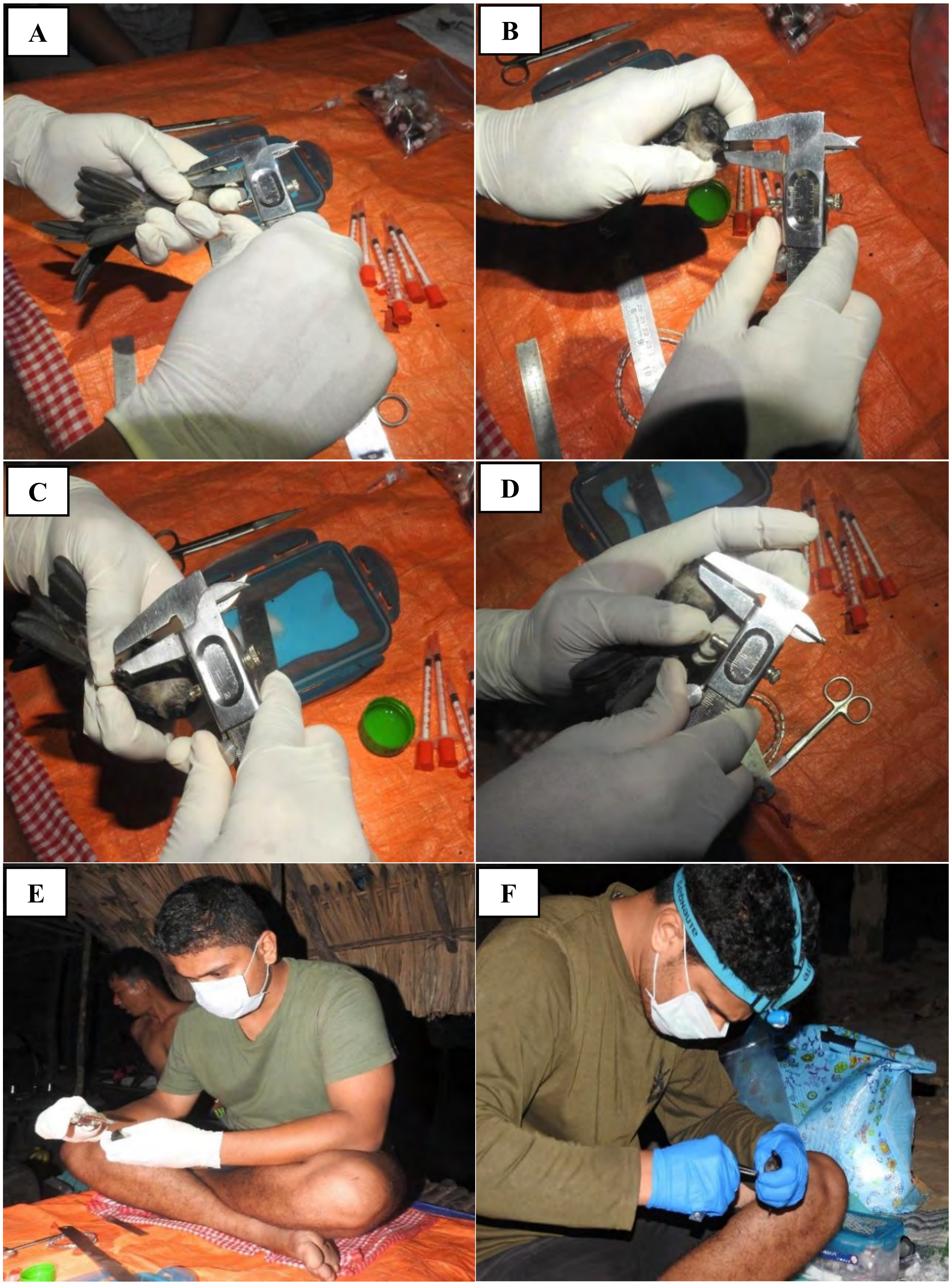


Plate 4.3: Morphometric Data collection of Edible-nest Swiftlet- A: Measuring Bill width; B: Measuring Bill length; C: Measuring Tarsus width; D: Measuring Bill depth; E & F: Collecting Morphometric measurement on-field

Descriptive Statistics

Descriptive statistical analyses were performed to derive indicators for each morphometric measurement. The differences between sexes were analyzed using t-tests, including the mean, maximum, minimum, and standard error.

Discriminant Function Analysis (DFA)

Using stepwise Discriminant Function Analysis, the difference between the sexes was determined. The steps included multi-collinearity statistics, an important statistical method to remove the collinear morphological factors and select the important factor for further analysis. The factors with r value<0.6 were discarded from the final analysis. XLSTAT-Student Version 2023.1.2 was used for the analyses.

4.5. RESULTS

4.5.1. Bird Capture and Marking

The adult and offspring were captured between the years 2017 to 2019. A total of 1545 adults were captured from 47 caves at three study sites (Baratang, n=28; Chalis Ek, n=16, and Interview Island, n=3; Figure 4.5). And 253 offspring were captured from the Baratang cave complex (n=14; Figure 4.5).

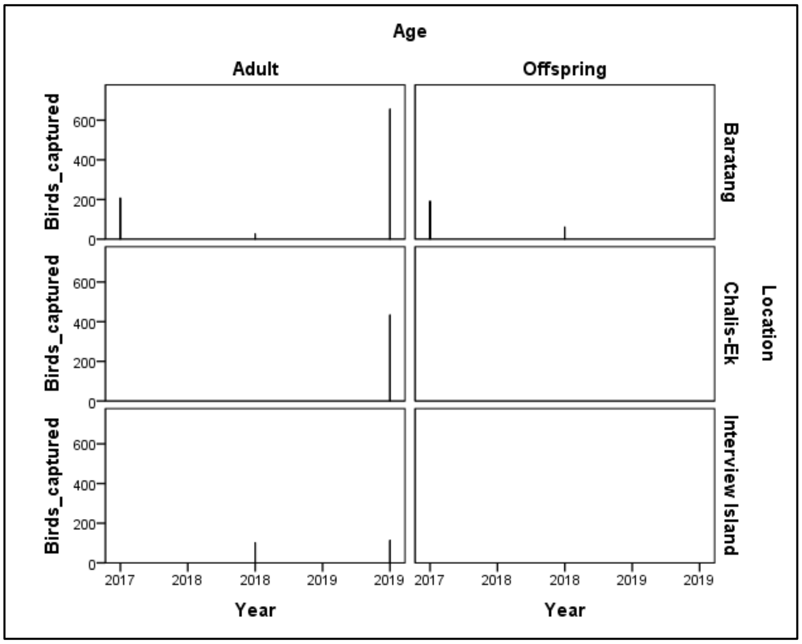


Figure 4.5: Adult and offspring captured from Baratang, Interview Island, Chalis Ek for the individual sex determination

4.5.2 Sex Identification

Initially, sex identification was accomplished using the method described by Griffiths et al. 1998, in which primer pair P8/P2 was used to amplify the CHD1 gene of the Edible-nest Swiftlet. Furthermore, after PCR amplification, P8/P2 alone resulted in a single band of ~380bp on 2% Agarose gel in males and females. Sex identification is impossible based on these results (Figure 4.6 & 4.7A). Another set of primers, 2550F/2718R (Fridolfsson & Ellegren, 1999), was used to resolve this problem. The PCR products run on 2% Agarose gel after PCR amplification. Female samples revealed a band of ~ 550bp, whereas male samples revealed no amplification (Figure 4.6 & 4.7B).

Polyacrylamide gel electrophoresis (PAGE) was used to differentiate sex in Edible-nest Swiftlet. This method uses a 15% polyacrylamide gel to separate PCR products amplified by the P8/P2 primer. The result showed successful male and female sex differentiation in Edible-nest Swiftlet. However, sex identification via PAGE is prohibitively expensive, time-consuming, and labor-intensive. Moreover, Polyacrylamide is a known potent carcinogen (Figure 4.6 & 4.8A).

The CHD1 gene was amplified using a multiplex PCR method that combined the P8/P2 and the 2550F/2718R primers in a single reaction to overcome this. This method successfully distinguished between sexes in Edible-nest Swiftlet and Chicken (Figure 4.6 & 4.8B). On agarose, two bands (380 bp and 550 bp) were observed in female Edible-nest Swiftlet and Plume-toed Swiftlet, but only a single thick band of 380 bp was observed in male Edible-nest Swiftlet and Plume-toed Swiftlet. The 380-bp common band in male and female Edible-nest Swiftlet and Plume-toed Swiftlet corresponds to CHD1Z/CHD1W fragment amplification using the P8/P2 primers. In female Edible-nest Swiftlet and Plume-toed Swiftlet, an additional band of 550 bp corresponds to CHD1W fragment amplification by the 2550F/2718R primers. Because of homogametic sex, the thickness of the 380 bp band was greater in males. Furthermore, these two primer pairs produced three bands in female chicken (380 bp, 460 bp, and 630 bp) and two bands in male chicken (380 bp and 630 bp). The differences in band patterns between the Chicken, Edible-nest Swiftlet, and Plume-toed Swiftlet are due to mutations in the primer annealing site (Fridolfsson & Ellegren, 1999). The multiplexing PCR method was used to sex 1798 Edible-nest Swiftlet samples, from which 942 samples were identified as male, while 856 were identified as female (Figure 4.6 & 4.9).

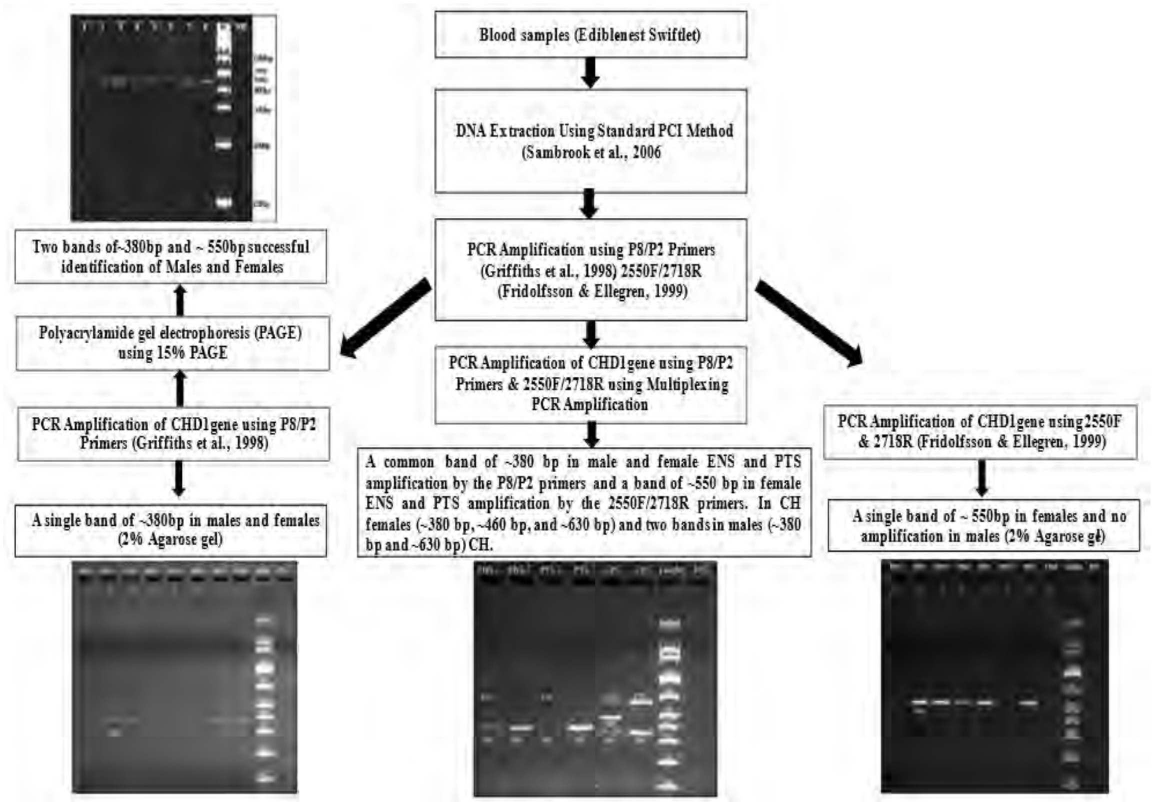


Figure 4.6: Illustration of Novel Molecular technique for sex identification in Edible-nest Swiftlet

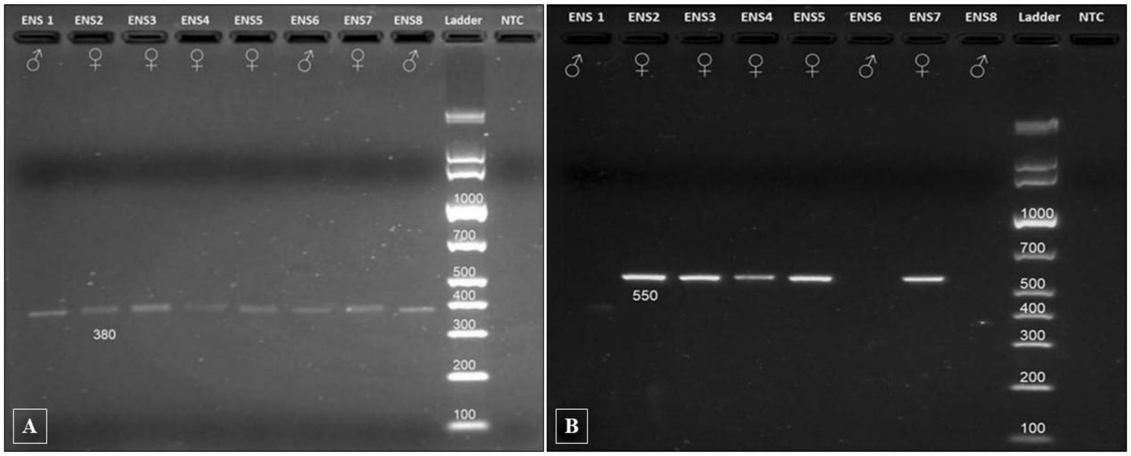


Figure 4.7: Agarose gel (2%) showing the band pattern of PCR A) Using P8/P2 primers B) Using 2550F/2718R primers (ENS Edible Nest Swiftlet, NTC Non-template control, Ladder 1 Kb)

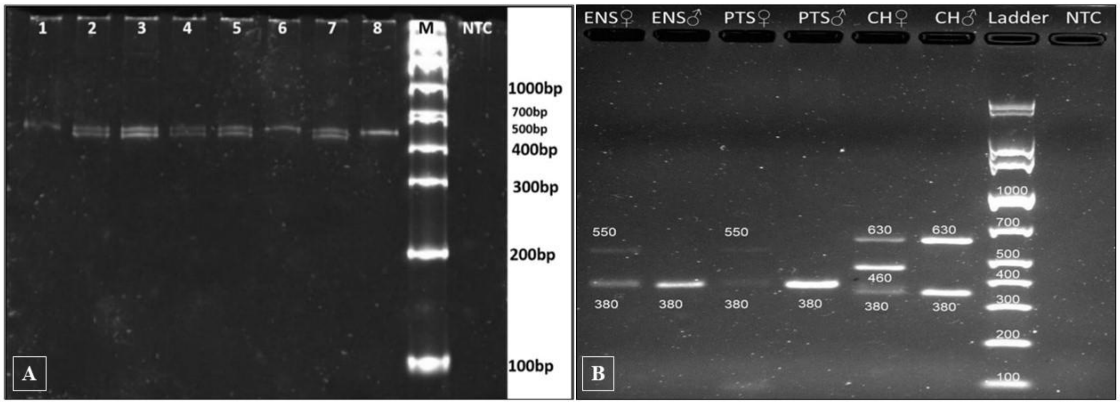


Figure 4.8: A) PAGE image showing the amplification in ENS samples using P8/P2 primers (NTC Non-template control, Ladder 1 Kb), B) Agarose gel showing the band pattern of multiplex PCR using the P8/P2 and the 2550F/2718R swiftlet, CH Chicken, NTC Non-template control, Ladder 1 Kb

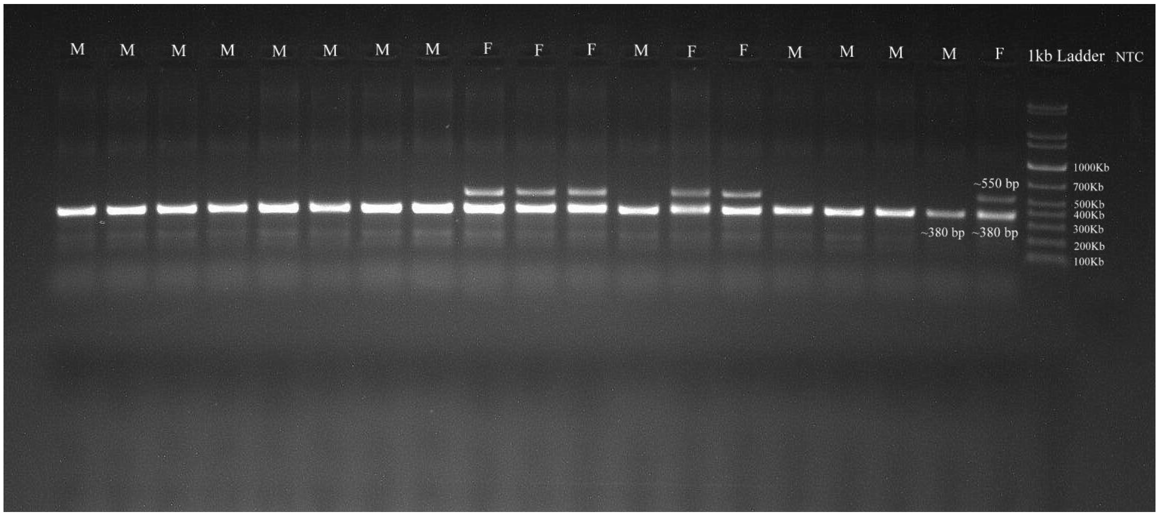


Figure 4.9: Agarose gel (2%) showing the band pattern of multiplex PCR amplification of ENS CHD1 Gene using the P8/P2 and the 2550F/2718R primers, M- Male, F- Female (Edible-nest swiftlet), Ladder 1 Kb, NTC Non-template control)

4.5.3. Sex Ratio in the Edible-nest Swiftlet Colonies

Adult Sex Ratio

Molecular Sex Identification of 1545 adults from all three study sites showed a 1.11:1 (M:F; 814:731) sex ratio. The colony-wise sex ratio in the 47 colonies of Edible-nest Swiftlet. suggests that most (72.91%) colonies maintain a 1:1 sex ratio, whereas the sex ratios are mostly male-biased in nine colonies, and three colonies had a female-biased sex ratio, where number of males was considerably low (Figure 4.10).

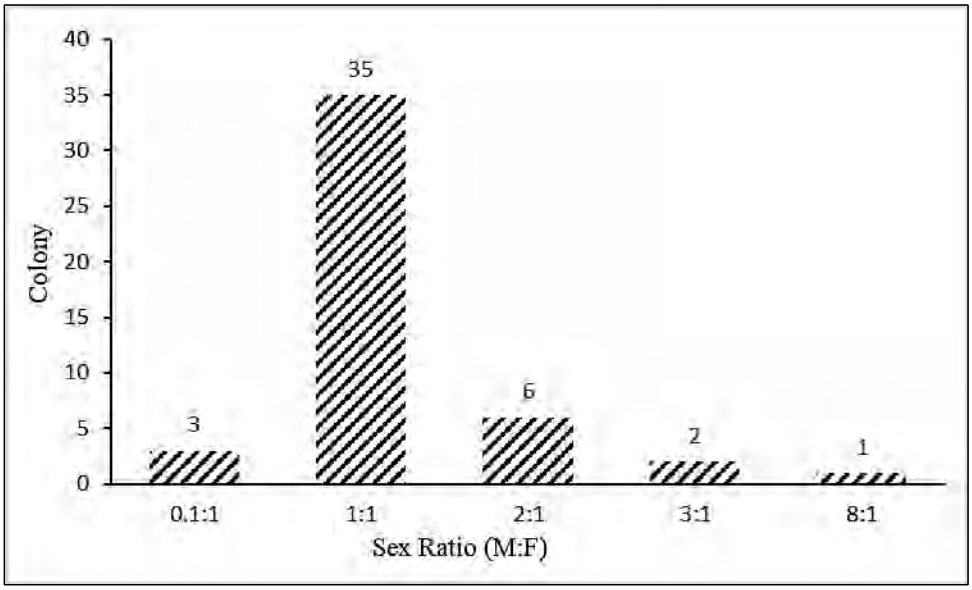


Figure 4.10: Colony-wise adult sex ratio in Baratang, Chalis Ek, and Interview Island caves

Offspring Sex Ratio

Molecular Sex Identification of 253 offspring from Baratang Island showed a 1:1 M:F; 128:125) sex ratio, confirming that Edible-nest Swiftlet colonies maintain a 1:1 (M:F) offspring sex ratio. As Baratang Island has a comparatively high Edible-nest Swiftlet population, data collected from the site was used to analyse the offspring sex ratio (Figure 4.11)

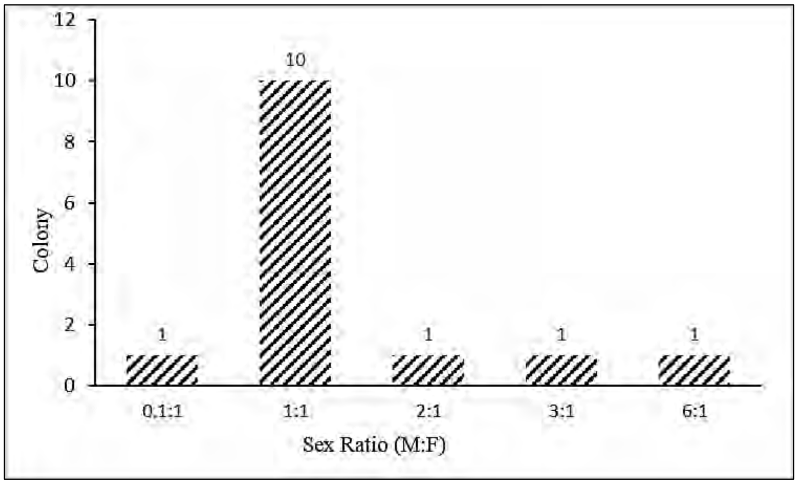


Figure 4.11: Colony-wise offspring sex ratio in caves from Baratang

4.5.4. Discriminant Function Analysis (DFA)

Based on the multi-collinearity statistics, among the nine morphological characters, the Body length and Wing Span are collinear to each other (Tables 4.2 & 4.3). Hence, the discriminant function analysis was conducted based on the eight morphological characters. The t-test conducted using the eight morphological characters for males and females shows no significant difference between the two sexes. However, only two factors contribute to cryptic dimorphism (Table 4.4). A stepwise discriminant analysis suggests that only two of the eight characters (Eigen value=0.02, χ^2=50.99, df=8, P <0.0001) were important in separating the two sexes. The discriminant function coefficient suggests that the sexes differed most for the body length (BL) followed by the body weight (BW). The sexual dimorphism index (SDI) suggests that the culmen width differentiates both sexes, but as the character has a non-significant p-value (>0.05), it is not considered a discriminating factor.

The linear discriminant function that best discriminates males and female Edible-nest Swiftlet was

D= -15.77+ 1.26 (body length) + 0.58 (body mass) + 0.16 (tail length),

where D is the discriminant score. The mean discriminant score of the females is 0.17, and for males is -0.15. The confusion matrix for the cross-validation results correctly classified 100% of 527 females and 30.82% of the 584 males. This implies that the females (Body Length between 12 -15.2cm) can be differentiated from the males based on body length.

Table 4.2: The correlation matrix between the nine morphological characters of the Edible-nest Swiftlet individuals

Variables	**Tail Length**	**Body Length**	**Wing Span**	**Culmen Width**	**Culmen Length**	**Tarsus Length**	**Tarsus Width**	**Hallux Length**	**Body Weight**
Tail Length	1								
Body Length	0.15	1							
Wing Span	0.11	**0.53**	1						
Culmen Width	0.00	-0.00	-0.00	1					
Culmen Length	-0.01	0.03	-0.01	0.03	1				
Tarsus Length	0.14	0.01	-0.06	0.04	0.05	1			
Tarsus Width	0.18	0.05	-0.04	0.00	0.09	0.20	1		
Hallux Length	0.12	0.03	-0.07	0.00	-0.01	0.19	0.30	1	
Body Weight	0.06	0.12	0.05	0.03	0.03	0.13	0.10	0.14	1

Table 4.3: Multi-collinearity statistics of the morphological characters of the Edible-nest Swiftlet individuals

Statistics	Tail Length	Body Length	Wing Span	Culmen Width	Culmen Length	Tarsus Length	Tarsus Width	Hallux Length	Body Weight
R^2	0.076	0.312	0.308	0.004	0.018	0.087	0.143	0.130	0.050
Tolerance	0.924	0.688	0.692	0.996	0.982	0.913	0.857	0.870	0.950
VIF	1.082	1.454	1.445	1.004	1.018	1.096	1.167	1.150	1.053

Table 4.4: Discriminant analysis of Edible-nest Swiftlet's eight morphometric characters as measured. Body weight is measured in grams (g) and length in centimeters (cm). Mean (SE), F-ratios Unidimensional test of equality of the means of the classes between the two sexes and discriminant function coefficients (DFC) from a Wilks' Lambda Test (Rao's Approximation) stepwise Discriminant Function Analysis

Morphological characters	**Male**		**Female**		**p-value (alpha=0.05)**	**F ratio**	**DFC**	**Sexual Dimorphism Index (SDI)**
	Mean ± SE	**Range (Min-Max)**	**Mean ± SE**	**Range (Min-Max)**				
Tail length (cm)	5.32±0.23	4.3-6	5.32±0.24	4.5-6	0.589	0.29	0.04	1
Body length (cm)	13.55±0.46	10.7-15.3	13.65±0.45	12-15.2	**0.00**	**12.56**	**0.58**	1.0
Culmen width (cm)	0.61±2.09	0.35-0.51	0.52±0.06	0.34-0.78	0.31	0.99	-0.18	1.17
Culmen length (cm)	0.45±0.02	0.32-0.57	0.44±0.03	0.05-0.72	0.24	1.37	-0.22	1.0
Tarsus length (cm)	0.85±0.05	0.8-1	0.84±0.05	0.8-1	0.36	0.81	-0.19	1.01
Tarsus width (cm)	0.21±0.03	0.1-0.5	0.21±0.02	0.17-0.52	0.34	0.87	-0.18	1
Hallux length (cm)	0.34±0.03	0.23-0.67	0.34±0.04	0.23-0.58	0.66	0.18	-0.11	1
Body Weight(g)	11.2±1.32	10.78-14.0	11.46±0.98	8-15	**0.00**	**14.21**	**0.69**	1.0

4.6. DISCUSSION

The 1798 Edible-nest Swiftlet individuals (1545 adults and 253 offspring) from the 47 caves were sampled from Baratang Island, Chalis Ek, and Interview Island for the present study. The individuals' sex is determined using the multiplex PCR method for sex identification based on the CHD1 gene that employs the P8/P2 and the 2550F/2718R primers. The sex of the Edible-nest Swiftlet was successfully determined by the new multiplex PCR technique. Because of its affordability, simplicity, and speed, a new adaptive molecular technique for sex identification in edible-nest swiftlets can also be used to identify other bird species.

On the identification of the sexes from the 1545 adults, the results showed that males are 52.69 % (n = 814) and females are 47.31% (n = 731). The overall adult sex ratio (ASR) in the Edible-nest Swiftlet colony is 1.11:1 ratio and 1:1 in the offspring. The skewed ASR is common in wild bird populations (Mayr, 1939; Donald, 2007). Therefore, the skewed ASR (Male biased) in the Edible-nest Swiftlet seems apparent. According to Fisher's theory (1930), when the costs of rearing males and females differ, the sex ratio at independence is expected to be biased towards the less expensive sex, i.e., the smaller sex (males in the Edible-nest Swiftlet). This further explains the skewness in the overall sex ratios in the Edible-nest Swiftlet colonies.

The skewness in the ASR raises questions about the monogamy of the colonial Edible-nest Swiftlet. Studies on socially monogamous birds, such as Eastern Kingbirds (Murphy 2007), found that the females were heavier than males (carried more fat affecting the body mass), thus exhibiting cryptic sexual size dimorphism. A similar trait is observed in the present study. Based on the DFA results, it is now determined that cryptic dimorphism exists in the Edible-nest Swiftlet. Female Edible-nest Swiftlet can be very well discriminated on the basis of body length (collinear to wing span) and weight. According to Anderson et al. (1993) and Krijgsveld et al. (1998), in the size-wise dimorphic species, the larger sex is predicted to have higher nutritional demands and, consequently, be costlier to produce. In the present study of the Edible-nest Swiftlet, the larger sex is female, and the overall sex ratio is male-biased. It explains the skewness in ASR, i.e., females are costlier, hence males are comparatively more in the colony.

In present study of sexual dimorphism DFA with better performance in classifying females than males depicted that the cryptically dimorphic Edible-nest Swiftlet can correctly classify females (100% of 527) and males (30.82% of 584). This implies that based on body length the females (Body length 12-15.2cm) can be differentiated from the males. On the contrary, many studies show successful sex differentiation for both sexes using bird morphometric data and DFA (Table 4.5), such as in White-bellied Sea Eagle *Haliaeetus leucogaster,* the predictive accuracy in identifying male and females is based on the Hallux claw length, Tarsal width, Wing cord, Tarsal joint as discriminating variables is 100% (Shephard et al., 2004) (Table 5). In Mediterranean Gull *Ichthyaetus melanocephalus,* DFA shows 100% predictive accuracy in male and female sex differentiation using Head length, Bill depth at the gonys, and Tarsus length as discriminating morphometric variables (Dubiec et al., 2015; Table 4.5). Further, In the Eurasian Scops Owl *Otus scops*, the discriminating variables were Wing length, Tail length, and Body weight, which show 50% & 59% predictive accuracy for male and female birds (Boano et al., 2019; Table 4.5).

According to Murphy (2007), the sexes generally differ based on the characteristic features of body size. It also presents an assumption where in most of the studies conducted on sexual dimorphism, the males and females are exact copies of one another that differ only in size. But, studies by Hammond et al. (2000) showed males of the Red Jungle fowl (*Gallus gallus*), have smaller peritoneal and reproductive organs than females, but also possess a significantly larger heart, leg muscles, and lungs. Similarly, Tree Swallows (*Tachcycineta bicolor*) showed fewer sexual differences, but males had larger pectoral muscles than females (Burness et al. 1998). Also, the existence of “cryptic sexual size dimorphism” of organ size and muscle mass is a possibility in species that are traditionally regarded as sexually monomorphic (Murphy 2007).

There are extreme examples such as Mallard or Wild Duck *Anas platyrynchus*. The sexes are so distinct that they were previously thought to be different species (Andersson, 1994; Owens & Hartley, 1998). However, while having almost identical plumage, male Corn Buntings *Miliaria calandra* is often 40% heavier than females, which is even more surprising. In birds such as Superb Fairywren *Malurus cyaneus* have comparable sizes for both sexes, but the males' iridescent blue plumage stands out from the females.

Table 4.5: Studies on birds Sex differentiation using morphometrics and Discriminate Function Analysis (DFA)

Species	**Discriminating Variables**	**% Predictive accuracy**		**References**
		Male	**Female**	
Common Raven (*Corvus corax)*	Footpad length and Body Mass	91	97	Bedrosian et al., 2008
White-bellied Sea Eagle (*Haliaeetus leucogaster*)	Hallux claw length, Tarsal width, Wing cord, Tarsal joint	100	100	Shephard et al., 2004
Common Snipe (*Gallinago gallinago*)	Outermost rectrix (R7)	80	80	Włodarczyk et al., 2011
Buff-breasted Wrens (*Thryothorus leucotis*)	Wing chord	95.5	95.5	Gill & Vonhof, 2006
Peruvian Boobies (*Sula variegata*)	Body weight and Wing chord	90	90	Zavalaga et al., 2009
Eurasian Scops Owl (*Otus scops*)	Wing length, Tail length, and Body weight	50	59	Boano et al., 2019
Black Terns (*Chlidonias niger*)	Head-plus-bill length and Body mass	81.5	79.3	Shealer & Cleary, 2007
White-crested Elaenia (*Elaenia albiceps chilensis*)	Wing length and Tail length	90	75	Cueto et al., 2015
Adélie Penguins (*Pygoscelis adeliae*)	Bill length, Bill depth, and Flipper width	89	89	Kerry et al., 1992

Species	Discriminating Variables	% Predictive accuracy		References
		Male	Female	
Mediterranean Gulls (*Ichthyaetus melanocephalus*)	Head length, Bill depth at the gonys, and Tarsus length	100	100	Dubiec et al., 2015
Eurasian Coots (*Fulica atra*)	Head length and Wing length	92	96.7	Minias, 2015
Yellow-legged Gull (*Larus michahellis lusitanius*)	Body length	91.8	85.3	Arizaga et al., 2008
Golden Eagles (*Aquila chrysaetos canadensis*)	Hallux claw and Head length	99.4	99.4	Harmata & Montopoli, 2013
Red-tailed hawks (*Buteo jamaicensis*)	Wing Chord and Body Mass	98	98	Donohue & Dufty, 2006
Great Cormorants (*Phalacrocorax carbo sinensis*)	Wing length, Culmen length, and Tarsus length	92.6	95.1	Liordos & Goutner, 2008
Osprey (*Pandion haliaetus*)	Forearm length and Tarsus length	96.8	93.3	Muriel et al., 2010
Rock Shag (*Phalacrocorax magellanicus*)	Wing length, Head length, and Bill length	83	88	Quintana et al., 2003
Shy albatross (*Diomedea cauta cauta*)	Upper bill depth and Head width	98	98	Hedd et al., 1998
Coscoroba Swans (*Coscoroba coscoroba*)	Head length and Tarsus length	95.2	95.9	Calabuig et al., 2011
Yellow-eyed Penguin (*Megadyptes antipodes*)	Head length and Foot lengths	95	90	Setiawan et al., 2004

The integration of size and plumage dimorphism in Red-winged Blackbirds *Agelaius phoeniceus* is impressive (Owens & Hartley, 1998). Finally, it is very clear that the cryptic sexual dimorphism needs detailed attention and has to be viewed from different parameters including sex-based differences in size, plumage colour, social and sexual behaviour, and parental care (Owens & Hartley, 1998).

Historically, differences in sexual dimorphism between species have been attributed to their mating and parental care practices (Darwin, 1871). According to more recent research, size dimorphism is generally explained by intra-sexual competition, but plumage colour dimorphism is explained by several evolutionary causes (Owens & Hartley, 1998). Adaptations for sexual selection, such as the exotic plumes and colours of the male bird-of-paradise (Family: Paradisaeidae), is an example of extreme variations. Many birds have at least some colour differentiations, with the female having cryptic colouring to blend in with the nest. Considering, the presence of the Sexual Size Dimorphism (SSD) in the Edible-nest Swiftlet, other parameters are recommended to be explored.

The equal 1:1 (M:F) offspring sex ratio determines that the investment in producing either of the two sexes is equal which correlates with Fisher's principle. According, to the Fisher (1930) & Beimborn (1976), both sexes are produced in equal numbers when the investment in producing either of the two sexes is equal. Also, according to Bowers et al. (2014), in the wild bird populations, the parents-rearing broods with equal sex ratio (1:1) are more productive (high in the Edible-nest Swiftlet) than parents-rearing broods biased more strongly towards males or females. This also points towards the selection favouring the production of mixed-sex broods. The authors also highlight that the interaction between the offspring sex and the neonatal environment influences offspring’s fitness, thus favouring sex-ratio adjustment by parents. However, sibling rivalry and environmental conditions such as resource availability with increased sensitivity of males, reduces the fitness returns from highly male-biased broods. This might be a probable reason for maintaining equal offspring ratios in the Edible-nest Swiftlet. Further, according to Szász et al. (2012), the brood sex ratio is not random in many bird species, rather it is related to parental quality and environmental conditions. Further studies focusing on the different environmental conditions and their correlation with the offspring sex ratio needs exploration with greater sampling efforts (similar to the efforts conducted for the ASR).

This study is a first attempt to understand the colony sex ratios in the Edible-nest Swiftlet and provides an intriguing glimpse into the colony structures of this cave-dwelling Apodids. This research also suggests that the Edible-nest Swiftlet are not monogamous species. This allows for detailed studies to be conducted to prove or disprove the same.

The novel findings from the morphology studies contribute to the understanding of the presence of cryptic Sexual Size Dimorphism in the Edible-nest Swiftlet, which has not been demonstrated in any other Apodids. Overall, this chapter adds new information to our understanding of swifts and swiftlets and allow us to study them in greater depth.

Chapter V

CHAPTER V

INTER-COLONIAL DISPERSAL PATTERNS AND FACTORS AFFECTING THE DISPERSAL OF THE EDIBLE-NEST SWIFTLET

5.1. INTRODUCTION

Population dynamics, part of population ecology, studies how population size and density for one or more species change over time and place (Harper et al., 1990). Population ecology has traditionally emphasized understanding the factors that control population dynamics (Murdoch, 1994; Krebs, 2002). However, because demographic processes are frequently governed by several biotic and abiotic processes functioning concurrently across vast geographical dimensions, the variables restricting population expansion still need to be better understood (Krebs, 2002). Population dynamics, influenced by environmental factors, food availability, and interactions between biotic organisms, transmit variations in population size, age class distribution, sex ratio, and behaviour through time and location.

Population dynamics parameters include density, birth rate, mortality rate, immigration, and emigration rates. Populations have quantifiable characteristics, including death and reproduction rates based on age, migration, and composition of sexes and ages. Dispersal significantly influences population dynamics as individuals move and breed from one area to another (Ferris & Wilson, 1987; Ramakrishnan, 2008).

Ornithologists define dispersal as the movement of an individual from the natal or earlier breeding site to the new breeding site. It differs from the migration of birds to and from often distant wintering areas. Natal dispersal involves an individual's movements from its natal, i.e., birth site to its first breeding site. The movement between the breeding sites is called "Breeding dispersal" (Greenwood & Harvey, 1982). Dispersal is fundamental to all living organisms (Comins et al., 1980). It is how a species maintains its current distribution and expands its range by occupying new or re-occupying vacated habitats (Greenwood, 1980; Howard, 1960). Dispersal studies in birds were initiated during the late 1940s by Werth (1947), followed by Austin (1951), who explored site fidelity in colonial birds. Then, Allee *et al.* (1949) explained density-dependent fitness in colonial birds. After testing it, Serrano et al. (2005) found both positive and negative opinions regarding the various species covered by the studies. Furthermore, studies were conducted to understand natal dispersal (Greenwood, 1980) and sex-biased dispersal in birds (Chabrzyk & Coulson, 1976; Greenwood & Harvey, 1976; Greenwood, 1980). Sex-biased dispersal is one of the mechanisms for inbreeding avoidance (Greenwood & Harvey, 1982). According to the study conducted by Greenwood (1980), the natal dispersal in birds is sex-biased, with females settling farther from their natal sites and establishing themselves in their natal territory. Longevity is one of the critical factors shaping the animal's colony along with the other factors affecting the population dynamics, including birth rate and mortality (Begon et al., 2009).

Lifespan, another name for longevity, is a crucial life-history characteristic that differs significantly between and within species. Farner (1945) made distinctions between various types of longevity. In contrast to "potential natural longevity," which is the oldest age attained in the wild, "potential longevity" refers to the maximum life span attained under ideal environmental conditions, such as captivity. In bird ecology, it is crucial to estimate the longevity and survival rates of wild birds and how they relate to other elements of their life histories, such as clutch size and nesting success (Lentino et al., 2003). Several studies show that certain innate factors, such as gender and body mass (Chen & Maklakov, 2014), are crucial for determining the longevity of a species (Lindstedt & Calder, 1976). Additionally, some studies indicate that habitat and the availability of resources may affect longevity (Gigliotti et al., 2020). These studies suggest that decreasing predation as an extrinsic stressor will increase lifespan and that predation may be required to reduce longevity in small prey species. Longevity is frequently influenced by gender, with females typically living longer than males (Chen & Maklakov, 2014). With a few female exceptions, the male of sexually dimorphic species is typically larger and more colorful to attract females during the breeding season. Simultaneously, sexually selected traits may attract the attention of predators, leading to higher predation-based mortality in males. On the other hand, predation might be anticipated to be similar between the sexes in sexually monomorphic species because males and females are morphologically identical. Theoretical explanations for the origin of long-life spans in animals like birds and bats. According to these theories, the average lifespan should rise as the likelihood of dying from extrinsic causes (such as accidents, infectious diseases, and predation) decreases (Austad & Fischer, 1991). In populations that do not have high extrinsic mortality at young ages, harmful mutations that act later in life will be subjected to relatively strong selection (Austad, 1997).

Due to their function in chromosomal integrity and cellular replication, telomeres, repetitive sequences that cap the ends of eukaryotic chromosomes, have lately been recognized as locations of interest for avian aging research (Pauliny et al., 2006). In sand martins *Riparia riparia*, residual telomere length predicts longevity, indicating that animals with longer telomeres may have longer lifespans (Pauliny et al., 2006).

The Bowhead Whale *Balaena mysticetus* (de Magalhaes & Costa, 2009) has a maximum longevity of up to 211 years. In contrast, the Pygmy Goby *Eviota sigillata* (Depczynski & Bellwood, 2005) has a maximum lifespan of just eight weeks. Bird species are prominently long-lived compared to mammals, with few exceptions (Holmes & Austad, 1995). Seabirds are relatively long-lived organisms, exhibiting low reproductive rates, delayed breeding maturity, and high annual adult survival (Gaston, 2004). Salmon-crested cockatoo *Cacatua moluccensis* in captivity shows the highest longevity record (65 Years) in order Psittaciformes (Brouwer et al., 2000). Great Horned Owl *Bubo virginianus* shows a longevity record of 28 years and seven months (Nero, 1992). The Seychelles Fody *Foudia sechellarumis,* a small olive grey passerine in the weaver family, Ploceidae, shows the highest longevity record of 14 years and three months (Oschadleus et al., 2013). The Pied stilt *Himantopus himantopus* shows a longevity record of 23 years and eight months (Habraken & Lawrie, 2020). Bank Swallow shows the highest longevity record of 10 years (Stoner, 1938). The maximum age observed for the Black-capped Vireo was 12 years (Cimprich et al., 2010). The Snowshoe Hares *Lepus americanus* shows the longest longevity record of 20 years (Theisen et al., 2019). Unfortunately, there is a lack of information on the longevity of Edible-nest Swiftlet worldwide.

5.2. OBJECTIVE

This chapter mainly focuses on understanding the inter-colonial dispersal patterns and factors affecting the dispersal. Further, Parameters of Population dynamics, namely Longevity, Mortality, Survival, and Life expectancy in Edible-nest Swiftlet, are discussed in this chapter.

5.2.1. Research Questions

1. Does the Edible-nest Swiftlet display a sex-biased dispersal pattern?
2. What is inter-colonial distance during the dispersal of the Edible-nest Swiftlet?
3. Is the Edible-nest Swiftlet dispersal affected by the caves' biotic and abiotic factors?
4. What is the Potential Longevity of Edible-nest Swiftlet?
5. What is the Mortality, Survival, and Life expectancy in Edible-nest Swiftlet?
6. Does the Edible-nest Swiftlet exhibit a density-dependent dispersal pattern, the "*Allee effect*"?

5.3. STUDY AREA

The study was conducted at three Andaman and Nicobar Archipelago cave complexes: Baratang Island, Challis-Ek, and Interview Island (for details, please refer to Chapter 2).

5.4. METHODOLOGY AND DATA ANALYSIS

5.4.1. Study Cave Selection

Initially, by visiting all the caves, the study confirmed that Edible-nest Swiftlet occupied 112 of the 175 caves known from the Baratang cave complex. The data concerning the breeding population in the 112 caves was collected using the nest count survey in the year 2017 to select the study caves. Further, using the Capture-Mark-Recapture method, 10% of the available caves (n=112) were selected to determine the Edible-nest Swiftlet population. Following the stratified random sampling method (Sutherland, 2006), caves were divided into various classes according to the breeding population sizes (0-10; 11-20; 21-30; 31-40 were pairs, Figure 5.1). Understanding the practical difficulties of using Capture-Mark-Recapture for caves with large swiftlet populations, the maximum class limit was retained at 31-40 pairs (Sutherland, 2006). In addition, the cave selection was greatly influenced by the accessibility of the cave and the feasibility of mist netting, considering the undulating terrain at the cave opening. In many places, setting up the mist net was difficult, and there was not enough place for a person to safely remove the birds from the mist net before they got badly entangled and injured. There was a risk of losing birds while capturing if a huge flock came at a time and got entangled in the mist net. The caves with large populations were avoided to prevent losing birds and causing errors in population estimation. Finally, to determine the population in various caves using the Capture-Mark-Recapture method, 12 caves from four different population classes were selected.

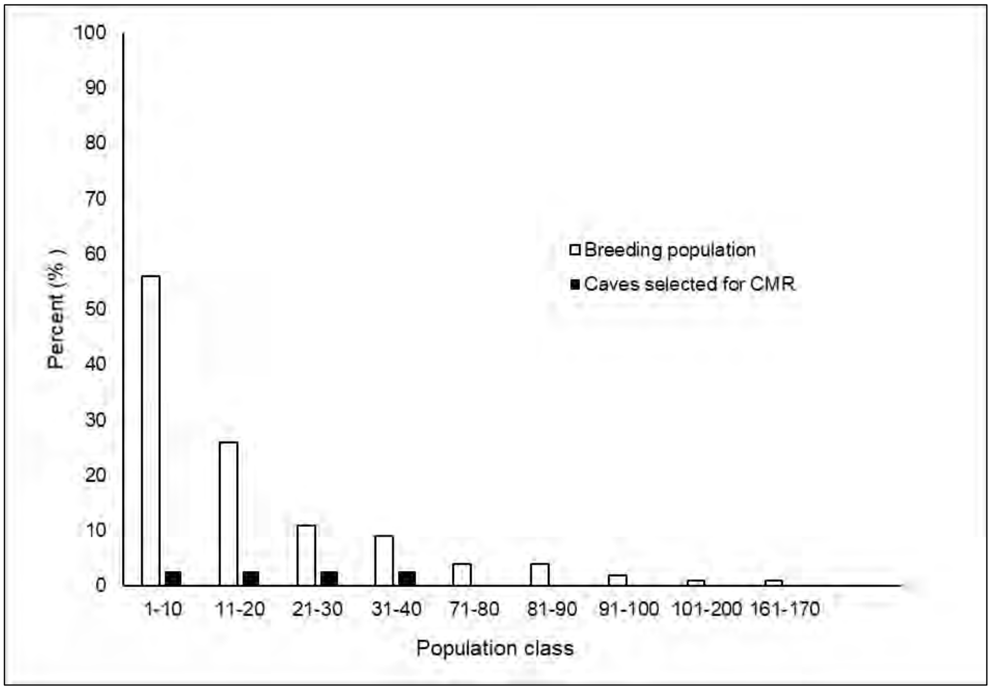


Figure 5.1: Three caves each from four population classes (0-10; 11-20; 21-30; 31-40 pairs) were selected for the Capture-Mark-Recapture method

5.4.2. Capture-Mark-Recapture Method (CMR)

The swiftlets' capture and marking were done in 2017. The recapture was done in all possible caves in the study area during 2018 and 2019.

Adult

Adult birds were caught using the capture-mark-recapture method (Sutherland, 2006). Sterilized nitrile gloves and face masks were worn during bird capture and handling as safety precautions to guarantee the birds' welfare. During the nest-building season (December-January), the adult birds were caught as they returned to their breeding caves by placing mist nets (6 m x 2.6 m; 30 mm mesh) at the entrances of each study cave

(Ralph & Dunn, 2004; Sankaran & Manchi, 2008; Manchi, 2009). First-time captures were marked with aluminum Z-rings bearing a special identification number. The cave number, ring number, and capture date were noted. All swiftlets that had been captured were released safely close to their respective breeding caves after data collection.

Offspring

The fledglings of the Edible-nest Swiftlet were captured on the nests and carefully removed from the nest before fledging (Plate 5.1). The average age of the Edible-nest Swiftlets' chicks is 35 days in the Andaman Islands (Manchi, 2009). The chicks attend to a body size almost equal to adult birds by 30 days after hatching, i.e., just before fledging. Before that, the tarsus of the individuals was found thicker. Therefore, the chicks above the period of 30 days were selected for ringing (Manchi & Sankaran 2008). All the nests from selected caves were checked every day in the early morning (6:00–6:30 am). The caves were surveyed physically from the start of the breeding season till the fledging of the nestlings to score the nest checks as an empty or occupied nest and to count the number of eggs and nestlings in the nests. The fledglings of the Edible-nest Swiftlet were marked using the aluminum Z-ring. The capture date, ring number, Nest number, and cave number were recorded. The birds were recaptured at the end of the next breeding season, placing the mist net at the entrance of all the possible caves in the area, including the cave selected for initial capture. Considering the chance of dispersal in adult swiftlets, the recapture was conducted in 29 Edible-nest Swiftlet-occupied caves in the study area, including study caves (Out of 112 Swiftlet-occupied caves). It is also essential for the error-less estimates of related parameters such as adult survival rate. Each recaptured individual was observed for the ring and its unique code number. The other individuals captured for the first time were marked using the aluminium Z-rings. All swiftlets that had been captured were released safely close to their respective breeding caves and the fledglings placed in their respective nests after data collection.

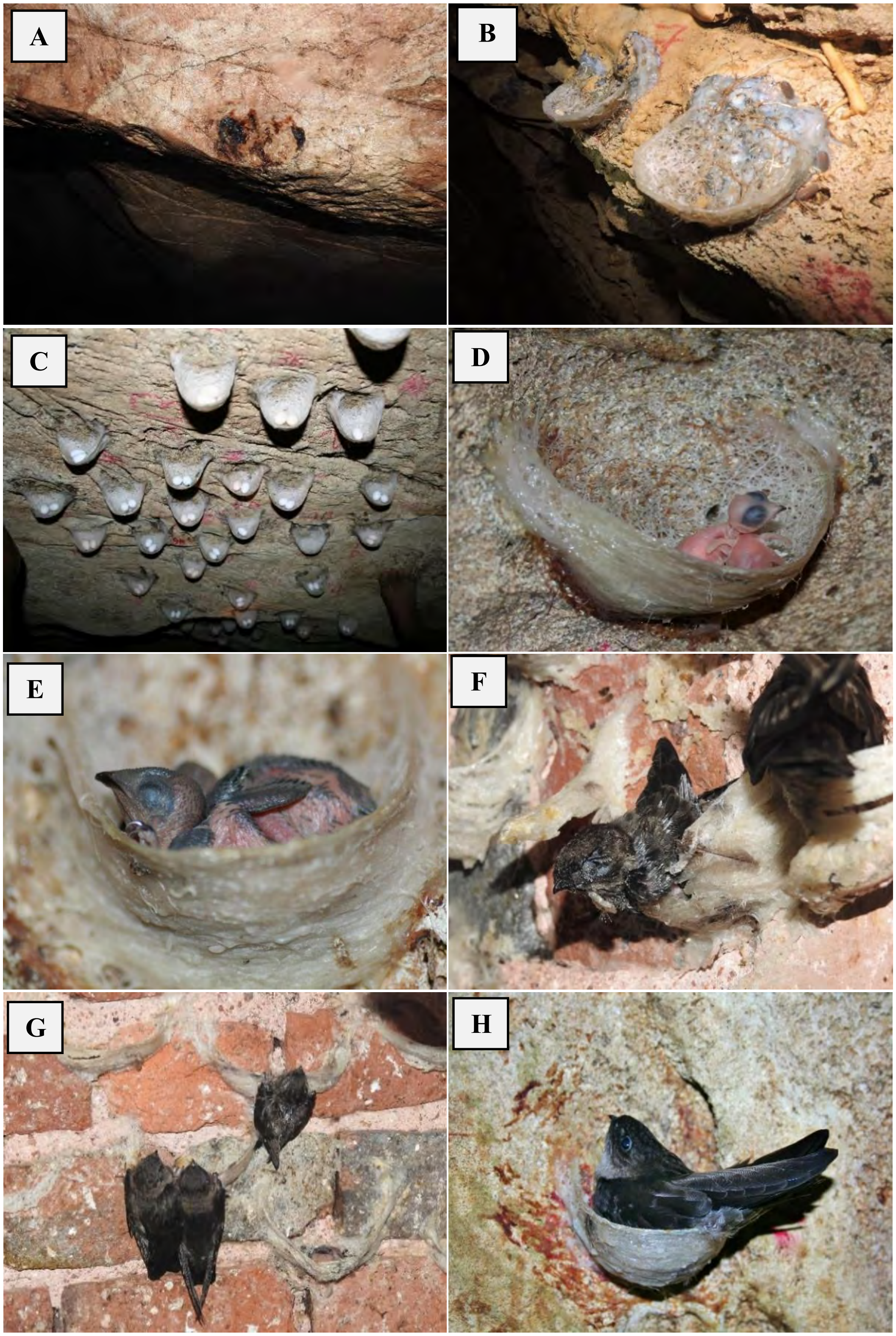


Plate 5.1: Breeding stages of Edible-nest Swiftlet- A: Nesting glue-on cave wall; B: Nest glued on wall; C: Nests with eggs; D: Pair of hatchlings in nest; E: Bird with initial growth of feathers sitting on nest; F: Nestling on nest; G: Fledglings on nest; H: Adult roosting on nest

5.4.3. Molecular Sex Determination

Similar to the other members of the Apodidae, the Edible-nest Swiftlet of the Andaman and Nicobar Islands is known to be monomorphic, where the male and female do not depict any morphological variations. Therefore, the molecular method was adopted for individual sex identification of the birds (adults and offspring) captured from the study area. All the necessary permissions for the bird handling and blood collection were procured from the Department of Environment and Forests of the Andaman and Nicobar Islands.

The blood samples (approximately 50µL) were collected from the wing veins (Brachial or Ulnar) using a sterile 1ml disposable syringe and stored in saline-saturated DMSO-EDTA buffer at Room Temperature for sex determination.

Blood Collection and DNA Extraction

The classical Phenol: Chloroform: Isoamyl alcohol method, with minor modifications, was used to isolate Genomic DNA from the blood sample using the following Protocol (Sambrook & Russell, 2006; Sharma et al., 2021):

- 50 µL of blood sample was taken in a sterilized tube.
- Added 330 µL of Lysis Buffer 10mM Tris (pH 8.0) + 10mM EDTA) + 10 µL 10% SDS + 3 µL Proteinase K. Vortex the sample using Vortex Shaker.
- The samples were kept at 50^{0}C in a Dry Bath Overnight.
- After Overnight Digestion, 400 µL of Tris-saturated phenol was added to the Samples. Test tubes were gently mixed by inverting slowly. Test tubes were incubated at room temperature for 10min.
- After incubation, the test tubes were centrifuged at 14,000 rpm for 10 min. We took the upper aqueous layer from the sample in the new set of test tubes.
- Then 400 µL of Phenol: Chloroform: Isoamyl Alcohol (25:24:1) (Tris Saturated) was added. Test tubes were gently mixed by inverting slowly. Test tubes were incubated at room temperature for 10min.

- After incubation, the test tubes were centrifuged at 14,000 rpm for 10 min. The upper aqueous layer was taken from the sample in the new set of test tubes.
- Then 400 µL of Phenol: Chloroform (25:24) was added. Test tubes were gently mixed by inverting slowly. Test tubes were incubated at room temperature for 10min.
- After incubation, the test tubes were centrifuged at 14,000 rpm for 10 min. The upper aqueous layer was taken from the sample in the new set of test tubes.
- Add 250 µL of Chilled Isopropanol + 50 µL of 0.33M Sodium Acetate were added to the samples. Then, samples were Kept at -20^{0}C for 1 Hour.
- After 1 hour, the samples were centrifuged at 14,000 rpm for 10 min. The Supernatant was decanted from the test tubes.
- 1 mL 70% Ethanol was added to test tubes. Test tubes were gently mixed by inverting slowly. The test tubes were centrifuged at 14,000 rpm for 10 min. The Supernatant was Decanted from the test tubes. Repeat this step for 2 times.
- Further, The DNA pellet was dried at 45^{0}C until completely dry. Then, 50 µL of Nuclease-free water was added to it.
- Test tubes were incubated at 55^{0}C for 1 hour. Samples were kept at -20^{0}C for Further PCR Analysis.
- The concentration and purity of DNA were determined spectrophotometrically using Nano Drop™ 2000c Spectrophotometer at OD 260/280.

PCR Conditions and Analysis

The classical PCI method with minor modifications was used to isolate DNA from blood. Two sets of primers- P8(5′-CTCCCAAGGATGAGRAAYTG-3′) /P2(5′-TCTGCATCGCTAAATCCTTT-3′) described by Griffiths et al. (1998) and 2550F (5′-GTTACTGATTCG TCTACGAGA-3′) /2718R (5′-ATTGAAATGATCCAGTGC TTG-3′) by Fridolfsson and Ellegren (1999) were used in combination (for multiplex PCR) to amplify regions of CHD1 gene in Eppendorf thermal cycler. PCR amplification was performed in a 10 µL reaction using the 5 µL Taq PCR Master Mix (Qiagen, Hilden, Germany), 20 ng DNA, 1 μM 2550F/2718R primers, and 0.5 μM P8/P2 primers in a single reaction. The amplification protocol included initial denaturation at 95 °C for 5 min followed by 35 cycles of denaturation at 95 °C for 30 sec, annealing at 45.4 °C for 45 sec, and extension at 72 °C for 50 sec with a final extension of 72 °C for 10 min. The multiplex PCR products were visualized with UV light using 2% agarose and stained with Hi-SYBr Safe Gel Stain (Himedia Laboratories, Mumbai, India).

Gel Electrophoresis

- Gels are prepared as percentage weight/volume solutions. To prepare 2% gel, 2g agarose was added in 100ml 0.5x TBE buffer.
- The microwave oven was used to dissolve the Agarose. After the solution was clear, the flask was removed from the oven. Then, the flask was kept at room temperature to get cool.
- The gel-stained dye binds to DNA and fluoresces under ultraviolet light. Traditionally, ethidium bromide (EtBr) is used for this purpose. EtBr is mutagenic and must be handled as hazardous waste. Recently, nontoxic dyes like Hi-SYBr Safe DNA Gel Stain have been introduced. Then, 6 μL/100 mL Hi-SYBr Safe Gel Stain (Himedia Laboratories, Mumbai, India) was added to the gel. The gel was mixed correctly. All the bubbles were removed from the flask before pouring into the gel tray.
- Then, this solution was poured into the Gel tray. An appropriate size comb was inserted into the gel. The gel was allowed to solidify at room temperature.
- The comb was removed carefully without breaking the wells.
- Then, the gel was kept in an electrophoretic chamber containing 0.5x TBE buffer and attached electrodes. Remember: DNA is negatively charged and runs towards the positive electrode. The black electrode should be closest to your samples, and the red electrode should be farthest.
- 3-4 μL of Loading dye was added to the PCR product. Samples were mixed using a vortex shaker and spinner before loading in gel wells.

- Samples were loaded into wells carefully without breaking wells using a micropipette, and with the sample, one negative control and one DNA Ladder were added according to the requirement.
- The power pack was started, and the current/voltage was set according to requirement.
- The Gel was run up to 3/4th of its size. The gel was checked occasionally to ensure that the last tracking dye never got outside the gel.
- The power pack was switched off before removing the Gel. The gel was kept inside the Gel Documentation System, and images were captured under UV- light.
- A commercial 1 kb plus DNA Ladder (Qiagen) was used as size slandered (Sambrook & Russell, 2006; Sharma et al., 2021).
- The image captured by Gel doc was saved using the appropriate name and in a designated folder.

5.4.4. Distance Analysis

During the study, the locations of the caves from all three study areas were recorded using a Handheld Global Positioning System (GPS; Model: Garmin Montana 680). To calculate the inter-colonial dispersal distance, a distance analysis was performed using QGIS (Ver. 3.24).

5.4.5. Colony Characters

Data concerning the seven colony-site characters of Edible-nest Swiftlet nesting locations was collected from all the colony sites: (i) the distance of the nesting location from the nearest cave opening, (ii) the distance of the nesting location from the 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 (Table 5.1 & Table 5.2) using a Distometer (Model: Leica S910). In addition, the micro-climatic data (Temperature, Relative Humidity, Atmospheric Pressure, and Wind speed) were collected at every nesting site using a Handheld Environment Meter (Model: Kestrel 5000).

5.4.6. Population, Survival Estimates, Mean Life Span, and Capture Probability

The capture-recapture data was to estimate the populations of the Edible-nest Swiftlet using the Lincoln Index (Cooch & White, 2001) (Equation I). It is based on the principle that a proportion of the marked population returns somehow to the original population. Then, after complete mixing, when a second sample is taken, the proportion of the marked individuals in the second sample would be the same as initially marked in the total population. Further, a goodness of fit test (Student's t-test) was performed to understand the significance between the two populations.

The formula of the Lincoln Index is as follows;

$$N = \frac{M*T}{R} \qquad \text{(Equation I)}$$

(Where, N=Total population size, M=Initially marked birds, T=Total in the second sample, R=Marked recaptures)

For survival estimates and capture probability, the program MARK (Ver. 9.0, Build 9200) was used with the Live Recaptures (CJS) model (Cooch & White, 2001). The following four predefined models were used to check the dependence of survival and capture probabilities as the function of time: (1) ϕ (t) p (t) (standard Cormack-Jolly-Seber model, Cormack, 1964; Jolly, 1965; Seber, 1965; Cormack, 1989) with time-dependent survival and capture probability, (2) ϕ (.) p (t), with constant survival and time-dependent capture probability, (3) ϕ (t) p (.), with time-dependent survival and constant capture probability and (4) ϕ (.) p (.), with constant survival and capture probability. Based on the lowest Akaike's Information Criterion (AICc), Delta AICc >2 (difference in AICc between models), and superiority of the Akaike's Information Criterion Weight (AICc weight) the best model fit was selected. Also, The Likelihood Ratio Test (LRT) was used to assess the goodness of fit of two competing statistical models using their likelihood ratio. The mean life span (Msl) was calculated using Equation II, i.e.

Msl= $\frac{1}{(-\log \phi)}$ (where ϕ is adult survival) (Tarburton, 1987) (Equation II)

5.4.7. Longevity

The longevity of the Edible-nest Swiftlet was calculated by using the following formula,

If the bird was initially marked as an adult, then

Age of the bird (Minimum) = $RC - C + 2$ (Equation III)

(RC = Year of the recapture of an individual, C = Year of the first capture of the same individual,

The Edible-nest Swiftlets are known to breed only in the alternate year after fledging, Juvenile bird age = 2)

If the bird was initially marked as a nestling, then

Age of the bird = $RC - C$ (Equation IV)

5.4.8. Allee Effect

The nesting area was calculated using the Distometer (Model: Leica S910). The Edible-nest Swiftlet population in each study cave was estimated, and based on this, the population density was estimated by using the following formula,

Population density, $D_p = N/A$ (Equation V)

(Where D_p is the population density, N is the total population, and A is the area covered by the population)

To determine the association between population size and density as well as population size and sex ratio, linear regression modeling was carried out using SPSS (Ver. 20). The nest count data was used for population size (total nest*2), and the sex ratio (females per male) was used for the analysis. The population size and sex ratio were independently calculated for 2017 and 2018. The number of caves sampled for estimating the population size is 12, whereas, for capture-mark-recapture, 12 caves were sampled in 2017. Still, due to weather conditions and a lack of human resources, six caves were sampled in 2018. The analysis was conducted independently for 2017 and 2018.

5.5. RESULTS

5.5.1. Inter-Colonial Dispersal and Individual Sex

None of the marked adult birds (n=207) dispersed between the colonies. This depicts that there are no adult dispersal phenomena in the Edible-nest swiftlet. The finding also supports the existence of breeding site fidelity in the species.

The 245 juveniles were initially captured in 12 caves on Baratang Island between 2017 and 2018 and then attempted to be recaptured in 49 caves from the three study sites (Baratang Is., n= 29, Interview Is., n= 3, Chalis Ek, n=16). In Interview Island and Chalis Ek, recapture was done to capture ringed birds from previous studies conducted between 2002 and 2013 (Sankaran & Manchi, 2008; Manchi & Mane, 2012). 34 Edible-nest Swiftlet Individuals, initially marked as juveniles from 2002 to 2013 (n=20) and 2017 to 2019 (n=14), were recaptured from all three study sites. Proportionately, 38.23% of these recaptured individuals [Interview Is. (n=4), Baratang Is. (n=7) and Chalis Ek (n=10)] were from the same caves, showing philopatry, whereas 61.77% of individuals depicted natal dispersal by commencing first breeding away from the birth cave. Natal dispersal detected in Edible-nest Swiftlet was female-biased of the 21 dispersed individuals 12 were females, and 9 were males (Figure 5.2 & 5.3). The remaining 13 individuals (8 females and 5 males) showed philopatry (Figure 5.2 & 5.3).

5.5.2. Inter-Colonial Dispersal Distance

The dispersal distance of the individuals varied between 0.01km and 4.07 km (Figure 5.5 & Figure 5.6). The average natal dispersal range of females was 0.57km, and that for males was 0.16km. The maximum natal dispersal distance covered by a female was 4.07km on Interview Island, and for a male was 0.75km on Baratang Island (Figure 5.4). Overall, the female Edible-nest Swiftlet shows a longer natal dispersal distance than males who choose to disperse in a cave near their natal site.

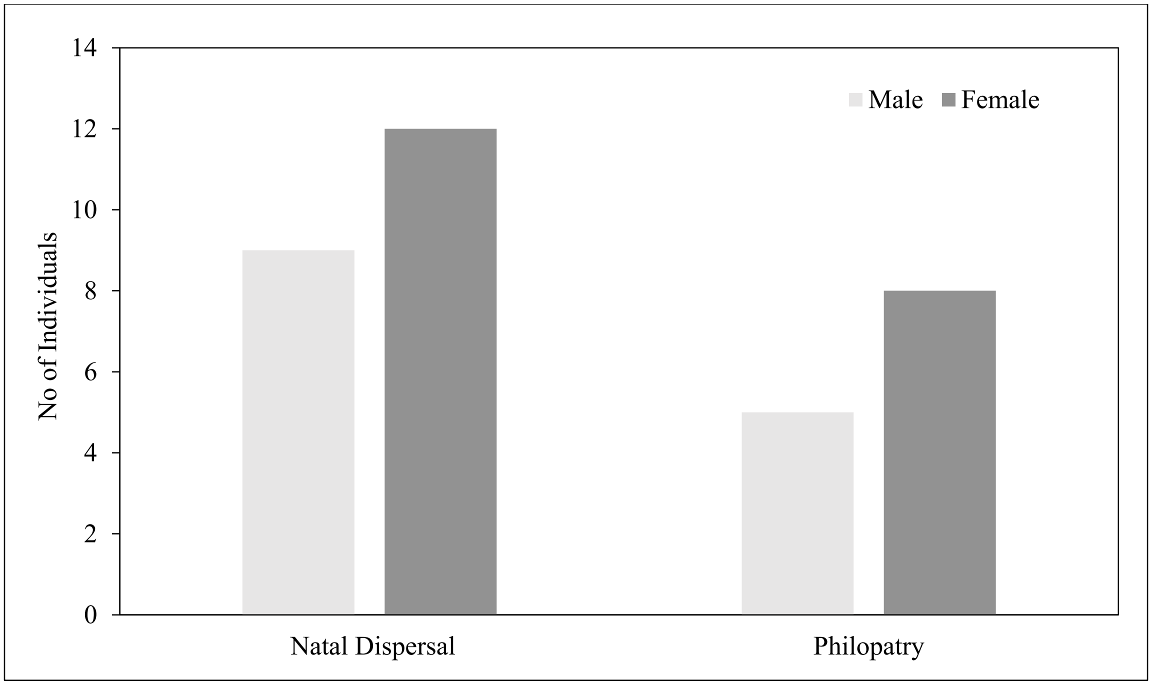


Figure 5.2: Sex-biased Natal Dispersal and Philopatry in Edible-nest Swiftlet of the Andaman Islands

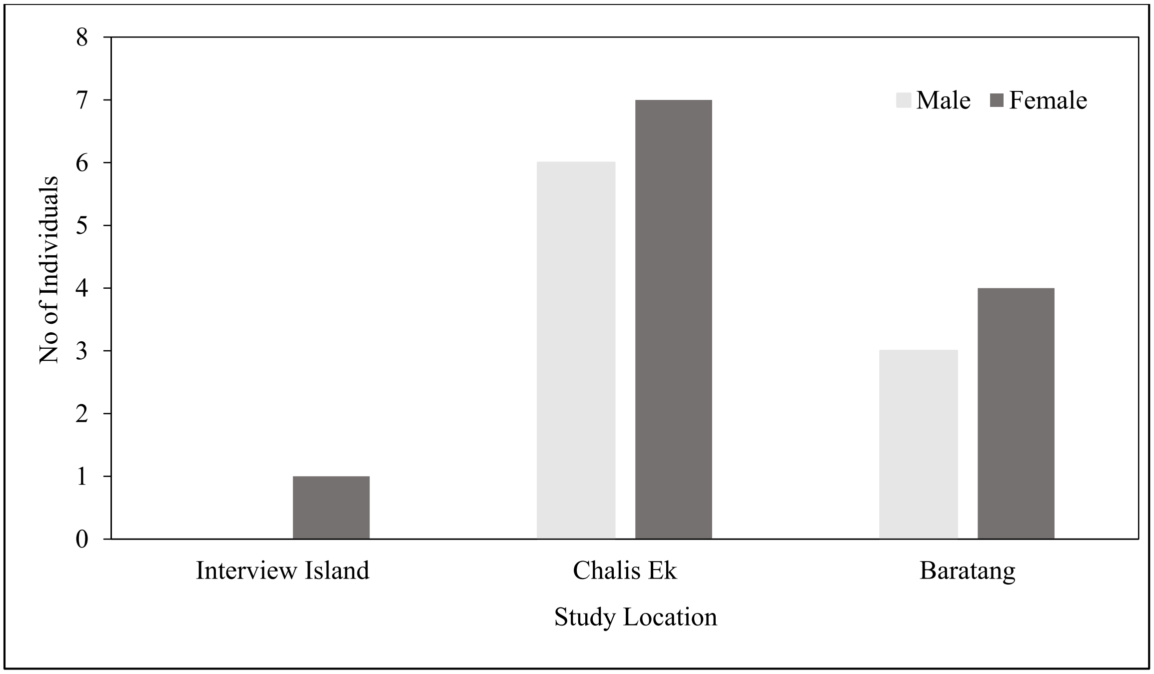


Figure 5.3: Sex-biased inter-colonial Natal dispersal in Edible-nest Swiftlet of three study locations: Interview Island, Chalis Ek, and Baratang Island

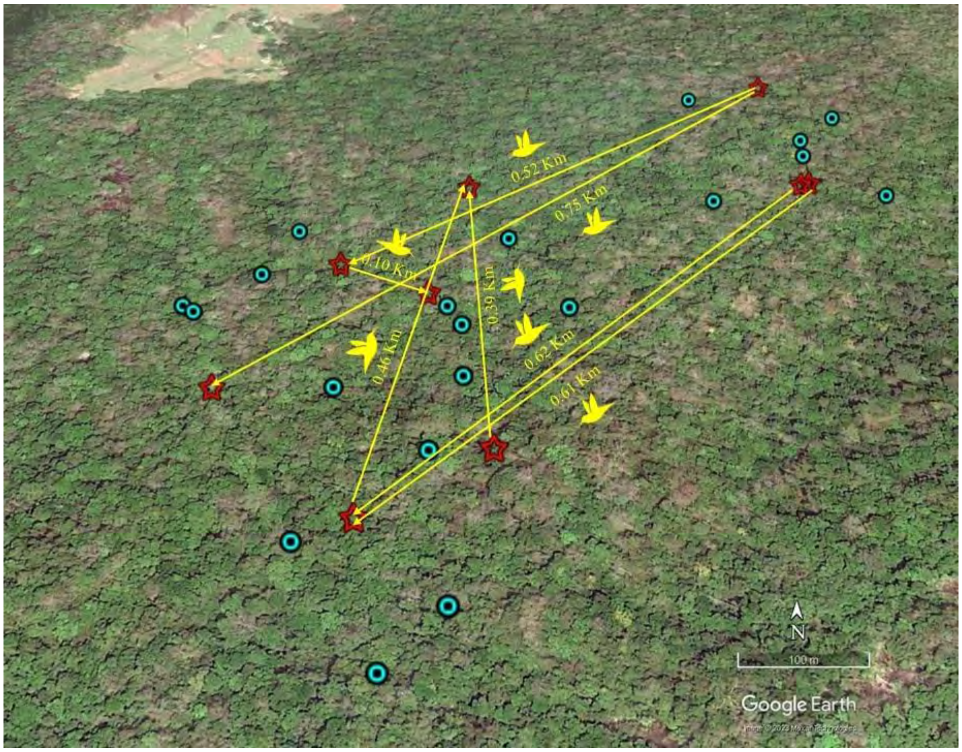


Figure 5.4: Edible-nest Swiftlet's Inter-colonial Dispersal and Dispersal Distance observed within the cave complex at Baratang Island

Figure 5.5: Edible-nest Swiftlet's Inter-colonial Dispersal Distance observed on the Interview Island

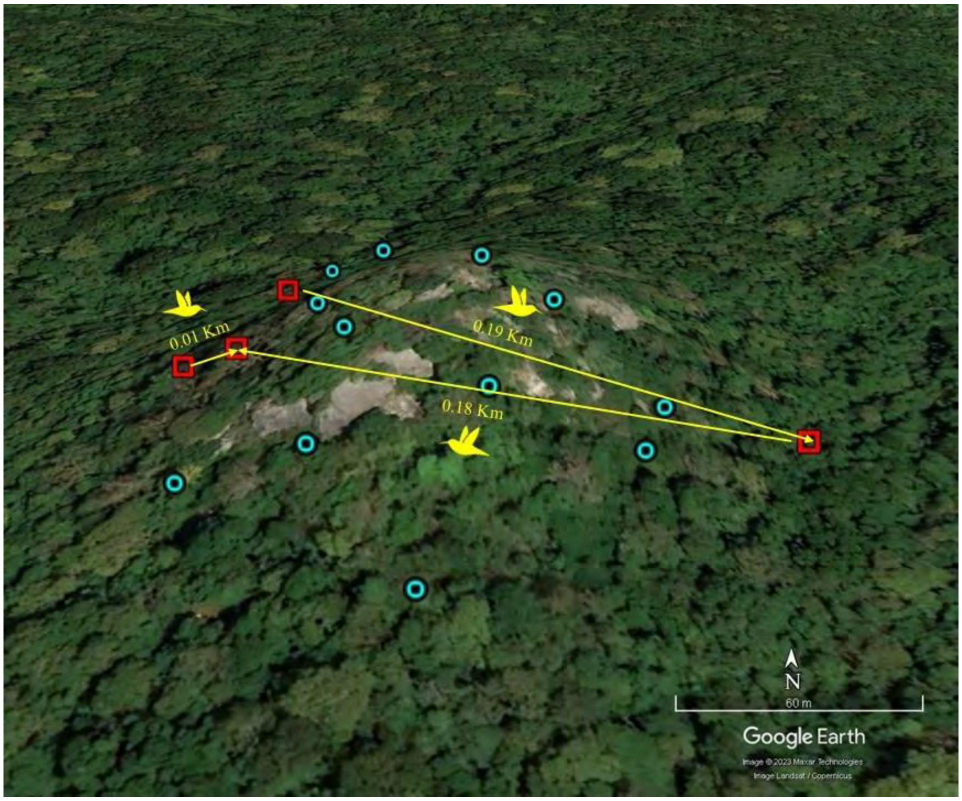


Figure 5.6: Edible-nest Swiftlet's Inter-colonial Dispersal Distance observed at Chalis Ek

5.5.3. Colony Characters

Twelve colony-site characters were collected, and none was significantly related to the colony-site selection (Table 5.1 & Table 5.2). However, a few of these parameters are known to contribute to the selection and use process. In the study caves of Baratang and Chalis-Ek, the study height of the swiftlet colony is between 1.83m to 9.39m and 1.69m to 15.97m, respectively. This factor does not affect the colony-site selection of the Edible-nest Swiftlet. The selection may be influenced by the height and angle of the cave wall in a way that is impenetrable to predators. However, the current study did not find evidence of such a relationship. The present study did not find that the vertical angle of the cave wall affected the choice of nest site. However, swiftlets were less common in the caves with a high bat population, according to observations made in the Baratang and Chalis-Ek.

The relative humidity and temperature in Baratang and Chalis-Ek are significantly different ($p<0.05$). The wind speed and light intensity are 0.00 km/hr and 0 lux at the colony-site location, implying that the birds chose the nest site where it is not windy and completely dark.

Table 5.1: Colony-site characters of caves where the Edible-nest Swiftlet was captured and recaptured within the cave complex of Baratang Island

Morphometric parameters	Capture Caves	Recapture Caves	p
Height	4.83±2.42	6.07±2.41	p>0.05
Nest angle	74.80±9.72	73.61±11.28	p>0.05
Length	0.75±0.64	0.79±0.64	p>0.05
Width	1.07±1.48	0.96±0.76	p<0.05
Perimeter	4.09±5.26	4.72±3.51	p>0.05
Direction	209.17±107.77	148.52±111.95	p>0.05
Distance from bat colony	5.25±3.92	9.68±9.66	p>0.05
Distance from the cave entrance/ nearest opening from the bird colony (m)	19.58±6.70	27.92±15.84	p>0.05
Temperature	28.47±0.41	27.92±1.01	p>0.05
Humidity	90.15±5.96	85.05±20.61	p>0.05
Barometric Pressure	29.77±0.04	29.73±0.10	p>0.05
Atmospheric Pressure	29.77±0.04	29.72±0.09	p>0.05
Wind speed	0	0	NA
Light intensity (Lux)	0	0	NA

Table 5.2: Morphometric characters of caves where the Edible-nest Swiftlet was captured and recaptured within the cave complex of Baratang Island

Morphometric parameters	**Capture Caves**	**Recapture Caves**	**p**
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.	32.42 ±13.41	43.88±21.69	$p>0.05$
Horizontal Length (m): The map-derived parameter tells us the length of the cave covered horizontally on the earth's surface.	19.54±7.66	27.68±14.06	$p<0.05$
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	139.83±151.56	149.1±139.79	$p>0.05$
Cave depth (m): It is the distance down of a cave from its opening at the earth's surface	25.05±10.56	32.86±16.73	$p>0.05$
Surface length (m): It is the measurement or extent of the cave ceiling from end to end	7.99±5.00	10.5±5.07	$p>0.05$
Surface width (m): It is the horizontal length of the cave surface	11.45±3.58	14.22±5.18	$p>0.05$
Surface area (m^2): It is a map-derived parameter that gives the area of the cave surface, mostly the ceiling	99.12±73.08	157.6±116.97	$p>0.05$
Cave Volume (m^3): It is a three-dimensional space enclosed by the cave.	187.47±215.79	520.31±403.70	$p>0.05$
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%.	2.13±1.01	2.73±1.16	$p>0.05$
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	325.05±222.32	514.43±363.47	$p>0.05$
Average Inclination (°): This considers the average of all the vertical angles recorded at every survey station	50.96±4.97	49.03±7.44	$p>0.05$
Inclination (°): It tells at which angle, vertically or horizontally, the cave is inclined in the three-dimensional space	49.75±25.08	40.4±29.33	$p>0.05$

5.5.4. Population Estimation, Survival Estimates, Mean Life Span, and Capture Probability

Population Estimation

The population of the study species in each cave was estimated using the nest count and roost count techniques (Medway, 1962a; Medway, 1962b; Manchi & Mane, 2012; Manchi & Sankaran, 2014; Mane & Manchi, 2017). Those with experience in nest protection and former nest collectors helped with the nest counts. The walls and ceilings of the cave were thoroughly searched for the nests after entering. The nests were noted as soon as they were discovered. To track the breeding populations of the Edible-nest Swiftlet, counts are made at the end of each month from December to June (Medway, 1962a; Sankaran, 2001; Manchi & Sankaran, 2014). When nest construction is complete, and chicks are in the nest, i.e., in April-May, the final nest count is taken into account. Due to the monogamous nature of the Edible-nest Swiftlet (Lim, 2002; Winkler et al., 2020), each nest was viewed as representing two individuals (Sankaran, 2001; Sankaran & Manchi, 2008; Manchi & Sankaran, 2014).

The roost counts were conducted to determine the total Edible-nest Swiftlet population in the caves. During the roost count, the observer sat close to the cave mouth and recorded the number of individuals entering and exiting. At dark hours, the audible echo clicks (frequency between 1.5 kHz and 10 kHz) produced by the birds (while entering and exiting) for navigation were counted (Medway, 1962a; Medway & Pye, 1977; Mane & Manchi, 2017) and recorded. The roost count method provides a total population estimate of the birds by subtracting the number of breeding individuals (Nest counts) from the entire assessment. It gives the number of non-breeding individuals in the colony. Combining the outcomes of these two methods, the breeding, non-breeding, and total population of the cave-dwelling Edible-nest Swiftlet were estimated (Equations VI, VII and VIII).

Based on the estimated breeding and total populations in each cave (Figure 5.7), we estimated the average proportions of the breeding and non-breeding populations in a colony using Equation VI. Total Population (TP) derived from the roost count is considered 100% of the population of a colony.

$$BP\ (\%) = (100*BP)/TP \qquad \text{(Equation VI)}$$

$$BP\ (\%) = (100*876)/963$$

Which estimated the proportionate breeding population in a colony as,

BP (%) = 91.95

Further, to estimate the proportionate non-breeding population

TP (%) = BP (%) + NP (%)

NP (%) = TP (%) – BP (%)

Which estimated the proportionate non-breeding population in a colony as,

NP (%) = 8.05

Where TP = Total Population derived from roost count, BP = Breeding Population derived from the nest count, NP = Non-breeding Population

Regarding the above mathematical calculations, each study cave had an average of 8.05% of non-breeding and 91.1% of the breeding population.

Therefore, the equation to estimate the Non-Breeding Population using the nest count method would be;

$$NP = \frac{8.05 * BP}{91.1} \quad \text{(Equation VII)}$$

(Where NP = Non-breeding Population, BP = Breeding Population derived from the nest count method)

Further, the equation to estimate the Total Population inside the cave would be;

$$TP = BP + NP \quad \text{(Equation VIII)}$$

(BP = Breeding Population derived from nest count method, NP = Non-breeding Population derived from Equation VI)

Using the nest count method, the Breeding Population (BP) in the 12 study caves was estimated as 460 birds. So, the Non-Breeding Population (NP) can be determined using Equation VII:

$$NP = \frac{8.05 * 460}{91.1}$$

which equals to 40.64, i.e., ~41 birds, putting the value 41 in Equation VIII,

$$TP = 460 + 41; \text{ are 501 birds}$$

Simultaneously, the Lincoln Index was used (using CMR data) and estimated 486±28 (Estimate±SE) birds (Figure 5.7). The goodness of fit test revealed that there is no significant difference between the total populations estimated using both the methods: the CMR method with Lincoln Index (Equation I) and the nest and roost count methods with a combination of Equation VII and VIII ($p>0.05$; Figure 5.7).

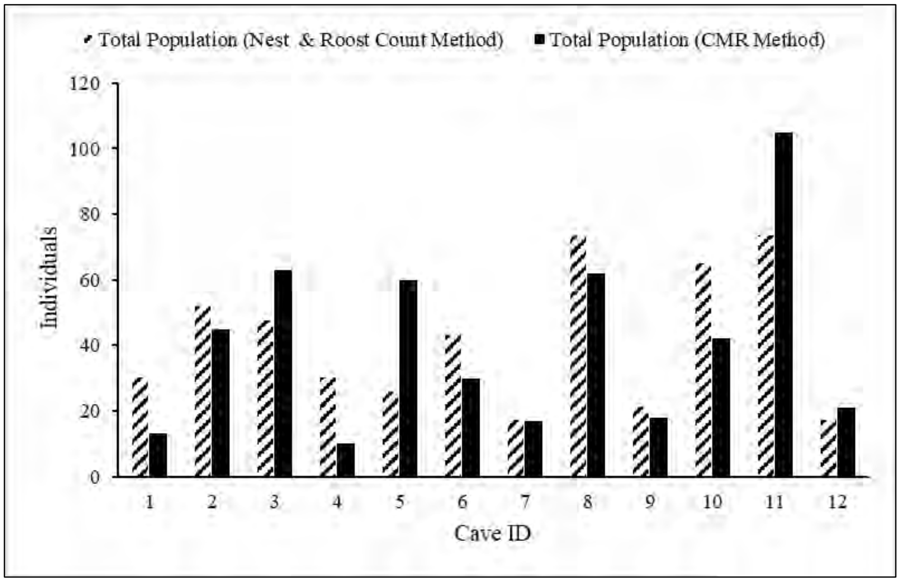


Figure 5.7: Population estimation using Nest Count, Roost Count Method, and Capture-Mark-Recapture (CMR) Method

Survival Estimates, Mean Life Span, and Capture Probability

Out of the estimated population of 501 birds, 75.64 %, i.e., 379 adult individuals, were captured and marked between December 2017 and June 2019. From every study cave, 31.58%±17.1% of birds were captured. The overall recapture rate (% adult survival) in the study caves was 42.22% (n=379). The CMR models (Table 5.3), along with the LRT (Table 5.4), suggested that the two models $\{\phi_t\, p_t\}$ and $\{\phi.p.\}$ are competing statistically based on the goodness of fit ($p<.0001$). The first model's time-dependent predicted annual survival rate is 0.97, and the capture probability is 0.21±0.03. When the annual survival rate is constant (i.e., 1.00 for the Edible-nest Swiftlet), the capture probability is 0.35±0.02. The annual survival between the sampling periods is 0.42; hence, the species' predicted Mean life span (Msl) is 2.85 years (Equation II).

Table 5.3: Population parameters and the outputs of the MARK program for the Edible-nest Swiftlets in Baratang

Model No	**Model and explanation**	**AI Cc**	**Delta AICc**	**AICc weight**	**Model Likelihood**	**No. Par.**	**Deviance**	**-2Log(L)**	**(ϕ) ±SE (Annual survival)**	**p (capture probability)**
1	$\{\phi_t\ p_t\}$, both survival and encounter probability time-dependent	621.9	0	0.5	1	3	615.83	615.83	0.97 ± 0.10	0.21± 0.03
2	$\{\phi.p_t\}$, survival constant over time, encounter probability time-dependent	621.9	0	0.5	1	3	615.83	615.83	0.97 ± 0.10	0.21± 0.03
3	$\{\phi_t\ p.\}$, survival time-dependent, encounter probability constant over time	664.8	42.9	0	0	3	44.1	658.73	1.00 ± 0.00	0.35± 0.02
4	$\{\phi.p.\}$, both survival and encounter probabilities constant over time	662.8	40.86	0	0	2	44.1	658.73	1.00 ± 0.00	0.35± 0.02

Table 5.4: Likelihood–ratio (LR) test between the predefined models

Reduced model	**General model**	**Chi-sq**	**Degrees of freedom (df)**	**Probability (p)**
{ϕ (.) p (.) PIM}	{ϕ (t) p(t) PIM}	42.901	1	<.0001
{ϕ (t) p (t) PIM}	{ϕ (.) p (t) PIM}	0.00	0	******
{ϕ (.) p (.) PIM}	{ϕ (t) p (.) PIM}	0.00	1	******
{ϕ (.) p (t) PIM}	{ϕ (t) p (.) PIM}	-42.901	0	******
{ϕ (t) p (t) PIM}	{ϕ (t) p (.) PIM}	-42.901	0	******

5.5.5. Longevity

During this study, 48 Edible-nest Swiftlets were recaptured from 1545 captured birds from all three study sites between 2017 and 2019. One female bird recaptured in a cave at Chalis Ek showed the highest longevity at 17 years and six months (Calculated using equations II and III). Around 35% (n= 17) of the number of birds recaptured individuals were found between the ages of 11-15 years, from which nine were identified as female and eight as male. I found 49% (n= 22) recaptured individuals between the ages of 6-10 years, from which 15 were identified as female and seven as male. Around 16% (n=8) recaptured birds between ages 0-5, of which four were identified as female and four as male. Of the 48 recaptured birds, 60% (n=29) were identified as female and 40% as male (n=19) (Table 5.5 & Figure 5.8).

Table 5.5: Showing different age classes of recaptured birds from all study sites

Age of the birds (Years)	**Year of Capture**	**Year of Recapture**	**Number of Individuals**	**Male**	**Female**
0-5	2013	2018	8	4	4
6-10	2008-2011	2018-2019	22	7	15
11-15	2004-2007	2018-2019	17	8	9
16-20	2002	2019	1	0	1

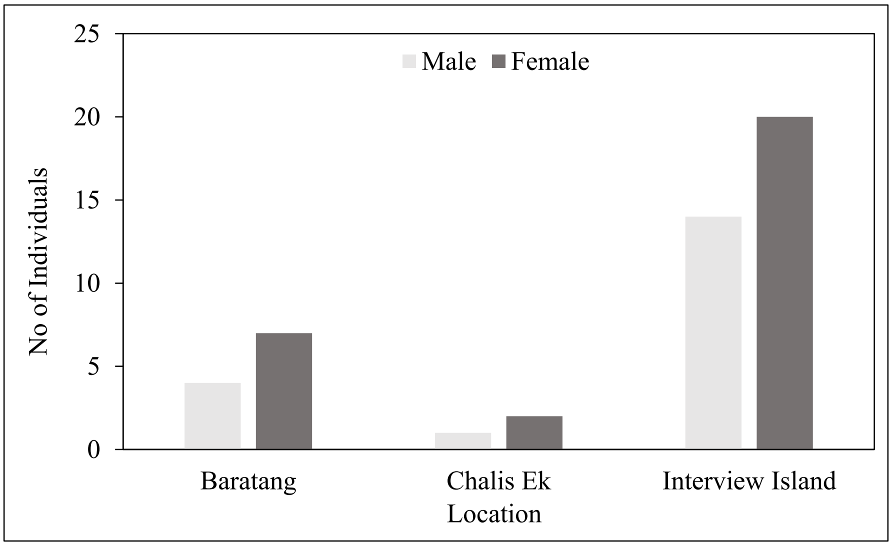


Figure 5.8: Edible-nest Swiftlet recaptured from study location: Baratang, Chalis Ek, and Interview Island for Longevity study

5.5.6. Allee Effect

Population Size and Density

In the year 2017, it is seen that there is no correlation ($R^2=0$) between the population size (independent variable) and the density (dependent variable, calculated using Equation V) (Figure 5.9A). Similarly, no difference was seen in 2018 ($R^2=0.12$) (Figure 5.9B). This indicates that the density does not affect the population size change in the Edible-nest Swiftlet colonies. It confirms that the Edible-nest Swiftlet does not follow the density-dependant Allee Effect.

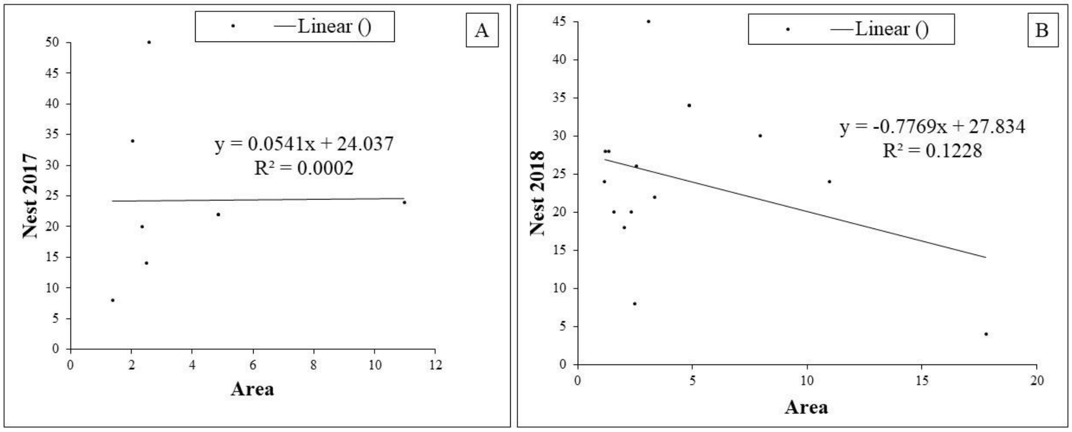


Figure 5.9: Linear regression of Population size and Density for the years A) 2017 and B) 2018

Population Size and Reproductive Success

The Edible-nest Swiftlet does not follow the Allee effect, i.e., the decline in population does not affect the reproductive success in the colony. The relationship between the population size and reproductive success was checked independently for 2017 and 2018 (Figure 5.10 & 5.11). There is no significant decline ($p > 0.05$) seen between the population sizes in 2017 and 2018; however, the reproductive success changed significantly ($p < 0.05$) between the years (Figure 5.12).

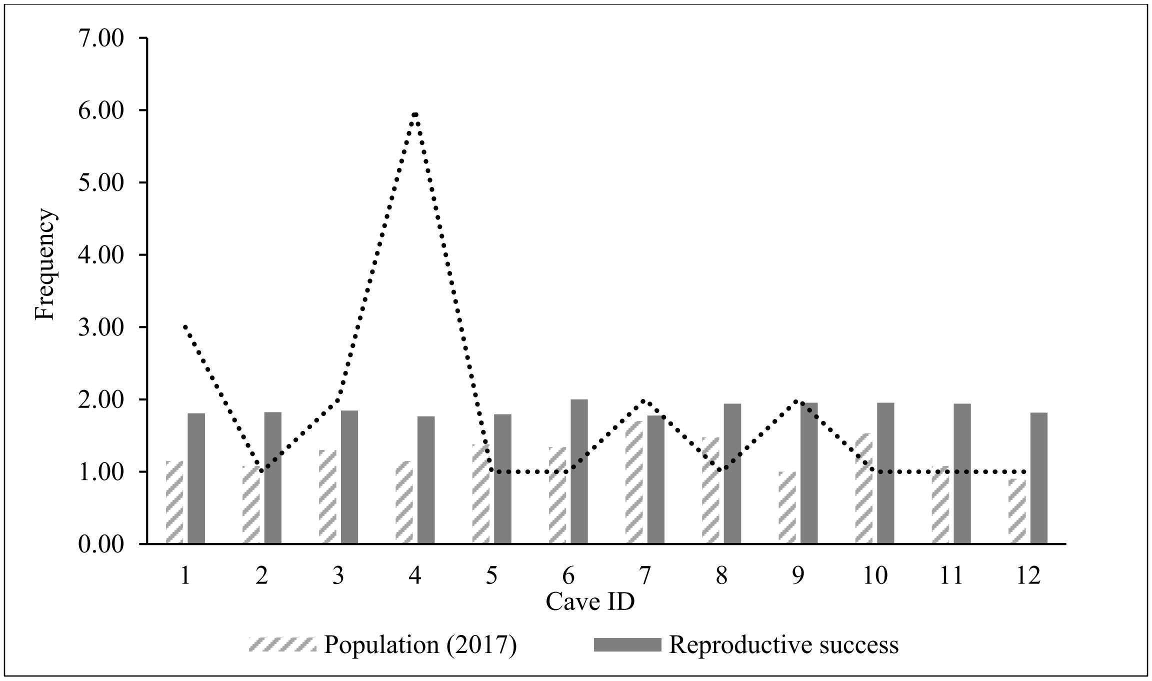


Figure 5.10: The population, reproductive success, and sex ratio observed in the colonies of the Edible-nest Swiftlet in the study caves at Baratang Island during the year 2017

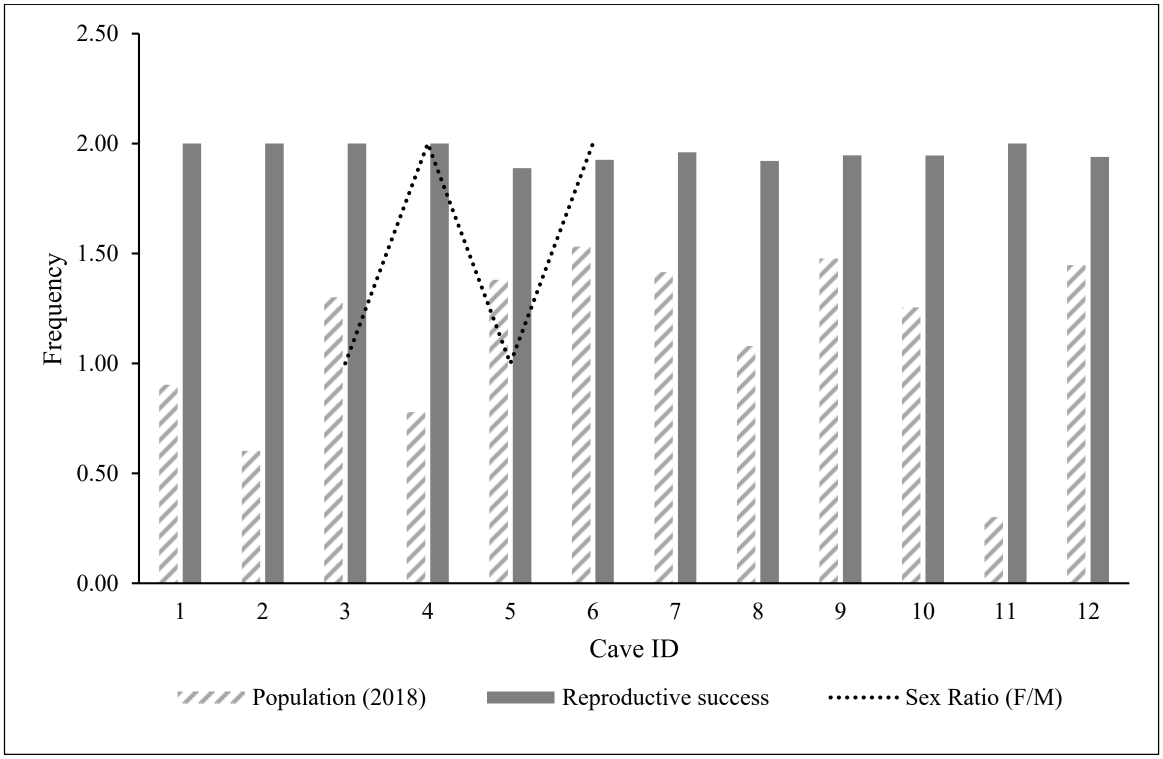


Figure 5.11: The population, reproductive success, and sex ratio observed in the colonies of the Edible-nest Swiftlet in study caves at Baratang Island during the year 2018

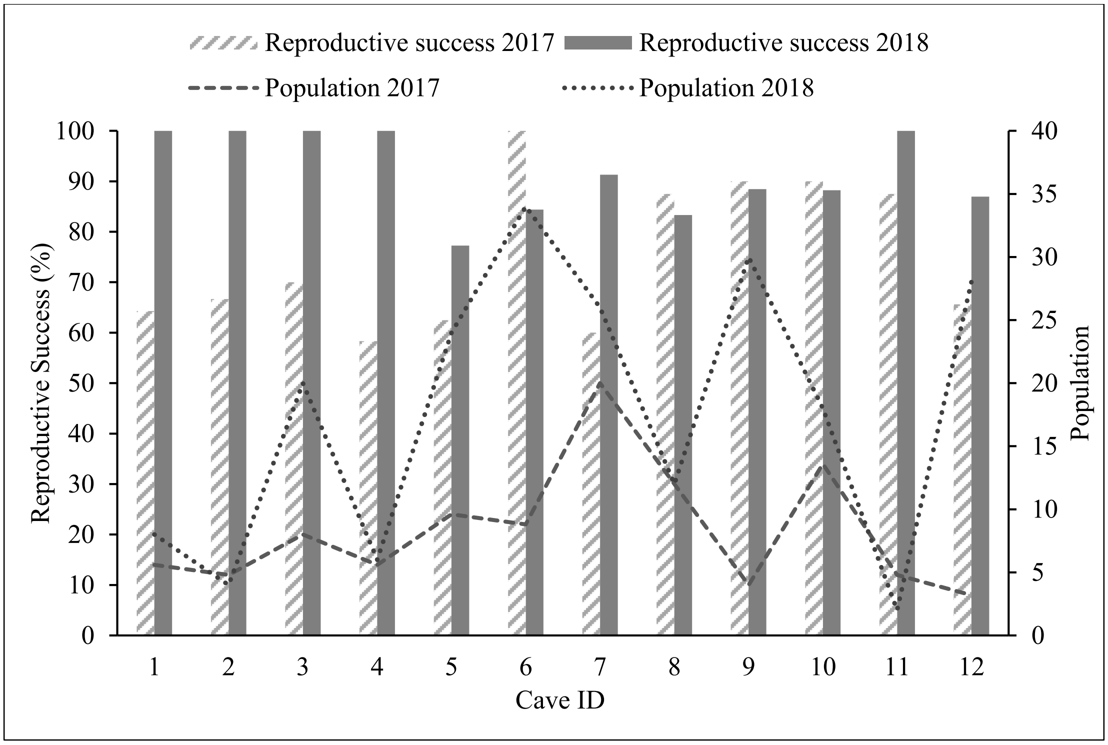


Figure 5.12: The population, and reproductive success observed in the colonies of the Edible-nest Swiftlet in study caves at Baratang Island during the years 2017, 2018.

5.6. DISCUSSION

Population dynamics can be defined as analyzing the factors that affect populations' increase, stability, and decrease over time (Mehner, 2009). Population density, sex ratio, dispersal, birth rate, mortality rate, longevity, and survival rate are population dynamics parameters (Ferris & Wilson, 1987). The population dynamics of the cave-dwelling, colonial birds belonging to the family: Apodidae, have not received much attention. The current study aims to learn more about the traits and population dynamics of the Edible-nest Swiftlet, which is unique to the Andaman and Nicobar Islands. There have been few studies on Population dynamics in swifts and factors affecting it. Studies on Common House-Martin (*Delichon urbicum*) and Common Swift (*Apus apus*) indicate the relative influence of environmental changes on population dynamics while the birds are on breeding and wintering grounds. It reveals that the population of Common House-Martin was most affected by spring rainfall (43%–47.7%) and Normalized Difference Vegetation

Index (24%–26.9%), while the Common Swift population was primarily affected by the Normalized Difference Vegetation Index (22.7%–34.8%) (Ambrosini et al., 2011).

In this study of the monogamous Edible-nest Swiftlet, females showed a high rate of natal philopatry (61.77%) as compared to males (38.23%). In monogamous birds, the probability of female's natal philopatry was significantly higher than in males (Liberg & von Schantz, 1985). The Charadriiformes (sandpipers, gulls, curlews, and godwits), Tree Swallow (*Tachycineta bicolor*), Banded Savannah Sparrows *Passerculus sandwichensis,* Florida Sandhill Cranes *Grus canadensis pratensis*, Stripe-backed Wrens *Campylorhynchus nuchalis,* Pinyon Jay *Gymnorhinus cyanocephalus*, White Storks *Ciconia ciconia* depict greater natal dispersal of females (Clarke et al., 1997; Wright & Mauck, 1998; Nesbitt et al., 2002; Yaber & Rabenold, 2002; Winkler et al., 2004; Chernetsov et al., 2006). In Black Brant *Branta bernicla nigricans*, natal philopatry was significantly higher for females than males (Lindberg et al., 1998). Semipalmated Sandpiper *Calidris pusilla,* California Spotted Owls *Strix occidentalis occidentalis* (Lahaye et al., 2001) Florida scrub Jay *Aphelocoma coerulescens*, Mexican Jay *Aphelocoma ultramarine* no influence of sex on dispersal (Gratto, 1988). In polyandrous Red-necked Phalarope *Phalaropus lobatus*, Spotted Sandpiper *Actitis macularius* (Reed & Oring, 1993), White-throated Magpie-Jay *Calocitta formosa* there was evidence of greater natal dispersal by males (Schamel & Tracy, 1991; Reed & Oring, 1993; Williams & Rabenold, 2005). Cooperatively breeding Red-cockaded Woodpecker *Picoides borealis* dispersal and philopatry in males depends upon social dominance relationships, reproductive competition among male fledglings, distribution of high-quality territories and vacant territories in the neighbourhood of the natal site (Pasinelli & Walters, 2002). The Bull-Headed and Brown Shrikes study on philopatry and habitat selection shows that Bull-headed shrikes show lower philopatry than Brown Shrikes. Studies show that Brown Shrikes declined due to habitat loss because they lost their nesting sites due to gravel operations and industrialization. On the other hand, Bull-headed Shrikes remained constant. These population trends appear inconsistent with the difference in their return rates due to the differences in philopatry and habitat selection between the two species (Takagi, 2003). However, the Edible-nest Swiftlet females are more philopatric than males.

In Black Kite *Milvus migrans*, the median natal dispersal distance was 4.8 km, with males often dispersing shorter distances and females dispersing equally at all distance categories. Single and first-hatched males born in high breeding density areas disperse across shorter distances. Dispersal distances between siblings tended to be correlated, possibly due to sharing similar environmental conditions. Males who dispersed across shorter distances had higher lifetime reproductive success. Lifetime reproductive success did not differ between females dispersing across various distances, but females that dispersed farther to mate with more experienced males. The discrepancy between sexes in breeding duties in this species may explain these sex variations in dispersal patterns and their effects. (Forero & Hiraldo, 2002). Dispersal distance of Mountain Plovers *Charadrius montanus* was also independent of sex at any stage, within the year, and between years (Skrade et al., 2010). Recapturing the dispersed offsprings as breeding adults during the study revealed that female Edible-nest Swiftlet has longer natal dispersal distance than males who choose to disperse in a cave near their natal site. A female's maximum natal dispersal distance was 4.07km on Interview Island; for a male, it was 0.75km on Baratang Island. The Average natal dispersal range for females was 0.57km, and that for males was 0.16km. This confirms that Natal dispersal in birds is sex-biased, with females settling farther from their natal sites and establishing themselves in their natal territory. While dispersing to unknown territory, birds' colony-site selection is paramount.

For Colony site selection, out of all the parameters, a few are known to contribute to the selection and use process. However, as a species belonging to the Apodidae, these aerial insectivores, with poorly developed legs and strong feet, nest mainly on the vertical surface (Lovette & Fitzpatrick, 2016). Hence, the swiftlets have stringent requirements for their breeding sites and are directly influenced by the available useful area in cave (Nguyên et al., 2002). Nguyên et al. (2002) recorded the White-nest Swiftlets nest at three locations: at the top of the cave, the bottom, and at the opening. In this study, in the dry caves of Baratang and Chalis-Ek, the study height of the swiftlet colony (useful area) is between 1.83m to 9.39m and 1.69m to 15.97m, respectively. This factor, however, does not seem to affect the colony-site selection of the Edible-nest Swiftlet in the present study. The vertical angle of the cave wall did not contribute to the nest site selection in the present study. Also, according to Viruhpintu et al. (2002), the wall's height and angle may influence the selection in a way inaccessible to predators. But, none of such probability is seen in the present study. According to Manchi and Sankaran (2011), the Edible-nest Swiftlet selects a specific location to build the nest. The results show that nest-site selection in the Andaman and Nicobar Islands is by the unique characters of the nest-site parameters (individual-level) (Manchi & Sankaran, 2011). The micro-climatic factors depicted a significant correlation with the mean temperature ($rs = -0.985, P < 0.001$) and relative humidity ($rs = 0.997, P < 0.001$). A strong negative inverse relation exists between the temperature and the nesting success. Nest success did not correlate with height ($rs = 0.022, P = 0.584$) and nest density ($rs = 0.314, P = 0.544$) (Manchi, 2009). The results of the present study show that the temperature ($R^2=0.002, p>0.05$) and relative humidity ($R2=0.008, p>0.05$) do not affect the breeding success of the bird.

As the Edible-nest Swiftlet is known to attach its nest to the cave walls inside the dark zone of the caves, the nest site characters play an essential role in selecting specific places for nest-building. Manchi and Sankaran (2011) state the importance of Colony-site characters, their selection, and preference towards nest success by the Edible-nest Swiftlet. It was recorded that the birds preferred the colony sites with rough surfaces on inwardly inclined walls with/without support. Further, the slightly rough rock surface and the nest height were the significant predictors of nesting success in Edible-nest Swiftlet (Manchi & Sankaran, 2011), which points towards the direct proportionality of the specific selection of nesting sites.

Inside the caves, swiftlets build their nest only in the suitable nesting area (on the vertical or near vertical walls), the size of which sets an upper limit to the number of nests the birds can build in a cave (max density ~100 nests/m²). The suitable nesting area extends 1m up from the cave ground in dry caves and 3m above the high tide in the marine caves in Viêtnam (Nguyên & Voisin, 1998), whereas ranges from 2.5 m to > 10 m in the swiftlet caves of Si-hi Islands, Thailand. Also, as Manchi and Sankaran (2011) documented, the nesting site's height did not correlate to nesting success. However, notable differences were recorded in the proportions of nests constructed on inwardly inclined walls (<90°) in Andaman and Nicobar Islands (Manchi, 2009; Manchi & Sankaran, 2011) and in Si-Ha Islands, Thailand (Viruhpintu et al., 2002).

Bats echolocate predators at night, whereas swiftlets feed primarily on daylight predators. In instances when Molossids and swiftlets live in the same cave, the former leave at about the time when the second comes back, which creates a niche separation because of different feeding habits (Medway, 1959). However, few studies have documented that the distribution of swiftlets belonging to the Collocalia group coincides with the depauperate bat fauna and is responsible for the competitive exclusion of bats (especially the Molossids; Fention, 1975; Salomonsen, 1983). Also, as per observations in the Baratang and Chalis-Ek, the caves with a high population of bats had fewer swiftlets conversely. A few species of bats, such as the Intermediate Roundleaf Bat *Hipposideros larvatus* and the Greater Bent-winged Bat *Miniopterus schreibersi*, are found in the Viêtnamese swiftlet caves. Intermediate Roundleaf Bat *Hipposideros larvatus* roost separately (in cave entrances or remote areas in the cave) and does not compete with swiftlets. However, Greater Bent-winged Bats *Miniopterus schreibersi* settle down near swiftlet nesting areas and frequently cling to the swiftlet nest. When their mothers are away foraging, young bats concentrate in large swarms (~2m^2), covering the rock surface of the walls and the nests. As a result, the swiftlets are driven away, or the breeding success is drastically affected. As observed, the bats do not roost at the places where the birds build their nest (Nguyên et al., 2002), so there is a visible niche separation between swiftlets and bats. Medway (1959) and Harrisson (1974) have mentioned only marginal competition for roosting/ breeding sites. However, in the Nicobar Islands, Sankaran (1995) reported that bats co-exist with swiftlets in Nicobar Island but did not mention any competition. Further studies regarding the niche separation and feeding habits of both swiftlets and bats can shed light on the competitive exclusion of bats by swiftlets and vice-versa.

The breeding cycles of Edible-nest Swiftlet are well-adapted to the environmental conditions inside the caves (Nguyên et al., 2002). The slow development (compared to the other small birds) is permitted because the nest of the swiftlet is in the most inaccessible places inside the caves, wherein the micro-climate is stable, and predators are few (Tarburton, 2009; Johnson et al., 2017; Gurjarpadhye et al., 2021). The relative humidity and temperature in Baratang and Chalis-Ek are significantly different ($p<0.05$). The wind speed and light intensity are 0.00 km/hr and 0 lux at the colony-site location. The findings of Nguyên and Voisin (1998) suggest that when the swiftlet caves (Dry) are not exposed to the winds, relative humidity decreases below 70%-80%, and the nests fall off the walls.

Similarly, the environmental stability and humidity favour the species diversity, but the temperature is a limiting factor for several bat species (de Sousa Barros et al., 2020). While all other variables remain constant, the insectivorous bat uses atmospheric pressure to predict the abundance of aerial insects outside (the atmospheric pressure increases, and the number of bats leaving the roost declines) (Paige, 1995). Barometric/Atmospheric pressure tracking can be an alternative evolutionary strategy to torpor and may be a widespread phenomenon amongst insectivorous bats. As swiftlets are also aerial insectivores, it is possible that the atmospheric pressure also affects the times the swiftlets leave the roost like other birds (Lehner & Dennis, 1971; Kreithen & Keeton, 1974). Further confirmation is needed with other swiftlets.

The birds tend to select a specific location to build the nest. Similar to the results of Viruhpintu et al. (2002) in Vietnam, the nest-site selection in the Andaman and Nicobar Islands is by the unique characters of the nest-site parameters (individual-level). Manchi and Sankaran (2011) recorded the presence of a slightly rough surface, inwardly inclined wall, with/without support, and of a rough surface, outwardly inclined wall. This combination of characters contributes the most to the nesting success.

The Jolly-Seber model using the Capture-Mark-Recapture data suggested that the swifts have high rates of annual survival (34%-100%) and a life span (Collins, 1985). However, survival during the first year of life is much lower in most Apodid species (Boano et al., 1993; Chantler & Driessens, 1995). The present data concerning the Edible-nest Swiftlet shows high annual survival rates ranging between 97-100%, whereas the overall apparent adult survival rate is 42.22%. Hence, as Pichorim and Monteiro-Filho (2010) and Boano et al. (1993) proposed, a survival estimate based on capture-recapture data should be considered as a minimum, owing to the dispersal of some individuals to the other colonies.

Compared with the Edible-nest Swiftlet, the average survival rate of the White-rumped Swiftlet (64%-73%) is higher. Also, the estimated mean life span of the Edible-nest Swiftlet (2.8 years) in the Andaman Islands is shorter than the mean life span of the

White-rumped Swiftlet (3.2 years) in Fiji (Tarburton, 1987). The best-fit models for the Edible-nest Swiftlet colonies in the caves of Baratang are typical of a closed population (i.e., constant survival), and capture probability (0.35) is independent of time. It corresponds to the fact that, with the assumption of constant survival in the Edible-nest Swiftlet, one can give a reliable estimate of the breeding and non-breeding populations with a 35% rate of recapture between 17:00 hrs to 20:00 hrs (IST) regardless of a capture season.

Capture probabilities vary by species and sex and are primarily determined by whether the populations are closed, partially open, or open (Nichols et al., 1981). The capture probabilities (when using mist nets) are interpreted to understand the adult-sex ratios (Senar et al., 1999; Amrhein et al., 2012; Lovász et al., 2018) and to estimate the population size (Whitman et al., 1997; Dunn & Ralph, 2004; Sæther et al., 2004). Unfortunately, the lack of relevant studies and a limited understanding of cave ecosystems with closed populations makes it difficult to make broad statements about the potential applicability of the Capture-Mark-Recapture method for estimating population size in cave-dwelling Apodids. Studies on seals and dolphins, on the other hand, indicate that capture probability larger than 0.3 are trustworthy and reflect the correctness of mark-recapture estimations (Otis et al., 1978; Speakman et al., 2010). Based on the occupancy models, the capture probability of insectivores and frugivorous birds is moderate (0.43–0.60) and is independent of habitat types (Hernandez et al., 2013). Nonetheless, additional research using different methods and statistical models may help support the current Capture-Mark-Recapture method's findings.

Longevity in *Aerodramus sp*ecies is poorly understood. According to the present study, the longest interval of the capture-recapture was 17 years and six months old. The individual was captured and marked as a nestling during the year 2003. Tarburton (1987) documented the 12-year lifespan of the White-rumped Swiftlet in Fiji. The findings of this study show that presently, the Edible-nest Swiftlet (*Aerodramus fuciphagus inexpectatus*) has the longest lifespan known among all swiftlets. The Alpine swift (26 years) has the longest lifespan compared to any swiftlet or swift (Table 5.6). This study discovered that the *Aerodramus fuciphagus inexpectatus* is the world's longest-living *Aerodramus* species.

Table 5.6: The longevity recorded in different species of Swifts and Swiftlets

Common Name	**Scientific Name**	**Longevity Recorded (Years)**	**Important references**
Common Swift	*Apus apus*	21.1	Fransson et al. (2010), EURING list of longevity records for European birds
Chimney Swift	*Chaetura pelagica*	15	Clapp et al. (1983), Longevity records of North American birds: Columbidae through Paridae
Alpine Swift	*Apus melba*	26	Fransson et al. (2010), EURING list of longevity records for European birds
White-throated Swift	*Aeronautes saxatalis*	10	BBL - Longevity Records of North American Birds
Black Swift	*Cypseloides niger*	18.2	BBL - Longevity Records of North American Birds
Vaux's Swift	*Chaetura vauxi*	5.1	Clapp et al. (1983), Longevity records of North American birds: Columbidae through Paridae
Grey-rumped Swift	*Chaetura cinereiventris*	7	Lentino et al. (2003), Longevity records of wild birds in the Henri Pittier National Park, Venezuela
White-tipped Swift	*Aeronautes montivagus*	10.4	Lentino et al. (2003), Longevity records of wild birds in the Henri Pittier National Park, Venezuela
White-collared Swift	*Streptoprocne zonaris*	5.1	Lentino et al. (2003), Longevity records of wild birds in the Henri Pittier National Park, Venezuela
Chestnut-collared Swift	*Streptoprocne rutila*	10.5	Pichorim et al. (2010), Population size, survival, longevity and movements of Biscutate swift in southern Brazil
Biscutate Swift	*Streptoprocne biscutata*	18.0 (Avg)	Pichorim et al. (2010), Population size, survival, longevity and movements of Biscutate swift in southern Brazil
Horus Swift	*Apus horus*	13	Pichorim et al. (2010), Population size, survival, longevity and movements of Biscutate swift in southern Brazil

Various mechanisms that affect reproduction and survival can cause a positive relationship between fitness and population size. The Allee effect is a positive association between absolute average individual fitness and population size over some finite time interval. Mate limitation, for example, may result in undercrowding in species that reproduce sexually because sexual reproduction necessitates contact between male and female gametes. Mate limitation occurs when plants or animals release gametes into the environment or when males and females cannot find each other. When cooperative behaviors such as breeding, feeding, and defense occur in larger social groups, they become efficient or successful, resulting in increased reproductive success or survivorship (Courchamp et al., 1999). Although cooperative behaviors are most evident in social vertebrates such as prairie dogs, ungulates, and birds, Allee effects can occur in insects such as bark beetles, and aquatic organisms, such as Cichlid Fish (Friedenberg et al., 2007; Balshine et al., 2001).

This study demonstrates that Edible-nest Swiftlet does not exhibit the "Allee effect". There is no correlation between Edible-nest Swiftlet population size and density, Sex ratio, and Reproductive success. However, Blue-footed Booby *Sula nebouxii*, simultaneously positive and negative density-dependent dispersal distances are seen in males and females' natal and breeding dispersal within the colony (Kim et al., 2009). In Lesser Kestrels *Falco naumanni*, adult nest predation decreases with the colony. Survival probability was higher in large colonies than in medium or small colonies size (Serrano et al., 2005). The study on cooperatively breeding Arabian Babblers *Turdoides squamiceps* demonstrated that breeding individuals in big groups results in more benefits than breeding individuals in small groups, with larger groups surviving longer. This supported the existence of a component Allee effect. It demonstrated a demographic Allee effect by demonstrating that population density has a favourable impact on the per capita population growth rate. A demographic Allee effect can result from component and group-level Allee effects, even though emigration and immigration rates rely on group size (Keynan & Ridley, 2016).

Population dynamics parameters, namely longevity, mortality, survival, and life expectancy dispersal, are of critical ecological and evolutionary importance in population biology, particularly population synchrony, colonization, range expansion, metapopulation, and population genetic structure in animals. but it has not previously been studied in Swiftlet species, especially cave-dwelling, endemic Edible-nest Swiftlet from Andaman and Nicobar Islands.

Chapter VI

CHAPTER VI

CONCLUSIONS

This study examines population dynamics and variables such as population density, sex ratio, dispersal, birth rate, mortality rate, longevity, and survival rate in the cave-dwelling Edible-nest Swiftlet *Aerodramus fuciphagus inexpectatus* of the three priority locations (Baratang, Chalis Ek and Interview Island) in the Andaman and Nicobar Islands. Following are a few highlights of the findings and significance of the present study.

- The study reveals site fidelity by rejecting the decision rule phenomenon and prior-experience hypothesis in adult Edible-nest Swiftlet on Andaman and Nicobar Islands. The study also found no relationship between cave morphology and breeding success, suggesting that microclimate variations inside the cave may not affect breeding success in the Edible-nest Swiftlet.
- The study also discovered a novel method of sex identification based on the CHD1 gene for Edible-nest Swiftlet, Plum-toed Swiftlet, and other avian species. The Multiplexing method of primer pair 2550F/2718R and P8/P2 is a rapid, simple, safe, and cost-effective procedure for gender identification in swiftlets.
- In the Edible-nest Swiftlet colony, the overall adult sex ratio was unveiled to be 1.11:1 (M:F) and 1:1 (M:F) in the offspring. The skewness discovered in the overall sex ratios (1.11:1) in the Edible-nest Swiftlet colonies questions the monogamous nature of the species.
- The discriminant function analysis (DFA) results demonstrate that females in the Edible-nest Swiftlet can be distinguished from males based on body length and weight, indicating the presence of the cryptic Sexual Size Dimorphism (SSD) in the species Edible-nest Swiftlet. It is the first-ever attempt to determine sex in Apodids based on morphometric factors.
- 38.23% of Edible-nest Swiftlet offspring’s exhibited natal philopatry compared to 61.77%, who preferred starting their first mating season away from the birth cave, exhibiting natal dispersion.

- The natal dispersal distance of female Edible-nest Swiftlet was longer than that of males, who preferred to disperse in the caves close to their natal location. The average natal dispersion range for males is recorded to be 0.16 km, compared to 0.57 km for females.
- The nest-site selection in caves is influenced by unique nest-site parameters, such as rough surfaces, inwardly inclined walls, and outwardly inclined walls. However, the nesting site's height did not correlate to nesting success in the present study.
- The Edible-nest Swiftlet *Aerodramus fuciphagus inexpectatus* is the swiftlet with the highest longevity of (17 years and six months), making it the longest-surviving *Aerodramus* species worldwide.

The study provides essential details on the species' dispersal pattern, colony sex ratio, and how biotic and abiotic variables affect population dynamics. The results of this study offer a chance to comprehend the monogamous or polygamous sexual mating behaviour of the Edible-nest swiftlet. This study offers a baseline for population monitoring and the habitat requirements of the species in the islands. It is the first attempt to understand the population dynamics of the cave-dwelling swiftlets. The study also understands the characteristics of the colony sites, the shape of the environment, and the significance of the microclimate for breeding success. These findings will further benefit the design of the ex-situ swiftlet houses for ranching this economically important species. The foundation for further investigation and chances to gain a deeper comprehension of dispersal in ex-situ settings is laid by this work.

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ORIGINAL ARTICLE

Stay or shift: does breeding success influence the decision in a cave-dwelling swiftlet?

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Abstract

Decision rules allow individuals of a species to decide whether or not to return to the same site in the following year or season, based on their immediate breeding success. We checked the decision rule phenomenon and simultaneously tested the prior-experience hypothesis for the cave-dwelling Edible-nest Swiftlet (*Aerodramus fuciphagus inexpectatus*; ENS) in the Baratang Cave Complex, Andaman and Nicobar Islands, India. We used the capture-mark-recapture method to understand the decision rule in ENS. Assuming that breeding success affects the decision, we monitored 234 individuals for two consecutive breeding seasons (2017 and 2018). We also documented habitat variables (cave morphometry and microclimate) to understand the correlates of breeding success. We captured 88% (207 birds) of adult birds from the study caves in 2017 and recaptured 66% (137 birds) of adults from the same caves in 2018, which confirmed fidelity towards the cave by the species. There was no significant correlation between the rates of breeding success in 2017 and 2018. Multiple regression models revealed an insignificant relationship between cave structure and breeding success of the species. Additionally, microclimate variables (temperature and humidity) did not influence the breeding success of the birds. Our results indicate that ENS individuals seem to chose decision rule by rejecting the prior-experience hypothesis. The existing conservation strategies associated with enhancing the ENS population in the Andaman and Nicobar Islands can benefit from our findings. We further recommend long-term studies and population monitoring to understand the breeding cave fidelity in ENS.

Keywords Andaman and Nicobar islands · Breeding success · Decision rule phenomenon · Edible-nest swiftlet · Prior-experience hypothesis

Zusammenfassung

Bleiben oder Abwandern - Beeinflusst der Bruterfolg die Entscheidung bei höhlenbrütenden Salanganen?

Anhand von gewissen Entscheidungsregeln beschließen Individuen, ob sie im folgenden Jahr oder in der folgenden Saison an denselben Brutort zurückkehren oder nicht. Diese Entscheidung beruht auf den unmittelbaren Bruterfolg der Vögel. Wir untersuchten das Phänomen der Entscheidungsregel und gleichzeitig die Erfahrungshypothese (engl. *prior experience hypothesis*) anhand von 243 Individuen einer Unterart der höhlenbrütenden Weißnestsalanganen (*Aerodramus fuciphagus inexpectatus*) im Höhlenkomplex von Baratang Island, eine Insel der Andamen und Nikobaren. Wir verwendeten die Fang-Wiederfang-Methode zur Überprüfung der Brutortstreue. Da der Bruterfolg die Entscheidung beeinflussen kann, beobachteten wir 234 Individuen (117 Nester) in zwei aufeinanderfolgenden Brutsaisons (2017 und 2018). Weiterhin notierten wir Habitatvariablen, um die Korrelationen der Brutortstreue zu verstehen. Wir erfassten die Morphometrie der untersuchten Höhlen zusammen mit den darin vorhandenen mikroklimatischen Verhältnissen. Im Jahr 2017 fingen wir 88% (207 Individuen)

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der in der Untersuchungshöhle lebenden adulten Vögel. Am Ende der darauffolgenden Brutsaison wurden 66% der adulten Vögel aus denselben Höhlen wiedergefangen, was die Brutortstreue der Art bestätigt. Eine lineare Regression zeigte keine signifikante Korrelation zwischen den Bruterfolgsraten 2017 und 2018 gab. Ein multiples Regressionsmodell zeigte keinen Zusammenhang zwischen der Höhlenlänge und dem Bruterfolg und auch die mikroklimatischen Verhältnisse (Temperatur und Luftfeuchtigkeit) hatten keinen signifikanten Einfluss auf den Bruterfolg. Die Individuen der Weißnestsalanganen scheinen eher der „Win-stay "-Strategie als der „Lose-shift "-Strategie zu folgen, sodass die Erfahrungshypothese abgelehnt wird.

Introduction

Breeding is amongst the most crucial phases of any animal life cycle and involves two stages, the decision to reproduce and to contribute to the ongoing reproduction (Pradel et al. 2012). Breeding in birds is highly specialized and occurs in a diversity of habitats from high elevation mountains to deep and dark subterranean habitats. Individuals can return to their known habitats, exhibiting site fidelity, or disperse to the available suitable areas between breeding attempts in a season or breeding seasons (Greenwood 1980; Greenwood and Harvey 1982). According to the decision rule, individuals assess their breeding success as prior experience and use the information to decide whether or not to return to the same breeding site during the subsequent season (Doligez et al. 1999). The win-stay or lose-shift strategy predicts the preference of an adult bird to exhibit site fidelity (stay) when confident of producing offspring at the same site with the social mate, or disperse (shift) to other suitable locations for subsequent breeding attempts when unable to produce offspring at the same location. This strategy enables adults to maximize the number of broods produced over their lifetime (Campomizzi et al. 2012). Individuals experiencing high breeding success often have a higher probability of returning to the same breeding site in the following year (Krištín et al. 2006). This behavior may serve to increase fitness (Bergerud and Gratson 1988) of individuals if the quality of a site (as determined by breeding success) is auto-correlated in time (Hoover 2003). Otherwise, individuals located in a low-quality habitat may disperse in search of other more suitable sites (Robinson 1985). Site fidelity is directly influenced by fecundity and survival of the individuals and can affect population dynamics and demography (Hoover 2003).

Adult birds tend not to return to the same site in the following years if they fail to produce young (Gavin and Bollinger 1988; Haas 1998) or produce fewer than two broods in cases of multiple-brooded species (Trine 1996). For instance, in waders, such as the European Oystercatchers (*Haematopus ostralegus*), stronger site fidelity was shown towards territories where chicks fledged successfully (Hazlitt and Butler 2001). Species such as the Greater Flamingo (*Phoenicopterus roseus*), Ovenbird (*Seiurus aurocapilla*), and Bobolink (*Dolichonyx oryzivorus*) also signified the importance of prior experience (Gavin and Bollinger 1988; Bernard et al. 2011; Pradel et al. 2012). All swiftlets exhibit site fidelity (Medway 1962a, b). Swiftlets show site tenacity by building their nests repeatedly at the same site year after year (Koon and Cranbrook 2002; Nguyên Quang et al. 2002). The birds also breed year-round, although the percentage of birds nesting varies depending on the weather conditions, particularly rainfall (Koon and Cranbrook 2002; Viruhpintu 2002).

The cave-dwelling Edible-nest Swiftlet *(Aerodramus fuciphagus inexpectatus*) is subspecies endemic to the Andaman and Nicobar Islands (Cranbrook et al. 2013; Gill et al. 2020). The Edible-nest Swiftlet breeds between December and August and has a clutch size of two eggs with an incubation period of 22–25 days (Manchi 2009). Recent ecological studies (Manchi 2009; Manchi and Sankaran 2011; Mane and Manchi 2017) considered microclimate (temperature and humidity) and physical characteristics of cave surfaces as influential parameters of breeding and roosting habitat of the ENS. Further studies on ENS habitat by Manchi and Sankaran (2011) revealed the importance of nest-site characteristics, nest-site selection, and preference towards nest success. Moreover, the *ex-situ* conservation efforts of this species in the Andaman and Nicobar Islands have recently documented nesting in urban areas (Sankaran and Manchi 2008; Manchi and Mane 2012).

As the basic understanding of the decision to stay or shift by the species is a critical component for conservation, management, and restoration efforts (Hoover 2003), this study aims to understand the decision rule in the case of Edible-nest Swiftlets and testing the prior-experience hypothesis. We also attempted to explore correlates of breeding success using cave morphometrics and microclimate as variables.

Methods

Study area

The Andaman and Nicobar Islands (06° 45′ 9 N and 13° 41′ 9 N, and 92° 12′ 9 E and 93° 57′ 9 E, Fig. 1) extend from the Arakan–Yoma ranges of western Myanmar (Burma) in the North and are flanked by the Andaman Sea in the east and Bay of Bengal to the west. The Andaman and Nicobar group comprise 572 Islands. Presently, of the 394 limestone caves known from the Andaman and Nicobar

Islands, 324 are located in the Andaman group (Manchi 2014).

We conducted this study at the largest known cave complex in the islands, on Baratang Island (12° 05′ N, 92° 45′ E, Fig. 1). The area of the cave complex, containing 175 caves, is 0.77 km^2 and is situated between Wraffter's Creek and Naya Dera (Sankaran 2001; Manchi and Sankaran 2014; Mane et al. 2019). The mean annual air temperature on Baratang Island is 26.2 °C, and the mean annual rainfall is 2870 mm (Kedzierski and Gargol 2016). The area is a Reserve Forest and protected under the Indian Forest Act, 1927. The most dominant vegetation types in this karstland forest are Andaman tropical evergreen forest, Andaman semi-evergreen forest, littoral forest, and mangrove forest (Champion and Seth 2005), with exclusive diversity patterns (Mane et al. 2019). These caves are under legal protection since the year 2010, towards the *in-situ* conservation of the ENS (Manchi and Sankaran 2014).

Selection of study caves

We stratified the caves according to the ENS population size inside. Initially, we grouped all of the caves into five different population classes ranging from 0 to 50 breeding pairs, with a class interval of 10. Randomly, we selected a minimum of two caves from each class for the detailed study. Of the 113 total caves occupied by the ENS, we selected 12 caves for this study. These caves were also chosen based on accessibility, feasibility to capture swiftlets, and presence/absence of bats inside.

Monitoring population and breeding success

The population size of ENS inside each study cave was estimated using the nest count method (Sankaran 2001; Manchi and Sankaran 2014). As ENS are known to be monogamous (Koon and Cranbrook 2002), each nest was considered equal to a breeding pair or two adults (Manchi 2009). The ENS starts nest-building during December and continues till mid-February when the egg-laying starts. The hatching of eggs begins by the second week of March till the end of April. The nestlings start fledging by end of April. The ENS lays the second bout of eggs between May and June, and the second batch of fledging occurs from July till mid-August (Manchi 2009; Mane and Manchi 2019). We conducted the nest count surveys between January and June in the years 2017 and 2018. The presence of an incubating adult and nestlings facilitated the visibility of active nests. During the breeding season, we counted all the nests in each study cave at the end of each month. We used four observers to conducted six nest surveys in the year 2017 and six nest surveys in 2018. All the surveys were carried out during day time to minimize disturbance to the birds.

All the nests from selected caves were checked every day in the early morning (6:00–6:30 a.m). We visited the caves physically from the start of the breeding season till the nestling to the fledgling stage, to score the nest checks as an empty or occupied nest and to count the number of eggs and nestlings in the nests. Following Jehle et al. (2004) and Manchi (2009), we estimated the breeding success of the ENS, using the formula:

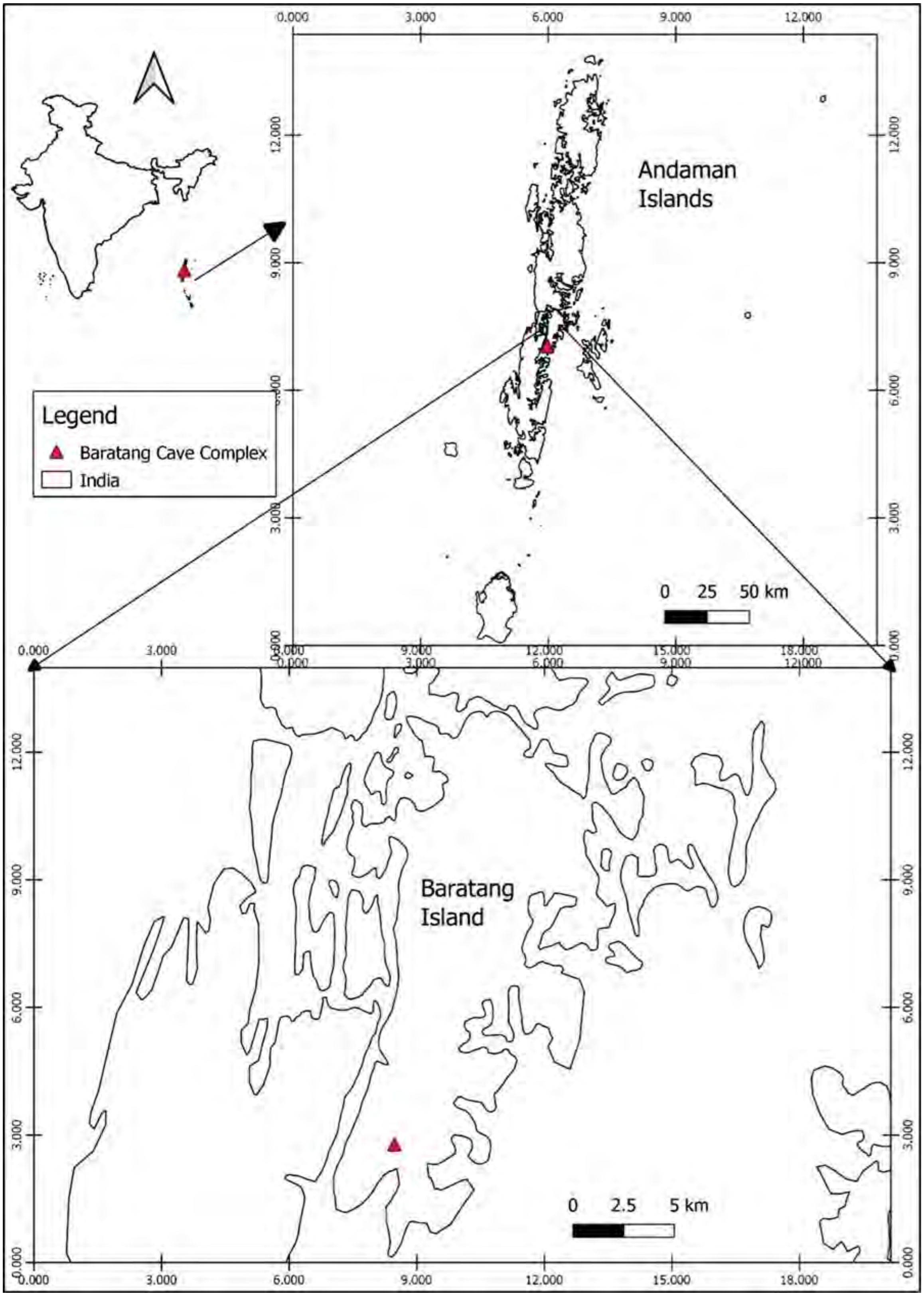
$$\text{Breeding success} = \frac{\text{number of clutches that produce young}}{\text{total number of clutches}}.$$

Determining cave fidelity

We used the capture-mark-recapture method to determine cave fidelity. We ensured safe handling of the birds and carefully released them back near their breeding caves. We captured the adult birds while they return to their breeding caves (between 5:00 and 8:00 p.m.), during the nest-building period (December–January), by placing the mist nets (6 m × 2.6 m; 30 mm mesh) at the entrances of each study cave (Erica and John 2004; Sankaran and Manchi 2008; Manchi 2009). Individuals captured for the first time were marked using aluminium *Z*-rings with a unique identification number. We recorded the date of capture, ring number, and cave number. We recaptured adult birds at the end of the 2018 breeding season to determine if the birds, regardless of their breeding success, returned to the same cave for breeding. During the 2018 recapture, we marked the first-time captured individuals and noted capture date, ring number, and cave number. Once the birds were recaptured, we recorded the capture date, ring number, and cave number where they were marked initially. Following the data collection, all captured swiftlets were released safely near their respective breeding caves.

Cave morphometry and microclimate variables

Of the 12 selected study caves, we could gather morphometry data of 11 caves, as the 12th cave was not accessible. Using a Leica DISTO™ S910 P2P (https://leica-geosystems.com/), we implemented a standard survey method for recording morphometric measurements of each study cave (Ford and Cullingford 1976; Kawalkar and Manchi 2020; Fig. 2) between January and June 2018. We fixed several survey stations in each of the study caves, with a 1-m distance between the two survey stations. Each cave mapping survey began at the cave entrance (e.g., survey station 1) until the end of the cave (Fig. 2). At each survey station, we measured the distance (meters) to the left wall (L), distance to the right wall (R), distance to the cave ceiling (U), distance to the cave floor (D), vertical angle (Θ),


Andaman
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▲ Baratang Cave Complex
☐ India
0 25 50 km
Baratang
Island
0 2.5 5 km
0.000
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6.000
9.000
12.000
15.000
18.000

◂**Fig. 1** Study area; the karstland with the largest limestone cave complex between Naya Dera and Wraffter's Creek on Baratang Island, North and Middle Andaman district, Andaman and Nicobar Islands

and bearing from true North. We used these measurements to produce 12 map-derived cave morphometric parameters (Table S1). Cave measurements obtained were processed using WinKarst (Ver12.5, http://www.resurgentsoftware.com/winkarst.html) and Compass 32 Project manager software (https://fountainware.com/compass/).

To collect microclimate data (temperature and humidity), we placed HTC-Easy Log data loggers (http://htcinstruments.com/humidity-temp-meter.html) at the cave entrances and the nesting locations for several months (December, March, April, and May) during the ENS breeding season. We used the average mean temperature (°C) and relative humidity (RH %) values for further analysis. Using the XLSTAT software Ver 2020.2.1 (Addinsoft 2020), we performed the goodness of fit statistics, Spearman's correlation test, and linear and multiple regression modeling. Pairs of the habitat variables (Table 1) were tested for correlation using Spearman's rank correlation test to reduce the effects of multicollinearity (Golawski and Mroz 2019). If two variables were positively correlated ($r > 0.60$), only one data set was selected for further analysis. We used the ecological understanding of the cave morphometric parameters as the basis to choose amongst the correlating parameters. Further, only non-collinear variables (i.e., cave length, cave bearing, cave inclination, surface length, and wall area) were used for modelling to avoid the possibilities of error. We used multiple-regression modelling to predict the influential factors and to develop inferences about the determinants of patterns (Mac Nally 2002) affecting breeding success. Further, the linear and multiple regression model assumptions were checked using the normal distribution of residual plots.

Results

Population monitoring and capture-mark-recapture

Collectively, the 12 study caves had a breeding population of 234 ENS individuals (117 nests) in 2017 and 212 individuals (106 nests) in 2018, respectively (Fig. 3). We captured 88.4% (207 birds) of adult birds from the study caves in 2017 and recaptured 66.2% (137 birds) of the adult individuals in 2018 marked in 2017.

Decision rule and testing prior-experience hypothesis in ENS

The monitoring of 234 ENS individuals during the breeding seasons confirms that the species decides to stay regardless of prior experience. Comparative analysis (Fig. 3) showed that the overall breeding success of ENS was significantly higher in 2018 ($p < 0.05$, 91.5 ± 7.1%) than in 2017 (74.9 ± 12.9%). Linear regression ($R^2 = 0.08$, $p > 0.05$) showed that the breeding success of the ENS in 2018 was independent of breeding success in 2017 (Fig. 4).

Fig.2 Illustration of the dummy cave with the survey stations at a one-meter distance, across the caves, beginning from the cave entrance. *L* left, *R* right, *U* up, *D* down

Table 1 Table 2: Multicollinearity between morphometric variables of 12 caves on Baratang Island of the Andaman and Nicobar Islands

Variables	Cave length	Horizontal length	Cave bearing	Cave inclination	Cave depth	Surface length	Surface width	Surface area	Cave volume	Average diameter	Wall area	Average inclination
Cave length (CL)	**1**	**0.834**	−0.136	−0.005	**0.945**	0.200	**0.873**	0.591	0.145	−0.068	0.445	0.319
Horizontal length (HL)		**1**	−0.228	−0.018	**0.702**	0.364	**0.638**	**0.615**	0.401	0.183	**0.615**	0.126
Cave bearing (CB)			**1**	−0.018	−0.127	−0.491	−0.027	−0.264	−0.173	−0.191	−0.109	0.196
Cave inclination (IN)				**1**	0.237	−0.374	−0.241	−0.533	−0.355	−0.416	−0.237	**0.689**
Cave depth					**1**	0.145	**0.800**	0.482	−0.027	−0.237	0.291	0.528
Surface length						**1**	0.155	**0.800**	0.564	0.515	0.491	−0.305
Surface width							**1**	**0.627**	0.136	−0.055	0.418	0.241
Surface area								**1**	0.400	0.278	0.491	−0.109
Cave volume									**1**	**0.961**	**0.927**	−0.369
Average diameter										**1**	**0.802**	−0.491
Wall area											**1**	−0.087
Average inclination												**1**

Values in bold shows that variables are collinear to each other

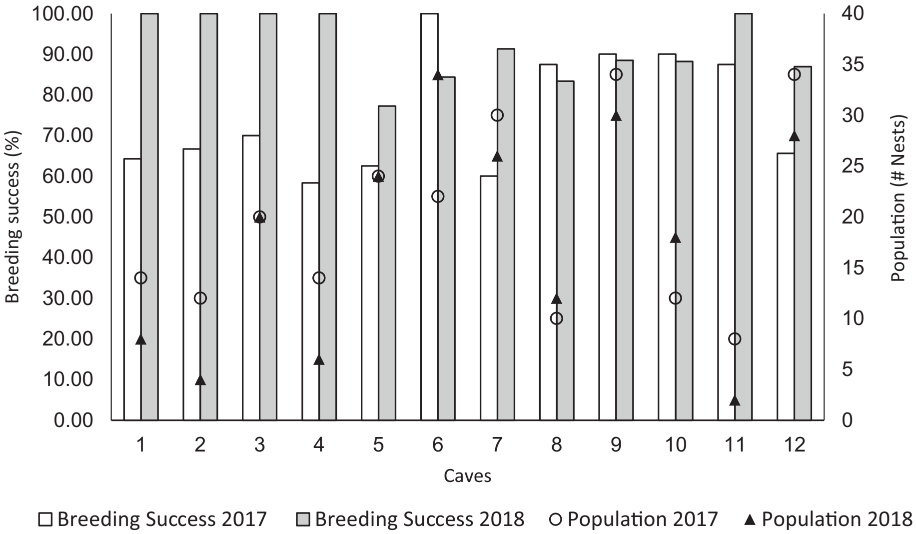

Fig. 3 Breeding success of the Edible-nest Swiftlet in 2017 and 2018 at 12 study caves on Baratang Island, Andaman Islands

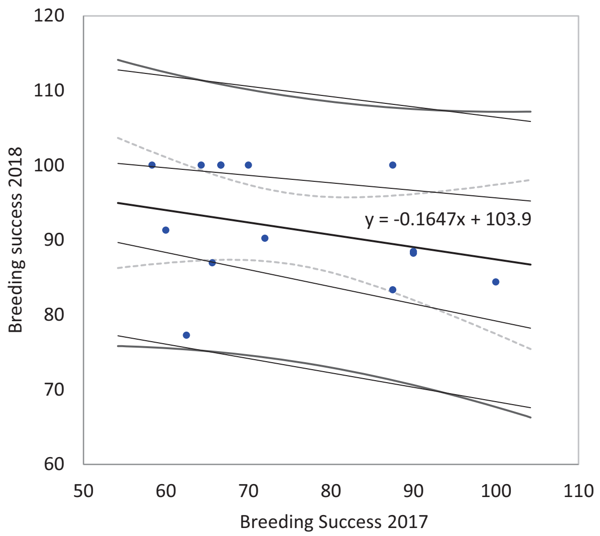

Fig. 4 Regression of breeding success of 2018 by breeding success of 2017 ($R^2 = 0.08$, $p > 0.05$)

Factors influencing breeding success

Cave morphometry

The 11 accessible caves had a varied range of morphometric measurements (Table S1). The multicollinearity test for 12 morphometric variables resulted in the removal of correlated parameters (Table 1). The non-collinear variables (cave length, cave inclination, surface length, wall area, and cave bearing) were then selected based on their logical relatedness with the bird's ecology. Further, multiple regression model performed using the five non-collinear variables (cave length, cave inclination, surface length, wall area, and cave bearing) revealed that there is an insignificant relation between breeding success and cave structure ($R^2 = 0.57$, $p > 0.05$, Table 2).

Table 2 Multiple regression fit of morphometric variables of 12 caves and Edible-nest Swiftlet breeding success on Baratang Island, Andaman Islands

Source	Value	Standard error	*t*	Pr > |*t*|	Lower bound (95%)	Upper bound (95%)
Intercept	124.486	24.808	5.018	0.004	60.716	188.256
Cave length	0.565	0.547	1.033	0.349	−0.841	1.971
Cave bearing from true north	−0.026	0.023	−1.135	0.308	−0.086	0.033
Cave inclination	−0.366	0.352	−1.040	0.346	−1.270	0.539
Surface length	−0.946	1.819	−0.520	0.625	−5.623	3.731
Wall area	−0.061	0.031	−1.962	0.107	−0.141	0.019

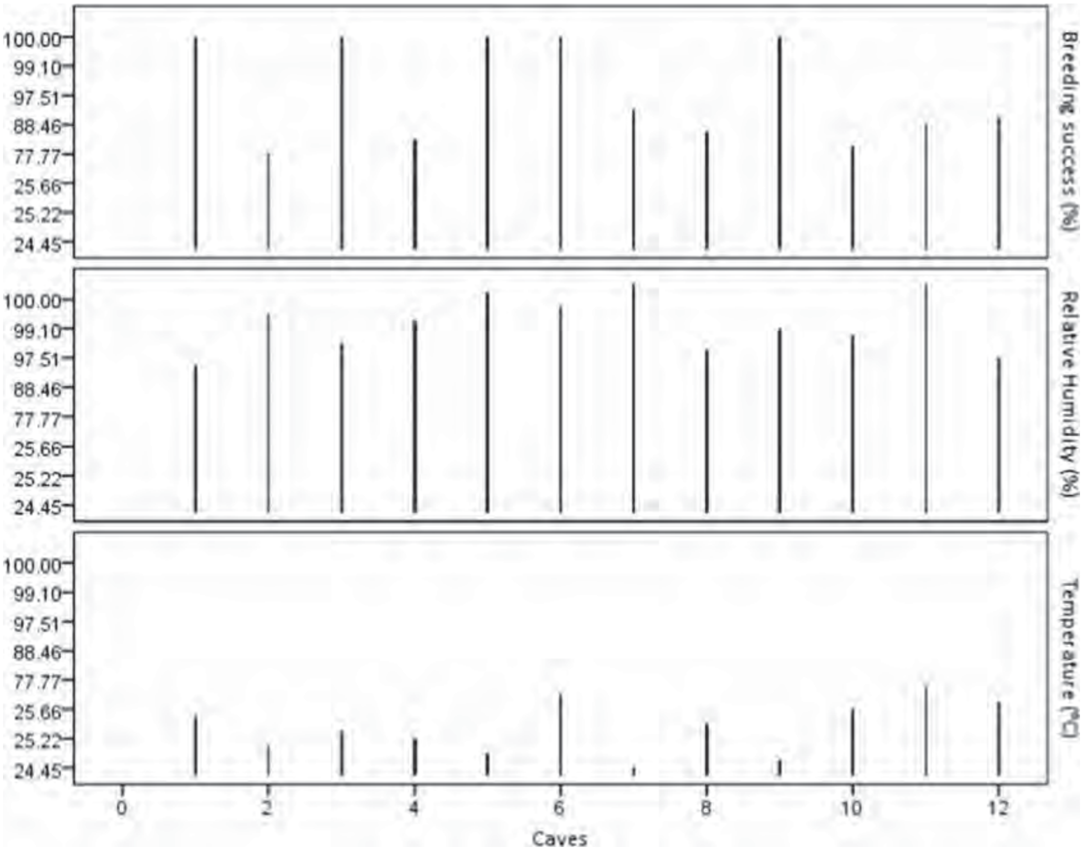

Fig. 5 Breeding success of the Edible-nest Swiftlet and average temperature and relative humidity in 12 study caves on Baratang Island, Andaman Islands

Microclimate variables

The limestone study caves on Baratang Island maintained nearly stable temperatures throughout the study period, with a slight variation of 2 °C (23–25 °C, Fig. 5). Whereas, the relative humidity in the study caves varied considerably between 92 and 105% (Fig. 5). The goodness of fit statistics shows that the temperature ($R^2=0.002$, $p>0.05$) and relative humidity ($R^2=0.008$, $p>0.05$) does not affect the breeding success of the bird.

Discussion

Rejecting the prior-experience hypothesis, the ENS individuals returned to the same caves for breeding despite the previous year's lower breeding success. The average rate of breeding success of ENS in the present study was higher as compared to the most members of genus:*Aerodramus* except, Germain's swiftlet (*Aerodramus germani*; 77%), Mountain Swiftlet (*Aerodramus hirundinaceus*; 77%) and Mascarene Swiftlet (*Aerodramus francicus*; 81%). The ENS individuals exhibited variation in the rates of their breeding success in 2017 (74.9%) and 2018 (91.5%). In two caves (4 and 7) the breeding success increased to 91.3% in 2018 from 60% in 2017. Despite the lower overall breeding success in 2017, the ENS individuals choose to stay and use the same caves for breeding in 2018. This finding supports Switzer (1993), as caves are unpredictable habitat with semi- (stable) mircroclimatic conditions. Moreover, the ENS breeding success in 2018 was independent of breeding success in the previous year. Langham (1980) recorded the decline in breeding success in ENS in Malaysia with successive clutches, being highest in November (53.6%) and February (55.6%). Our study revealed that the ENS has fidelity towards their breeding caves, as documented in other Apodidae species (Dexter 1969; Medway 1962a, b; Tarburton 1987; Koon and Cranbrook 2002; Nguyên Quang et al. 2002).

The re-capture rate of the marked adult individuals in the present study was high (66.2%), as observed in Common swifts (*Apus apus*) by Lebreton et al. (1992). As both the swiftlets (Medway 1962a, b; Tarburton 1987; Koon and Cranbrook 2002; Nguyên Quang et al. 2002) and swifts (Dexter 1969) are faithful to the colonies where they breed, it is apparent that they have high return rates. However, Johnson et al. (2018) could recapture only one individual of Mariana Swiftlet (*Aerodramus bartschi*) from the roosting/nesting tunnel on the Mariana island, USA. Also, based on numerous studies involving marked individuals, return rates to breeding sites by birds are known to be highly variable and influenced by various factors, including previous breeding success, sex, and age of the returning individual (Newton and Marquiss 1982; Shields 1984; Warkenton et al. 1996). However, the present two years study indicates that the return rates of ENS do not directly depend on breeding success or failure of the previous year. Nonetheless, further studies are required to finally answer the question whether ENS individuals are 'always' site faithful and understand the effect of other factors (sex, age) on the return rates of the individuals.

We found an insignificant relationship between cave structure and breeding success of the ENS. Overall, R^2 value of the multiple regression model indicates that the selected non-collinear variables explain together 57% of the variability in the breeding success. None of these variables show any significant effect on the breeding success of the species ($p > 0.05$). Nevertheless, from the greater values of cave length and surface length (Table 2), we understand that these two variables in some way affect the breeding success of the study species. However, this needs further confirmation through much detailed study. Furthermore, several studies have pointed out the significance of the cave structure for the safety of the individuals as the presence of the predators in caves is affected by the cave morphometry (Tarburton 2009; Johnson et al. 2018). Effect of the cave morphometry on the presence of several predators such as feral cats and crabs is well documented (Tarburton 1990, 2009). For example, cave length seems to be affecting the presence of one of the most well-known predators like the rats (Johnson et al. 2017). Moreover, we encountered the rats in the study caves during various visits. However, we did not find any predation of swiftlets by the rats in the study caves. Also, Manchi and Sankaran (2009) described the rats as the predators of the edible nests fallen on the cave floor. The echolcation developed in the Paleotropical swiftlets enables these cave-dwelling birds to explore the darker regions for safer breeding (Griffin 1958; Brinkløv et al. 2013; Fenton 1975).

The caves are known to be the natural laboratories as they maintain an almost constant temperature throughout the year (Mammola 2018). However, the microclimate variables (temperature and relative humidity) inside the study caves indicated slight variations. These microclimate variations did not affect the breeding success of the ENS, unlike the findings of Manchi and Sankaran (2011) from the caves in the Northern part of the Andaman Islands. We understand this difference in output might be a result of various aspects like variations in local climate and in the type of caves. The caves at Chalis-ek are mostly above-ground caves, unlike our study caves on the Baratang Islands (Manchi 2009, 2014; Manchi and Sankaran 2009). Though the microclimate inside a cave does not directly influence the breeding success of the ENS in the caves on the Baratang Island, we agree with Manchi (2009) and Manchi and Sankaran (2011) that the high relative humidity during peak summer maintains the rigidity of the edible nest and might contributes in hatching success. The nests are also known to become hard in dry conditions, resulting in cracks and breakage or nests falling from the cave wall or ceiling, subsequently hindering breeding success (Koon and Cranbrook 2002; Nguyên Quang et al. 2002; Manchi and Sankaran 2011).

Our study indicates that ENS is faithful to their breeding caves, irrespective of breeding success or failure. Therefore, following the decision rule phenomenon, the birds chose to “always-stay” and reject the prior-experience hypothesis. Our findings imply improving the existing conservation strategies associated with enhancing the ENS population in the Andaman and Nicobar Islands. However, long-term capture-mark-recapture studies are necessary for a detailed understanding of the site-fidelity behavior of swiftlets.

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Author contributions PG: conceptualization, data curation, writing—original draft, methodology. DK: writing—original draft, data curation, formal analysis, software. SSM: conceptualization, funding acquisition, project administration, writing—review and editing, validation, methodology, supervision. RPS: funding acquisition, validation, writing—review and editing.

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Availability of data and material (data transparency) All the authors agree for the data transparency.

Compliance with ethical standards

Conflict of interest The authors have no conflicts of interest to declare.

Ethics approval The Research Advisory Committee of the Department of Environment and Forests, Andaman and Nicobar Islands, approved the capture and ringing procedure involved in the study. Based on which the Principal Chief Conservator of Forest, Wildlife Division, Department of Environment and Forests, Andaman and Nicobar Islands permitted to conduct the study. Vide Letter- CWLW/WL/134/25 dated on 13 April 2016.

Consent to participate The authors provide consent to participate.

Consent for publication The authors provide consent for publication.

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TECHNICAL NOTE

A simple and cost-effective test for sex identification in edible-nest swiftlet (*Aerodramus fuciphagus inexpectatus*) and plume-toed swiftlet (*Collocalia affinis*)

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Abstract

Existing molecular methods of sex identification have mixed success in different classes of birds. We report a new multiplex PCR method for sex identification based on *CHD1*gene using the P8/P2 and the 2550F/2718R primers. The new multiplex PCR approach successfully identified sex (two bands in female, single band in male) in edible-nest swiftlet (ENS) (*Aerodramus fuciphagus inexpectatus*) and plume-toed swiftlet (PTS) (*Collocalia affinis*). The new approach required agarose gel electrophoresis to resolve multiplex PCR products. The simplicity, speed and low cost make this method an adaptable molecular tool for sex identification in ENS and PTS with a possibility in other bird species.

Keywords Multiplex PCR · *CHD1* gene · Sex identification · Edible-nest swiftlet · Plume-toed swiftlet

Sex identification plays a vital role in avian research; specifically in avian behaviour, ecology, evolutionary biology, genetics, forensic studies and captive breeding programs (Morinha et al. 2012). However, identification of sex based on plumage and other morphological characters is impossible in monomorphic and young birds (Griffiths 2000). A number of DNA-based sex identification methods that target *CHD1* gene (*Chromo-helicase-DNA-binding protein* 1) have been developed for birds over the past decades (Griffiths et al. 1998; Lessells and Mateman 1996; Fridolfsson and Ellegren 1999, 2000). The *CHD1* gene is present on both W and Z chromosomes in most birds (Griffiths and Korn 1997), and size differences between *CHD1W* and *CHD1Z* introns have been exploited to differentiate the sex of an individual bird. Among all the molecular methods, sex identification using the P8/P2 and the 2550F/2718R primer pairs for *CHD1* has been successfully used for a variety of avian species (Fridolfsson and Ellegren 1999, 2000; Griffiths et al. 1998). The P8/P2 primer pair is effective in Passeriformes, whereas the 2550F/2718R is effective in Falconiformes and Pelecaniformes (Kocijan et al. 2011). Each of these methods have limitations, for example the 2550F/2718R primer results in a single band of about 645 bp on agarose for female (heterogametic sex) whereas the male bird (homogametic sex) do not show any amplification in select species. The P8/P2 primer set results a single band on agarose in both male and female, and needs hazardous, and combursive Polyacrylamide gel electrophoresis for resolving sex-specific bands. Several scientists have tried to overcome these method-specific limitations by combining more than two primers, Wang et al. (2011) used a combination of three primers (P8/WZ/Z) for identifying sex in Chinese Egret and other ardeid birds. Similarly, Rahim et al. (2012) multiplexed CHD1F/CHD1R and P8/P2 primers and resolved the resultant PCR product on 8% PAGE to identify sex in select Galliformes. We report for the first time multiplexing of the P8/P2 and the 2550F/2718R primers to differentiate sex in ENS and PTS. The new approach is cost-effective and fast as it requires only agarose gel electrophoresis to visualize PCR product of multiplex PCR.

To develop the multiplex PCR method, DNA was isolated from blood samples (adult male and female) of chicken (CH, $n=2$), ENS ($n=8$) and PTS ($n=2$). Prior permission was obtained (Permission No. CWLW/WL/134/480 dated 20/03/2015) from Forest Department of Andaman and Nicobar Islands. Blood was drawn from wing vein

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using sterile 1 ml disposable syringe and stored in saline saturated DMSO-EDTA buffer. Classical PCI method with minor modifications was used to isolate DNA from blood. Two sets of primers: P8 (5′-CTCCCAAGGATGAGRAAYTG-3′) /P2 (5′-TCTGCATCGCTAAATCCTTT-3′) described by Griffiths et al. (1998) and 2550F (5′-GTTACTGATTCGTCTACGAGA-3′)/2718R (5′-ATTGAAATGATCCAGTGCTTG-3′) by Fridolfsson and Ellegren (1999) were used alone or in combination (for multiplex PCR) to amplify regions of *CHD1* gene in Eppendorf thermal cycler. PCR amplification was performed in 10 µL reaction using the 5 µL Taq PCR Master Mix (Qiagen, Hilden, Germany), 20 ng DNA, 1 µM 2550F/2718R primers and 0.5 µM P8/P2primers in a single reaction. The amplification protocol included initial denaturation at 95 °C for 5 min followed by 35 cycles of denaturation at 95 °C for 30 s, annealing at 45.4 °C for 45 s and extension at 72 °C for 50 s with a final extension of 72 °C for 10 min. The multiplex PCR products were visualized with UV light using 2% agarose, stained with Hi-SYBr Safe Gel Stain (Himedia Laboratories, Mumbai, India). A commercial 1 kb plus DNA Ladder (Qiagen) was used as size slandered.

The multiplex PCR using the P8/P2 and the 2550F/2718R in a single reaction amplified *CHD1* gene, and successfully differentiated sex in ENS, PTS and CH (Fig. 1). Two bands (~ 380 bp and ~ 550 bp) were observed on agarose in ENS and PTS females, whereas only a single thick band of ~ 380 bp was observed in ENS and PTS males. The common band of ~ 380 bp in male and female ENS and PTS corresponds to *CHD1Z/CHD1W* fragment amplification by the P8/P2 primers, whereas an additional band of ~ 550 bp in ENS and PTS female corresponds to *CHD1W* fragment amplification by the 2550F/2718R primers. The thickness of ~ 380 bp band was more in males due to homogametic sex. Further, these two primer pairs resulted three bands in female (~ 380 bp, ~ 460 bp and ~ 630 bp) and two bands in male (~ 380 bp and ~ 630 bp) chicken. The difference in band patterns between CH and ENS/PTS can be attributed to specific mutation/s in the primer annealing site (Fridolfsson and Ellegren 1999). The P8/P2 alone resulted a single band in male and female ENS on agarose (Fig. 2a), whereas the 2550F/2718R resulted a single band only in female ENS (Fig. 2b) on agarose. However, multiplexing of these two primer pairs provides an accurate, safe and cost-effective method of sex identification in ENS and PTS. We have sexed over 1000 ENS samples using the new multiplexing approach, and expect that this method would be equally

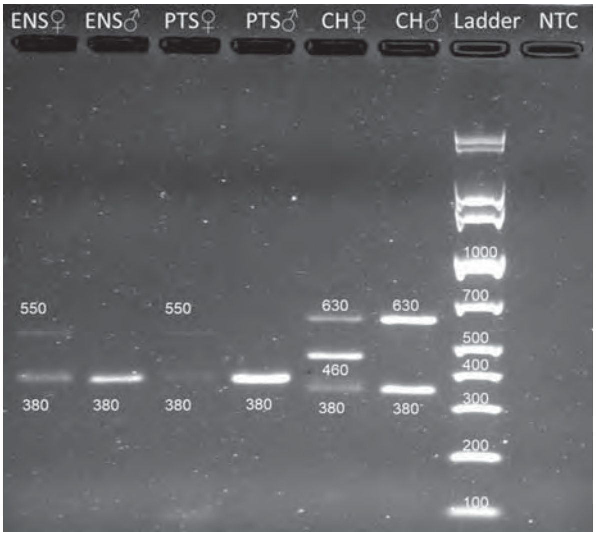

Fig. 1 Agarose gel showing the band pattern of multiplex PCR using the P8/P2 and the 2550F/2718R primers (*ENS* Edible Nest Swiftlet, *PTS* plume-toed swiftlet, *CH* chicken, *NTC* non template control, *Ladder* 1 Kb)

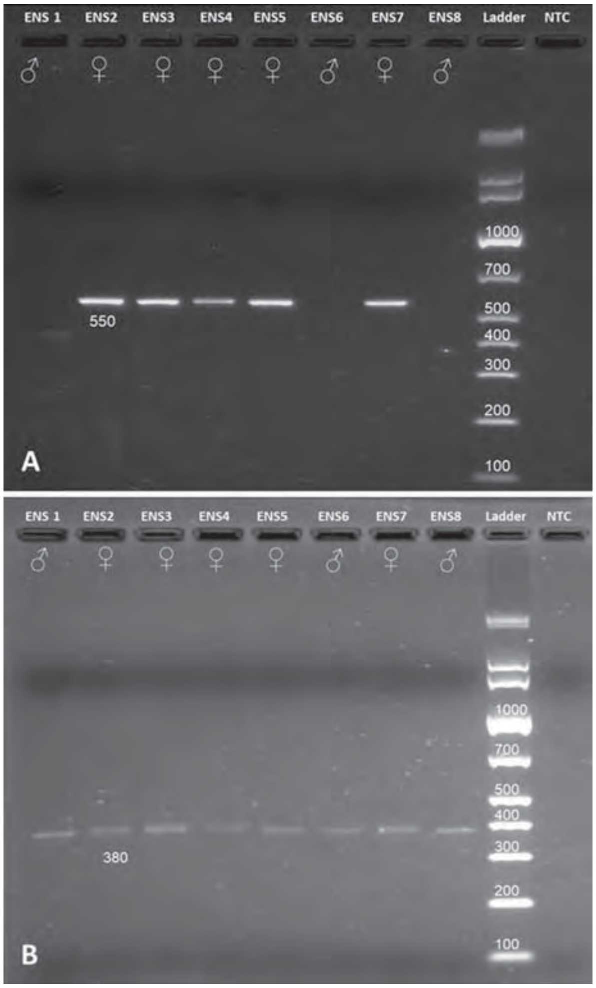

Fig. 2 Agarose gel showing the band pattern of PCR using the 2550F/2718R (**a**) and P8/P2 (**b**) primers alone (*ENS* Edible Nest Swiftlet, *NTC* non template control, *Ladder* 1 Kb)

useful in other bird species where the existing molecular sexing methods fail to identify sex.

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Compliance with ethical standards

Conflict of interest The authors have no conflicts of interest to declare.

Ethical approval The Research Advisory Committee of the Department of Environment and Forests, Andaman and Nicobar Islands, approved the capture and ringing procedure involved in the study. Based on which the Principal Chief Conservator of Forest, Wildlife Division, Department of Environment and Forests, Andaman and Nicobar Islands permitted to conduct the study. Vide Letter- CWLW/WL/134/25 dated on 13 April 2016.

Informed consent The authors provide consent to participate. The authors provide consent for publication.

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DEVELOPING A MOLECULAR SEXING TECHNIQUE FOR CAVE-DWELLING SWIFTLETS (FAMILY: APODIDAE)

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Sex identification is essential for the effective management and conservation of birds. In monomorphic bird species, the male and female birds cannot be identified based on phenotypic traits. Therefore, molecular techniques were used for reliable sex differentiation. The polymerase chain reaction (PCR) based methods have been widely used in molecular sexing of birds, using sex-linked markers. In the present study, initially, we used existing methods for sex identification in the monomorphic Edible-nest Swiftlet (ENS) (*Aerodramus fuciphagus inexpectatus)* & Plume-toed Swiftlet (PTS) (*Collocalia affinis)*. We followed three different protocols; primer pairs 2550F/2718R, P8/P2, and multiplexing of 2550F/2718R and P8/P2 sets of primers in a single reaction for sex identification.

CHD1 gene of ENS and PTS were successfully amplified using 2550F/2718R primer pair with ENS female samples, but it could not be amplified with male samples. CHD1 gene was successfully amplified using P8/P2 primer pair with males and female ENS samples and yielded single-band using agarose gel electrophoresis. This PCR product was subjected to expensive and prolonged PAGE analysis, which yielded double band for the female and a single band for the male ENS sample. As to overcome from PAGE limitations, we invented multiplexing PCR method using the primer pair 2550F/2718R and P8/P2. We observed two bands for females and a single-band for males after running the multiplex PCR product on 2% agarose gel, which identified males and females. This newly developed, simple, cost-effective, less time-consuming, high-throughput applicability of bird sex identification technique has implications for understanding the population dynamics of birds.