Ecological and Phylogenetic Aspects of an Avian Aerial Insectivore: The Barn Swallow in the Himalaya

Thesis submitted for the award of the degree of

Doctor of Philosophy

In

WILDLIFE SCIENCE

By

Amarjeet Kaur

To

Saurashtra University
Rajkot- 360005 (Gujarat)

Under the supervision of

Dr. R. Suresh Kumar

भारतीय वन्यजीव संस्थान
Wildlife Institute of India

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Altitude and Arc: A Barn Swallow's pursuit of prey in the Himalaya
Illustration by Karmannye Om Chaudhary

This work is dedicated to the people of the Indian Himalayan Region and Northeast India, who whole-heartedly allowed me access to their properties and even let me observe and catch "their" birds for the purpose of this research.

भारतीय वन्यजीव संस्थान
Wildlife Institute of India

DECLARATION

I, hereby, declare that the work conducted under this thesis titled "**Ecological and Phylogenetic Aspects of an Avian Aerial Insectivore: The Barn Swallow in the Himalaya**" is a record of original and independent research work done by me and subsequently submitted for the award of the degree of **Doctor of Philosophy in Wildlife Science** to the **Saurashtra University, Rajkot (Gujarat)**. This research work has been carried out under the guidance and supervision of Dr. R. Suresh Kumar of Wildlife Institute of India, Dehradun. The work has not formed the basis for the award of any other degree, diploma or any other qualification. I also declare that the thesis embodies my own work, analysis, observation, understanding and the particulars given in it are true to the best of my knowledge.

(AMARJEET KAUR)

Place: Dehradun

Date: 22.01.2026

22/01/2026

Supervisor

Dr. R. Suresh Kumar
Scientist-F
Endangered Species Management
Wildlife Institute of India

पत्रपेटी सं. 18, चन्द्रबनी, देहरादून-248 001, (उत्तराखण्ड), भारत
Post Box No. 18, Chandrabani, Dehradun-248 001, (Uttarakhand), **INDIA**
ई.पी.ए.बी.एक्स. : +91-135-2640111 से 2640115, एवं 2644462 से 2644464, फैक्स: 0135-2640117, तार: **WILDLIFE**
EPABX : +91-135-2640111 to 2640115 & 2644462 to 2644464 **Fax** : 0135-2640117, **GRAM** : **WILDLIFE**
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भारतीय वन्यजीव संस्थान
Wildlife Institute of India

Date: 22.01.2026

CERTIFICATE

This is to certify that **Miss Amarjeet Kaur** thesis, **" Ecological and Phylogenetic Aspects of an Avian Aerial Insectivore: The Barn Swallow in the Himalaya"** submitted for the degree of **Doctor of Philosophy in Wildlife Science at Saurashtra University, Rajkot, Gujarat**, embodies original research work carried under our guidance and supervision.

Miss Amarjeet Kaur has researched on this thesis for more than six terms under my supervision and guidance. The work presented in this thesis has not been submitted for any other degree. It meets all of the specifications stated forth in the ordinances of Saurashtra University in Rajkot, Gujarat, and the Wildlife Institute of India.

Forwarded by:

Ruchi

Dean
Faculty of Wildlife Science
संकायाध्यक्ष / Dean
भारतीय वन्यजीव संस्थान
WILDLIFE INSTITUTE OF INDIA
देहरादून / Dehradun

Date: 22.01.2026
Place: Dehradun

WILDLIFE INSTITUTE OF INDIA
CHANDRABANI, DEHRADUN

22.01.2026
Supervisor
Dr. R. Suresh Kumar
Scientist-F
Endangered Species Management
Wildlife Institute of India

पत्रपेटी सं. 18, चन्द्रबनी, देहरादून-248 001, (उत्तराखण्ड), भारत
Post Box No. 18, Chandrabani, Dehradun-248 001, (Uttarakhand), INDIA
ई.पी.ए.बी.एक्स. : +91-135-2640111 से 2640115, एवं 2644462 से 2644464, फैक्स: 0135-2640117, तार: WILDLIFE
EPABX : +91-135-2640111 to 2640115 & 2644462 to 2644464 Fax : 0135-2640117, GRAM : WILDLIFE
ई–मेल/E-mail : wii@wii.gov.in

SAURASHTRA UNIVERSITY
P.G.T.R Section
Main Office, First Floor
University Road
Rajkot - 360 005 (Gujarat)
Phone No. : 2578501
Fax : (0281)2856983
www.saurashtrauniversity.edu

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I certify that the research work was appreciated by all who were present, and the comments made by the faculty and researchers have been appropriately included in the thesis.

Ruchi
(Dr. Ruchi Badola)
21/01/2026
Dean
Faculty of Wildlife Science
संकायाध्यक्ष / Dean
भारतीय वन्यजीव संस्थान
WILDLIFE INSTITUTE OF INDIA
देहरादून / Dehradun

WILDLIFE INSTITUTE OF INDIA
CHANDRABANI, DEHRADUN

21.01.2026
(Dr. R. Suresh Kumar)
Supervisor
Dr. R. Suresh Kumar
Scientist-F
Endangered Species Management
Wildlife Institute of India

भारतीय वन्यजीव संस्थान
Wildlife Institute of India

CERTIFICATE OF PLAGIARISM CHECK

It is certified that the Ph.D. thesis entitled **"Ecological and Phylogenetic Aspects of an Avian Aerial Insectivore: The Barn Swallow in the Himalaya."** submitted by **Amarjeet Kaur** has been examined by us for plagiarism check as per UGC (Promotion of Academic Integrity and Prevention of Plagiarism in Higher Educational Institutions) Regulations. The following inferences are drawn from this check:

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Chandrabani, Dehradun - 248 001

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(Dr. R Suresh Kumar)
Supervisor

Dr. R. Suresh Kumar
Scientist-F
Head of Department
Endangered Species Management
Wildlife Institute of India

WILDLIFE INSTITUTE OF INDIA
CHANDRABANI, DEHRADUN

Dr. Ruchi Badola
Dean, FWS

संकायाध्यक्ष / Dean
भारतीय वन्यजीव संस्थान
WILDLIFE INSTITUTE OF INDIA
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पत्रपेटी सं0 18, चन्द्रबनी, देहरादून – 248 001, उत्तराखण्ड, भारत
Post Box No. 18, Chandrabani, Dehradun - 248 001, Uttarakhand, INDIA
ई.पी.ए.बी.एक्स : +91-135-2640111 से 2640115 फैक्स : 0135-2640117
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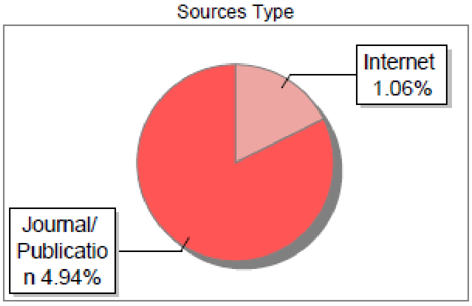

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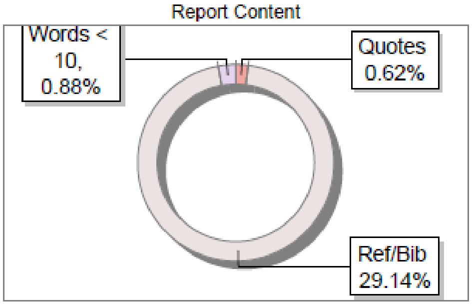

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List of publication(s) and conferences (National & International) attended

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Peer-reviewed Publications (Annexure 1)

- **Kaur, A**., Chauhan, H., and Kumar, R. S. (2026). Prey composition in the diet of an avian aerial insectivore – the Barn Swallow (*Hirundo rustica*) in the Indian Himalaya submitted in *Avian Conservation and Ecology ISSN: 1712-6568* (**accepted for publication, Impact Factor 1.6**).

- **Kaur, A**., and Kumar, R. S. (2026). Barn Swallows of the Imphal Valley – a potential case of past climatic events leading to year-round residency in the population in Northeast India submitted in *Journal of Wildlife Science ISSN (Online): 3048-7803* (in review)

Popular Article Publications and Popular Talks (Annexure 2)

- **Kaur, A.** (2024). Barn Swallow: A tale of homecoming. WII Newsletter, Vol. 31, Issue 1, pp. 30–31.

- **Kaur, A.** (2024). The Beloved *Katij* of Kashmir. Nature inFocus.

- Kumar, R. S. and **Kaur, A**. (2023). Barn Swallow – the aerial insectivore of the Himalayas. Podcast episode no. 33. Heart of Conservation. https://open.spotify.com/episode/5xGdSTrE14Gix0FtVeGfuk?si=7v0qbSUpTxKQ00mE-3RnlQ

- **Kaur, A.** (2025). Looking for a home within a home – the Barn Swallows in the Himalayas. Live Webinar. Hindustan Times. https://www.youtube.com/watch?v=9IST36u37FQ

Conferences – National and International (Annexure 3)

- **Kaur, A**., and Kumar, R.S (2021). Poster presentation titled "Common birds in a changing world: Monitoring Barn Swallow populations in the Himalaya" held on 26th – 27th March 2021 (online mode) at Bird Monitoring Symposium 2021.

- **Kaur, A**., and Kumar, R.S (2023). Oral presentation titled "Population-level structuring of Barn Swallow *Hirundo rustica* across the Himalaya based on morphological traits", held on 12th – 14th September 2023 at 16th Internal Annual Research Seminar, WII.

- **Kaur, A**., and Kumar, R.S (2025). Oral presentation titled "Common Birds in a Changing World: Nesting Ecology of Barn Swallow in the Himalayas" held on 5th – 6th September 2025 (online mode) at Bird Monitoring Symposium 2025.

- **Kaur, A**., and Kumar, R.S (2023). Oral presentation titled "A Close-Knitted Relationship: Barn Swallows (*Hirundo rustica*) and the Humans of the Himalaya" in the session Nature and Humans - Human-wildlife interactions at the British Ecology Society Annual Meeting 2023, Belfast, United Kingdom.

Acknowledgement

“Come! says the mother. "Try your wings!"
But the baby swallows huddle in fright,
Gazing down from the dizzy height.
The babies flutter and flap their wings;
They squeak and twitter and chitter and cling.
For they hate to leave, and the hate to try
To test their wings and learn to fly.
But Mother and Father know what's best,
So they push their babies out of the nest.”

-By Dahlov Ipcar (1967)

This excerpt from *From Whisperings and Other Things* by Dahlov Ipcar perfectly sums up my PhD journey - from registration to the submission of my thesis. The only difference is that, unlike the baby swallow in the poem, I was ready to leave the nest and had to gently push my mother and father to help me learn to fly. I believe this was indeed the best decision, one that eventually shaped my research journey.

However, this baby swallow could truly fly only because of the guidance and encouragement of my PhD supervisor, Dr. R. Suresh Kumar. From mentoring a novice researcher like me to helping me choose and shape my research topic, and instilling a deep interest in avian ecology, I am also sincerely thankful for his support during fieldwork, including assistance with catching swallows, taking measurements, and collecting blood samples for this research. I am forever grateful to him. I am also sincerely grateful to my PhD supervisor for involving me in the Amur Falcon project which played a significant role in strengthening my research abilities.

I would like to thank my institute, the Wildlife Institute of India (WII), which has shaped my research career over the past years. I am grateful to the Director, WII, for enabling timely permissions to carry out this research work; the Dean, WII, for consistently facilitating the smooth completion of academic requirements; and the Registrar, WII, along with the administrative and academic staff, for their support throughout my PhD journey. I would also like to extend my thanks to the teaching laboratory and genetic laboratory facilities at WII, without which the analysis of my data would not have been possible. I further extend my sincere gratitude to Dr. V. P. Uniyal, former Scientist–G and NOEA at WII, for going out of his way to assist me with my timely registration. I am also thankful to the current NOEA, Dr. Samrat Mondol, Scientist – F, WII for his guidance on the submission. I am truly grateful for the necessary push by Mr. Virendra R. Tiwari, former Director, WII for completing this PhD.

I would like to convey my heartfelt thanks to my M.Sc. mentor, Dr. Sanjay K. Das, Assistant Professor at Guru Gobind Singh Indraprastha University, Delhi, who showed me the right direction at the very beginning of my academic journey. I am also grateful to him for encouraging me to apply for the DST–INSPIRE Fellowship for my PhD, which I was awarded successfully. I sincerely thank the Government of India's INSPIRE Fellowship programme for financially supporting my doctoral research, and I am also thankful to the staff at the DST office and the Accounts Section at WII for the timely transfer of fellowship funds. I am also obliged to the Forest Departments of Jammu & Kashmir, Uttarakhand, West Bengal, and Manipur for granting the necessary permissions to undertake research activities in their respective states. I am thankful to Dr. S. Sathyakumar, former Scientist – G, WII for his support and DST- NMSHE Phase II project for funding this research for two years. I sincerely thank Dr. Trevor Price and Dr. Dhananjai Mohan for their valuable guidance, insights, and encouragement, which greatly enriched my academic perspective.

Although this thesis is presented as an independent piece of work and is written largely in the passive voice to avoid the use of personal pronouns, it has benefited from the contributions, guidance, and support of many individuals and institutions. Foremost, gratitude is extended to those who assisted in carrying out fieldwork. Special thanks are due to Harsh Chauhan, who was like a younger brother and was always willing to travel to remote areas for data collection. He consistently ensured that Barn Swallows were observed even while engaged in other work. I also thank Ms. Mahi Noor, a local resident at my field site in Kempty, whose curiosity about the birds nesting in her shop led her to join me in data collection there over two years. I am further grateful to the interns, Dr. Manisha Bisht, Ms. Yamini Nayal, Ms. Divya Bhatt, Ms. Khushi Soni, Ms. Lakshita Bhatti - who assisted during different phases of data collection and learned alongside the project.

I also extend special thanks to Deepak *bhaiya* and his reliable Alto, which proved to be a great relief during extensive field travel. During challenging travel conditions across different field sites in Uttarakhand, Deepak *bhaiya* ensured my safety while driving me to various locations for data collection.

I am deeply thankful to the people of Uttarakhand, particularly in Kempty and Nainital, for their warmth and cooperation during my fieldwork. I owe special gratitude to Deepti Bhatt (*Bhabhi*) for granting me unrestricted access to her home, taking care of me with immense kindness, and consistently offering food whenever I visited to check nest status. I also sincerely thank Samar Ahmed, her parents, and extended family in Nainital for welcoming me into their home, allowing me to stay with them, and making me feel like part of their family. I am especially grateful to Ms. Samar Ahmed for conducting fieldwork in Nainital under challenging conditions and for helping collect information on swallows even during the COVID-19 period.

I also acknowledge the support received during surveys and sampling across different regions. In Kashmir, I thank Mr. Harsh Chauhan for accompanying me and travelling extensively in the region to document Barn Swallow breeding locations. I am grateful to Mr. Abdul Sofi Qayoom (Senior Forester, Jhelum Valley Forest Division, Baramulla) for his immense support in identifying suitable sampling sites for Barn Swallows in Kashmir, as well as for his hospitality during our stay at his home. I also thank Mr. Nazir Ahmed from Wular Lake for granting access to his property to capture swallows.

For field surveys in North Bengal, I am thankful to Mr. Rajdeep Mitra for connecting me with appropriate local support during fieldwork. I am sincerely grateful to Ms. Manju, who not only hosted me at her homestay in Ghoom but also provided invaluable support as a cook, field assistant, and translator, and who later became a dear friend. I am also thankful to Rajdeep for his support in field in Kashmir, North Bengal and Manipur.

I thank DFO Mr. Kharibom Singh H., for his consistent support during my stays in Manipur and for helping me connect with the appropriate people to carry out field surveys. I am grateful to Mr. Indra from Loktak Lake, Imphal, who travelled with me to various sites in search of swallows and assisted by translating conversations with local communities. I also sincerely thank Mr. Khogen Singh Rao and for connecting me with his sister who generously hosted me in her home and treated me like family. I further extend my thanks to Mr. Victor and Mr. Johnson R.O. for their assistance during fieldwork.

I am grateful to Dr. Stefanie LaZerte, Adjunct Professor at Brandon University, for her active support in helping me understand and develop R code for analysing eBird data. I sincerely thank her for her consistent guidance and support at every step. I also thank my colleague at WII, Mr. Varun Kher, for helping clarify doubts related to R. I am further thankful to Dr. Roxy Mathew Koll, Scientist–F and his students at the Indian Institute of Tropical Meteorology for their assistance in learning the basics of Python and for climate data analysis. I am grateful for generous support by Mr. Bhakta Pattnaik for supporting my travel to attend the BES conference through funds from Trilegal Firm, Mumbai and Mr. Ravindra Kumar for supporting my living expenses at UK through CSR Funds, TATA Motors, Mumbai.

A significant part of this thesis involved laboratory work, for which I sincerely thank the interns, Ms. Raveena and Ms. Palak for their initial efforts in testing faecal samples in the laboratory, and to Mr. Harsh Chauhan for his major contribution in assisting with subsequent laboratory analyses. The laboratory work would not have been possible without guidance in insect identification from the "insect people" in my life – Dr. Ritesh Kumar Gautam, Dr. Shabnam Rana, and Dr. Uttaran Bandyopadhyay - whose continued assistance and support were invaluable throughout various stages of laboratory work. Another lab work was for the genetics work and for that I am thankful for intellectual discussions and lab-based inputs from Dr. Roi Dor, Associate Professor, The Open University of Israel. His support in designing the study was critical. I am also thankful to Dr. Bhim Singh, Dr. Kumudani Bala for their consistent help. I thank Ms. Shrewshree, Ms. Farah, Dr. Bhawna and Ms. Sneha for their selfless support in lab work.

There are many individuals with whom I interacted during my fieldwork. Across all field sites, local people generously welcomed me into their homes and allowed me to search for swallows. In Kashmir, I was never allowed to leave a house without being offered tea or a snack. In Manipur, people were often amused to see a stranger travel such long distances to study swallows. In Ghoom, North Bengal, local residents even guided us to sample swallows roosting inside kitchens late at night. People in Kashmir, Uttarakhand, North Bengal, and Manipur placed great trust in us by granting access to their properties, often during late evening and night hours, sometimes as late as 2 a.m.

There were numerous people whom I met during fieldwork, whose kindness and warmth stayed with me throughout my PhD journey. Two individuals whom I would like to acknowledge with heartfelt gratitude are Mr. Jagat Singh from the remote village of Rarikhooti in Champawat district, Uttarakhand, and Mr. Rajendra Singh from Thoubal district, Manipur, both of whom encouraged me by saying, *"you are doing good work."* These words of support meant a great deal to me during my doctoral journey.

My deepest personal gratitude goes to my constant supporters - my parents, and my source of strength, my brother. I feel deeply privileged to have received their unwavering support, love, and care throughout and during the challenging period of the COVID-19 pandemic, when I lost crucial field seasons and moments of hope. I am also grateful for the love and support of my sister-in-law and my nephew, who came into my life bringing happiness. I thank my family for patiently listening to me and for allowing me to miss family functions to meet my research commitments. I am equally thankful for their understanding and support when vacations had to be cancelled due to the demands of my PhD.

I am most thankful to my all-time supporter – Akshita Chaudhary—whose unwavering belief in me carried me through the most challenging phases of this journey. She was always there helping me personally as well as professionally. I am also thankful to my dearest Vani Rijhwani and Kashish Madan. WII made me make many friends and I am thankful for their time in my life. I am with all my heart truly grateful to Alex Jacob for being there throughout this journey. I thank my brother from another mother – Vignesh Chandran for being a solid support. I am thankful to Sarabjeet Kaur for helping me learn birds and many important lessons in life. I thank Renu Bala for her constant support both personally and professionally. I thank my friends, Rohit Jha, Jithin V, Vabesh Tripura, Niazul Hassan Khan, Sameeha Pathan and colleagues Aksheeta Mahapatra, Harindra Baraiya, Gaurav Sirola, Mohit Mudliar for their help during my PhD.

It is often said that the most difficult phase of a PhD comes toward the end, and I experienced this profoundly. I was fortunate to have been surrounded by people whose love and support helped me through this period. I owe special thanks to Anoop Raj Singh for his constant encouragement, meaningful conversations, and for proofreading my writing. I also thank Praveen Krishna for conversations over evening teas that helped me cope during difficult times. I am thankful to Karmannye Om Chaudhary for having thoughtful discussions about birds and work and for making me a beautiful illustration of Barn Swallow for my thesis. I am grateful to Ritesh Kumar Gautam for his genuine support in motivating me to work harder and for standing by me during many challenging moments. I am also thankful to the parents of Ritesh, whose warmth and care made me feel like part of their family when I was away from my own. I was fortunate to meet two remarkable individuals during this journey – *Bhauji* (Shankhamala Ghosh) and *Dada* (Uttaran Bandyopadhyay)—whose support and affection during some of the most difficult moments meant a great deal to me.

Lastly, I apologise to anyone I may have inadvertently missed who was part of this journey, and I sincerely thank you all.

Executive Summary

This thesis is a first to document the ecology of a common and widespread species yet is declining in many parts of its range, the Barn Swallow (*Hirundo rustica*). The species breeds in the Northern Hemisphere and undertake long-distance migratory movements every year to its non-breeding grounds in Southern Hemisphere. Owing to its close association with humans – the nature of nest building in human artefacts, the Barn Swallow is a well-known human commensal species globally. Due to its widespread distribution, populations show variations in their morphological as well as genetic traits, and globally six subspecies of *H. rustica* are recognized, of which two are sedentary or non-migratory. Though common, this aerial insectivore is experiencing severe population declines in Canada, North America and parts of Europe with global population trend status is declining. The widespread declines in Barn Swallow populations have alarmed the scientists across the world with the urgent need for ecological monitoring and identification of region-specific drivers of decline.

In India, three out of six subspecies of Barn Swallow are reported to occur - two subspecies, *H. r. rustica* and *H. r. gutturalis* breed in Himalaya while the third *H. r. tytleri* is a winter visitor in Northeast India. Given the documented alarming declines across regions, population trends of Barn Swallows in India remain unknown. This formed the basis of this thesis wherein the knowledge gaps on species are addressed with three major components. First, given the absence of any population trend, eBird data - citizen-science observations was utilised to examine the species' breeding and non-breeding distribution across the Indian subcontinent. Second, field surveys were conducted across the Himalayan region to document the breeding sites of Barn Swallows with main focus of documenting breeding ecology in the Uttarakhand Himalaya. Third, Barn Swallow populations across the Himalayan range were examined to assess morphological and genetic variations. Finally, the thesis is concluded by synthesising ecological and evolutionary findings, while also highlighting the strong cultural relationship between Barn Swallows and the people of the Himalaya.

The first objective focuses on eBird locations to document the occurrence of Barn Swallows in the Indian subcontinent. eBird platform is valuable particularly in parts of the world where long-term species monitoring programs are limited and access to ecological data remains constrained. eBird data was utilized with the objective of investigating the occurrence and seasonal movements of the Barn Swallow in the Indian Subcontinent. With five years of data

(2019 – 2023), following eBird best practice criteria, checklists were filtered and considered for the analyses. Barn Swallows presence data was compiled for the Indian subcontinent region, divided into equal-area icosahedron hex grids (25 km^2). For each cell, daily presence was calculated and then weighted daily mean location was calculated using the central longitude and latitude of each cell. A generalized additive model (GAM) was applied on the weighted mean daily locations for each year to model latitude and longitude separately as functions of time (Julian day). Combining the predicted latitude and longitude values from the fitted GAM, daily population-level centroids were generated. From the GAM predicted occurrence centroids, migration timing, migration speed and migration distance was calculated, and seasonal and annual variations were compared using linear regression and linear mixed models.

Across five years, Barn Swallows bred at a mean latitude of 28.18°N and wintered around 16.19°N, with marked interannual variation in both breeding extent and migration timing. Spring migration began on average in late March and was faster than autumn migration (23.7 vs. 20.1 km/day), although this difference was marginal. Migration distances were similar between seasons (≈1550 km in spring; ≈1670 km in autumn). Migration timing influenced latitudinal positions, with later spring departures associated with more northerly locations and later autumn departures with more southerly positions. Weak northward shifts in migration routes and breeding latitudes were observed over time, indicating subtle directional changes in the migratory system.

This eBird analysis provides the first broad-scale synthesis of Barn Swallow migration within the Indian subcontinent, revealing that Himalayan-breeding populations consistently occupy higher latitudes during breeding and overwinter predominantly in southern India, underscoring India's central role in Asian migratory connectivity. Migration phenology showed spring departure in late March and residence at breeding sites until late July, with faster and slightly shorter spring migration compared to autumn, consistent with optimal migration theory and monsoon-driven resource tracking. Interannual variation in timing, speed, and distance likely reflects environmental variability along migratory routes. Weak but consistent northward shifts in breeding and migratory latitudes suggest early climate-driven range adjustments that may be especially consequential in the rapidly changing Himalayan landscape. Despite limitations of citizen science data, these findings establish a critical baseline for understanding the migration ecology of Himalayan Barn Swallows and highlight the need for integrated tracking and ringing studies to resolve population-specific routes, identify key non-breeding habitats, and assess future climate and land-use impacts.

The second objective focuses on documenting breeding distribution and nesting ecology of Barn Swallows in the Indian Himalayan Region. Systematic surveys across the Himalayan range from west to east axis between 2019 and 2023 (excluding two years- 2020 and 2021 of COVID-19 pandemic) were carried out. On locating a nest, nest-site characteristics and nest attributes were recorded. Systematic nest monitoring was conducted across four sites in Uttarakhand to quantify breeding parameters and nest success of Barn Swallows, with nests monitored every 5–7 days from initiation to outcome. Breeding metrics including clutch size, brood size, fledgling number, and nesting duration were estimated, and nest success was assessed using both apparent success and Mayfield nest survival estimates to account for unequal exposure times. Spatial and temporal variation in nest success was analysed using binomial generalized linear models. To examine nestling diet and prey selection, faecal samples were collected from active nests and prey remains were identified to insect order using microscopy, while aerial insect availability was quantified through sweep-net sampling along foraging transects at rural and urban sites. Diet composition and prey availability were compared across settlement types using frequency of occurrence, PERMANOVA, and NMDS based on Jaccard dissimilarity, allowing assessment of dietary differences between urban and rural habitats and evaluation of prey use relative to local insect communities.

Across the Indian Himalaya, 1,450 Barn Swallow nests were recorded between an elevation belt of 489 and 2,317 m, with a mean nesting elevation of ~1,500 m and high concentration within the mid-elevational range (1,000–2,000 m). Nesting records spanned 24.4–34.2°N and were unevenly distributed among states, with Uttarakhand contributing the majority of nests and exhibiting the broadest elevational range. Across the region, over 70–90% of nests were located inside buildings, most commonly on walls, bulb holders, and other artificial supports, with commercial structures such as shops dominating in most states.

In Uttarakhand, breeding activity extended from late February to late June, with mean nest initiation around day 102 of the year and clear advancement in nest initiation, egg-laying, and fledging dates across years, particularly in 2023. Mean clutch size was 3.88 eggs, mean brood size 3.25 chicks, and successful nests fledged an average of 2.63 young, though reproductive output varied across sites. Apparent nest success was 62.2%, while Mayfield estimates indicated higher overall nest survival (mean 76.5%), reflecting differences in exposure time and daily survival rates among sites and years. Nest success varied significantly among regions but not among years, with Nainital and Bageshwar showing consistently higher success than Kempty. Diet analysis of 240 nestling faecal samples identified six insect orders, dominated by Coleoptera (96.7%) and Hymenoptera (75%), with significant differences in prey composition between rural and urban settlements and weaker spatial structuring within settlement types. Aerial insect sampling revealed distinct insect communities between rural and urban habitats, yet nestling diets differed significantly from local prey availability at both settlement and site levels, indicating selective foraging rather than passive prey use.

This objective's findings provide the first comprehensive assessment of Barn Swallow breeding ecology across the Indian Himalaya, demonstrating that the species is a widespread and regular breeder across a broad elevational range, with nesting concentrated at mid-elevations where it is likely that climatic conditions and prey availability are most favourable. The strong association with human-made structures - particularly indoor nesting in shops and traditional buildings - highlights the species' long-standing commensal relationship with people in the region and complete dependence on human structures for nesting in the region. Spatial variation in breeding distribution and reproductive success appears to be driven by regional climate, monsoon dynamics, and local habitat quality, while the observed advancement in breeding phenology between 2019 and 2023 is consistent with climate-driven shifts documented in migratory birds globally.

Dietary analyses revealed selective foraging, with nestlings fed predominantly large-bodied insects, especially Coleoptera and Hymenoptera, and clear differences between rural and urban settlements reflecting habitat-specific prey availability. The mismatch between available insects and prey consumed indicates active prey selection rather than opportunistic feeding, though reliance on faecal analysis may underrepresent soft-bodied taxa. Collectively, these findings underscore the vulnerability of Himalayan Barn Swallow populations to rapid changes in architecture, land use, and insect communities. The ongoing replacement of traditional buildings with sealed modern structures, combined with widespread declines in aerial insects, may create ecological traps where nesting opportunities persist but food resources do not. Conservation efforts in the Himalaya should therefore integrate nest-friendly architectural practices, protection of insect-rich foraging habitats, and long-term monitoring to safeguard this culturally valued and ecologically important aerial insectivore in a rapidly transforming mountain landscape.

The third objective of the thesis is aimed to fill the gap in identity and origin of Barn Swallow populations breeding in the Indian Himalayan region. Despite well-documented morphometric variation among Barn Swallow subspecies, the identity, breeding distribution, and evolutionary history of populations breeding in the Indian Himalayan region remain poorly understood. In particular, it is unknown when Barn Swallows colonized the Himalaya, how Pleistocene glacial events shaped their present-day distribution, and how or whether geographically isolated populations - such as the sedentary population in Manipur - diverged from the largely migratory Himalayan populations. Addressing this gap, the third objective of this study investigates the phylogeography of Barn Swallow populations breeding in the Indian Himalaya within a global context, integrating Indian populations with well-studied breeding populations worldwide to elucidate their evolutionary relationships, historical connectivity, and region-specific adaptations.

For this objective, adult Barn Swallows were captured at breeding sites across Kashmir, Uttarakhand, North Bengal, and Manipur using mist-nets and customized butterfly nets, and standard morphometric measurements were recorded. Birds were banded, and small blood samples were collected from adults for genetic analysis. Morphometric variation among regions was examined using principal component analysis, one-way ANOVA, and post-hoc tests, with wing length used as a proxy for body size and additional regression analyses conducted to assess latitudinal trends; sexually dimorphic tail streamers were analysed separately by sex. For phylogeographic analysis, mitochondrial Cytochrome b and ND2 gene sequences were generated from blood samples, following DNA extraction using standard kits and PCR amplification with published primers. Sequences were edited, aligned, and analysed alongside global Barn Swallow subspecies sequences retrieved from GenBank. Genetic diversity was estimated, phylogenetic relationships were reconstructed using Bayesian inference in BEAST with appropriate substitution models and outgroup rooting, and haplotype relationships were visualized using median-joining networks, with genetic distances calculated under the best-fitting evolutionary model.

Barn Swallow populations across the Indian breeding range showed pronounced variation in plumage, morphology, and genetic structure. Plumage colouration varied geographically, with buff-bellied birds with broken or broad breast bands dominating Uttarakhand and North Bengal, mixed white to rufous-bellied individuals with complete breast bands in Kashmir, and predominantly rufous to chestnut-orange birds with broken or complete breast bands in Manipur. Morphometric analyses of 158 adults revealed clear regional structuring, with principal component analysis separating populations primarily along a body size axis (PC1) and a bill morphology axis (PC2), together explaining 58.6% of total variance. Birds from the Srinagar Valley were significantly larger, exhibiting the greatest wing lengths, while individuals from the Imphal Valley were smallest; Himalayan populations (Uttarakhand and North Bengal) were intermediate but showed greater variability in bill traits. Sexually selected outer tail length was consistently longer in males than females, with both male and female Kashmir birds exhibiting significantly longer streamers than those from other regions. Across all populations, wing length, tarsus length, body mass, and head length increased significantly with latitude, indicating strong latitudinal clines in body size.

Phylogeographic analyses based on mitochondrial Cyt b and ND2 genes revealed two genetically distinct Barn Swallow lineages within India. All samples from Kashmir, Uttarakhand, and North Bengal clustered into a well-supported and genetically distinct Himalayan clade, whereas samples from Manipur, along with two individuals from Uttarakhand, grouped with the East Asian subspecies *Hirundo rustica gutturalis*. Both Bayesian phylogenetic reconstruction and haplotype network analyses consistently supported this deep genetic separation, indicating that Himalayan Barn Swallow populations represent a distinct evolutionary lineage, clearly differentiated from other recognized subspecies across the species' global range.

This study demonstrates strong geographic structuring in morphology and genetics of Barn Swallows across the Indian Himalayan region, shaped by latitude, ecology, and historical biogeography. Birds breeding at higher latitudes in Kashmir were consistently larger, with longer wings and exaggerated male tail streamers, conforming to well-established latitudinal size clines and suggesting adaptation to colder climates, migratory demands, or flight efficiency. Central Himalayan populations (Uttarakhand and North Bengal) showed intermediate morphology with greater trait variability, indicating partial phenotypic cohesion along the Himalayan axis, potentially constrained by geographic barriers such as the Pir Panjal range. In contrast, the newly documented resident breeding population in Manipur exhibited distinct plumage and smaller body size, with morphometric traits that do not align cleanly with described subspecies, instead appearing intermediate between *H. r. tytleri* and *H. r. erythrogaster*. This challenges traditional subspecies assignments in South and Southeast Asia and highlights unresolved complexity in the region's biogeographic history.

Phylogeographic analyses revealed two well-defined mitochondrial lineages within India: a distinct Himalayan clade encompassing Kashmir, Uttarakhand, and North Bengal, and an eastern lineage aligned with *H. r. gutturalis* that includes all Manipur samples and a small subset from Uttarakhand, suggesting secondary contact or admixture. The concordance between morphometric differentiation and genetic structure indicates that geographic isolation, local adaptation, and sexual selection may jointly reinforce divergence despite the species' high dispersal ability. The Manipur population may have arisen through secondary colonization and introgression or through a shift from migratory to sedentary breeding within a former wintering range, underscoring the Barn Swallow's capacity for rapid evolutionary and behavioural change. While these patterns point to the Himalaya as an important axis of divergence, the Himalayan lineage is best viewed as an incipient evolutionary or management unit rather than a fully differentiated subspecies, emphasizing the need for genome-wide data and migratory tracking to resolve evolutionary status and inform conservation in this climatically sensitive region.

Thie last chapter discusses on Barn Swallows as one of the world's most successful avian commensals, whose close association with humans emerged relatively recently alongside permanent settlements during the Holocene. Across cultures, their reliance on human-made structures for nesting has fostered deep symbolic, religious, and emotional connections, particularly in breeding regions. In the Indian Himalaya, where Barn Swallows are summer breeders nesting predominantly inside houses and shops between 1000–2000 m elevation, these cultural relationships had not previously been documented. By combining large-scale surveys with ethnographic-style interviews, this study demonstrates that Barn Swallows occupy a unique socio-ecological niche in the Himalaya, where their breeding ecology is inseparable from human tolerance, daily routines, and traditional belief systems.

Survey results across the Himalayan region revealed overwhelmingly positive perceptions of Barn Swallows, reflected in vernacular names that associate the species with gods, prosperity, and domestic well-being. In Uttarakhand, residents reported nesting histories extending back several decades to over a century, strong nest-site fidelity, and widespread nest protection practices, including deliberate avoidance of disturbance. Despite threats such as competition with House Sparrows, nestling mortality from ceiling fans, and predation by domestic animals, human tolerance remained high. The COVID-19 lockdown provided a natural experiment demonstrating the strength of this relationship: even when shops were closed, many owners actively ensured access for swallows by modifying shutters or maintaining openings, allowing most nests to persist. These findings highlight cultural values as an unrecognized yet critical buffer supporting Barn Swallow breeding success in human-dominated Himalayan landscapes.

However, the findings of the chapter also underscore emerging vulnerabilities. Rapid urbanisation, architectural modernisation, tourism pressure, and changing hygiene norms threaten the availability of traditional nest sites and may erode long-standing cultural tolerance. While positive perceptions remain deeply rooted across much of the Himalaya, early signs of shifting attitudes mirror trends already documented in parts of East Asia, where modernization has led to nest exclusion. Given the Barn Swallow's near-total dependence on human structures, the persistence of culturally mediated coexistence may be as important as ecological factors for its future in the region. This chapter therefore emphasizes that conserving Barn Swallows in the Himalaya requires not only habitat and insect prey management, but also the recognition, preservation, and integration of traditional cultural values into conservation and development planning.

Overall, my thesis provides the first integrated ecological, evolutionary, and socio-cultural assessment of Barn Swallows in the Indian Himalayan region, revealing the Himalaya as a key axis of divergence, connectivity, and human–wildlife coexistence within the species' Asian range. By combining citizen-science–derived migration analyses, extensive field-based breeding ecology, detailed dietary and reproductive assessments, phylogeographic and morphometric analyses, and cultural perspectives, the study demonstrates that Himalayan Barn Swallow populations are shaped jointly by climatic gradients, historical biogeography, selective pressures linked to migration and reproduction, and an unusually strong dependence on human tolerance. The identification of a distinct Himalayan genetic lineage, the reporting of a resident breeding population in Manipur, evidence for climate-linked phenological shifts, and the documentation of culturally mediated nest persistence together underscore the species' capacity for rapid ecological and behavioural adaptation, but also its vulnerability to accelerating environmental change. Collectively, these findings establish a critical baseline for monitoring population trajectories in India, challenge simplified subspecies boundaries in Asia, and highlight that effective conservation of this declining aerial insectivore in the Himalaya will require integrative approaches that link evolutionary history, migration ecology, insect prey documentation, urban architecture-sensitive planning, and the preservation of traditional human values that have long enabled coexistence of Barn Swallows with humans in this complex mountain landscape of the Himalaya.

Chapter 1
Introduction

1.1 Introduction

*"If the land mechanism as a whole is good, then every part is good, whether we understand it or not. If the biota in the course of aeons, has built something we like but do not understand, then who but a fool would discard seemingly useless parts? **To keep every cog and wheel is the first precaution of intelligent tinkering**."*

-Aldo Leopold, from The Round River, 1953

The ethos of conservation rightly put by Leopold (1953) "to keep every cog and wheel is the first precaution of intelligent tinkering" is to care for existence of the ecosystem as a whole. The global biodiversity is declining at an unprecedented pace (Butchart et al., 2010), still conservation programs largely focus on species facing the greatest risk of extinction – the rare species (Baillie et al., 2004; Gaston, 2010). Such a species-centric conservation approach, however, often neglects focus on common and widespread species (Baillie et al., 2004; Gaston & Fuller, 2008; Gaston, 2010), which comprises a large part of the ecosystem and therefore have a significant role in ecosystem functioning (Geider et al., 2001). This is particularly true when growing body of research highlights some common species to be equally or even more important (Gaston, 2010). Certainly, these arguments do not indicate the non-importance of rare species rather provide ample evidence to give priority and retain different kinds of Leopold's cogs and wheels to ensure the functioning of ecosystem.

The growing evidence highlights conservation concern for common and widespread species for three inter-linked reasons (Gaston & Fuller, 2008). Many species currently threatened or extinct were once common, large number of common species are undergoing serious declines, and third, the process causing these declines are going to alarmingly accelerate in the future. This is concerning as reported by (Rosenberg et al., 2019) the loss of nearly a third of all North American avifauna within just past five years. Similarly, most abundant European birds also appear to be declining (Gregory et al., 2005; Inger et al., 2015; Burns et al., 2021). The global insect decline found to be more evident in the most abundant species while the less abundant species remain stable (van Klink et al., 2020). In similar lines, a recent study by (Dupont & Dobson, 2025) demonstrate the relation between species decline and their abundance and carrying capacity, wherein less abundant species have increased while species nearing their carrying capacity to have declined.

The declines in widespread species posit more concern as they are also driven by anthropogenic activities that extend beyond classical extinction risk focused on rare taxa. The four major drivers of extinction given by Diamond (1984) - overexploitation, habitat loss and degradation, introduction of invasive species, extinction cascades have affected the numbers and distribution of previously known common species. Accelerated land conversion and climate change have significantly altered the natural ecosystems (Hansen et al., 2001; Foley et al., 2005; Jetz et al., 2007). Once common and now Critically Endangered the Yellow-breasted Bunting (*Emberiza aureola,* IUCN, 2017), Endangered - Grey Parrot (*Psittacus erithacus,* IUCN, 2021), and now Vulnerable European Turtle-dove (*Streptopelia turtur,* IUCN, 2019) are following the similar trends of decline (BirdLife International, 2026). In 1994, 75% of the world's 16 Old World vulture species were classified as Least Concern, however, today populations all across their global distributional range are declining due to anthropogenic reasons. Eleven of these 16 vulture species are now globally threatened and classified as Critically Endangered or Endangered, with steepest and rapid declines in Asia's vultures (BirdLife International, 2025).

One group of birds although common are notably affected by anthropogenic factors including agricultural intensification and changing farming practices (Conrad et al., 2006; Donald et al., 2006) are the aerial insectivores. These are a guild of birds that spend much of their time foraging on wings and feeding on aerial insects and include families such as the Hirundinidae (swallows), Apodidae (swifts), Tyrannidae (flycatchers) and Caprimulgidae (nightjars). The decline of North American Avifauna includes the decline of the species of aerial insectivores where ~73% of 26 species are exhibiting negative population trends (Rosenberg et al., 2019). The declines are evident in other parts of their distributional range (Smith et al., 2015; Sauer et al., 2017; Bowler et al., 2019). An alarming 59% decline in this guild is reported in Canada since 1970 (NABCI, 2019) resulting in inclusion of these species in Canada's Species at Risk Act (Nebel et al., 2020). This has led to increase in scientific research to identify the risks behind these losses particularly in regions where long-term monitoring has revealed the most dramatic population declines (Nebel et al., 2010; Rosenberg et al., 2019; Kardynal & Imlay, 2022).

These declines are unequal in resident and migratory aerial insectivores where long-distance migrants are severely affected (Nebel et al., 2010; Vickery et al., 2013; Spiller & Dettmers, 2019). One of the common and widespread aerial insectivores is the Barn Swallow (*Hirundo rustica*), a long-distant migrant experiencing significant declines across many parts of its range (Lee et al., 2011; Ambrosini et al., 2012; Vickery et al., 2013). Barn Swallow breeds throughout most of the northern hemisphere, and winters in the southern hemisphere (Møller & Gregersen, 1994; Turner, 2004) and is one of the most widely distributed and abundant swallows in the world. Owing to its habit of building open-cup mud nests on human artefacts, Barn Swallow shows close association with humans all across its breeding range (Turner, 2004). Originally, thought to have nested in caves and crevices but now, benefitting from expansion of human habitations (Zink et al., 2006), the species mainly nests in artificial structures, such as buildings, bridges, culverts and ditches (Møller & Gregersen, 1994). This widespread availability of breeding sites is believed to result in dramatic range and population expansion of Barn Swallow across Europe (Møller 1994), North America and Asia (Zink et al., 2006). Moreover, its broad ecological plasticity possibly allowed the Barn Swallows to exploit high mountain habitats (up to 3000m above sea level) to wetlands and deserts (Turner, 2006).

Considering the circum-global distribution and large population size, Barn Swallows are currently evaluated as Least Concern, though globally population trend is reported declining (BirdLife International, 2019). Recent reports of large-scale decline in population in parts of species range have been observed. Long-term monitoring in Canada has revealed more than 70% loss in population since 1980s, and similar declines are being observed in Europe with 19% decline between 1980 and 2023 (PECBMS, 2024). The reasons attributed to this decline include habitat modifications; changing land use practices, such as changes in agricultural practices, impact of dairy farming (Møller, 2001; Ambrosini et al., 2002) and changing climatic conditions and influence of global weather patterns (Both et al., 2006; Jetz et al., 2007; Balbontín et al., 2009; García-Pérez et al., 2014).

The sustained and widespread declines in Barn Swallow populations underscore the urgent need for ecological monitoring and identification of region-specific drivers, particularly in underrepresented regions such as Asia, where data are scarce. The population status in Asia is unknown, however, a study by Lee et al. (2011) based on model simulations suspect an alarming population decline of over 99% in recent decades in breeding sites in Korea. Despite concerning population declines, there is no detailed ecological study on the species from India, particularly in the Himalaya, which marks its southern breeding boundary in South Asia.

In Indian subcontinent, three out of six subspecies of Barn Swallow occur, where two subspecies, *H. r. rustica* and *H. r. gutturalis* breed high up in Himalaya and the third subspecies *H. r. tytleri* is a winter visitor in Northeast India (Ali & Ripley, 1987). Even though the national conservation programs of India such as the National Wildlife Action Plan which supports the idea of establishing baseline information on indicator species to understand impact of landscape level changes. India's climate change initiative, National Action Plan on Climate Change focuses on National Mission on Sustaining Himalayan Ecosystem (NMSHE) and the National Mission on Strategic Knowledge on Climate Change (NMSKCC), still a huge gap is prevalent in the ecology of such species. With respect to these missions, baseline data even on the now common species is crucial for understanding long-term effects of changing habitats and climate on the sensitive ecosystem such as the Himalaya.

The whole debate of conserving common species is because of their substantial role in functioning of ecosystems. Cascading effects on ecosystem services such as pollination, pest control, and nutrient cycling can result in even modest proportional declines in common species (Gaston & Fuller, 2008). Species commonness and ecosystem service provisioning are so interlinked that this is demonstrated across wide range of ecological systems including plants, insects, and birds (Gaston & Fuller, 2008; Winfree et al., 2015; Lemanski et al., 2022; Genung et al., 2023). The declining population paradigm, a foundational idea in conservation biology by Caughley (1994) press upon the need of effective conservation is to first understand the causes of population declines. This thesis was worked on the idea that understanding the common species such as the Barn Swallow, documenting its current distribution, ecology and populations across the Himalaya is a prerequisite to first fill the critical gap in species global ecology, and second build a baseline on an ecologically sensitive species in the region for any future research work.

1.2 Justification of the study

The breeding population of the Barn Swallow in the Himalayan region has not previously been studied, making this doctoral research the first comprehensive ecological investigation of the species in this landscape. Given the documented alarming declines across regions, population trends of Barn Swallows in India remain largely unknown. The Himalayan region is undergoing rapid anthropogenic change, including shifts in land-use practices such as agricultural intensification, mechanisation, and increased pesticide application. Concurrently, large-scale human out-migration from mountainous areas has led to the abandonment of traditional agricultural lands, resulting in the conversion of cultivated fields into fallow land. These changes may substantially alter the availability of aerial invertebrates, the primary prey of Barn Swallows, with potential consequences for breeding success and population viability.

In addition, the species' long-distance migratory behaviour renders it particularly vulnerable to climate change, including altered weather patterns and phenological mismatches between migration timing and prey availability. While this thesis focuses primarily on the breeding ecology of the species, understanding conditions at non-breeding grounds - many of which are also experiencing rapid anthropogenic transformation - remains equally important for comprehensive conservation assessments.

An additional and particularly intriguing aspect of Barn Swallow ecology is its close association with humans, especially its tendency to nest in and around human habitations. The species is believed to have originated in Africa before radiating into other parts of the world, giving rise to multiple geographically structured populations. However, the timing and pathways through which Barn Swallows colonised the Indian Himalayan region remain unknown. Given the relatively recent geological history of the Himalaya, it is plausible that the species established its breeding populations in this mountainous landscape comparatively recently. Accordingly, this study also aims to elucidate patterns of colonisation and evolutionary diversification of Barn Swallows in the Himalayan region, thereby contributing to a broader understanding of the species' historical biogeography and population differentiation within this part of its range.

To address these knowledge gaps holistically, this thesis is structured into three major components. First, the only large-scale dataset currently available for Barn Swallows in India - citizen-science observations from the eBird platform is utilised to examine the species' breeding and non-breeding distribution across the Indian subcontinent. Using a multi-scale spatial and temporal approach, seasonal patterns are analysed, including the timing of spring and autumn migration and broader patterns of seasonality over a seven-year period (Objective 1; Chapter 3).

Second, intensive field-based studies are conducted at selected breeding sites within the Uttarakhand Himalayan region to investigate breeding ecology, with a focus on nest-site selection, nesting periodicity, reproductive parameters, and breeding success (Objective 2; Chapter 4). In parallel, prey composition is examined and the availability of insect prey is assessed in relation to local land-use practices, enabling an evaluation of how environmental modification influences foraging ecology and reproductive outcomes.

Third, breeding populations are surveyed across the Himalayan range and individuals are sampled from multiple locations to assess morphological and genetic variation. By analysing two mitochondrial genes, Himalayan breeding populations are placed within the global phylogenetic framework of the species, and population-level differentiation and subspecies affiliation are evaluated (Objective 3; Chapter 5).

Finally, the thesis is concluded by synthesising ecological and evolutionary findings, while also highlighting the strong cultural relationship between Barn Swallows and the people of the Himalaya. During field surveys, a close and enduring association between local communities and the species was observed. Consequently, nature–culture linkages are explored in the final chapter (Chapter 6), examining how traditional beliefs and human perceptions may facilitate coexistence and contribute to the conservation of Barn Swallows in India.

1.3 Objectives

1. To investigate the role of global weather patterns on the distribution and seasonal movements of Barn Swallows
2. To investigate the breeding ecology of Barn Swallow population in Indian Himalayan region
3. To determine the evolutionary history of Barn Swallow populations in the Himalaya, and explore for morphological differentiation and genetic variation between populations

1.4 Research Questions

Research question 1a: What is the seasonal distribution with respect to breeding, migration and wintering ranges of Barn Swallows across the Indian subcontinent?
Research question 2a: Do weather patterns influence the seasonal movements of Barn Swallows?

Research question 2a: Is nesting success influenced by nesting site characteristics and associated land-use practices?

Research question 2b: Does prey species composition in the diet influence nesting success across different breeding sites?

Research question 3a: How old is the Barn Swallow lineage breeding in the Himalaya and how many sub-populations occur in the region?

Research question 3b: How the subspecies are separated geographically and is there any hybrid zone formation in their breeding range in the Himalaya?

1.4 Study Area

The first objective of the study is centred on understanding the spatial and temporal distribution of Barn Swallows across the Indian subcontinent using eBird data and therefore encompasses the entire subcontinent. For nesting ecology, surveys to delineate the breeding distribution were conducted across the Indian Himalayan region, with particular emphasis on the Uttarakhand Himalayan region for detailed nest-ecology investigations. Finally, sampling to assess population-level variation was carried out at selected sites across the Himalayan states of Kashmir, Uttarakhand, North Bengal, and the northeastern Indian state of Manipur (Fig 1.1).

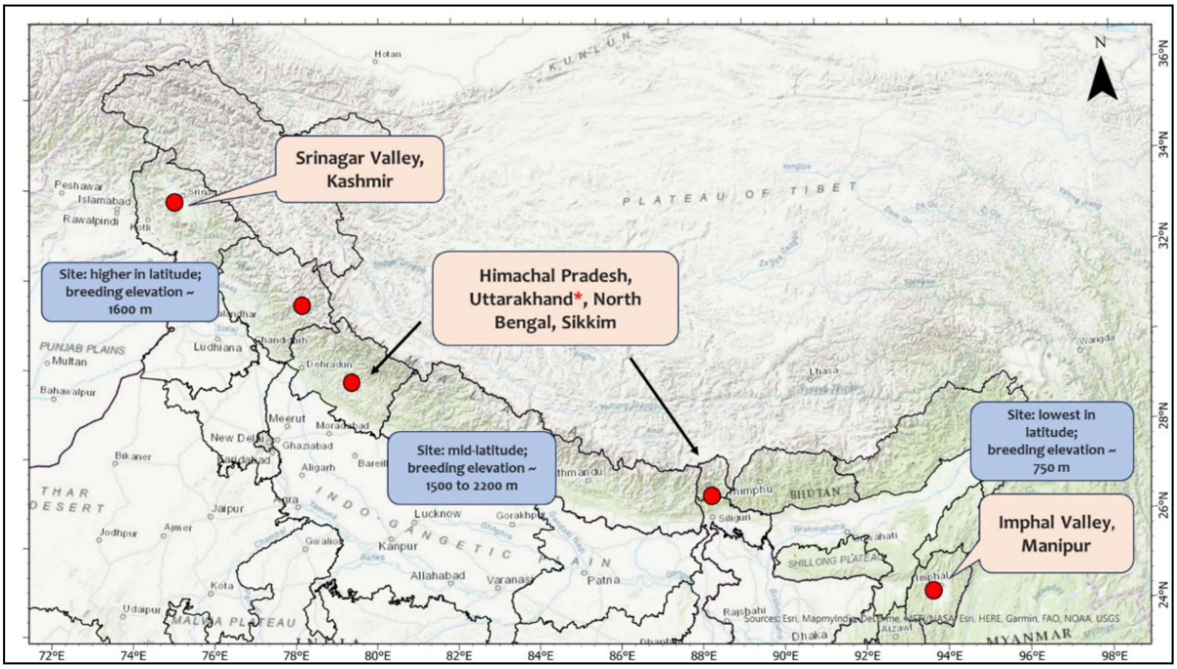

Fig 1.1 Map of study locations across the Himalayan region. Systematic surveys were conducted in Jammu and Kashmir, Himachal Pradesh, Uttarakhand, North Bengal, Sikkim, and Manipur to document the breeding distribution of Barn Swallows. Detailed nest-ecology studies were undertaken at selected sites in Uttarakhand, while sampling for morphological and genetic variation was carried out in Kashmir, Uttarakhand, North Bengal, and Manipur.

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Chapter 2
Literature Review

2.1 Common Species in a Changing World – Aerial Insectivores

Common and widespread species are of significant conservation concern for three linked reasons. First, a number of species that are presently highly threatened or have recently become extinct could previously have been described as common and widespread. Second, there is growing evidence that large numbers of presently still common and widespread species are undergoing massive declines, with major ramifications for ecosystem functions and services, and potentially for many other species. Third, the processes that underlie these declines seem likely to intensify in many regions in the future (Gaston & Fuller, 2008). Studies have reported on the importance and studying common species (Lindenmayer et al., 2011) as they play important roles in ecosystems (Dickman & Steeves, 2004; Gregory et al., 2005; Sekercioglu, 2006; Gaston, 2010) and comprise the dominant structure and overall biomass in ecosystems (Gaston & Fuller, 2008; Gaston, 2010) contributing significantly to spatial and temporal species richness patterns (Vázquez & Gaston, 2004).

Owing to their widespread distribution, common species particularly birds stand out as a good subject to study the impacts of changing environment and habitats. Projects such as the Pan-European Common Bird Monitoring Scheme (PECBMS) commenced in 2002 focuses on monitoring common birds as indicators of general health of the ecosystems. The PECBMS regularly reports the status of commonly occurring birds across Europe using large-scale and long-term monitoring data on changes in the breeding populations. The latest report highlighted an alarming decline of 60% in the breeding population of common farmland birds (PECBMS, 2025, *Fig 2.1*). A recent study by (Rosenberg et al., 2019) documented a dramatic net loss of approximately 2.9 billion breeding birds (29% decline) in North America bird populations since 1970s. Astonishingly, this loss disproportionately affected common and widespread species, with 90% of the decline concentrated among just 12 bird families, including swallows, sparrows, finches, and warblers.

Similar to this, aerial insectivores, birds that forage on insects in flight are one of the steeply declining bird groups across the globe (Smith et al., 2015; Sauer et al., 2017; Bowler et al., 2019; NABCI, 2019; Rosenberg et al., 2019; Kardynal & Imlay, 2022). The guild includes members of Hirundinidae (swallows), Apodidae (swifts), Tyrannnidae (flycatchers), and Caprimulgidae (nightjars) families. Rosenberg et al., (2019) documented cumulative decline of 160 million individuals, representing a decline of over 30% in aerial insectivore populations in North America since 1970 (*Fig 2.2*). Globally, the declines are thought to be a result of climate and land-use changes (García-Pérez et al., 2014; Weegman et al., 2017; Cox et al., 2020), agricultural intensification, pesticide use (Rioux Paquette et al., 2014; Stanton et al., 2017; Imlay & Leonard, 2019), and the loss of breeding and non-breeding habitats (Spiller & Dettmers, 2019). Among these, the global decline in insect populations (Narango et al., 2021; Sánchez-Bayo & Wyckhuys, 2021; Wagner et al., 2021) is increasingly recognized as a primary driver.

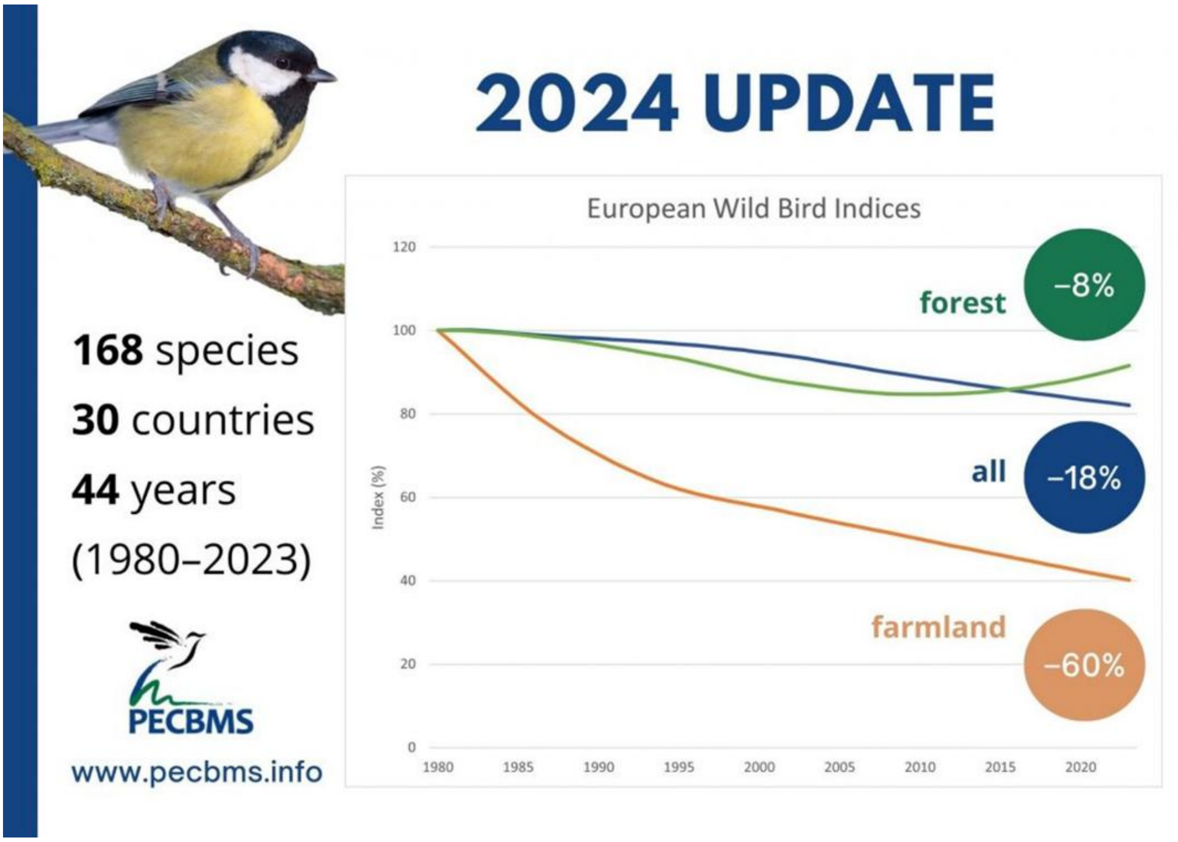

Fig 2.1 The Pan-European Common Bird Monitoring Scheme (PECBMS) analyses of European common bird indicators from 1980–2023. As per PECBMS indicators for assessing changes in commonly occurring wild bird populations, all bird Index (168 species; in blue line) has declined by 18%; while Forest Bird Index (34 species; in green line) has declined by 8%; and Farmland Bird Index (39 species; in red line) has undergone severe decline of 60%.

The decline is more profound in species that are migratory in nature. In North America long-distance migratory aerial insectivores have reportedly undergone steeper declines than the short-distance migrants (Nebel et al., 2010; Vickery et al., 2013; Spiller & Dettmers, 2019).

Barn Swallow is one such long-distance migratory and a widely distributed species that have experienced significant population declines across most parts of its distribution (Lee et al., 2011; Ambrosini et al., 2012; Vickery et al., 2013). In Canada, populations have declined by more than 70% decline since 1980, and similar trends have been observed in Europe, where Barn Swallows have undergone 26% decline since 1980 (PECBMS, 2024). Owing to these declines, Barn Swallows have been listed in Canada's Species at Risk Act (Nebel et al., 2020). Although data from Asia are limited, similar severity in declines in Barn Swallows have been reported from across breeding sites in Korea over the past five decades (Lee et al., 2011). While the extent and causes of decline vary by region (Shutler et al., 2012; Smith et al., 2015; Michel et al., 2016), the global drivers remain poorly understood and are often regionally scattered (Zhao et al., 2022).

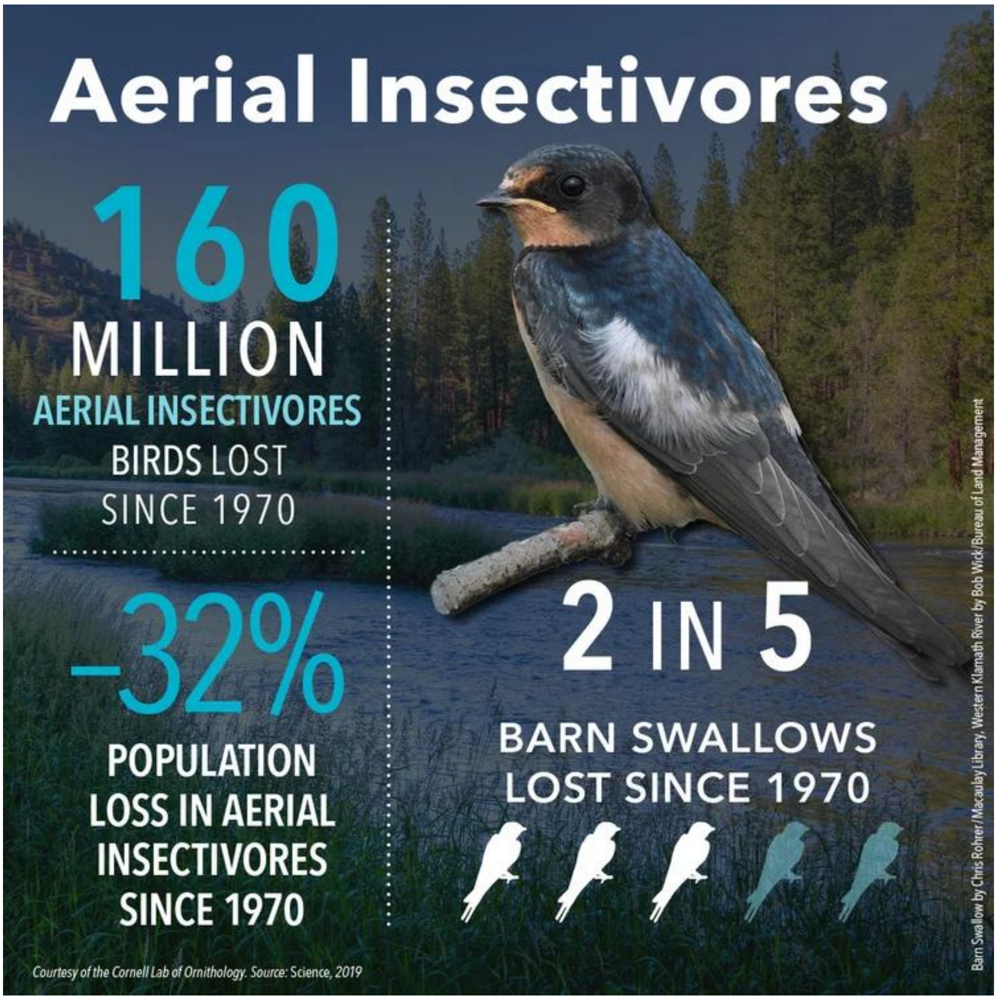

Fig 2.2 Alarming loss of Aerial Insectivores in North America since 1970 as reported by Rosenberg et al. (2019), image courtesy- Cornell Lab of Ornithology. Source: Science, 2019.

2.2 Barn Swallow – Origin and Phylogeography

The Barn Swallow is a member of the most species-rich genus *Hirundo*, in the swallow family Hirundinidae, comprising 14 described species (Turner 2004). At the species level, reconstructions based on mitochondrial DNA (mtDNA) and nuclear sequences (Sheldon & Winkler, 1993; Sheldon et al., 2005) showed that the genus *Hirundo* is grouped within the ‘‘mud-nesting” swallows together with the crag martins (*Ptyonoprogne*), house martins (*Delichon*), cliff swallows (*Petrochelidon*) and red-rumped swallows (*Cecropis*).

Barn Swallow is the only member of *Hirundo* that has a broad Holarctic breeding distribution and a species that has been studied extensively through molecular and phylogenetic research. Studies show *H. rustica* to have an African origin which is supported by their close affinity to African congeners such as *H. aethiopica* and *H. angolensis* (Dor et al., 2010; Carter et al., 2020). It is estimated that around 493 kya, divergence from these relatives occurred and the ancestral lineage emerged during Pleistocence (between 280 and 300 kya), a period of major climatic oscillations that likely facilitated dispersal out of Africa (Lombardo et al., 2022; Teglhøj, 2020). Phylogeographic studies reveal the role of glacial-interglacial periods in shaping the subspecies divergence supporting the hypothesis that subspecies differentiated primarily because of range expansions and contractions in response to climatic shifts (Turner & Rose, 2010).

Studies carried out using mitochondrial DNA (mtDNA) confirm that Barn Swallow species complex is monophyletic and different subspecies forms two major phylogenetic clusters, possibly diverged ~100 kya and geographically correspond to Europe-Middle East clade and Asia-America clade (Zink et al., 2006; Dor et al., 2010; *Fig 2.3*). European and West Asian populations differentiated around the onset of the Holocene (~11 kya), coinciding with post-glacial warming and the stabilization of breeding habitats (Smith et al., 2018). In contrast, East and South Asian lineages colonized independently during the late Pleistocene, while the colonization of the Americas, a relatively recent event likely within the past 20–50 kya and possibly facilitated by both natural dispersal across Beringia and subsequent human-mediated processes (Hobson et al., 2015; Scordato et al., 2017; Lombardo et al., 2022). There was also a secondary dispersal event occurred about 7 kya from North America back into the Asia (Zink et al., 2006) suggested by the close phylogenetic relationship between Asian *tytleri* and American *erythrogaster.* Further, Dor et al. (2010) using mtDNA also suggest intermingling of nominate *rustica* (migratory) with the resident *transitiva* in Israel.

The dynamic demographic history of Barn Swallows reflects a series of founder effects, bottlenecks, and secondary expansions linked to past climate fluctuations. Studies carried out using mitogenomic data show distinct haplogroups corresponding to isolated refugia, while at the same time multiple studies also revealed repeated episodes of secondary contact particularly across Eurasia resulting into formation of subspecies and hybrid zones (Santure et al., 2010; Scandolara et al., 2014; Scordato and Safran, 2014; Lombardo et al., 2022; *Fig 2.4*). Nuclear genomic evidence further emphasizes species to have traits of high connectivity and adaptability that likely facilitated survival through repeated climatic oscillations (Safran et al., 2016; Liu et al., 2018).

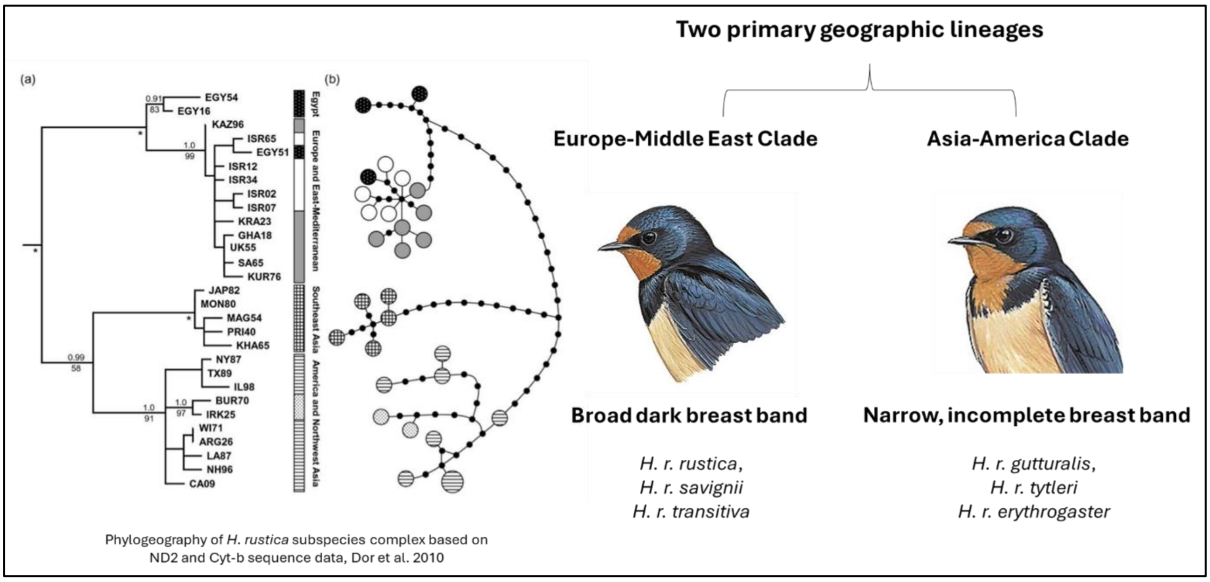

Fig 2.3 Phylogeography of monophyletic *Hirundo rustica* (Dor et al. 2010). *H. rustica* clusters into two primary geographic lineages Europe-Middle East clade and Asia-America clade (Zink et al. 2006; Dor et al. 2010).

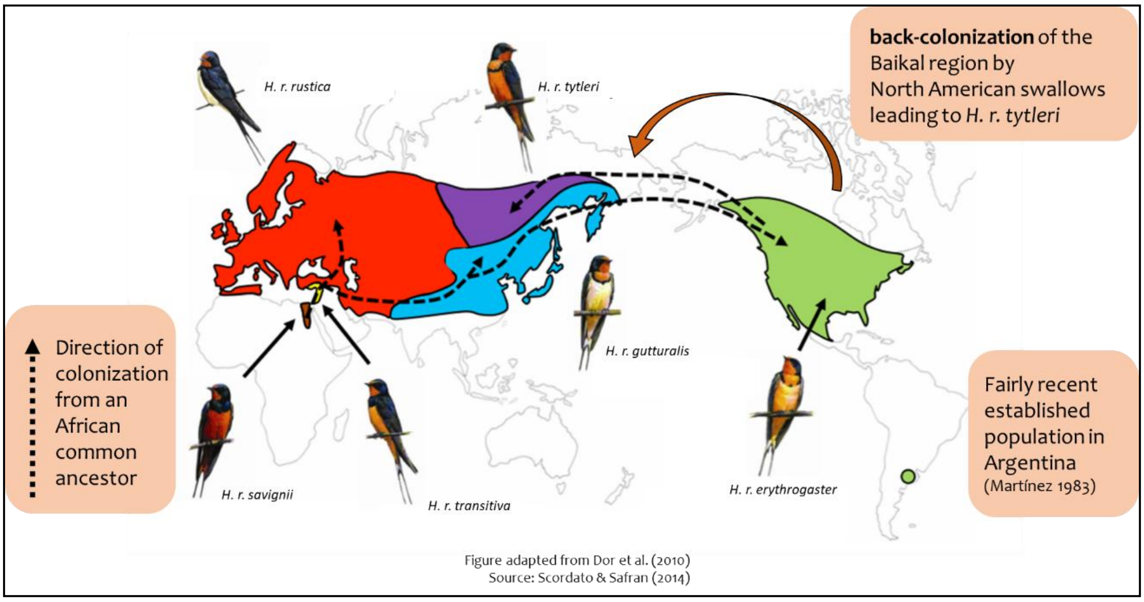

Fig 2.4 Barn Swallow subspecies complex, figure shows directions of colonization of different subspecies across the breeding range (figure adapted from Dor et al. 2010 and Scordato and Safran 2014).

2.3 Barn Swallow – Morphology and Population Differences

The Barn Swallow weighs about 20g and like many other aerial insectivorous birds, has small beak, wide gape, streamlined body shape, very long pointed wings, and a long-forked tail. Their characteristic plumage features include shining metallic blue-black dorsal body with chestnut forehead, chin and throat patch, a distinctive dark blue breast-band and elongated outermost tail feathers which form a distinct V-shape (Møller & Gregersen, 1994; Turner, 2004). While ventral coloration varies from buff-white to red-buff, and usually females are paler than males and have shorter tail streamers and smaller tail spots (on inner rectrices) (Møller & Gregersen, 1994).

Morphologically, the subspecies (*described in section 2.2*) vary in certain traits such as body size, ventral coloration, extent of breast band, and tail streamer length, and in life-history traits such as migration patterns (Turner & Rose, 1989; Turner, 2004, 2006; Winkler, 2006; Winkler et al., 2017; Seifert et al., 2018; Turbek et al., 2022; Anisimova et al., 2025). The largest of all is the European *rustica* with white to pale buff ventral coloration and moderately broad and complete breast band while Asian subspecies *gutturalis* is small and buff-bellied with narrower, often broken breast band. Siberian *tytleri* is intermediate in body size and has dark brown ventral colour with narrow and complete breast band (Scordato & Safran, 2014; *Fig 2.4*). American *erythrogaster* is similar to *gutturalis* with extensively rufous throat, broken breast band diffused with rufous throat, underparts rufous chestnut to orange. Two sedentary subspecies Egyptian *savignii* is smaller and has rufous-chestnut underparts while Middle Eastern subspecies *transitiva* is similar to *rustica* but has broader breast band and much darker rufous-buff vent (Dor et al., 2010).

2.4 The Barn Swallow – Global Distribution and Migration Pattern

Barn Swallow, a human-commensal is well known among the local people across its distribution range owing to its nature of building its cup-shaped mud nest in human-inhabited areas. Consequently, it is the most widespread and abundant swallow species in the world, breeding in Eurasia and North America and migrating long-distances to winter in south to tropical Africa, northern Australia, Central and South America. Globally, six subspecies have been recognized of which four are strict migrants and two are residents (Turner & Rose, 1989; Dor et al., 2010; Brown & Brown, 2020).

Recent advances in tracking technology, particularly the use of light-level geolocators, have significantly expanded knowledge of Barn Swallow migration across its global range (Winkler et al., 2017; Seifert et al., 2018; Turbek et al., 2022; Tian et al., 2024; Anisimova et al., 2025). The nominate subspecies *H. r. rustica*, breeding across Europe, North Africa, and western Russia, typically winters in the Mediterranean basin and sub-Saharan Africa, with some Eurasian populations also moving into South Asia (Seifert et al., 2018; Turbek et al., 2022). In contrast, populations of *H. r. gutturalis* breeds in far eastern Russia, China, Korea, and Japan and likely passes across the Qinghai–Tibetan Plateau to reach wintering grounds in Southeast Asia (Heim et al. 2020; Tian et al. 2024), while *H. r. tytleri*, breeding in Siberia and Mongolia, appears to follow a more direct north – south route into mainland Southeast Asia (Anisimova et al., 2025). The new world subspecies, *H. r. erythrogaster*, breeds throughout North America and overwinters in Central and South America. A breeding population has also recently established itself in Argentina (Martínez, 1983). *H. r. savignii* in Egypt is largely sedentary while *H. r. transitiva* in the Middle East exhibits short-distance migration (Dor et al., 2010).

Interestingly, some populations exhibit diverse migratory strategies, particularly where the populations form hybrid zones. Birds from the *rustica – gutturalis* hybrid zone in western China migrate either westward to Africa or south across the Tibetan Plateau into India (Turbek et al., 2022), and populations breeding in Amur contact zone winter in Southeast Asia (Heim et al., 2020). However, still important uncertainties remain, particularly in Asia where subspecies and hybrid populations exhibit diverse and poorly resolved migratory strategies. For instance, migration of Siberian *H. r. tytleri* is poorly known, with only one geolocator-tracked individual suggesting a direct route into Southeast Asia (Anisimova et al., 2025). These contrasting patterns highlight significant knowledge gaps in the migratory connectivity of Asian Barn Swallow populations, particularly those moving into or wintering within the Indian subcontinent.

2.5 Barn Swallow – Breeding and Nesting Ecology

Historically, prior to human settlements, Barn Swallows nested in natural features like caves, holes, crevices, and cliff ledges (Speich et al., 1986; Turner, 2006; Campbell et al., 2007). It is speculated that Barn Swallows began to build their nests in human-made structures by 1800s in North America (Brown & Brown, 2020). Møller & Gregersen (1994) describes similar patterns in Europe and Asia where Barn Swallows started to affix their nests to structures and bridges. In Baikal, Amur and Primor'e regions of eastern Russia, Barn Swallows were historically absent when native people lived mostly in subterranean structures and only with the arrival of people who built structures above-ground, Barn Swallows could potentially colonize the region (Smirensky & Mishchenko, 1981). With rapid expansion of human settlements leading to widespread availability of nest sites resulted in dramatic range expansion of Barn Swallows.

Nest-site selection is closely tied to landscape context and foraging opportunities. Barn Swallows typically select sites near open habitats (farmland, pastures) and water, and nest placement is influenced by substrate type, height and local disturbance (Møller & Gregersen, 1994; Turner, 2006). Adults show high site fidelity, frequently returning to the same breeding or nearby sites each year (Rowan, 1968; Moreau, 1972; Oatley, 2000), which has implications for local population persistence and for interpreting colony dynamics.

Breeding phenology follows a latitudinal gradient: birds arrive and begin breeding earlier in the south than in high latitudes, and timing varies across the species' range (Moreau, 1972; Turner, 2004).Typical reproductive parameters are well documented: mean clutch size ≈ 4–5 eggs laid over ~5 days, incubation ≈ 15 days, nestling period ≈ 21 days, with parents provisioning for a short period after fledging (Møller, 1991). A full brood cycle therefore requires roughly 45 days, and successive clutches are on average separated by ~47 days (Møller, 1991). Most populations produce one to two broods per season (occasionally three), with the frequency of second and third broods increasing toward lower latitudes; first broods are generally larger than later broods, while overall fledging success is often high (≈80–90%) in many studied populations (Moller, 1984; Cramp, 1988; Møller, 1989; Turner, 2004).

Barn Swallows specialise on aerial invertebrates (more than 80 insect families recorded), preferring large, fast-flying Diptera (e.g. Syrphidae, Tabanidae, Calliphoridae) during the breeding season; diet composition shifts seasonally with changes in prey availability. Because adults must frequently return to feed nestlings, prey abundance, prey type and distance from nest to foraging patches strongly influence parental provisioning rates and hence reproductive success (Bryant & Turner, 1982; Turner, 1982; Møller & Gregersen, 1994).

Outside the breeding season and during migration, Barn Swallows commonly form large communal roosts—often in reedbeds or tall grasses near water—whose size fluctuates with habitat and climatic conditions (van den Brink et al., 1997; Bijlsma & van den Brink, 2005; Turner, 2006). Migration timing and speed interact with breeding schedules: autumn (southward) migrations can be protracted (up to several months) whereas spring (northward) migrations are generally faster, which is thought to confer fitness advantages through earlier arrival at breeding grounds (Mead, 1970; Cramp, 1988; Huin & Sparks, 1998; Kokko, 1999).

First-year birds are immature in their first breeding season and attain adult status in year two (Møller & Gregersen, 1994). Most adults complete a full moult at the non-breeding grounds (Broekhuysen & Brown, 1963), although regional variation exists: juveniles often replace body feathers earlier than adults (Jenni & Winkler, 2020) some southern populations suspend or partially conduct moult during migration (Pilastro et al., 1998), and individuals from parts of southern Asia may begin primary moult on the breeding grounds (Moreau, 1972). Adults typically arrive earlier than juveniles at non-breeding sites and initiate moult sooner (Møller et al., 2011; Jenni & Winkler, 2020).

Because breeding success is tightly coupled to both nest-site availability and local prey resources, Barn Swallows are vulnerable to anthropogenic changes in land use and agricultural practice. Alterations in cropping patterns, loss of pasture/open foraging habitats, and pesticide-driven declines in insect prey can reduce provisioning rates and reproductive output; consequently, assessing nest-site characteristics alongside measures of foraging habitat and distance to feeding grounds is essential for understanding breeding outcomes (Møller & Gregersen, 1994).

2.6 Barn Swallow in a Changing World

Changing land-use practices and its influence on Barn Swallow populations

Land-use changes particularly agricultural intensification and loss of foraging habitat have primarily been identified as cause behind regional declines in Barn Swallow populations (Nebel et al., 2010; COSEWIC, 2011; Spiller & Dettmers, 2019). Several studies mainly conducted in Europe, have shown a strong link between maintaining farming activities with domestic animals (especially cattle) in the landscape and occurrence of large colonies of Barn Swallows (Møller, 2001; Ambrosini et al., 2002; Evans et al., 2007). Dramatic declines in the number of dairy farms in recent years have precipitated the decline in numbers in parts of the European range where local abundance of breeding Barn Swallows decreased significantly, with decrease in insect abundance as well (Møller, 2001; Evans et al., 2007) In North America, replacement of traditional farm structures by modern buildings, resulting in lack of easy access to nesting habitat has been cited as a principal reason for declining Barn Swallow population (Campbell et al., 2007; COSEWIC, 2011).

Large scale changes in prey populations

Global decline in insect populations (e.g. Hallmann et al., 2017; Sánchez-Bayo & Wyckhuys, 2019; Wagner et al., 2021), is thought to be another key factor responsible for the decline in Barn Swallow populations across parts of its distributional range (Nebel et al., 2010). Changes in agricultural land-use practices, loss of pasturelands, large-scale use of pesticides are reported to be few reasons causing changes in insect abundance (Nebel et al., 2010). Recent studies have shown a direct link of intensive agriculture; pesticide use and landscape homogenization to reduced insect prey and poor nestling condition and provisioning rates in Barn Swallows and other aerial insectivores (Kusack et al., 2021; Møller et al., 2021; Garrett et al., 2022). Experimental and field studies also point to combined effects of contaminants and parasite loads on reproductive health in aerial insectivores (Sigouin et al., 2021). Together these results suggest that lowered prey availability and contamination, rather than a single cause, are central to observed reproductive declines.

Environment and life history traits-survival and dispersal

Largescale weather phenomena such as the North Atlantic Oscillation (NAO) and the *El Nino* Southern Oscillation Index (SOI) have different effects on environmental conditions in different parts of the world frequented during the annual cycle of migratory birds. Long-term population study on Barn Swallow from two populations from Europe, Denmark and Spain wintering in South Africa and North Africa respectively, (Cramp, 1988; Møller, 2003; Saino et al., 2004; Turner, 2006), revealed that that climate change affects different populations differently and hence cause divergent patterns of selection in different parts of the range of birds (Balbontín et al., 2009). Due to different trends of rainfall because of *El Nino* and *La Nina* affects in wintering grounds, fluctuations in arrival to the breeding grounds was observed (Balbontín et al., 2009). Additionally, survival of yearlings was found to be related with global weather phenomenon NAO and years with positive NAO positively affected the survival of yearlings while negative NAO had negative effects (Balbontín et al., 2009).

Climate change induced range shift

General predictions about the response of migratory birds to climate change envisage that migrants should respond to milder climatic conditions at northern latitudes by arriving to the breeding grounds earlier (Visser et al., 2009). Temperatures in Europe increased by 0.9°C during the last century (Jones & Moberg, 2003; Parry, 2007) and, Barn Swallows are reported to have advanced their arrival on the breeding grounds in 80% of the European long-term time series of arrival dates (Lehikoinen et al., 2004). Constraints on the onset of spring migration (Coppack & Both, 2002) explained this northward shift in wintering grounds, which brought Swallows toward areas where ecological conditions have found to be worsened (Ambrosini et al., 2011). The shift in the wintering grounds is reported to have potential implications for the observed declining Barn Swallow populations as well as other migrants (Møller, 1989; PECBMS, 2024).

2.7 References

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Chapter 3
Seasonal Distribution and Migration Behaviour of Barn Swallows (*Hirundo rustica)* in the Indian Subcontinent

3.1 Introduction

Animal migration is a spectacular phenomenon closely linked with seasonal abundance of resources regulated by climatic cycles and photoperiodicity (Alerstam et al., 2003; Winger et al., 2018; Newton, 2023). With increasing shifts in climate the migration phenology particularly in birds is disrupting, altering not only the migration timing but also routes and speeds (Supp et al., 2015; Prytula et al., 2023). Further, mismatch in arrival timing and peak resource abundance at breeding sites can negatively impact reproductive output (Cresswell & Mccleery, 2003; Holmes, 2007), particularly in the case of long-distance migrants (Knudsen et al., 2011; Fraser et al., 2013; Lehikoinen et al., 2019). Such phenological mismatches disrupt ecosystem functions, triggering cascading ecological consequences. Coupled with climate-driven migration shifts, anthropogenic pressures such as land-use change, habitat alteration, etc., pose additional threats to migratory birds(Sherry & Holmes, 1996; Faaborg et al., 2010).

Migratory birds are faced with varying ecological conditions at breeding and non-breeding grounds and also habitats along their migration routes (Holmes, 2007; Newton, 2023). As conditions across these habitats play critical role in essential life-history stages such as moulting and preparation for long migratory flights (Bairlein, 2003; Newton, 2023). Growing evidence indicates that conditions at non-breeding grounds strongly determine the long-term survival of migratory species (Sherry & Holmes, 1996; Marra, 1998; Faaborg et al., 2010; Newton, 2023). Apart from these two destinations, stopover sites represent another crucial phase in the lifecycle of migratory birds and plays a critical role in determining the success of overall migration (Alerstam, 2011; Duijns et al., 2017; Gómez et al., 2017; Newton, 2024). Therefore, identification of critical migratory routes, breeding and non-breeding sites and stopover habitats (Stutchbury et al., 2009; Bächler et al., 2010; Briedis et al., 2018; Areta et al., 2021; López-Calderón et al., 2021), migratory strategies are critical for the conservation of species (Bradley et al., 2014) for predicting demographic consequences of habitat loss and climate change.

Traditionally, migration is studied by capturing birds at various sites along their migratory routes and marking individuals using uniquely coded bands. This approach relies on subsequent recaptures of ringed individuals across multiple years and across their range and is therefore limited by sample sizes and variation in recovery effort (Thorup & Conn, 2009). With the arrival of advanced tracking technologies, the field of migration ecology has been revolutionized. Tracking devices such as satellite and GPS transmitters provide high-resolution data on migration timing, routes, critical habitats and even flight behaviour (Bridge et al., 2013; Kays et al., 2015). Even recently, the limitation of such devices being large and heavy due to batteries for recording and transmitting data for tracking small passerines (<20g) has been resolved using light-level geolocators. This rapid miniaturization of tracking devices has led to the scientists to passively track small birds which was not possible before (Stutchbury et al., 2009; Bächler et al., 2010; Bradley et al., 2014; Arizaga et al., 2015; Blackburn et al., 2019; Areta et al., 2021; López-Calderón et al., 2021; Wong et al., 2022; Adamík et al., 2023). However, traditional banding as well as advanced tracking methods have logistical and financial limitations and without enough sample size is difficult to yield any meaningful population-level data (Hofman et al., 2019).

In this scenario, one powerful tool which has enabled the scientists from across the globe to study migration is the citizen science database, eBird developed by Cornell Lab of Ornithology. Observers from all around the globe upload their species checklists on the platform and freely accessible, eBird data therefore helps document and detect changes in species distributions and track species migration patterns across multiple years and over a large spatial scale (Heim et al., 2020; Prytula et al., 2023). Using eBird also enables accessing data from regions that are logistically challenging or otherwise under-studied (Dickinson et al., 2010). This makes eBird particularly valuable in parts of the world where long-term species monitoring programs are limited and access to ecological data remains constrained.

In this study, citizen science data on eBird was utilized to investigate the occurrence and seasonal movements of the Barn Swallow in the Indian Subcontinent. A commonly occurring species throughout the globe, Barn Swallows have undergone marked population declines across its breeding range in Canada, North America and parts of Europe (Ambrosini et al., 2012; Vickery et al., 2013; PECBMS, 2024). A long-term study on breeding populations in Northern Italy revealed decline at the rate of about 7% per year since 1999 (Ambrosini et al., 2012; Sicurella et al., 2015). However, of this only 5% is accounted by the habitat conditions at the breeding sites (Sicurella et al., 2015), indicating that populations are affected by conditions outside the breeding areas implying the importance of identification of non-breeding as well as stopover sites (Liechti et al., 2015).

While global population trends are concerning, however, still, no ecological research or population status of the species is known from the Indian region where the species is a summer breeding visitor in the mid-Himalayan region (~1000-2000 m). The species breeds from

Baluchistan Pakistan, Kashmir, Himachal, Uttarakhand, Nepal, till Sikkim towards east (Ali & Ripley, 1987). The findings of the third objective of this thesis indicated variations within Barn Swallow populations breeding across the Himalayan region wherein the western populations in Srinagar, Kashmir and Uttarakhand appeared to be closer to the European subspecies *rustica* morphologically and phylogenetically. Given this, it was expected that populations breeding across the Himalayan region, i.e., of Kashmir, Uttarakhand and North Bengal would show variations in their migration route and wintering grounds. Given the absence of baseline data from the region, eBird data was utilized to determine the distribution and migration pattern of Barn Swallows across the Indian Subcontinent. One question was to also assess the role of weather patterns on seasonal movements of the swallows, however, within the time frame this question could not be answered. With the available eBird records, migration routes and migration timings of Barn Swallows at a broad spatial and temporal scale was examined. Thereafter, their seasonal and annual movement patterns and migration speed during spring and autumn season was also tested for any variation.

3.2 Methodology

Species data

From the publicly available community database eBird (available online, www.ebird.org, eBird 2024), checklists of Barn Swallow observations from 2010 to 2023 were extracted. However, due to relatively low data from 2010 to 2018, checklists from 2019 to 2023 were only included for trend analysis (*Fig 3.1, Fig 3.2)*, for comparison across five years. Following eBird best practice criteria, 'complete' checklists which includes all observed bird species were used which accounted for locations where species were not present, that is to "zero-fill" data. Checklists that were submitted under the "traveling" and "stationary" sampling protocols, of duration between 0-5 hr, and distance travelled between 0-5 km (Strimas-Mackey et al., 2017) were considered for the analyses.

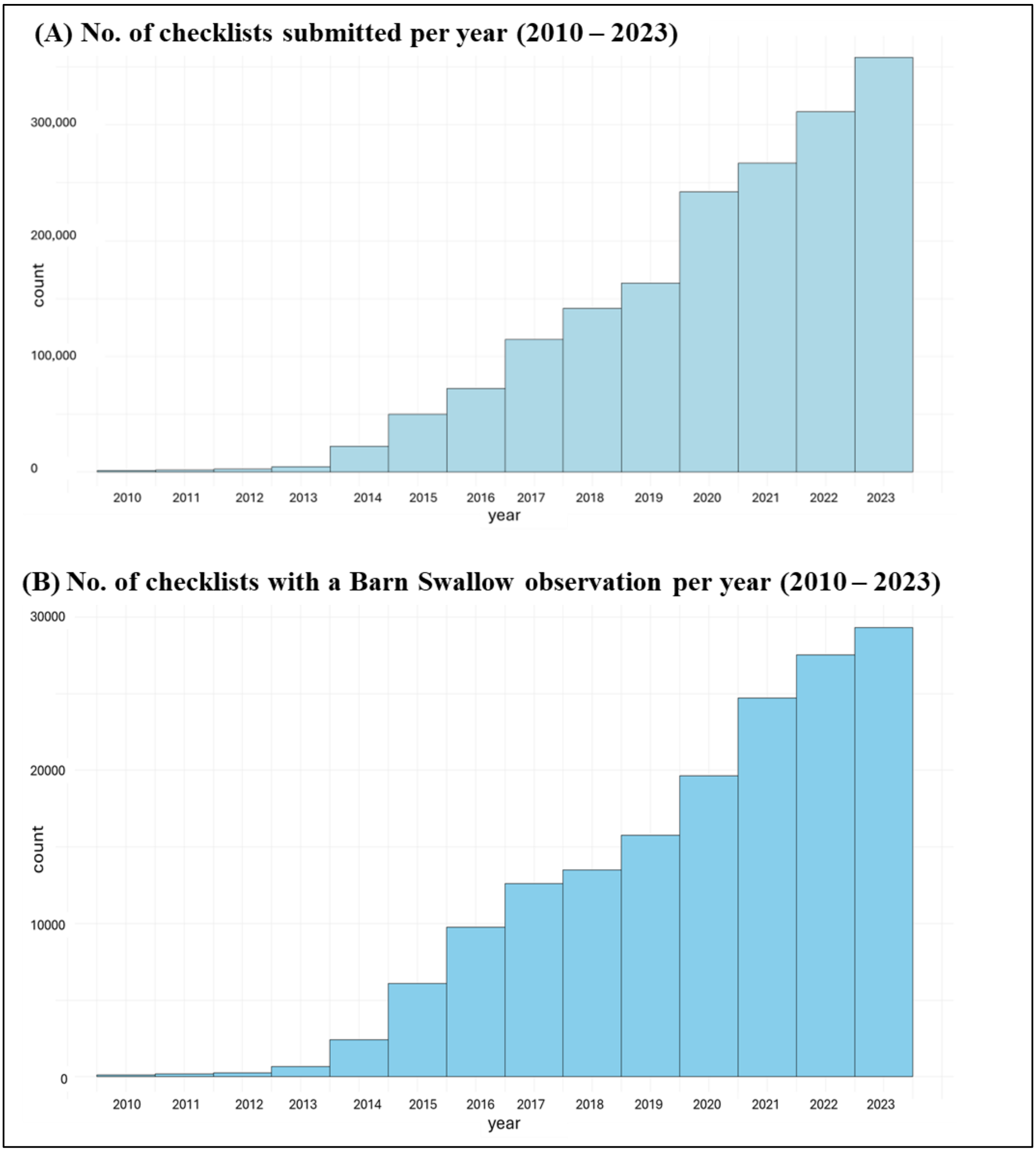

Fig 3.1 A) Count of checklists (complete) under "travelling" and "stationary" protocol submitted from 2010 to 2023 on eBird. B) Count of checklists with a Barn Swallow observation submitted from 2010 to 2023. To minimize the effect of extremely low counts before the year 2017, analyses was only undertaken from 2017 onwards.

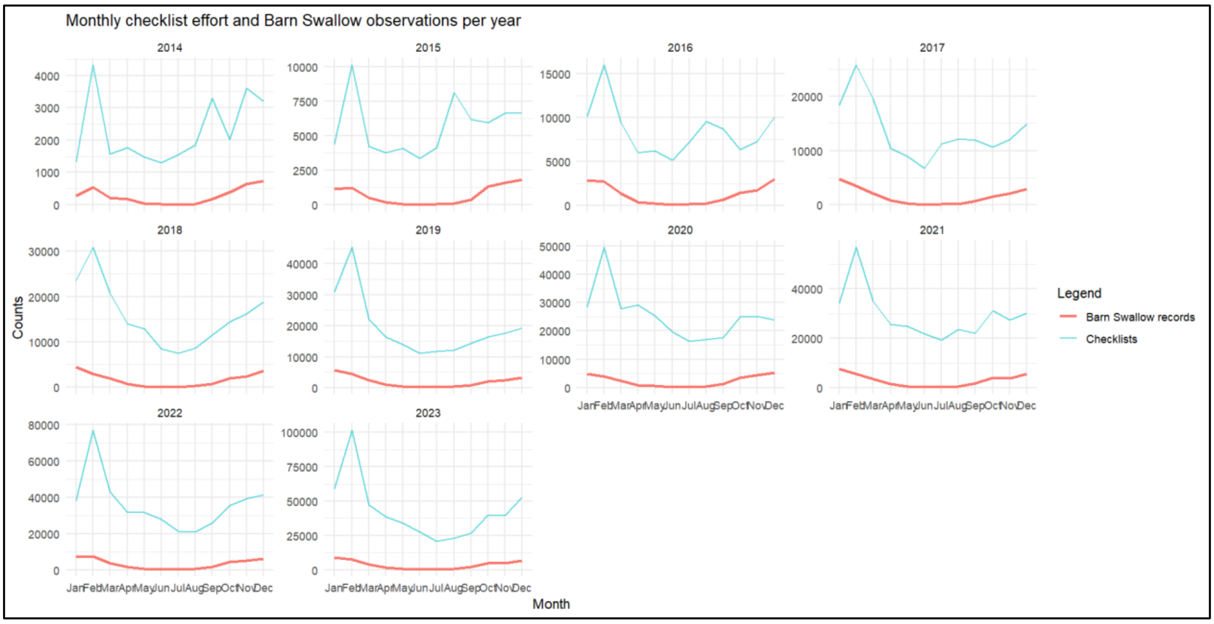

Fig 3.2 Summary plots of month-wise complete checklists (in blue) and checklists with a Barn Swallow observation (in red) on eBird (2014-2023).

Centroids for migration routes and timings

Following the methodology developed by Supp et al. (2015) and subsequently by Sonnleitner et al. (2022), Barn Swallows presence data was compiled from 2019 to 2023. The locations were then compiled for the Indian subcontinent region which was divided into equal-area icosahedron hex grids (25 km²) following the (SoIB, 2020), using the dggridR package (Barnes & Sahr, 2016). For each cell, daily Barn Swallow presence was calculated as the number of checklists with a Barn Swallow record divided by total number of checklists submitted for each date (*Fig 3.3*). The weighted daily mean location was then calculated using the central longitude and latitude of each cell. This acted as the proxy for total observer effect by accounting for spatial variation in the total number of checklists submitted per cell across time (Sullivan et al., 2014). Then a generalized additive model (GAM; package *mgcv*; Wood, 2017) was applied on the weighted mean daily locations for each year to model latitude and longitude separately as functions of time (Julian day). Combining the predicted latitude and longitude values from the fitted GAM, daily population-level centroids were generated (*Fig 3.3*), along with associated standard errors and 95% confidence intervals.

Migration timing

The onset and end of migration was based on the GAM-predicted occurrence centroid reaching a stable latitude (*Fig 3.4*). The minimum latitude was considered as species on its non-breeding grounds while the maximum latitude was considered the time of the species to be at the breeding grounds. Following Supp et al. (2015), the minimum and maximum latitude thresholds were used to determine the date of species leaving the stable latitude depicting start of the migration and reaching the stable latitude as the end of the migration. This was under the assumption that the period when species reached its maximum latitude or minimum latitude is when the entire population have established at breeding and non-breeding grounds, respectively and the migration has not yet started. Thereafter, based on 99% confidence interval of predicted daily locations a latitudinal threshold was established for each year and season. The minimum latitude of the upper confidence limit and the maximum latitude of the lower confidence limit was used to calculate the southern latitudinal thresholds as these dates are likely to include where migration was carried out. Specifically, the start of spring migration was considered to be within the period February to March 15 (ordinal date 32-74), the end of autumn migration to be within the period October to December 31 (274-365), the end of spring migration to be within the period March 16 to June 30 (75-181), and the start of autumn migration to be within the period August to September 30 (213-273).

Migration speed

The maximum population-level daily speed of migration for each year and season was calculated from the GAM-predicted occurrence centroid movements as the median kilometres per day over the five fastest days (km/day) following Supp et al. (2015). The median speed was considered to reduce the effect of potential outliers in the data. Between February 1– June 30 (ordinal dates 32–181) the fastest spring migration and between August 1–December 31 (213–365) the fastest fall migration dates was searched. To ensure the speeds at the start and end of migration were not excluded, date ranges extended into breeding and overwintering seasons.

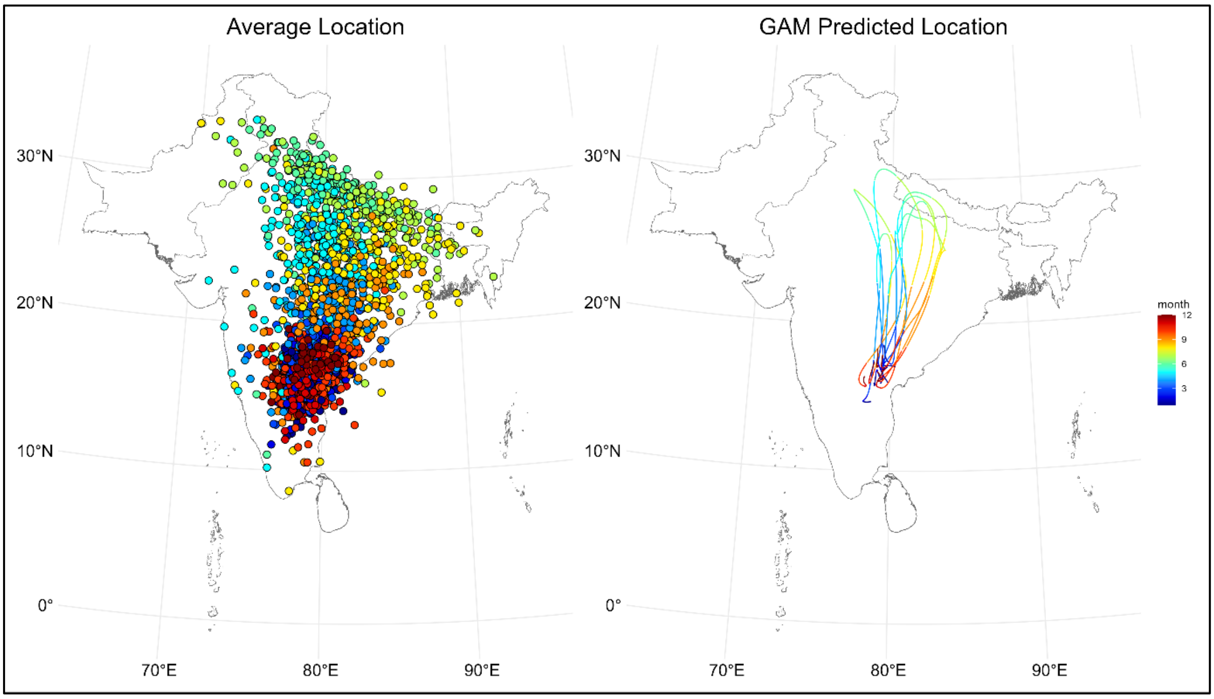

Fig 3.3 Mean location of Barn Swallow populations over five years (2019 to 2023) across the Indian subcontinent. Each point represents the daily mean weighted location of the population, coloured by month; lines represent generalized additive model (GAM) smoothed migration paths, one for each year, coloured by month.

Migration distance

Seasonal migration distances were calculated using the GAM-predicted population-level daily centroids. For each year, the great-circle distance (Vincenty ellipsoid method, package *geosphere*; Hijmans, 2019) between consecutive daily centroids was computed to estimate daily travel distance (km). Seasonal distance was then derived as the cumulative sum of daily distances across the spring and autumn migration periods, as determined by the onset and end dates of migration (*see Migration timing*). The mean and standard deviation of distances were computed for each year and season, providing measures of central tendency and annual variability.

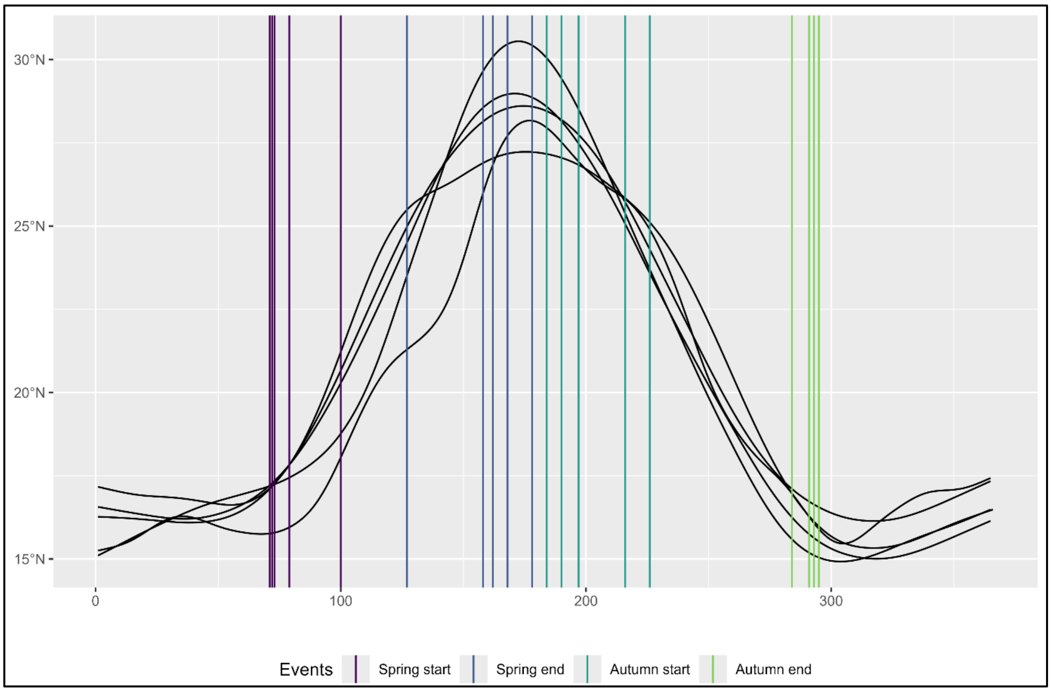

Fig 3.4 The latitude plot shows GAM smoothed predicted latitude (of the population centroid; black) overlaid with the calculated starts and ends of spring and fall migration.

Statistical analysis

To determine the magnitude of annual and seasonal variation the migration routes, timings and speeds across years was compared. Migration timing was assessed using the onset of spring migration, peak latitude, end of autumn migration, and population-level migration speed within and across years was compared using means and standard deviation and thereafter linear regression on the time series was used to understand directional trends in migration timing across years. Latitudinal extremes (maximum and minimum breeding and non-breeding latitudes) were used to identify annual geographic limits.

Migration speed was compared between spring and autumn using means and standard deviations, and differences between seasons were tested using a linear mixed model (LMM) with year as a random effect. Directional trends in migration timing and latitudinal shifts across years were evaluated using linear regression. To assess the relationship between migration timing and latitude, generalized additive models (GAM; package *mgcv*; Wood, 2017) were fitted with Julian date as a smooth predictor of seasonal median latitude (*Fig 3.3*).

To test for differences in migration distances between spring and autumn, we fitted a linear mixed-effects model (LMM; package *lme4*; Bates et al., 2015) with distance as the response variable, season as a fixed effect, and year as a random intercept to account for annual variation. This model was evaluated using Satterthwaite's method for denominator degrees of freedom (*lmerTest* package; Kuznetsova et al., 2017). All statistical analyses were conducted in R (v.4.0.2; R Core Team, 2024).

3.3 Results

Breeding and non-breeding distributions

Across five years of analysis, Barn Swallow seasonal movement records indicated the breeding locations in north of the Indian subcontinent while wintering locations in the deccan southern region (*Fig 3.5*). The 95% kernel density estimates indicated the Central Himalayan region to be the centre of the breeding ground for Barn Swallow populations (*Fig 3.6* A) and southeastern Indian region as wintering grounds (*Fig 3.6* B). The average breeding latitude of Barn Swallows was 28.18°N, with the highest breeding location at 30.55°N in 2021 and the southernmost at 25.20°N in 2020. Average non-breeding latitudes was found to be at 16.19°N (range:14.92°N to 18.67°N).

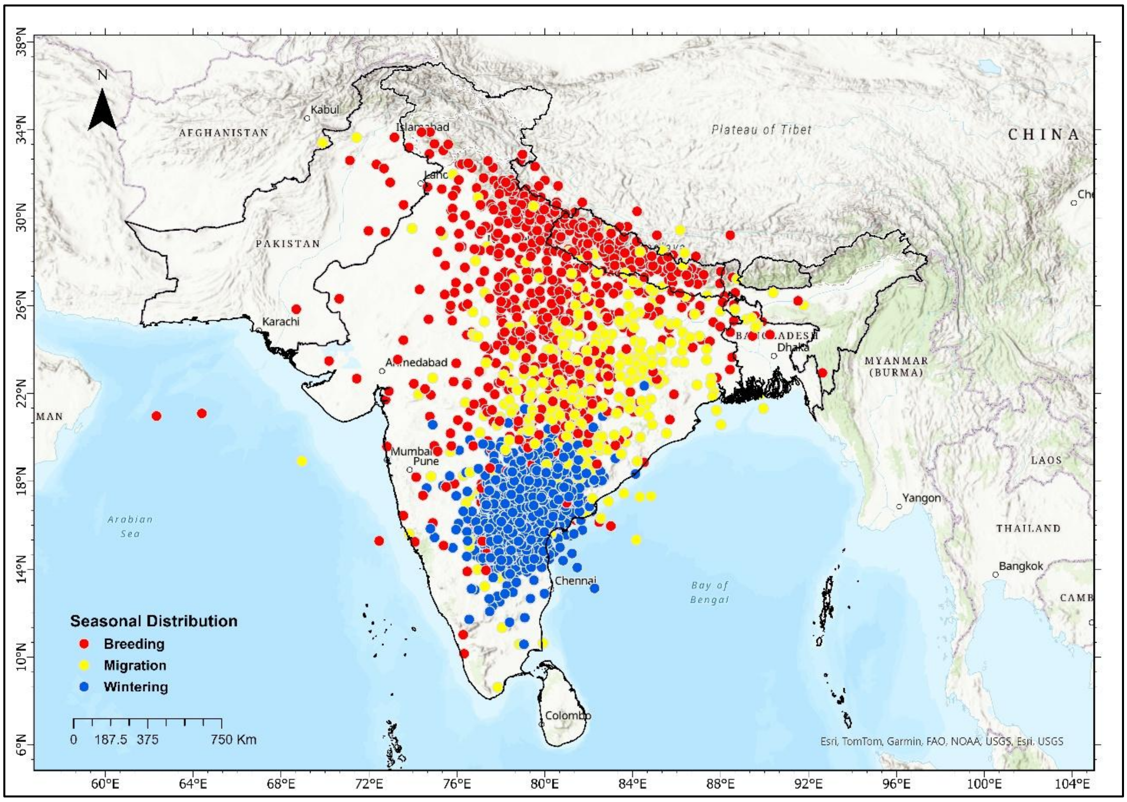

Fig 3.5 Barn Swallow seasonal distribution across years (2017-2023) calculated using GAM predicted daily weighted mean locations for the Indian subcontinent. The locations are coloured as per the seasons of breeding, wintering (non-breeding) and migration.

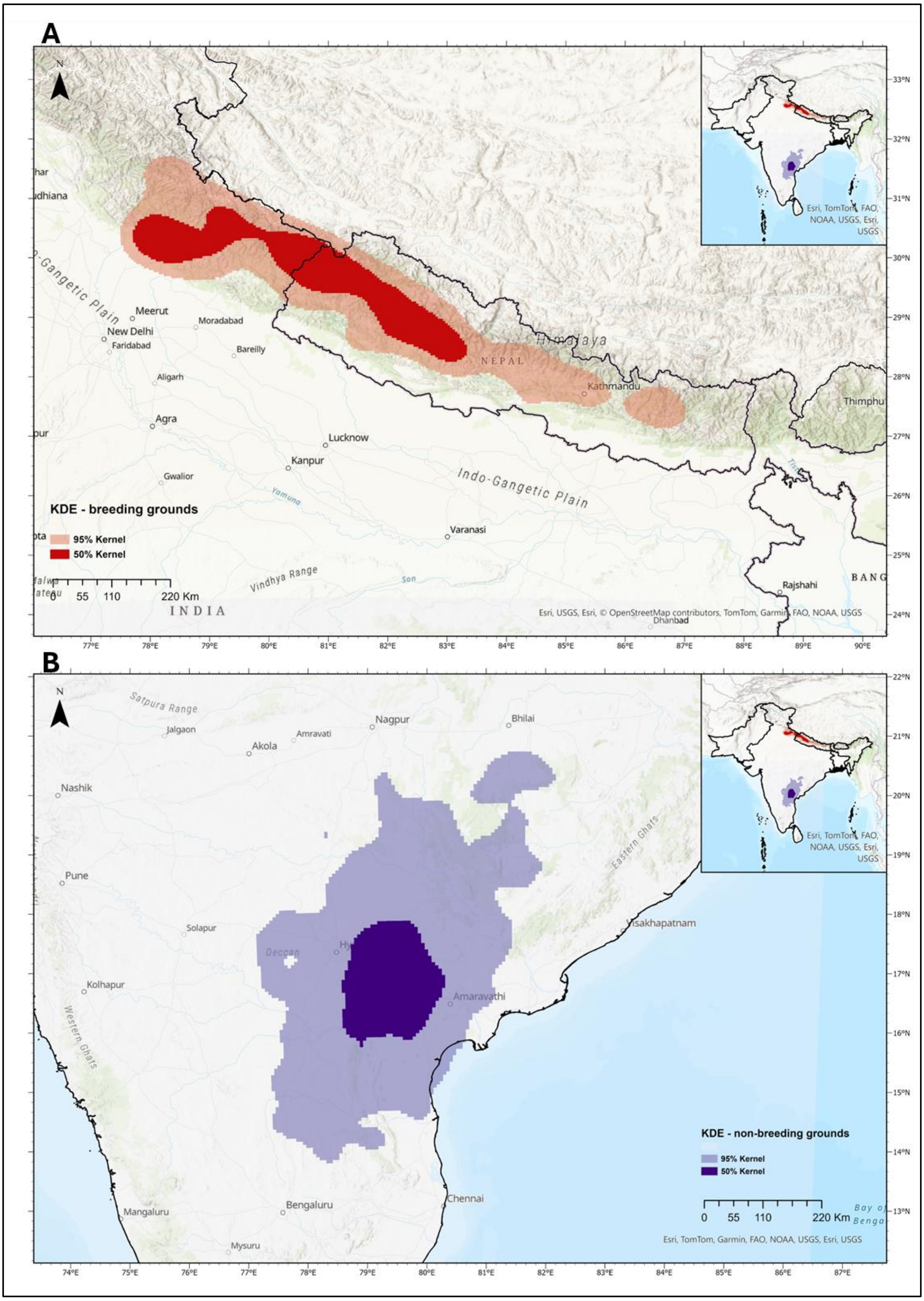

Fig 3.6 **A.** Kernel density map of the GAM predicted occurrence centroids for Barn Swallows in the breeding grounds and **B.** at non-breeding grounds across years of study (2017-2023). Inset map of the Indian subcontinent shows the pattern of breeding (in orange) and non-breeding range (in purple).

Migration timing

Spring migration on average started on the 20th of March (79th Julian day). Spring migration was earliest in 2023 i.e., on 12th March (71st day) and latest in 2021 on 10th April (100th day). The return migration started on the 22nd of July (203rd day) on average, with the earliest departure from breeding sites recorded on 3rd July (184th day) in 2021 while it started as late as 14th August (226th day) in 2020.

Migration speed

Spring migration was recorded to be faster (mean ± SD: 23.7 ± 6.2 km/day) than the autumn migration (20.1 ± 3.5 km/day). Migration towards the breeding grounds was fastest in 2019 2019 (33.4 km/day) and slowest in 2023 (18.3 km/day). In autumn, migration was fastest in 2020 (22.0 km/day) and slowest in 2022 (16.5 km/day). Migration speeds in spring were on average 3.6 km/day higher the speed in autumn (*Fig 3.7*), although it was found to be marginally non-significant ($p=0.075$).

Migration distance

Spring migration covered on average 1546.7 ± 292.3 km across the five study years. The shortest distance was recorded in 2020 (1105.6 km), while the longest was in 2019 (1918.2 km; (*Fig 3.8, Fig 3.9*). Autumn migration was generally longer (*Fig 3.10*), averaging 1671.2 ± 234.8 km, with the shortest journey in 2019 (1540.4 km) and the longest in 2021 (2134.4 km). The linear mixed model indicated no statistically significant difference between spring and autumn distances ($p = 0.41$).

Latitude dynamics and directional trends

GAMs suggested that the timing of migration influenced latitudinal positions: later spring departures were associated with slightly higher latitudes (R^2 adj = 0.59, deviance explained = 75.6%), while later autumn departures corresponded with slightly lower latitudes (R^2 adj = 0.45, deviance explained = 58.4%). Linear regressions across years indicated weak northward tendencies in migration routes (*Fig 3.11*). Spring median latitude increased by 0.51° per year ($p = 0.33$), autumn latitude by 0.57° per year ($p = 0.052$), and breeding latitude by 0.61° per year ($p = 0.31$).

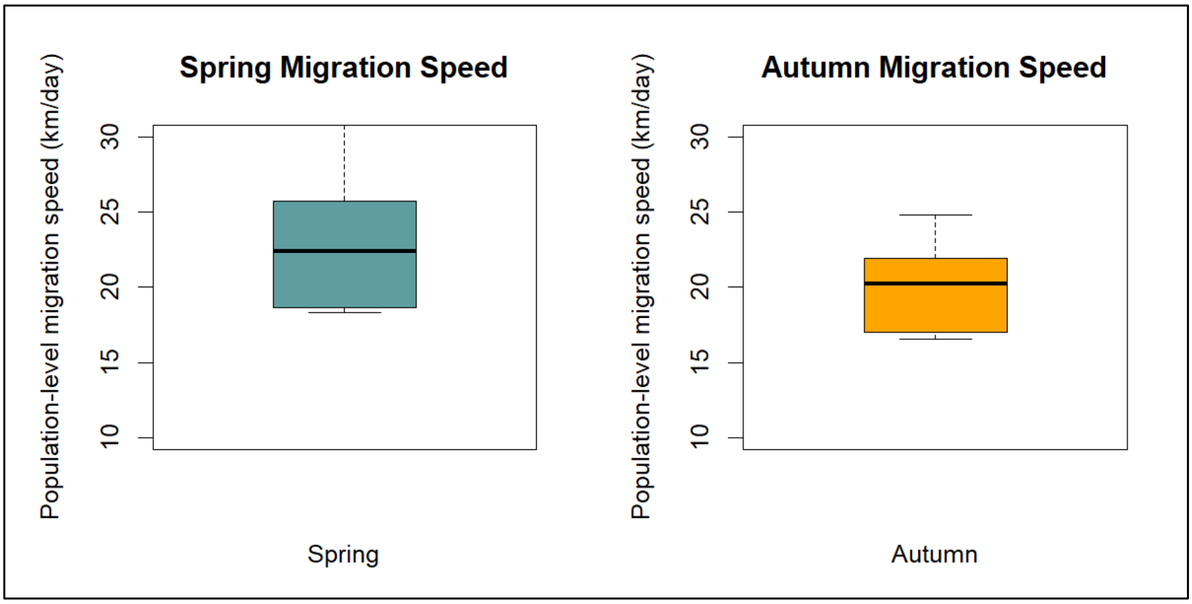

Fig 3.7 Differences in the spring (a) and fall (b) migratory speed of Barn Swallows. Speed of migration was calculated as the mean distance travelled (in kilometres) over the fastest 5 days. Boxplots represent the median value and interquartile range Q1 below as 25th percentile of data and Q3 above as 75th percentile of data).

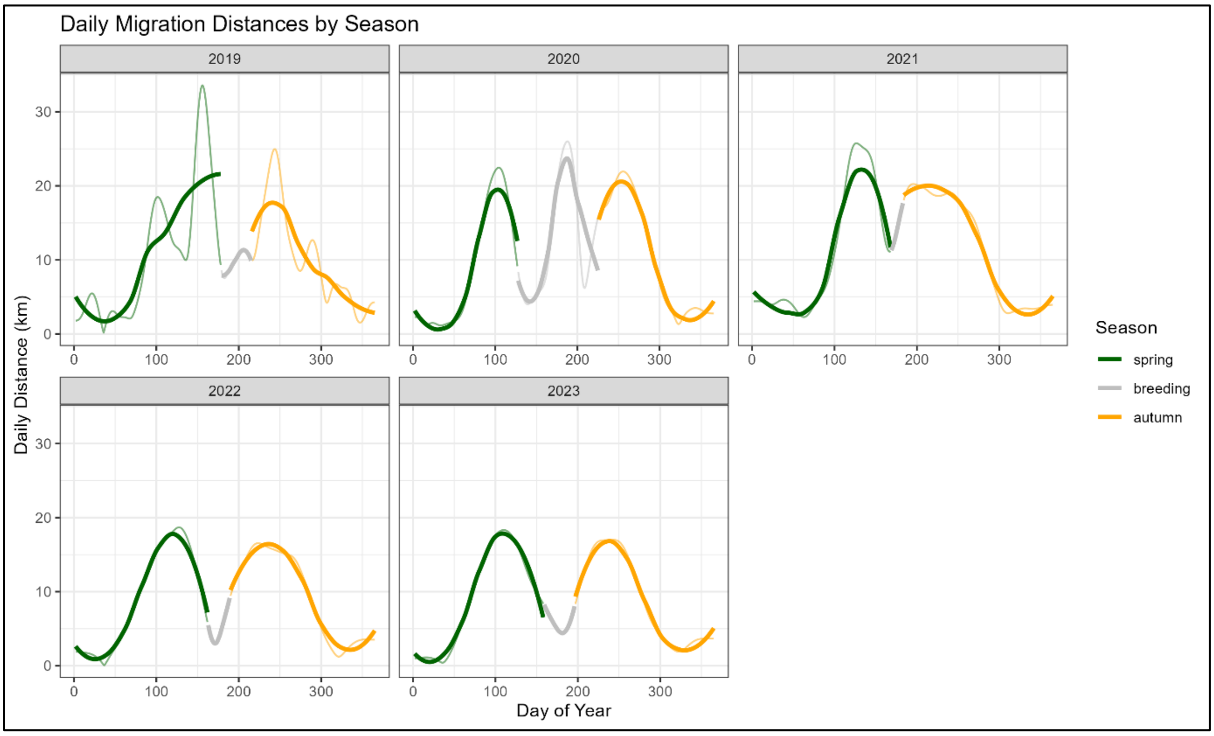

Fig 3.8 Daily migration distance travelled by Barn Swallows during spring migration (green), during breeding (grey) and autumn migration (orange), calculated from daily population centroid longitudes and latitudes predicted using generalized additive models across the period of study (2019-2023).

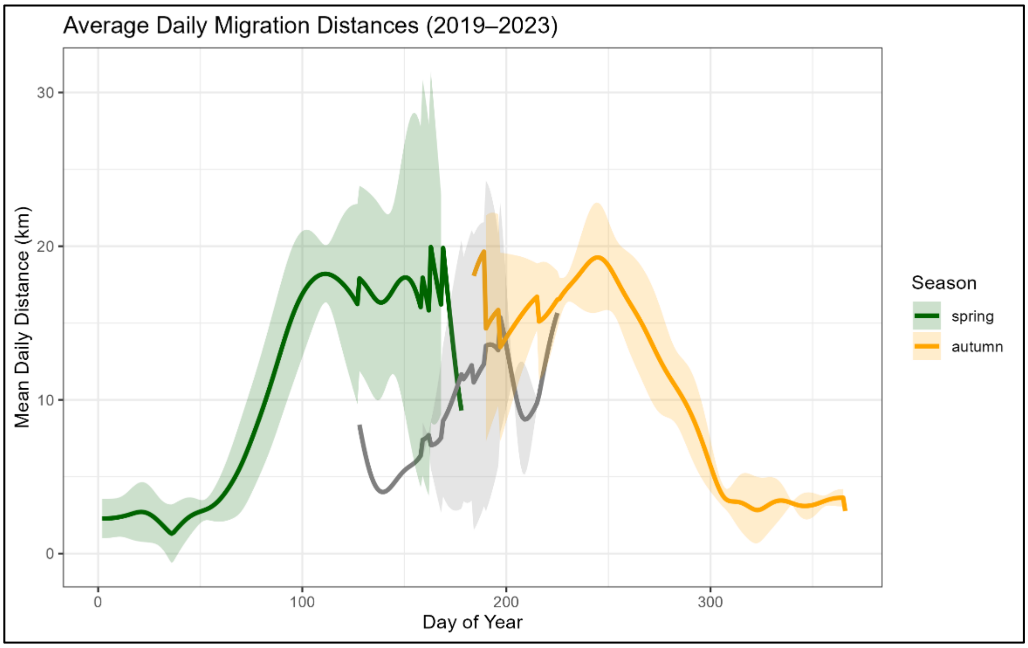

Fig 3.9 Average daily distance travelled by Barn Swallows during spring migration (green), during breeding (grey) and autumn migration (orange), calculated from daily population centroid longitudes and latitudes predicted using generalized additive models.

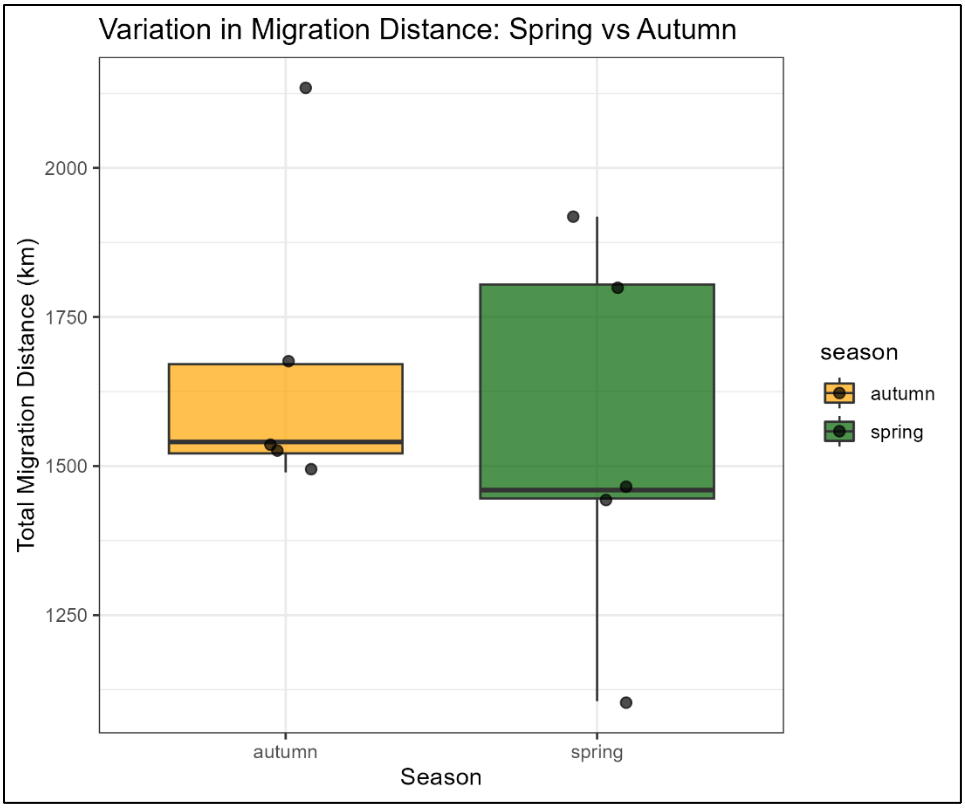

Fig 3.10 Variation in migration distance (in kilometres) during autumn and spring migration, calculated from daily population centroid longitudes and latitudes predicted using generalized additive models.

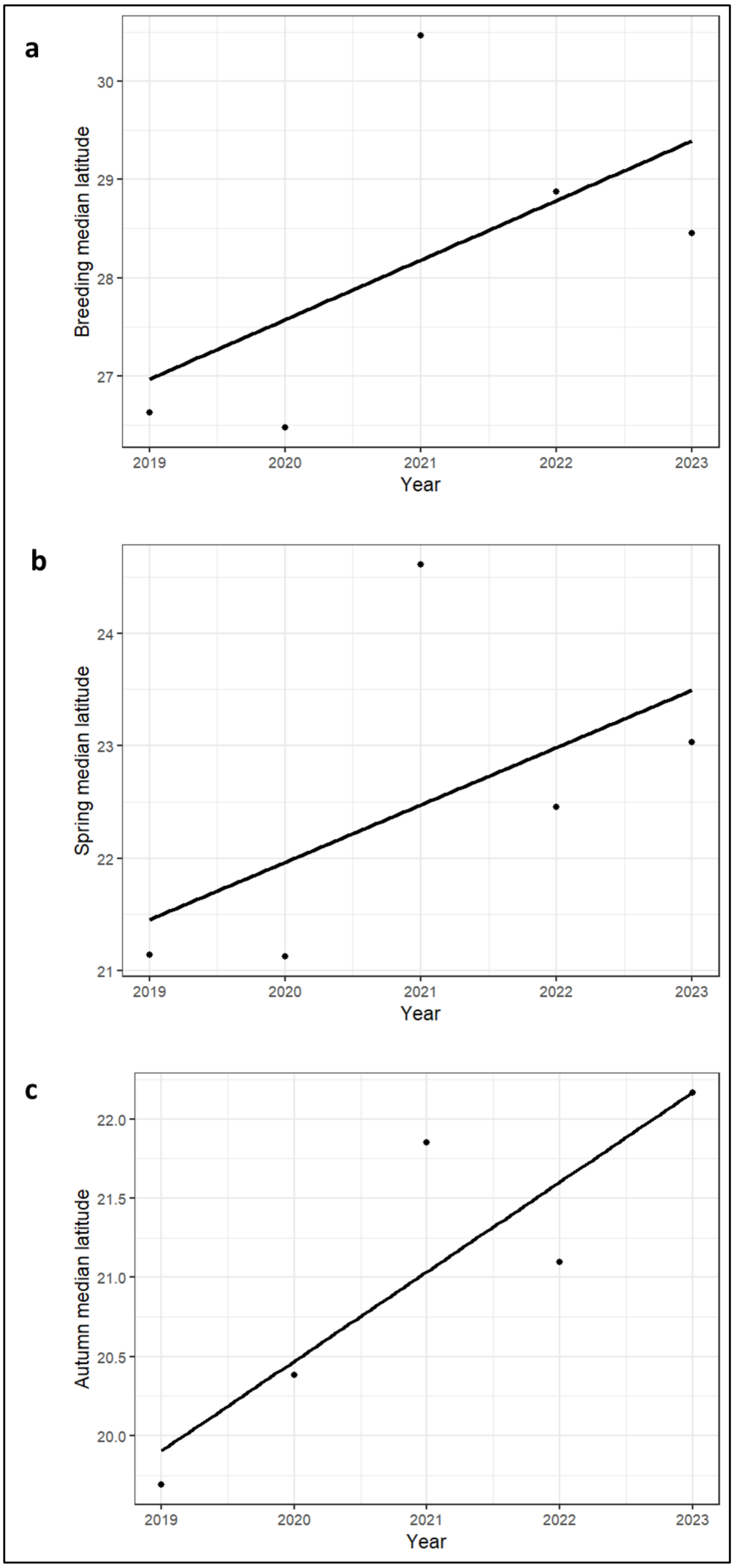

Fig 3.11 Changes in the breeding (a), spring (b), and autumn (c) median latitude during Barn Swallow migration (black points) from daily population centroid longitudes and latitudes predicted using generalized additive models.

3.4 Discussion

This study provides the first broad-scale temporal and spatial perspective on the seasonal movements and migration of Barn Swallows in the Indian subcontinent using publicly available citizen science data. This study enriches our understanding on migration connectivity specifically for populations breeding in Asia specifically in the Himalaya. As Barn Swallows across their wide breeding range have been extensively studied for their migration, the European populations migrating to overwinter in sub-Saharan Africa and North American populations migrating to South America (Hobson et al., 2015a; Saino et al., 2015; Imlay et al., 2018; Pancerasa et al., 2022), while the migratory connectivity of Asian breeding populations remains largely unknown, with only a few recent studies available (Heim et al., 2020; Turbek et al., 2022).

The findings indicate that in India, populations breed in the higher latitudes of the Himalayan region, which is in line with the only distribution record available from Ali and Ripley (1987). The analyses also suggest that the Himalayan breeding populations migrate and overwinter in southern India. These findings are interesting recent studies indicate southern India to be an important wintering ground for populations of *H. r. gutturalis*, an east Asian subspecies breeding in higher latitudes of China (Turbek et al., 2022). A study by Heim et al. (2020) further suggests populations from northern latitudes overwintering in north-east plains of India. However, it is to be noted that despite presence of eBird locations in Kashmir, Himachal Pradesh, and in western India (*Fig 3.5*), the generalized additive model showed no migratory routes of swallows in the westward direction (*Fig 3.3*). This is likely due to the possibility of these populations not staying in western India for winters and rather migrating further towards Africa on their migration. This should be further tested using geolocator tags to document the variation in migratory routes of swallow populations breeding across the Himalayan region.

The eBird analyses revealed that Barn Swallows departed on spring migration around March 20^{th}, and stayed at breeding sites till late July, consistent with our nesting ecology study on the species in the Himalayan region (*Chapter 4*). The spring migration was found to be faster than the autumn migration, and distance covered during spring was shorter than that of autumn, although not statistically significant. This pattern is typical for long-distance migrants, as faster spring migration leads to early arrival at breeding grounds, ensuring maximized reproductive success through territory establishment and resource utilization, following optimal migration theory (Alerstam, 2011; Newton, 2023).

Inter-annual variations in migration distances likely reflect responses to environmental variability, such as wind patterns, weather conditions, and resource availability along migratory routes. Similarly, inter-annual variations in departure and arrival dates suggest that migration timings are shaped by both endogenous rhythms and exogenous factors such as rainfall and insect abundance, a pattern widely reported in aerial insectivores (Rappole & Schuchmann, 2003; Russell et al., 1994). The arrival and departure from both breeding and non-breeding grounds are dictated by local climatic and habitat conditions (Alerstam & Lindström, 1990). The autumn migration of Barn Swallows begins at the onset of southwest monsoon in northern India which was also evident from the results of nesting ecology study (*Chapter 4*). It appears that populations track resources along their migratory routes to non-breeding grounds in southern India where they exploit resources during the northeast monsoon. Similarly, temperature at both breeding and wintering grounds appears to be dictating the migratory decisions, as Barn Swallows time their arrival at breeding sites only after the end of winter in the Himalayas and leave as temperatures begin to drop with the onset of monsoon in the region.

The findings suggest weak but consistent northward shifts in both breeding and migratory latitudes (~0.5–0.6° per year). This corroborates widespread climate-driven shifts reported in migratory birds, where breeding ranges often expand poleward or to higher elevations in response to warming temperatures and altered phenology (Thomas & Lennon, 1999; Rushing et al., 2020). For birds breeding in the Himalayan region, the northward shift is particularly significant. Given the rapidly changing Himalayan landscape, these shifts may affect breeding populations' ability to locate suitable breeding sites. The Himalayas face both natural and anthropogenic challenges, including rapid weather shifts and changing land-use patterns that alter habitat and limit nesting sites for swallows (*Chapter 4*). Therefore, any change in existing range will impact population dynamics.

Most importantly, this study establishes the Indian subcontinent as a critical region for Barn Swallow migration. Recent work by Heim et al. (2020) and Turbek et al. (2022) identified India as one of the wintering grounds for populations breeding in China and Russia. These studies highlighted the complexity of migration routes within Asia, where populations breeding over a large longitudinal range exhibit strong geographic structuring and follow strict migration routes. Using citizen science, ringing, and tracking data, Heim et al. (2020) described multiple population-specific migratory routes for Barn Swallow populations breeding through China to Southeast Asia (mainland corridor) and from Japan and eastern Russia to Taiwan and the Philippines (island corridor). They also identified major wintering grounds in the Ganges-

Brahmaputra floodplains, confirming that the Indian region supports not only local breeders but also long-distance migrants arriving from East Asia.

These population-specific migratory routes act as migratory divides and reinforce mechanisms of reproductive isolation (Irwin et al., 2005; Ruegg et al., 2012; Turbek et al., 2018; Scordato et al., 2020). Turbek et al. (2022) revealed a sharp migratory divide between two subspecies - *H. r. rustica* and *H. r. gutturalis* across central Asia. The east and west populations show contrasting migratory routes wherein populations breeding west of the hybrid zone cross the Taklamakan Desert and the Arabian Peninsula to overwinter in eastern Africa, while swallows to the east cross the Qinghai–Tibetan Plateau and the Karakoram to overwinter in southern India. Following optimal migration theory, these small-bodied passerines appear to avoid crossing formidable barriers of Central Asia, particularly the Taklamakan Desert, Tibetan Plateau, and Karakoram Range. Therefore, populations in the Indian subcontinent, by adopting different migratory routes, may follow historical and cultural routes to their respective breeding grounds.

The importance of India becomes evident as populations breeding further north circumvent ecological barriers including the Taklamakan Desert, Tibetan Plateau, Karakoram Range, and the Himalayan range. It appears that populations breeding in the Himalayas recently diverged from Eurasian populations and possibly overwinter in both Africa (as observed in European and East Asian populations) and southern India. For navigating formidable barriers, populations have adapted contrasting strategies via these divergent routes across Central Asia. As suggested by (Burman et al., 2018), the Great Escarpment, the mountain range that separates the central South African plateau from the coast acts as a migratory barrier and restricts Palearctic Barn swallows to overwintering in the coastal plain of South Africa. We believe that the Himalayan chain not only acts as a migratory barrier for Eurasian Barn swallow populations but also limits populations and creates genetic divergence.

The Indian subcontinent occupies a central position where multiple migratory strategies converge for different populations. Populations of long-distance migrants breeding in different regions tend to show high levels of mixing at their non-breeding grounds (Finch et al., 2017; Burman et al., 2018). This appears to be the case in India, which acts as central non-breeding grounds where it is likely that different Barn Swallow populations converge and adopt multiple migratory strategies. It is to be noted that the eBird analyses did not highlight populations breeding in Northeast India (*see Chapter 4*), indicating bias in the data for underrepresented regions. However, our observations and previous reports on Barn Swallow populations indicate that, apart from one sedentary population breeding in Manipur, one migratory population from East Asia also winters in the region (Ali & Ripley, 1987). Overall, the Indian region forms major migratory and wintering grounds for many populations breeding in northeast Asia.

These findings should be considered with the limitations of using citizen science data. Despite correcting for biases associated with eBird data through data filtering, spatial aggregation, certain regions, remain under-represented. Biases such as uneven observer effort, spatial clustering of checklists and potential reporting biases specifically in the case of species such as the Barn Swallow which is difficult to identify for many birders, can influence estimates of migration timing and distribution (Dickinson et al., 2010; Johnston et al., 2021). Nonetheless, the power of citizen science data can be utilised in describing species occurrence patterns specifically in regions where other studies are limited. The strength of citizen science lies in its broad spatial and temporal coverage, which, when combined with geolocators, ringing, and genomic approaches, offers a powerful framework for uncovering migratory connectivity at population scales (Marra et al., 2011; Saino et al., 2017).

Barn Swallow breeding in the Himalayan region is understudied and given rapidly changing climatic conditions coupled with anthropogenic pressures in this ecologically sensitive mountain chain, it becomes critically important to understand the migration ecology of these populations. Given that migration phenology of long-distance migrants is highly influenced by rapidly changing climate, understanding of migration strategies and key wintering and stopover habitats is essential (Jones & Cresswell, 2010; Knudsen et al., 2011) to determine conservation threats even outside the breeding region.

Future work should focus on extensive ringing effort across the Himalayan breeding populations as well as coordinated efforts at the non-breeding grounds, which would help in identifying and establishing the migratory connectivity of different breeding populations converging in southern India. The use of miniaturised technology of light-level geolocator tags has extensively been utilised for tracking small birds (Laughlin et al., 2013; Hobson et al., 2015b; Saino et al., 2015; Sicurella et al., 2016; Klvaňa et al., 2018; Seifert et al., 2018; Gow et al., 2019; Imlay & Taylor, 2020; Pancerasa et al., 2022). This can be utilized in identifying the stopover and overwintering sites as well as migratory timings and strategies of different populations.

While it has been observed that the Barn Swallow is able to exploit diverse conditions and is resilient, feeding on broad range of flying insects, despite this, steep declines are being reported in Europe and North America raises concerns. The steep decline in Barn Swallow populations across Europe and North America has resulted in studies understanding the impact of climate change on migration phenology (Liechti et al., 2015; Saino et al., 2017; Imlay et al., 2018; Pancerasa et al., 2018; Heim et al., 2020; López-Calderón et al., 2021). This study provides a preliminary understanding on the migration of Himalayan breeding populations and has provided key insight on how different breeding populations are utilising the Indian landscape for overwintering. This study will help in further understanding on how changes in climatic conditions as well as habitat would affect these different breeding populations across time.

3.5 References

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Chapter 4
Breeding distribution and Nesting ecology of Barn Swallow (*Hirundo rustica)* in the Uttarakhand Himalayan region

4.1 Introduction

Barn Swallow, a human-commensal, is well known among the local people across its distribution range owing to its nature of building its cup-shaped mud nest in human-inhabited areas. As a result, it is the most widespread and abundant swallow species in the world, breeding in Eurasia and North America and migrating long-distances to winter in south to tropical Africa, northern Australia, Central and South America (Turner, 2006). Historically, prior to human settlements, Barn Swallows nested in natural features like caves, holes, crevices, and cliff ledges (Speich et al., 1986; Turner, 2006). In Baikal, Amur and Primor'e regions of eastern Russia, Barn Swallows were historically absent when native people lived mostly in subterranean structures and only with the arrival of people who built structures above-ground, Barn Swallows could potentially colonize the region (Smirensky & Mishchenko, 1981). In North America it is speculated that by 1800s with the availability of human-made structures Barn Swallows shifted their nests within such structures (Brown & Brown, 2020). Møller & Gregersen (1994) describes similar patterns in Europe and Asia where Barn Swallows started to affix their nests to structures and bridges. The rapid expansion of human settlements leading to widespread availability of nest sites resulted in dramatic range expansion of Barn Swallows.

Owing to its wide distribution, Barn Swallows is one of the commonly occurring species, however still, across most parts of its range steep population declines have alarmed the scientists (Lee et al., 2011; Ambrosini et al., 2012; Vickery et al., 2013). In Canada, populations have declined by more than 70% since 1980, and similar trends in Europe have been observed, 19% decline between 1980 and 2023 (PECBMS, 2024) From Asia, the population status is still unknown, however, a study by Lee et al. (2011) based on model simulations suspect that pronounced delays in spring arrival of Barn Swallows at breeding sites in Korea may reflect an alarming population decline of over 99% in recent decades. A range of factors have been implicated in the decline of particularly climate and land-use changes (García-Pérez et al., 2014; Weegman et al., 2017; Cox et al., 2020), agricultural intensification, pesticide use (Rioux Paquette et al., 2014; Stanton et al., 2017; Imlay et al., 2018), and the loss of breeding and non-breeding habitats (Spiller & Dettmers, 2019). Among these, the global decline in insect populations (Sánchez-Bayo & Wyckhuys, 2021; Wagner et al., 2021) is recognized as a primary driver, resulting in decreased food availability and cascading impacts on insectivorous species such as the Barn Swallow (Imlay et al., 2018; Spiller & Dettmers, 2019; Michel et al., 2021). While the extent and causes of decline vary by region (Smith et al., 2015; Michel et al., 2016; Shutler et al., 2012), the global drivers remain poorly understood and are often scattered across regions (Zhao et al., 2022).

The sustained and widespread declines in Barn Swallow populations underscore the urgent need for ecological monitoring and identification of region-specific drivers, particularly in underrepresented regions such as Asia, where data are scarce. Despite being the most widely distributed bird species worldwide, no ecological study on Barn Swallow is available in India, particularly in the Himalaya, which marks its southern breeding boundary in South Asia. In this region, Barn Swallows primarily breed at elevations between 1500 and 2000 meters above sea level (Ali & Ripley, 1987), typically from February/March to July. Unlike in North America and Europe, where they primarily inhabit rural landscapes with livestock farms, in the Himalaya, they occupy a broad range of habitats - from villages to towns and cities.

Himalaya is an ecologically sensitive mountain ecosystem facing increasing vulnerability due to rapid urbanization, declining agricultural activity, climatic shifts, and large-scale human out-migration (Xu et al., 2009; Negi & Mukherjee, 2020). The Central Himalayan region has undergone profound changes, with many villages becoming depopulated or "ghosted" due to rural depopulation and agricultural abandonment (Naudiyal et al., 2019; Sati, 2021). These landscape-level changes may reduce suitable nesting habitats and prey availability - both key factors identified behind the decline of the Barn Swallow population (Møller, 2001; Lee, 2009; Nebel et al., 2010).

Because breeding success is tightly coupled to both nest-site availability and local prey resources, Barn Swallows are vulnerable to anthropogenic changes in land use and agricultural practice. Given this, this chapter focuses on documenting a) breeding distribution of Barn Swallows in the Indian Himalaya, b) nesting ecology across select sites in the Himalayas, and c) nestlings' dietary composition at selected breeding sites. This study focused on understanding the factors driving the nest-site selection, and nest success. Given the nesting periodicity is seasonal, whether nesting stages differ spatially and temporally was also documented. Further, whether nestlings' dietary composition varied with habitat type, in relation to local insect prey availability was also investigated.

4.2 Methods

Study sites

For documenting the breeding distribution, systematic surveys across the Himalayan range from west to east axis between 2019 and 2023 (excluding two years- 2020 and 2021 of COVID-19 pandemic) were carried out. For the nesting ecology and nesting's diet objective, four sites within the Uttarakhand Himalaya were selected. Barn Swallows typically breed within 1000 to 2500 m asl in the region, which is broadly characterized by subtropical to tropical climate, with mild, dry winters and a short, warm summer season (India Meteorological Department 2014). The study sites were selected based on the geographical location, elevation, and settlement type, particularly rural and urban settlements (*Fig 4.1*A).

The two rural sites selected were Kempty village (30°29'41.96"N, 78°2'22.32"E, 1500 m asl) in Tehri Garhwal district and Purola village (30°52'43.88"N, 78°5'6.58"E, 1300 m asl) in Uttarkashi district. These sites are characterized by sparse human settlements with interspersed agricultural land. Kempty is situated along a ridgeline and primarily dominated by terrace farming type, whereas Purola lies in a river valley along the banks of the River Kamal, supporting extensive cultivated fields. At both rural sites, Barn Swallows were predominantly observed foraging over agricultural areas. The two urban sites chosen for the study were Nainital (29°23'32.71"N, 79°27'12.14"E, 2000 m asl), and Bageshwar (29°50'25.25"N, 79°46'9.90"E, 1200 m asl), which serve as the district headquarters of Nainital and Bageshwar districts, respectively. These sites are characterized by dense built-up areas; however, Nainital has a large freshwater body (Naini Lake), whereas Bageshwar town is situated at the confluence of the Saryu and Gomati rivers. At both these sites, Barn Swallows largely foraged across a heterogenous landscape, including over roads, waterbodies as well as open drainage channels. The dietary analysis was carried out in 2023 for which the land use/land cover (LULC) data was extracted from ESA Sentinel-2 imagery at a spatial resolution of 10m (Esri and Impact Observatory 2023). To visualise the site-level habitat variation LULC was quantified within a 500 m buffer around nesting locations (*Fig 4.1*B), corresponding to foraging limits of breeding swallows (Diaz Bohorquez et al., 2025).

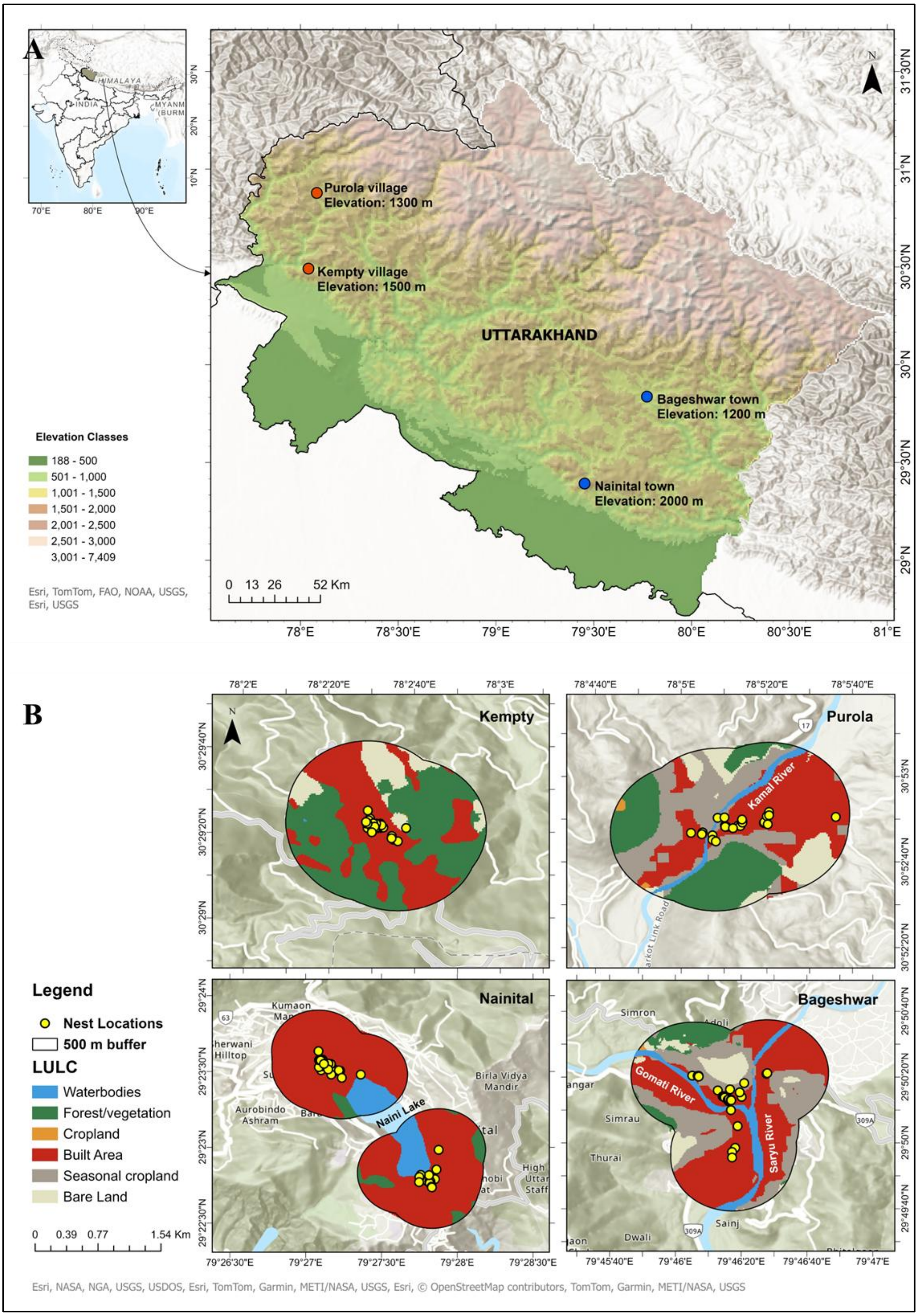

Fig 4.1 Study sites selected across the state of Uttarakhand where detailed nesting ecology study was carried out. A) enlarged map of the state shows geographical location and elevation variations across study sites while B) shows major land-use types in a buffer of 500 m around the Barn Swallow nesting colonies.

Methodology

Breeding distribution

Within the Himalayan region, following major highways and connecting road network, surveys were carried out across villages, towns and cities. Particularly in Uttarakhand, intensive surveys covering approximately a distance of 4500 km across the districts' administrative boundaries were undertaken. During the surveys, local people were enquired on the presence of Barn Swallows and nesting locations. Upon locating the colony, nest-site characteristics and nest attributes of about 80% of the nest within the site were documented. This included GPS location, elevation, aspect, type of building, number of nests within the building, nest height from ground, nest height from ceiling.

Nest monitoring and breeding parameters

During the breeding season (March to July), systematic nest monitoring surveys across the four select sites in Uttarakhand were carried out. A nest was considered active if any of the nesting activity (eggs, hatchlings or fledglings) was observed in the nest. Information was recorded for each of the located nest on the dates of nest construction, and once nest was observed to be active, regular monitoring of each nest was carried out every 5-7 days until the nesting attempt either succeeded or failed. During each visit, number of eggs or hatchlings with their developmental stages (C1 to C4) were recorded. These observations were used to estimate key breeding parameters, including clutch size, brood size, number of fledglings, incubation period, fledging period, and total nesting duration. The nest initiation dates and subsequent nesting stages were converted to the day of the year (DOY) to allow comparison across sites and years.

Nest fate and nest success

The nest fate was classified as successful if at least one chick fledged from the nest and failed if no fledglings were produced. Firstly, the apparent nest success was calculated as the proportion of successful nests relative to the total number of monitored nests for each site and year. Although widely used, apparent nest success does not account for differences in exposure time among nests and can overestimate true survival rates (Johnson, 1979; Mayfield, 1975). Therefore, to account for unequal monitoring intervals and varying exposure times, nest survival for each nest was estimated using the Mayfield method (Mayfield, 1975). For each nest, the number of exposure days was calculated as the total number of days the nest was known to be active and at risk of failure. Nest failures were assigned to the midpoint between the last active check and the visit when failure was detected.

Daily survival rate (DSR) was calculated as:

$$DSR = 1 - \left(\frac{\text{Number of failures}}{\text{Total exposure days}}\right)$$

Mayfield nesting success for the full nesting period was then estimated by raising the DSR to the power of the mean nesting length (in days) for each site and year. Mayfield estimates were calculated separately for regions, years, and region–year combinations.

Statistical analyses

To evaluate spatial and temporal variation in nest success, generalized linear models (GLMs) with a binomial error distribution and logit link function were used. Nest success (successful = 1, failed = 0) was modelled as a function of region and year. Because some regions were sampled in only a single year, temporal effects were evaluated separately for sites with multi-year data (Kempty and Nainital).

Model significance was assessed using likelihood ratio tests (analysis of deviance), and model fit was evaluated using Akaike's Information Criterion (AIC). All statistical analyses were conducted in R (version 2024.09.1+394, RStudio Team 2024), using base functions and the *lme4* package where appropriate.

Prey composition in the diet of Barn Swallow nestlings

Sample Collection and Examination

At the selected sites, the fresh nestlings' faecal samples were collected from under the active nests. The samples were taken using blunt-end forceps and stored them individually in a sealed microcentrifuge tube and labelled with location name and date at –20 °C. A total of 240 faecal samples (20 samples per site per month) during the 2023 breeding season from across four study sites was collected. To examine the prey remains, sample content from individual vials was first defrosted and then separated into a clean petri dish. Then the sample for examining the prey remains under a dissecting microscope (Stereo zoom Olympus SZX7 with 1.25X objective). Whenever required, a few drops of 70% ethanol were poured over the prey remains to aid the separation of clustered body parts. The prey remains, such as heads, mandibles, wings, and appendages, were then identified up to the order level and unidentified remains were categorised as unknown. To avoid potential overestimation due to repeated body parts (e.g., beetle elytra), only the presence or absence of each insect order was recorded and not abundance.

Insect prey availability

To investigate the prey selection by Barn Swallows with respect to the diversity of airborne insects, aerial insect sampling was conducted at 62 transects distributed between two sites – Purola, a rural settlement (n = 27) and Nainital, an urban settlement (n = 35). The other two sites sampled for diet analysis could not be included in the prey availability analysis due to logistics and persistent bad weather. Following the flight paths of foraging swallows, key feeding hotspots, such as agricultural fields, market areas, and roads, were identified, and insect sampling was carried out. The sampling was carried out on clear sunny days between 7:00 and 11:00 hours. Trails ranging from 50 to 100 m were walked at a constant speed, wherein insects were captured using a sweep-net of 0.3 m diameter attached to an extendible pole. After each sampling effort, insects captured in the net were carefully transferred to a killing jar containing ethyl acetate for later identification. Thereafter, insects of each sampling effort were stored separately in a labelled zip-lock bag at -20 °C. Insects were identified up to the order level later in the lab.

Statistical Analysis

For both the faecal and insect samples, the frequency of occurrence for insect orders was calculated as follows:

$$Frequency\ of\ occurrence\ (\%) = \frac{Number\ of\ samples\ where\ insect\ order\ was\ present}{Total\ number\ of\ samples} \times 100$$

Given the habitat differences across the four selected sites, the diet differences were examined at two levels: a) between settlement types (rural vs. urban), and b) within settlement types (sites within rural and urban categories). PERMANOVA (Permutational Multivariate Analysis of Variance) was performed to test for statistical differences in faecal samples of rural and urban settlements. The same analytical framework was employed to compare the diet composition and insect prey availability in the surrounding environment. Since the data was in binary form (presence/absence), Jaccard dissimilarity with 999 permutations per test was employed. To visualise multivariate patterns, we conducted Non-Metric Multidimensional Scaling (NMDS) based on Jaccard distances. The resulting NMDS axes (NMDS1 and NMDS2) were plotted to illustrate clustering and dissimilarity among samples. All analyses were performed in R Studio version 2024.09.1+394 (RStudio Team, 2024), and vegan version 2.6-10 (Oksanen et al., 2001) package was used for multivariate analysis and ggplot2 version 3.5.2 (Wickham et al., 2007) for data visualization.

4.3 Results

Breeding distribution of Barn Swallows across the Indian Himalaya

Across the Himalayan region, a total of 1450 Barn Swallow nests were recorded, spanning an elevational range from 489 to 2317 m above sea level (a.s.l), with a mean nesting elevation of 1505.6 ± 398.6 m. Nest records were unevenly distributed among states (*Table 4.1, Fig 4.2*), with Uttarakhand contributing the majority of nests (1103), followed by Himachal Pradesh (101), Sikkim (93), West Bengal (67), Manipur (57), and Jammu & Kashmir (29). Latitudinally, nesting records extended from 24.44°N in Manipur to 34.15°N in Jammu & Kashmir. Uttarakhand also exhibited the widest elevational range (489–2317 m), whereas Manipur showed a comparatively narrow elevational distribution (765–928 m). Across states, the majority of nests were located inside buildings, with proportions ranging from 71.9% in Manipur to over 90% in Himachal Pradesh. Commercial structures, particularly shops, represented the dominant nesting property type in most states, while houses were more frequently used in Manipur and Jammu & Kashmir.

Table 4.1 Breeding distribution of Barn Swallows across Indian Himalayan Range with minimum and maximum latitude limit and elevational limits.

State	Total nest	Latitude		Elevation (m)			% of nests located inside the property	Dominant property type
		Min	Max	Min	Max	Average		
Jammu & Kashmir	29	33.92	34.15	1585	1641	1605.7	75	House
Himachal Pradesh	101	30.77	32.49	695	2200	1259.2	92.1	Shop
Uttarakhand	1103	29.17	31.14	489	2317	1552.4	86.7	Shop
Sikkim	93	27.16	27.39	781	2040	1571.9	84.9	Shop
West Bengal	67	26.85	27.01	765	2277	1573.8	79.1	Shop
Manipur	57	24.44	25.04	765	928	796.4	71.9	House

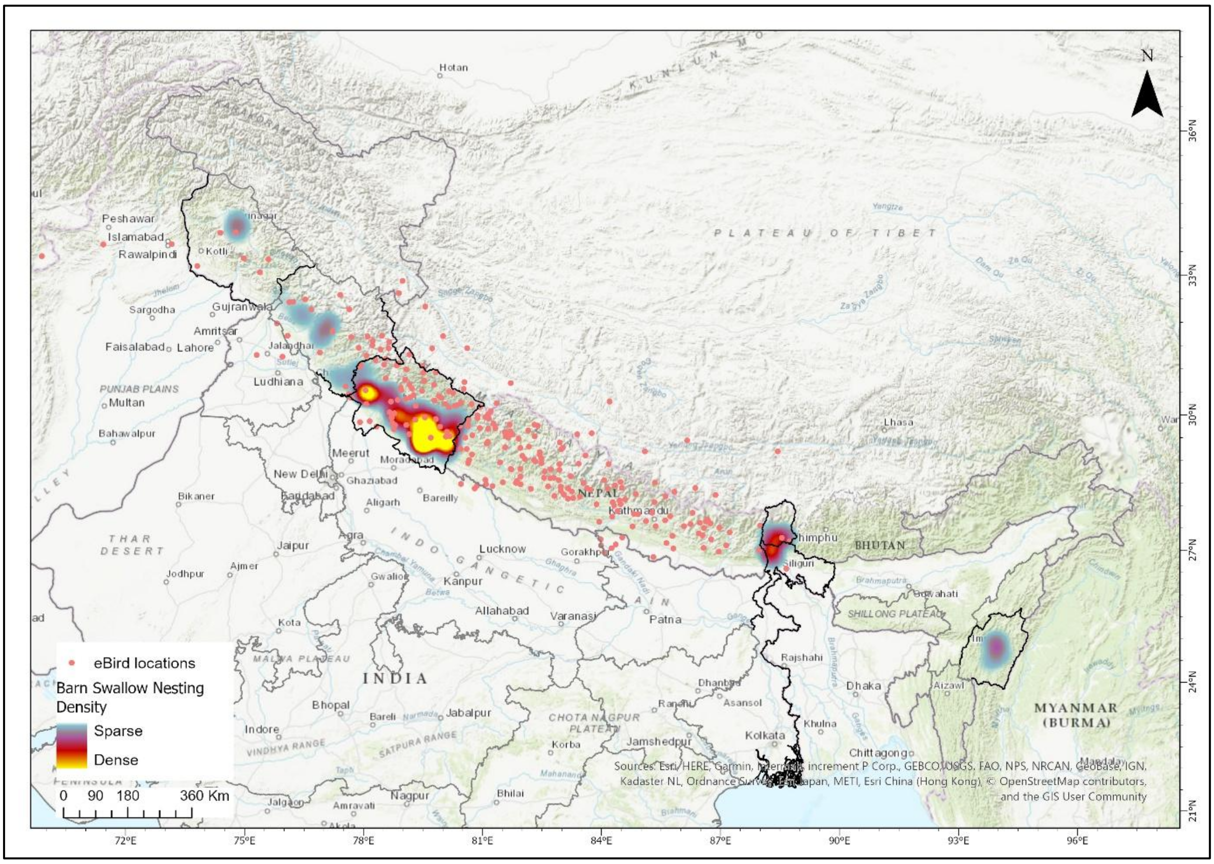

Fig 4.2 Barn Swallow breeding distribution documented across the Indian Himalayan Region during 2019, 2022 and 2023. The heat density shows nesting clusters with very dense clusters in Uttarakhand State (possibly an artefact of sampling bias). The eBird sighting locations of Barn Swallows across the region are also overlaid on the surveyed locations to visualise the overall breeding distribution.

Breeding distribution of Barn Swallows across Uttarakhand Himalaya

State-wide surveys across Uttarakhand documented approximately 1,200 Barn Swallow nests. Nesting was concentrated within the mid-elevational belt (1000–2000 m a.s.l.), which accounted for nearly 81% of all recorded nests (*Fig 4.3*). The lowest nesting elevation was recorded at 489 m a.s.l. in Rarikhooti village, Champawat district, while the highest nesting site occurred at 2317 m a.s.l. in Jwarna village, Tehri district. Spatially, nesting sites were more densely clustered in eastern Uttarakhand (*Fig 4.4*). When Barn Swallow nesting locations were overlaid with the climatic classification map of the Indian Meteorological Department (IMD, 2014), the majority of nests were found within the "tropical upland, mild and dry winter, short warm summer" climatic zone (*Fig 4.5*).

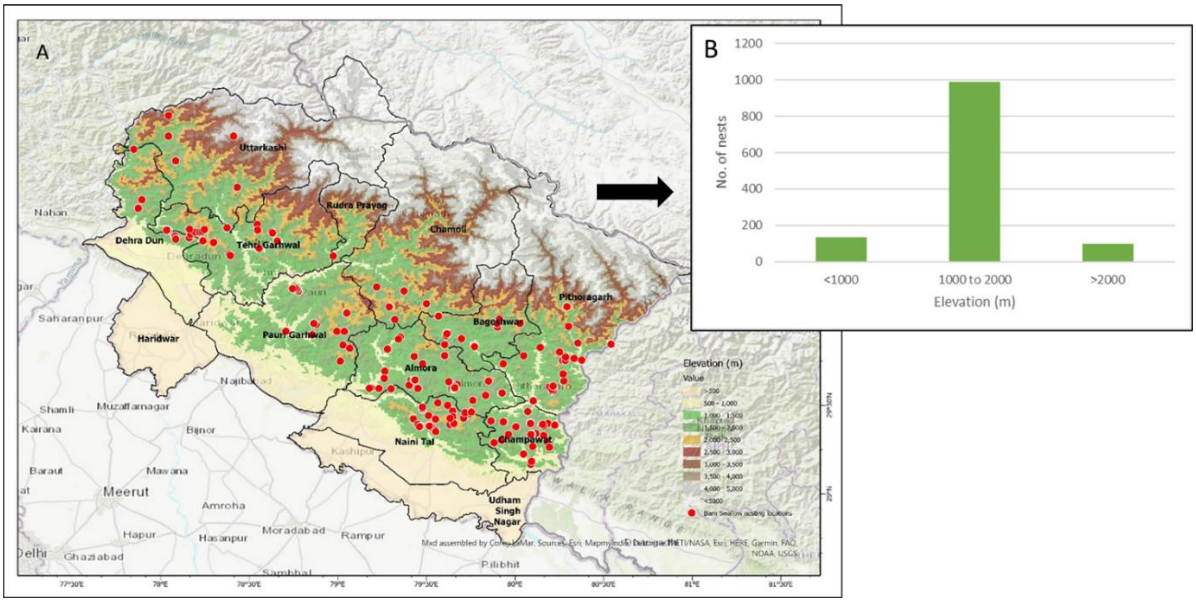

Fig 4.3 Barn Swallow breeding distribution recorded across the Uttarakhand State surveyed in 2022 and 2023 breeding season (A), wherein high density located between the elevation belt of 1000 to 2000 m asl (B).

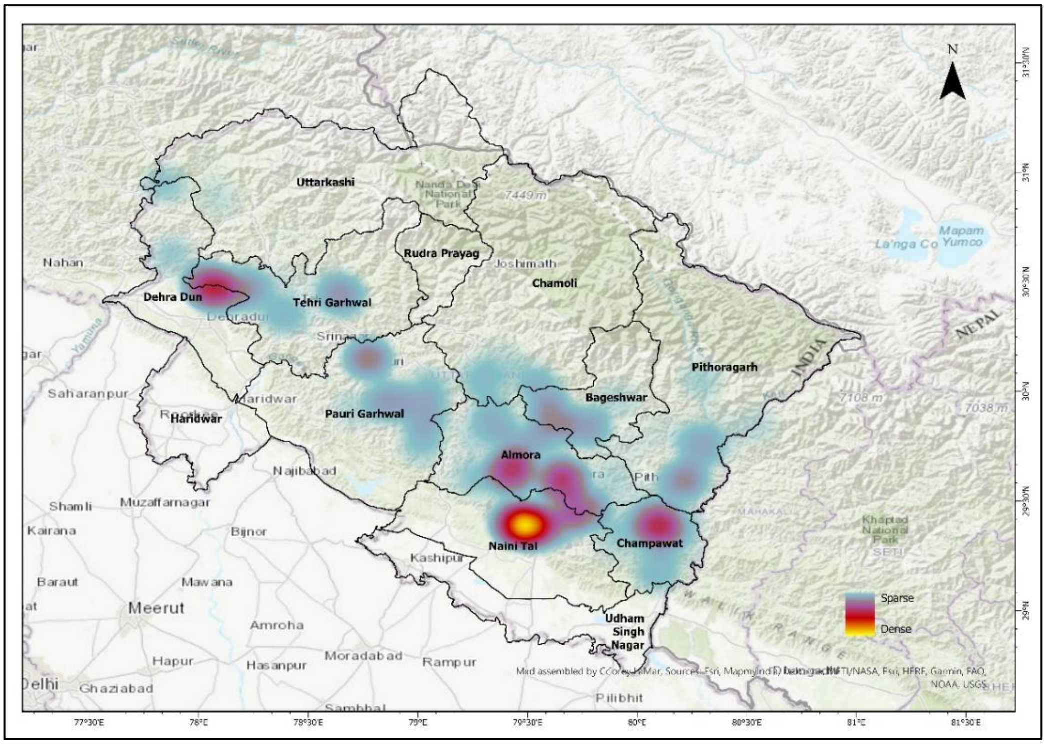

Fig 4.4 Barn Swallow nesting was recorded to occur densely in the eastern Uttarakhand corresponding to high precipitation region than that of western part of the State.

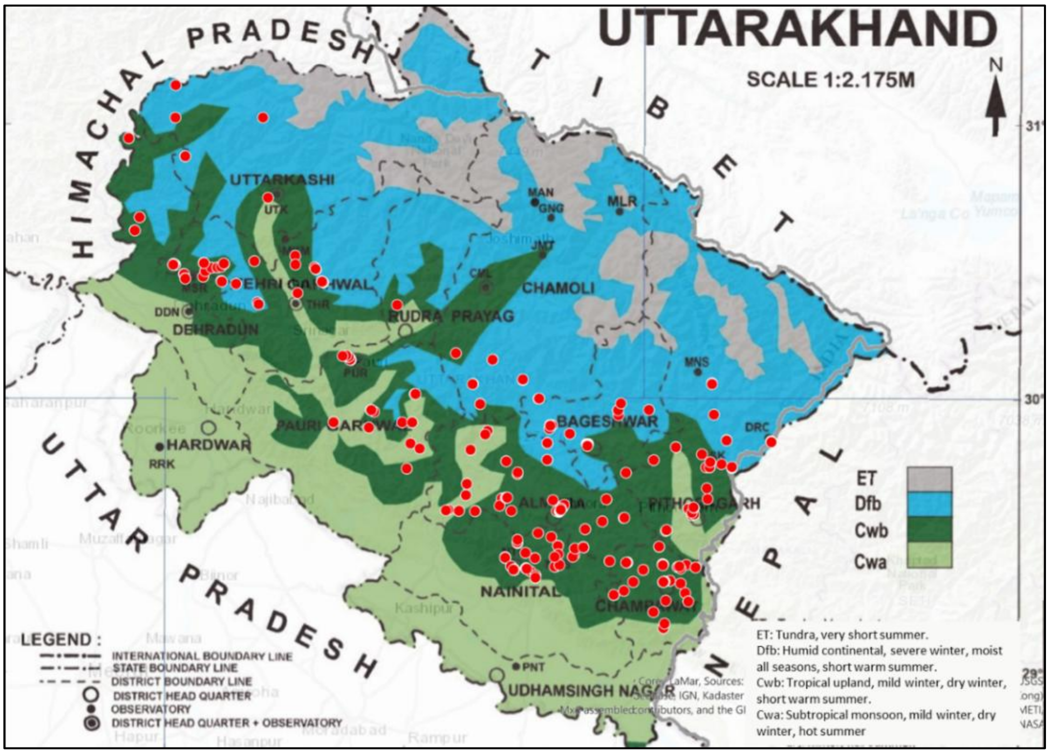

Fig 4.5 Barn Swallow nesting distribution overlaid on the Climatic Classification layer of Uttarakhand indicating nesting to predominantly in the tropical zone corresponding to mild and dry winter and short warm summer conditions.

Nest Attributes

Barn Swallow nests exhibited clear patterns in orientation, structural support, and placement height across the Himalayan breeding range. Nest orientation did not show a strong directional preference, with nests distributed relatively evenly across all aspects. In terms of structural support, nests were most frequently attached to walls (30.5%) and bulb holders (27.5%), followed by a substantial proportion using miscellaneous artificial supports (27.2%), while electric wiring (10.8%), beams (2.1%), and ledges (1.9%) were used less commonly (*Table 4.2*). Mean nest height from the ground was found to be at 10.1 ft and varied among states, ranging from an average of 9.2 ± 4.7 ft to higher placements at 12.2 ± 1.7 ft (*Table 4.3*).

Table 4.2 Number of nests built on varied substrate types in buildings across study sites in the Himalayan region and in Manipur (Northeast India)

Nest support substrate	Number of nests	in %
Wall	442	30.5
Bulb holder	399	27.5
Other	395	27.2
Electric wiring	157	10.8
Beam	30	2.1
Ledge	27	1.9

Table 4.3 Average nest height from ground across study sites in the Himalayan region and in Manipur (Northeast India)

State	Number of nests	Average height (mean ± SD) of nests from ground (in ft)
Jammu & Kashmir	29	9.27 ± 3.06
Himachal Pradesh	101	9.2 ± 4.71
Uttarakhand	1103	10.01 ± 2.55
Sikkim	93	12.17 ± 1.7
West Bengal	67	11.79 ± 4.3
Manipur	57	10.78 ± 2.64

Breeding parameters and nesting success of Barn Swallows in Uttarakhand

Breeding Periodicity in Uttarakhand Himalayan region

Across Uttarakhand, nest activity of Barn Swallows on average began on the 56th day of the year (late February) and extended until 176th day of the year (late June) (*Fig 4.6*). On average, nesting across years and sites began by 92nd day of the year (early April) with egg-laying by 97th day of the year and hatching by 108th day of the year and fledging by 131.5th day (mid-May).

Nest initiation dates were latest in 2019 (107th day), intermediate in 2022 (98th day), and earliest in 2023 (85th day). A similar advancement across years was observed for egg laying, hatching, and fledging, with 2023 consistently showing earlier median dates than previous years (*Table 4.4*). Across regions, median nest initiation was earliest in Purola (79th day) and Bageshwar (89.5 day), intermediate in Nainital (95th day), and latest in Kempty (100th day) (

Fig ***4.7***, Table 4.5). Median egg-laying and hatching dates followed a similar spatial pattern, whereas fledging occurred latest in Bageshwar (median 153rd day of the year).

Across three years of monitoring, a significant shift in nest initiation timing was detected among years in Kempty (Kruskal–Wallis test: H_2= 9.44, p < 0.05), with initiation occurring earlier/later in 2023 compared to 2019 (*Fig 4.8*). The median active date shifted from 107th day in 2019 to 99th day in 2022 and 84th day in 2023. A comparable advancement was observed in Nainital, where median initiation occurred at 98th day in 2022 and day 86th in 2023.

Table 4.4 Number of Active Nests across Uttarakhand across three years of surveys with days of nest activity, egg-laying, hatching and fledging.

Year	No. of Active Nests	Nest Active Day	Egg-laying Day	Hatching Day	Fledging Day
2019	41	107	109	121	142
2022	114	98	102	107	139
2023	173	85	89	104	123
Overall	328	92	97	108	131.5

Table 4.5 Number of Active Nests across select sites across three years of surveys with days of nest activity, egg-laying, hatching and fledging.

Region	Year	No. of Active Nests	Nest Active Day	Egg-laying Day	Hatching Day	Fledging Day
Kempty	2019	41	107	109	121	142
	2022	39	99	102	96	122
	2023	40	84	87	104	128
Nainital	2022	75	98	102	110	142
	2023	67	86	89	104	123
Purola	2023	36	79	81.5	101	115
Bageshwar	2023	30	89.5	92	108	153

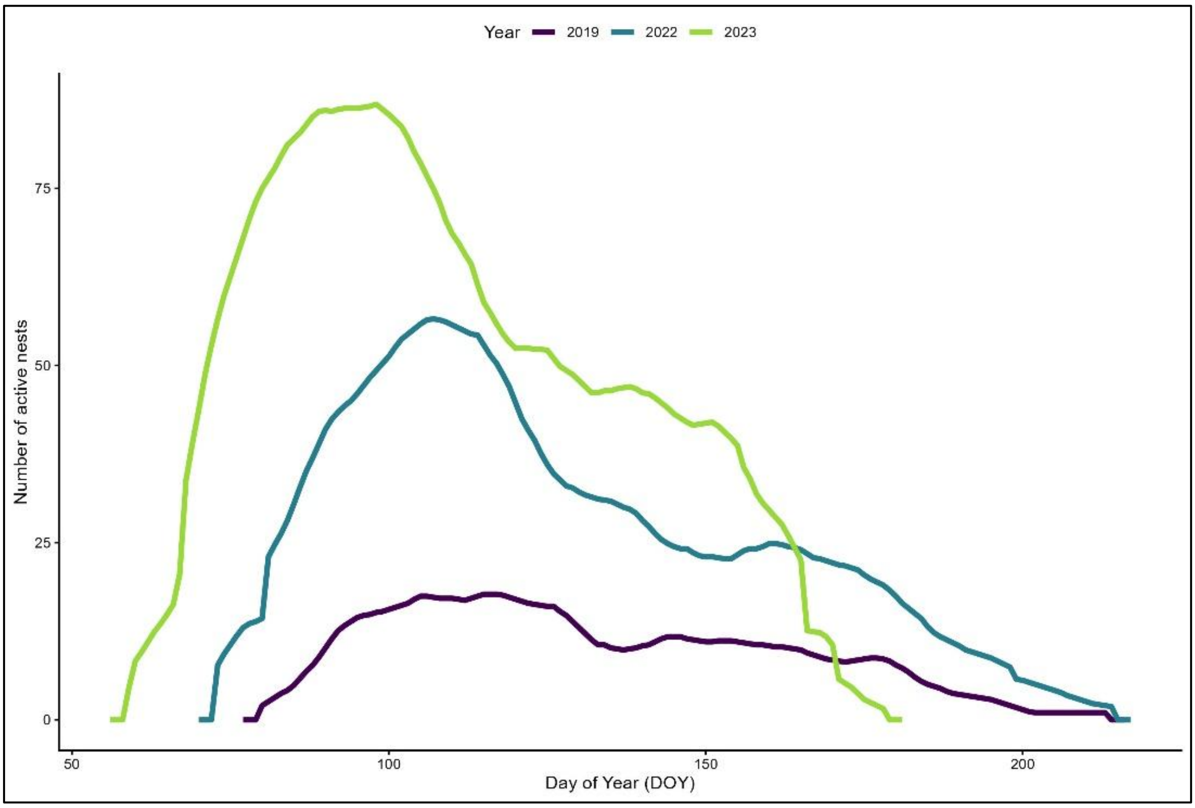

Fig 4.6 Nest activity of Barn Swallow in Uttarakhand Himalaya for three years of survey (2019, 2022 and 2023).

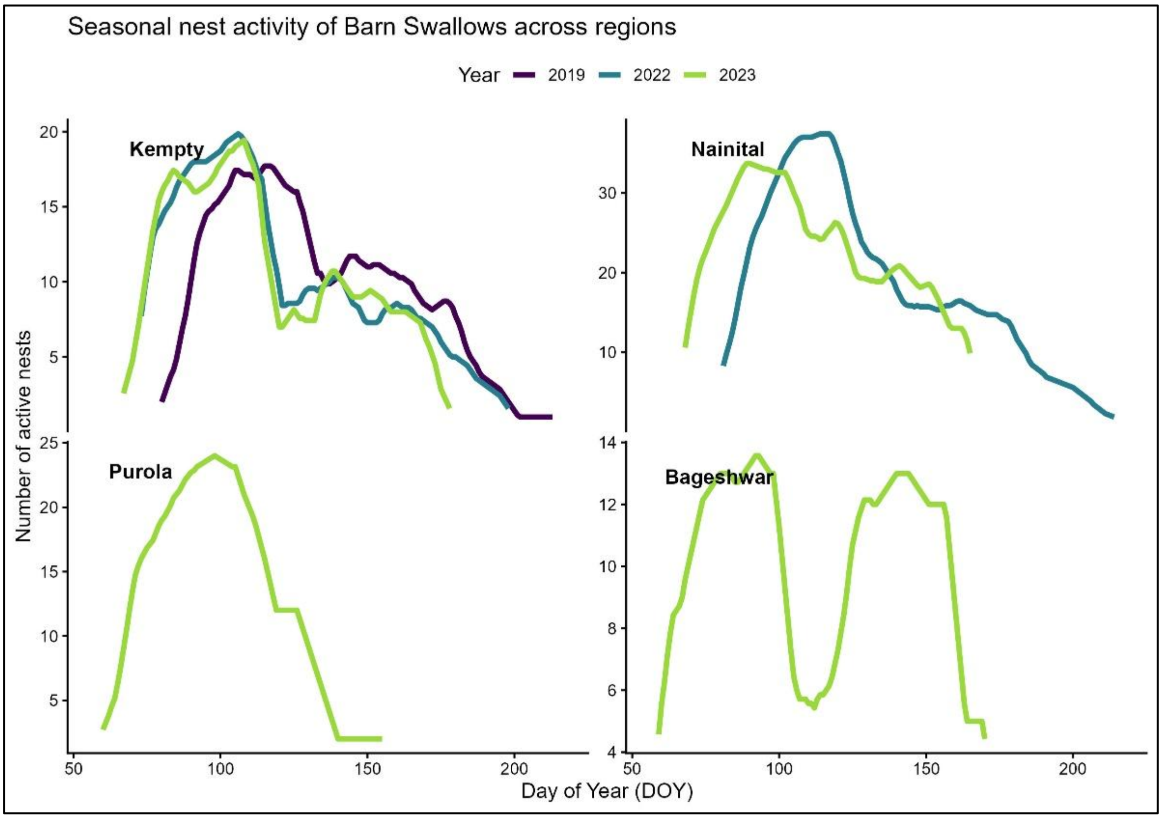

Fig 4.7 Nest activity of Barn Swallow across four sites – Kempty, Nainital, Purola and Bageshwar within Uttarakhand Himalaya.

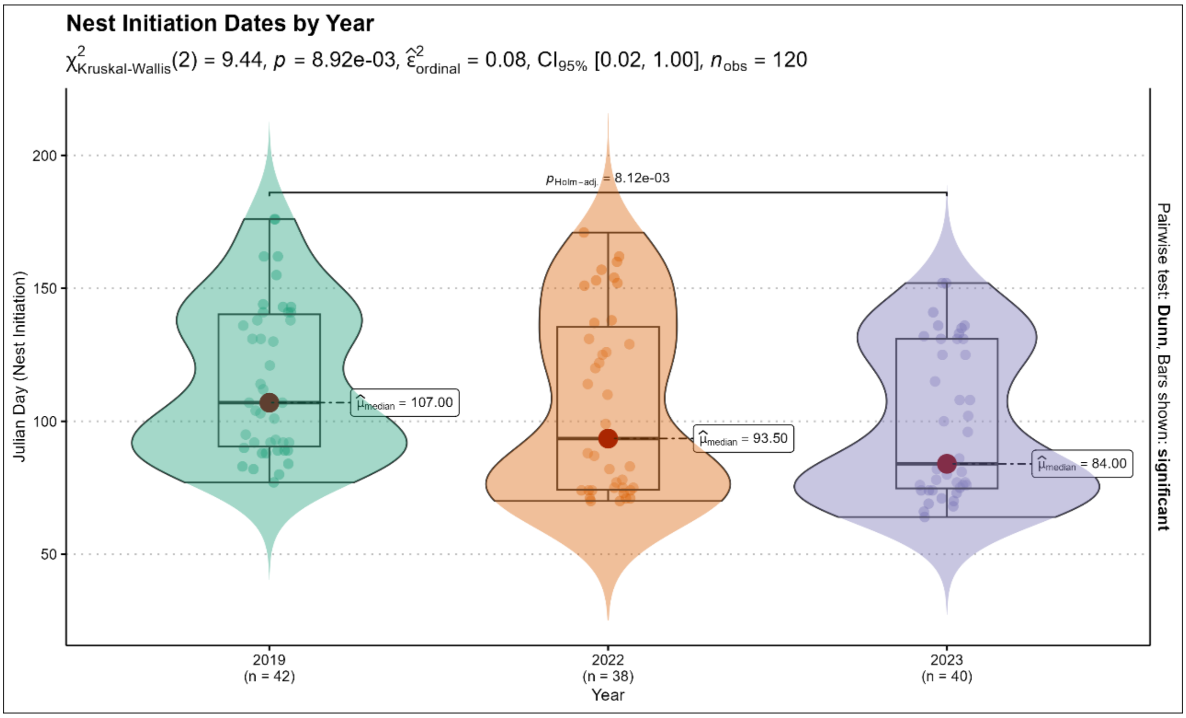

Fig 4.8 Variation in Barn Swallow nest initiation dates across three years of monitoring in Kempty, Uttarakhand.

Breeding Parameters across Uttarakhand

Across Uttarakhand, Barn Swallows initiated nests at a mean day of year of 102.2 ± 30.3 (n = 317 nests). Mean clutch size was 3.88 eggs per nest, mean brood size at hatching was 3.25 chicks, and successful nests fledged an average of 2.63 young per nest. Across years, mean clutch size ranged from 3.79 eggs in 2022 to 3.98 eggs in 2019, while mean brood size ranged from 3.00 to 3.34 chicks. Mean number of fledglings ranged from 2.32 fledglings per nest in 2019 to 2.69 in 2022 and 2.68 in 2023 (*Table 4.6*). Across sites (*Table 4.7Table 4.8*), mean clutch size was highest in Purola (4.0 eggs) and lowest in Nainital (3.77 eggs). Mean brood size was greatest in Bageshwar (3.57 chicks), while fledging output was highest in Bageshwar (3.07 fledglings per nest) and lowest in Kempty (2.18).

Table 4.6 Number of active nests and nesting periodicity and breeding parameters across years of monitoring.

Year	No. of Active Nests	Nest Active Day	Clutch size	Brood size	Fledgling Size
2019	41	116 ± 28.9	3.98	3	2.32
2022	103	109 ± 31.3	3.79	3.21	2.69
2023	173	94.9 ± 28.1	3.92	3.34	2.68
Uttarakhand	317	102 ± 30.3	3.88	3.25	2.63

Table 4.7 Number of active nests and nesting periodicity and breeding parameters across selected sites in Uttarakhand

Site	No. of Active Nests	Nest Active Day	Clutch size	Brood size	Fledgling Size
Kempty	120	107 ± 31	3.97	3.08	2.18
Nainital	131	103 ± 28.9	3.77	3.26	2.93
Purola	36	89 ± 28.8	4	3.52	2.75
Bageshwar	30	93.4 ± 30.2	3.9	3.57	3.07

Table 4.8 Number of active nests and nesting periodicity and breeding parameters across years and sites

Site	Year	No. of Active Nests	Nest Active Day	Clutch size	Brood size	Fledgling Size
Kempty	2019	41	116 ± 28.9	3.98	3	2.32
	2022	39	107 ± 33.9	4.1	3.05	2.08
	2023	40	98.9 ± 28.5	3.85	3.21	2.15
Nainital	2022	64	110 ± 29.8	3.59	3.31	3.07
	2023	67	96.3 ± 26.5	3.93	3.21	2.77

Nest Success

Across Uttarakhand, apparent nest success was 62.2%, with 204 of 328 monitored nests successfully fledging at least one young. Mean hatching success was 81.2%, while mean fledging success was 79.1% (*Table 4.9*). Apparent nest success varied moderately among years (*Table 4.9*), with lowest in 2019 (58.5%), increasing in 2022 (65.8%) and declining slightly in 2023 (60.7%). Across regions, apparent nest success varied ranging from 53.3% in Kempty to 80.0% in Bageshwar (*Table 4.10*). Mean hatching success was highest in Bageshwar (91.8%) and lowest in Kempty (73.6%), whereas fledging success ranged from 68.3% in Kempty to 87.4% in Nainital.

Within sites, nest success also varied across years (*Table 4.11, Fig 4.9*). In Kempty, apparent nest success declined from 58.5% in 2019 to 51.3% in 2022 and 50.0% in 2023, accompanied by consistently low hatching (70.5–77.2%) and fledging success (66.4–71.2%). In contrast, Nainital showed high apparent success in both 2022 (73.3%) and 2023 (59.7%), with consistently high fledging success (92.4% and 81.1%, respectively).

Table 4.9 Apparent nest success across years with mean clutch, hatching and fledgling size in Uttarakhand.

Year	No. of Active Nests	Clutch size	Hatching Success	Fledging Success	Nest Success
2019	41	3.98	73.4	71.2	58.5
2022	114	3.79	82.5	83.8	65.8
2023	173	3.92	82.4	77.9	60.7
Uttarakhand	328	3.88	81.2	79.1	62.2

Table 4.10 Apparent nest success across regions with mean clutch, hatching and fledgling size.

Region	No. of Active Nests	Clutch size	Hatching Success	Fledging Success	Nest Success
Kempty	120	3.97	73.6	68.3	53.3
Nainital	142	3.78	84.3	87.4	66.9
Purola	36	4	85.4	80.2	58.3
Bageshwar	30	3.9	91.8	81.5	80

Table 4.11 Apparent nest success across regions and years with mean clutch, hatching and fledgling size.

Site	Year	No. of Active Nests	Clutch size	Hatching Success	Fledging Success	Nest Success
Kempty	2019	41	3.98	73.4	71.2	58.5
	2022	39	4.1	70.5	66.4	51.3
	2023	40	3.85	77.2	66.7	50
Nainital	2022	75	3.62	89.7	92.4	73.3
	2023	67	3.93	79.1	81.1	59.7

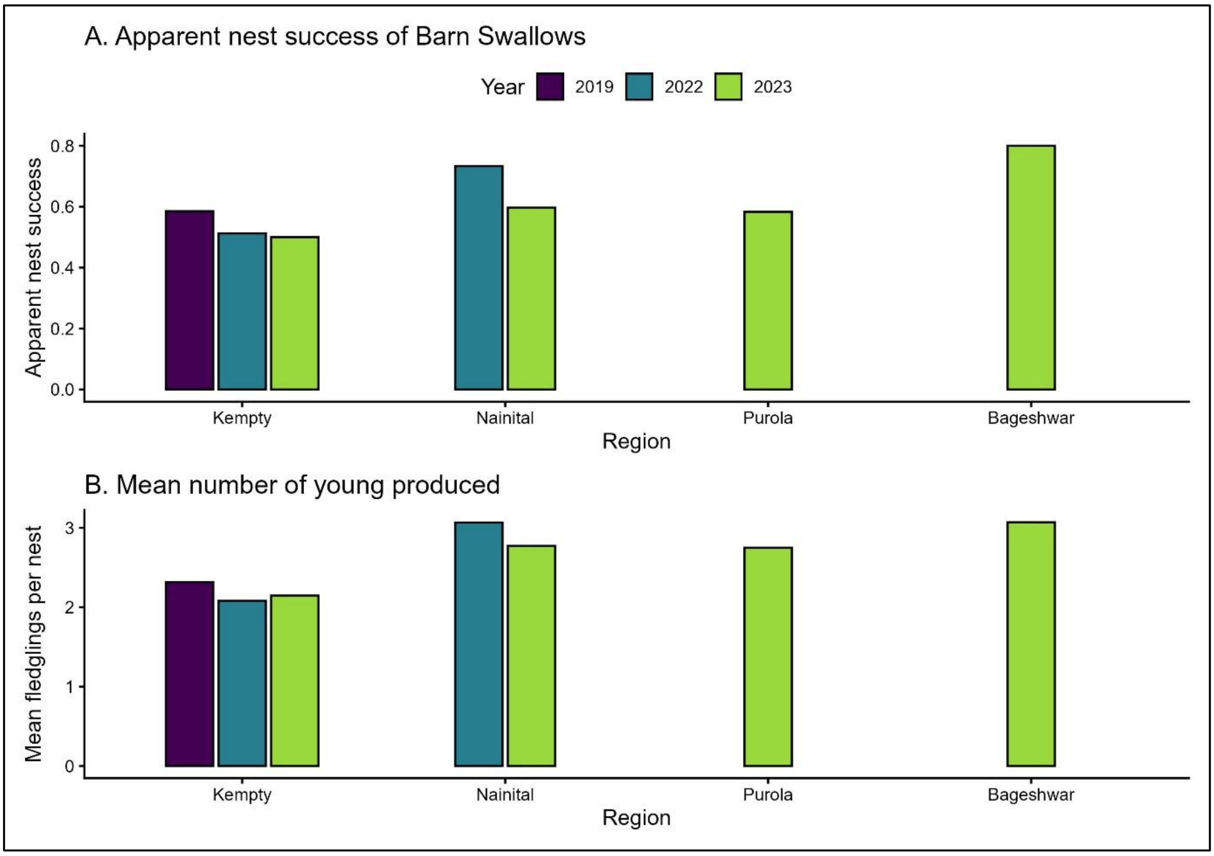

Fig 4.9 Apparent nest success (A) of active Barn Swallow nests with mean fledglings per nest (B) across regions and years.

Mayfield Nest Success

Across Uttarakhand the mean Mayfield nest success was estimated to be 76.5% (*Table 4.12*). Nainital showed the highest nesting success (84%), supported by a high DSR (0.995) and relatively long mean nesting length (32.2 days). Bageshwar also exhibited high nest success (87%), despite a shorter mean nesting length (27.8 days). In contrast, Kempty had the lowest Mayfield success (67%), associated with the highest number of failures (43 failures over 3,309 exposure days) and a comparatively lower DSR (0.987). Purola showed intermediate nest success (78%) with moderate exposure duration and failure rates (*Table 4.12, Fig 4.10*).

Across years, Mayfield nest success was lowest in 2019 (70%), based on 37 nests and 1,062 exposure days, with a DSR of 0.988 (*Table 4.13*). Nest success increased in 2022 (0.803), coinciding with a higher DSR (0.993) and longer mean nesting length (32.7 days). In 2023, despite the largest sample size (145 nests), Mayfield success declined slightly to 0.758, with a DSR of 0.991 and a mean nesting length of 31.9 days.

For sites with multiple year observations, Mayfield nest success declined from 0.702 in 2019 to 0.63 in 2022, before increasing slightly to 0.673 in 2023 at Kempty. While at Nainital, nest success was markedly higher, particularly in 2022, when Mayfield success reached 93%, supported by a very high DSR (0.998) and low failure incidence (4 failures over 1,926 exposure days). In 2023, Mayfield success at Nainital declined to 0.751, associated with an increase in failures (16 failures) and a lower DSR (0.991), despite a similar mean nesting length (*Table 4.14*).

Table 4.12 Mayfield nest success across regions with total exposure days, failures, daily survival rate (DSR) and mean nesting length.

Region	Total Active Nests	Total Exposure Days	Total Failures	Daily Survival Rate (DSR)	Mean Nesting Length	Mayfield success
Kempty	107	3309	43	0.987	30.9	0.667
Nainital	115	3705	20	0.995	32.2	0.84
Purola	28	1028	7	0.993	36.7	0.778
Bageshwar	28	778	4	0.995	27.8	0.867
Uttarakhand	278	8820.5	74	0.991	31.7	0.765

Table 4.13 Mayfield nest success across years with total exposure days, failures, daily survival rate (DSR) and mean nesting length.

Year	Total Active Nests	Total Exposure Days	Total Failures	Daily Survival Rate (DSR)	Mean Nesting Length	Mayfield success
2019	37	1062	13	0.988	28.7	0.702
2022	96	3134	21	0.993	32.7	0.803
2023	145	4624	40	0.991	31.9	0.758

Table 4.14 Mayfield nest success across regions and years with total exposure days, failures, daily survival rate (DSR) and mean nesting length.

Region	Year	Total Active Nests	Total Exposure Days	Total Failures	Daily Survival Rate (DSR)	Mean Nesting Length	Mayfield success
Kempty	2019	37	1062	13	0.988	28.7	0.702
	2022	37	1209	17	0.986	32.7	0.63
	2023	33	1038	13	0.987	31.4	0.673
Nainital	2022	59	1926	4	0.998	32.6	0.934
	2023	56	1780	16	0.991	31.8	0.751

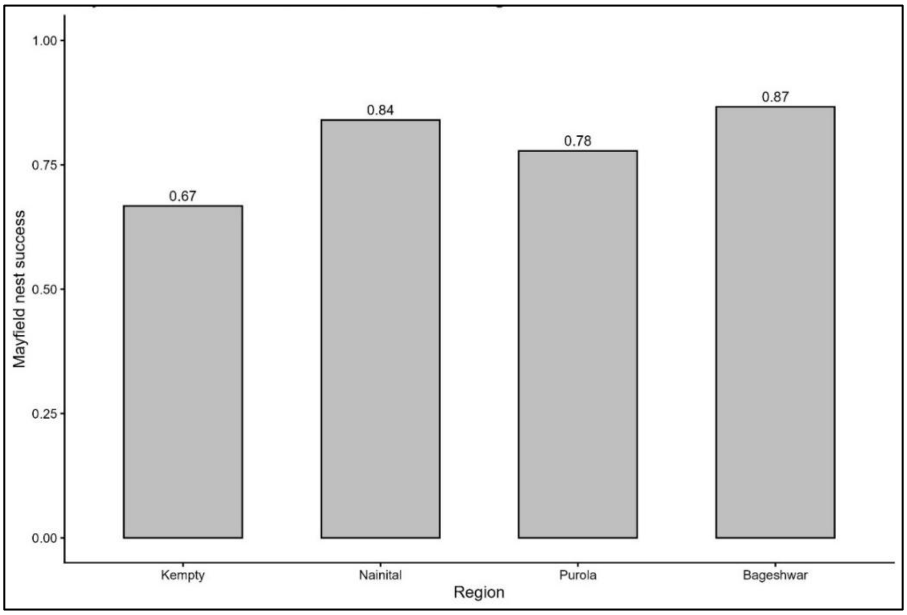

Fig 4.10 Mayfield nest success of Barn Swallow across four selected sites – Kempty, Nainital, Purola and Bageshwar in Uttarakhand.

Regional and temporal effects on nest success

The global GLM revealed a significant effect of region on nest success ($\chi^2 = 9.94$, df = 3, $P = 0.019$). In contrast, year had no significant effect on nest success ($\chi^2 = 1.66$, df = 1, $P = 0.20$). Relative to Kempty, nest success was significantly higher in Nainital (β = 0.72 ± 0.28 SE, $P = 0.010$) and Bageshwar (β = 1.48 ± 0.52 SE, $P = 0.005$), while differences between Kempty and Purola were not statistically significant. These results are consistent with patterns observed in Mayfield nest success estimates. Within Kempty, no significant inter-annual variation in nest success was detected (β = −0.09 ± 0.11 SE, $P = 0.41$). Similarly, in Nainital, nest success showed only a weak, non-significant decline between 2022 and 2023 (β = −0.62 ± 0.36 SE, $P = 0.09$).

Diet of Barn Swallows and Potential Prey availability

Prey composition in the diet of Barn Swallow nestlings

A total of six insect orders in the diet of nestlings Barn Swallows were identified (*Fig 4.11A*). The frequency of Coleoptera was the highest (96.7%) followed by Hymenoptera (75%), Hemiptera (15%), Diptera (13%), Isoptera (11%), and Odonata (0.4%). PERMANOVA analysis indicated a significant difference in insect prey community composition between rural and urban Barn Swallow populations ($R^2 = 0.17$, F = 49.18, p = 0.001), where settlement type accounted for 17.3% of the total variation in prey assemblages. Within settlement types, prey composition showed weaker but significant spatial structuring. Among rural localities, locality explained only 6.3% of the variation ($R^2 = 0.063$, F = 2.584, p = 0.029), whereas among urban localities, locality accounted for 10.5% of the variation ($R^2 = 0.105$, F = 4.417, p = 0.001). Consistent with these results, the NMDS ordination (*Fig 4.12*) showed clear separation between rural and urban samples, with tighter clustering of the rural prey community and more dispersed urban diets.

Across all sites, prey composition in the diet of Barn Swallow nestlings showed no significant temporal variation ($R^2 = 0.0084$, F = 1.981, p = 0.118). However, the two urban sites showed a weak but significant temporal variation in prey composition ($R^2 = 0.0287$, F = 3.395, p = 0.033).

Insect prey availability

Insect sampling through sweep-netting captured representatives from seven insect orders (*Fig 4.11B*). Across the two settlement types, Diptera exhibited the highest frequency of occurrence, followed by Coleoptera, Hymenoptera, Hemiptera, Aranea, Orthoptera and Lepidoptera. Hymenoptera was the only order with a significantly different frequency of occurrence between the two sites (Mann-Whitney U = 587.5, $p < 0.05$). The PERMANOVA analysis showed a significant difference in insect community composition between rural and urban settlements ($R^2 = 0.085$, F = 5.58, p = 0.001), however it accounted for 8.5% of the total variation in insect presence-absence data.

Insect prey availability vs. dietary composition

Across all sites, the insect prey composition in nestlings' diet and insect prey in the surrounding environment showed a significant difference ($R^2 = 0.225$, F = 86.39, p = 0.001, *Fig 4.13 A*). Similarly, when compared at the settlement level, significant differences were observed for both rural ($R^2 = 0.292$, F = 35.03, p = 0.001, *Fig 4.13 B*) and urban settlement types ($R^2 = 0.256$, F = 31.68, p = 0.001, *Fig 4.13 C*).

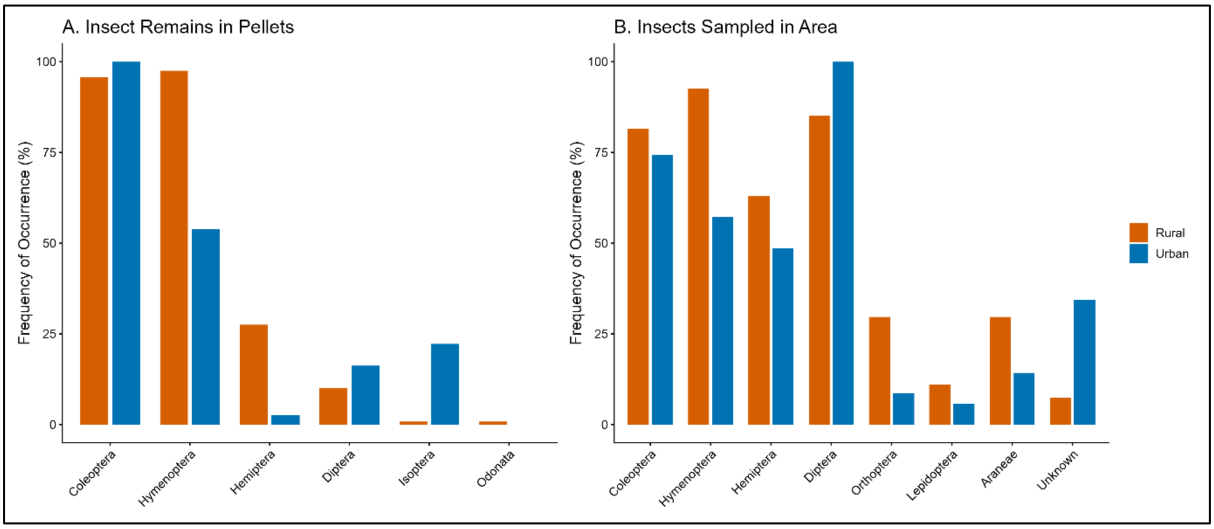

Fig 4.11 Frequency of occurrence of insect prey remains from Barn Swallow nestling pellets (A) and insect taxa sampled in the surrounding environment (B) across rural and urban sites. Note that environmental insect sampling (B) was conducted at only two locations: one rural site (Purola) and one urban site (Nainital).

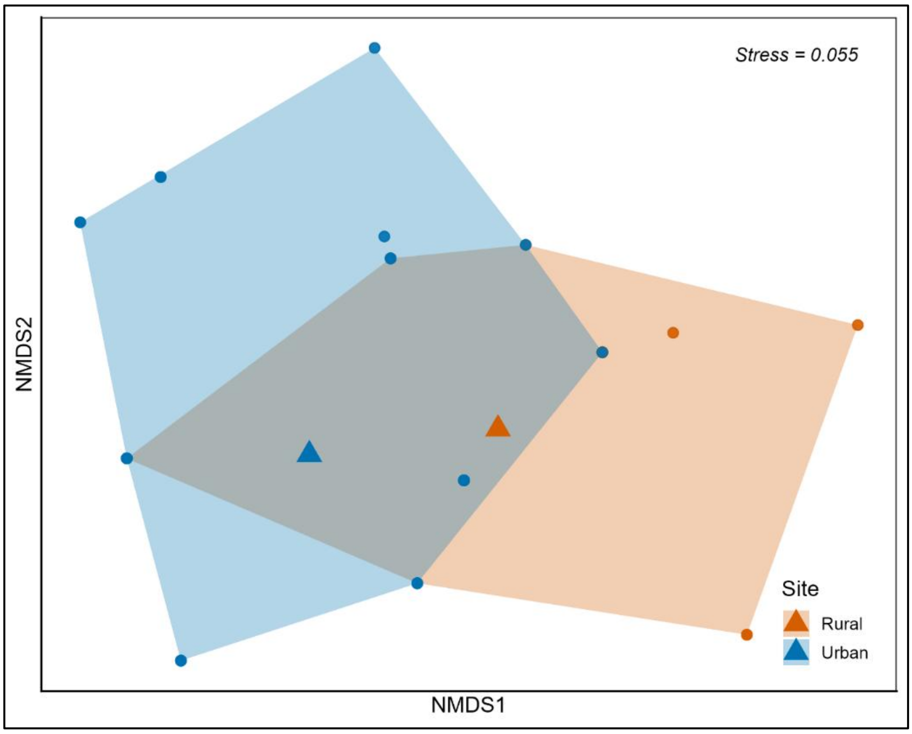

Fig 4.12 NMDS plot representing relative similarity/dissimilarity between faecal samples of nestlings' Barn Swallows. Points that cluster together indicate similar prey composition, while points that are farther apart depict more distinct prey composition. Polygons delineate the multivariate diet space occupied by rural (orange polygon) and urban (blue polygon) samples, illustrating within-group variation in prey assemblages.

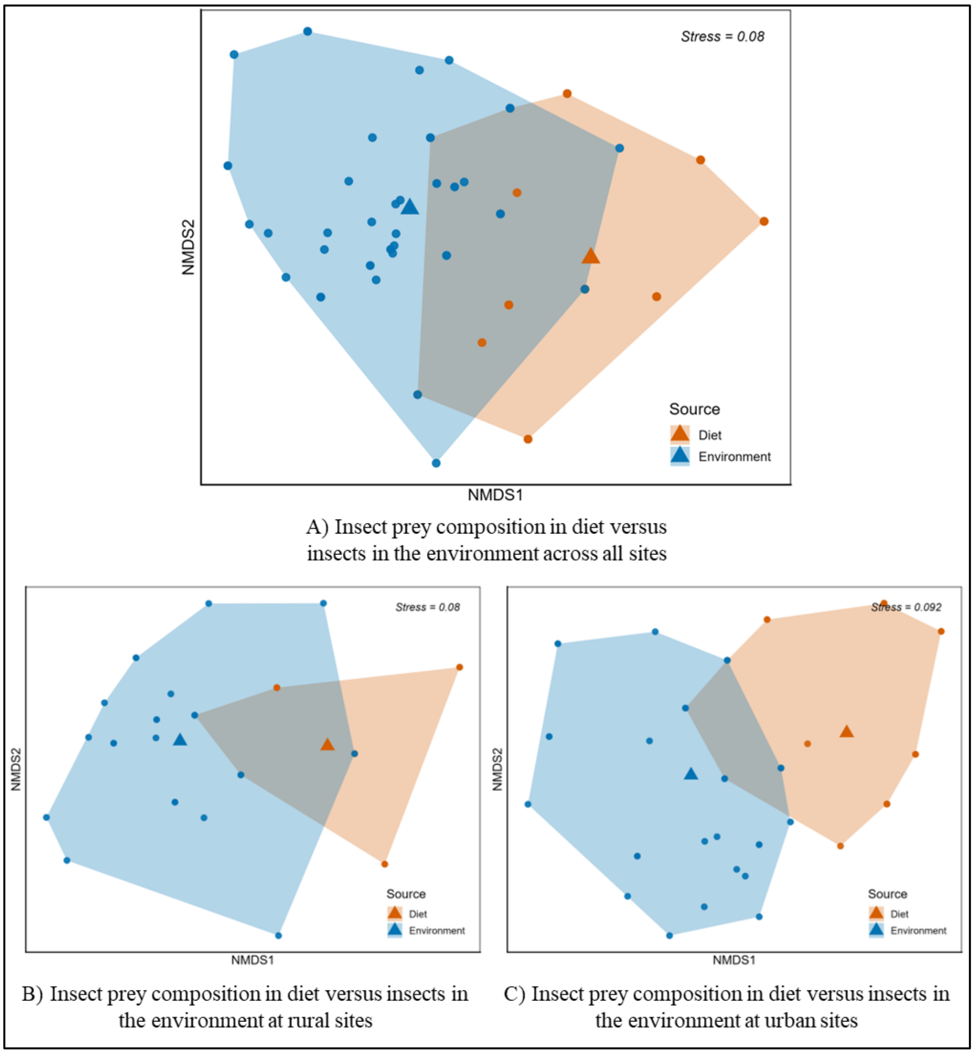

Fig 4.13 NMDS ordination plots showing differences between insect prey availability (blue-coloured polygon) and prey detected in Barn Swallow nestlings' diet (orange-coloured polygon) across all sites (A), the rural site Purola (B), and the urban site Nainital (C). The ordinations indicate different insect composition between available prey and consumed prey. Note: Stress values indicate good model fit as values <0.1 indicate a reliable ordination, and values <0.05 are considered excellent.

4.4 Discussion

Breeding distribution of Barn Swallows across the Indian Himalaya

This study provides the first large-scale, systematic assessment of the breeding distribution of the Barn Swallow across the Indian Himalayan region. Nesting records spanning from 489 to 2317 m a.s.l. confirm that the Barn Swallow is a widespread and regular breeder across much of the Himalayan arc, extending from the western Himalaya (Jammu & Kashmir) to the easternmost ranges in North Bengal and Sikkim and then in Northeast India in Manipur. This elevational span closely aligns with the upper breeding limits reported for the species in other mountainous regions of Eurasia, where breeding is largely constrained by temperature, season length, and prey availability (Turner, 2006; Newton, 2023). Moreover, the breeding surveys also confirms the only one earlier record of Ali & Ripley (1987) to be a summer-breeding visitor in the Himalaya. This study provides a novel information on species distribution from Imphal valley in Manipur.

The predominance of nesting records within the mid-elevational belt indicates the presence of mid-domain effect (MDE) hypothesis on the species occurrence (Colwell & Hurtt, 1994). This signifies that intermediate elevations provide optimal trade-offs between climatic suitability and resource availability (McCain, 2009). Further, the elevational distribution of species proposed to be dictated by various processes such as climate, productivity, habitat heterogeneity and mass effects (Kattan & Franco, 2004; Rahbek, 2005). In the Himalaya, low elevations experience harsh summers and heavy monsoon rainfall while also is under high urbanisation pressure while at high elevations the extremely low temperatures and shorter day length might limit the species distributional range. The concentration of nests between 1000 and 2000 m elevational belt therefore likely reflects a combination of favourable temperature conditions, extended breeding windows, and presence of sufficient insect prey during the breeding season. Similar mid-elevation optima have been reported for a range of Himalayan bird species, suggesting that this zone represents a biodiversity hotspot driven by favourable climatic and ecological conditions (Acharya et al., 2011).

Within Uttarakhand, higher concentration of Barn Swallow nests in the eastern region suggests that regional climatic factors likely play an important role in shaping breeding distribution. In the Himalayan ranges, rainfall reduces from east to west along the path of travel of southwest monsoon, as the number of days between its onset and withdrawal reduces (Kansakar et al., 2004). Therefore, relatively higher precipitation in the eastern Uttarakhand might result in more productive agroecosystems supporting higher insect diversity and abundance and could therefore possibly be responsible for higher number of nests of Barn Swallows. Overall, the nesting locations when overlaid with climatic classification layer, the majority of nests fell in the climatic zone characterised by mild, dry winters and short, warm summers. These conditions likely facilitate early breeding onset, prolonged breeding activity, and improved reproductive outcomes. Interestingly, the reason for resident Barn Swallow populations at the lower latitudes in Imphal valley, Manipur indicate the stable weather conditions as well as productivity in the region throughout the year. These conditions likely enable the Barn Swallows to reside in the region and unlike the Himalayan populations not undertake long migrations.

Nest site characteristics and attributes

Historically, Barn Swallows have been observed to nest on cliffs, in caves and tree holes (Speich et al., 1986). It is only with the arrival of human settlements during the Holocene that the species adapted to build its nest in human properties (Zink et al., 2006; Brown & Brown, 2020). In the Himalaya, it appears that the species has completely shifted its nesting on human-made structures as is evident from my findings that more than 70% of nests were located inside buildings with some regions exhibiting indoor nesting rates exceeding 90%. The adaptation of nesting inside human properties provided additional protection to their nests from predators (Møller, 2010). The dominance of commercial structures, particularly shops, as nesting sites in most Himalayan states suggest species preference for nesting as in addition to protection from predators, shops typically offer open entrances throughout the day hours. In contrast, houses were more frequently used in regions such as Jammu & Kashmir and Manipur, reflecting the presence of traditional architecture which allows the swallows to fly in and out through large ventilation windows or spaces (Kaur, 2024). Across sites, nest orientation did not show a strong directional bias with nests distributed relatively evenly across aspects. In many bird species, nest orientation reflects microclimatic optimisation, particularly in exposed environments (Ambrosini et al., 2012). However, some birds depict no preference for directionality in nest building (Ardia et al., 2006; Kim et al., 2023) Given their behaviour of nesting indoors, swallows likely avoid exposure to weather extremities and thereby do not prefer for any direction to orient their nests.

Globally the association of Barn Swallows with humans reflects their long evolutionary history as commensal breeders (Stetzel, 2001; Turner, 2006) . The high adaptability of Barn Swallows, along with the cultural association that local people in the Himalaya have enabled the species to nest for long in the region. Local people across the region regard swallows nesting in one's property to be auspicious, and particularly the older generation of people view the swallows as an embodiment of "Goddess Laxmi", the goddess of wealth, and so a sign of prosperity. The tradition of swallows nesting inside shops in the area is reportedly a longstanding one, closely tied to the daily opening and closing routines. These cultural values for the Barn Swallow in the Himalayan region are vital for their survival. Globally, despite being common, significant declines in Barn Swallow populations have been reported (Vickery et al., 2013; PECBMS, 2024), primarily due to loss of traditional nesting sites and decreasing aerial insect prey linked to changing land-use practices (Teglhøj, 2017; Imlay & Leonard, 2019; Spiller & Dettmers, 2019).

Breeding phenology in the Uttarakhand Himalaya

The breeding season of Barn Swallows in Uttarakhand extended from late February to late June, with most nesting activity concentrated between early April and mid-May. This timing is broadly consistent with breeding schedules reported from other temperate and montane regions, where breeding is closely linked to seasonal peaks in insect availability (Turner, 2006; Winkler et al., 2014). The relatively short breeding window reflects the constraints imposed by elevation, climate, and monsoon onset in the Himalaya (*Fig 4.14*). It was observed that before the onset of southwest monsoon, the nesting is completed, this finding was consistent across years and across sites.

Notably, the spatial variation in nest commencement at some sites may reflect local climatic conditions, elevation, aspect, and microhabitat characteristics. However, it could also be a sampling bias as these sites were surveyed for only one breeding season. One of the most significant findings of this study is the advancement of breeding phenology across years, particularly between 2019 and 2023. Nest initiation, egg-laying, hatching, and fledging all occurred progressively earlier, with 2023 exhibiting the earliest median dates across multiple sites. Such temporal shifts are consistent with widespread phenological advances documented in birds globally in response to climate warming (Both et al., 2006; Dunn et al., 2011).

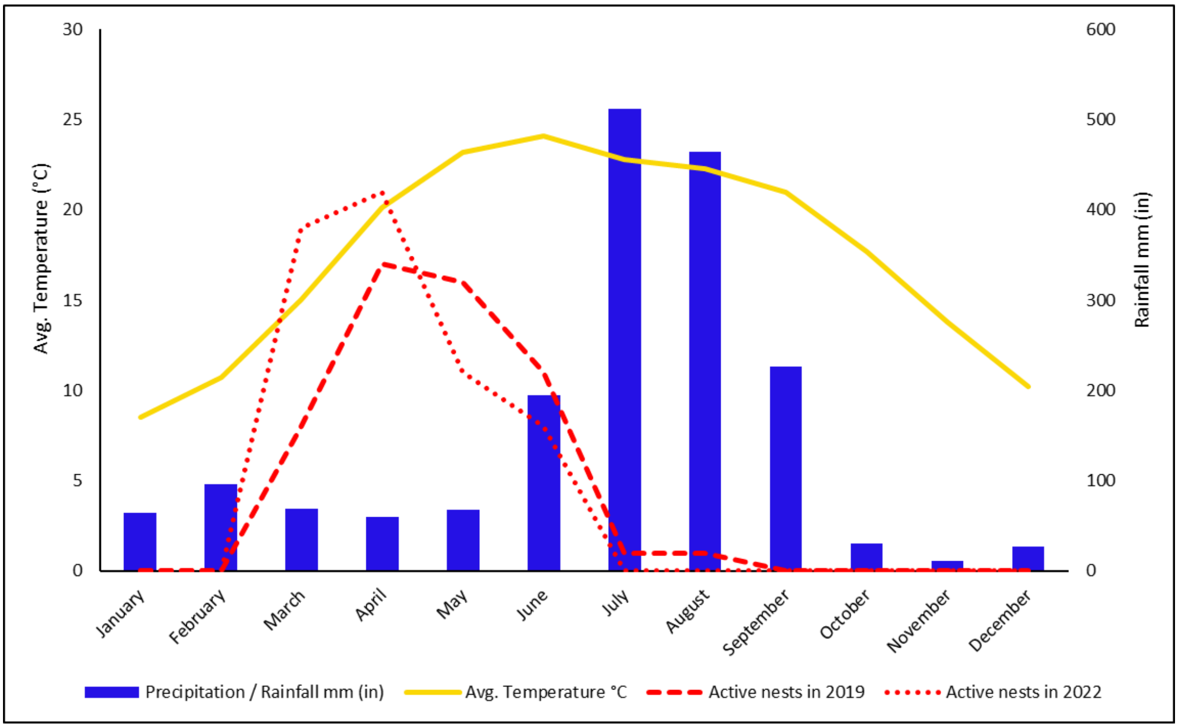

Fig 4.14 Representation of Barn Swallow breeding periodicity with average temperature and rainfall trend in the region in Uttarakhand.

Breeding parameters in a Himalayan context

Mean clutch size of approximately four eggs aligns with values reported from Europe and Asia, suggesting that Himalayan populations do not exhibit strong reductions in clutch size despite the constraints of elevation and shorter breeding seasons (Stetzel, 2001; Turner, 2006). However, the observed decline from clutch size to fledging output indicates that a substantial proportion of reproductive potential is lost during incubation and chick-rearing stages. Mean fledging success of approximately 2.6 young per nest suggests moderate reproductive performance, potentially constrained by factors such as weather variability, food availability, predation, and competition. Spatial variation in breeding parameters among sites further indicates that local habitat quality and disturbance levels play a critical role in shaping reproductive outcomes.

Nest success patterns

Both apparent nest success and Mayfield estimates revealed moderate overall nesting success across Uttarakhand. The use of Mayfield methods provided more robust estimates by accounting for exposure days and uneven monitoring effort, highlighting the importance of methodological rigor in nest success studies (Mayfield, 1975; Johnson, 1979). Regional differences in nest success were pronounced. Kempty consistently exhibited lower nest success, lower hatching success, and lower fledging success compared to other sites, whereas Nainital and Bageshwar showed substantially higher success rates. These patterns were supported by both apparent and Mayfield estimates, as well as by GLM results indicating a significant effect of region but not year on nest success.

The consistently lower success observed at Kempty likely reflects a combination of high nest density, increased competition (particularly with House Sparrows), and higher levels of human disturbance. High-density breeding can lead to increased competition for nest sites and food, as well as elevated parasite loads, all of which can reduce reproductive success (Put et al., 2021). In contrast, sites with lower nest density or more stable nesting substrates may provide higher-quality breeding environments. However, the absence of multi-year data from other site restricts us to say that regionally Barn Swallows are exhibiting differences in nesting success.

Nest Failure

The strong dependence on specific building types observed in the Himalaya underscores the vulnerability of Barn Swallows to rapid infrastructural transformation and the loss of traditional architectural features. The widespread loss of anthropogenic nesting structures is consistently identified as a major limiting factor for Barn Swallow reproduction in human-dominated landscapes (Campbell et al., 2007; COSEWIC, 2011; Brown & Brown, 2020). In the Himalaya, with rapid shifts towards changing traditional architecture to modern buildings, nest sites will become increasingly limited for Barn Swallows. My observation on changing buildings in small village Kempty resulted in loss of nests that were earlier inside the shops which resulted in pair to build nest outside. However, nesting outside escalated the competition with other human-commensal species (*Fig 4.15*) such as the House Sparrow (*Passer domesticus*) and Red-rumped Swallow (*Cecropis daurica*).

Barn Swallow nests loss occurs due to various biotic as well as abiotic reasons, for instance, in temperate and tropical regions, weather extremes result in nest deterioration especially if nests are built on old unstable substrates on human structures (Turner, 2006; Tian et al., 2022). Like our findings, egg and nestling disappearance, commonly interpreted as predation by avian or mammalian predators or accidental loss during provisioning, represents another widespread cause of failure across breeding sites (Safran, 2006; Tian et al., 2022). At study site Kempty, the presence of ectoparasites which resulted in failure of all broods in one nest in 2019 was recorded during the study. Nests loss due to ectoparasite infestation has been reported contributing substantially to breeding failure in North American and European populations (Shields & Crook, 1987; Barclay, 1988; COSEWIC, 2011). In addition, interspecific interference competition, most notably from House Sparrows has been documented to cause nest failure through nest usurpation, destruction of eggs or nestlings, and displacement of breeding adults, leading to reduced fledging success in sympatric populations (COSEWIC, 2011; Brown & Brown, 2020).

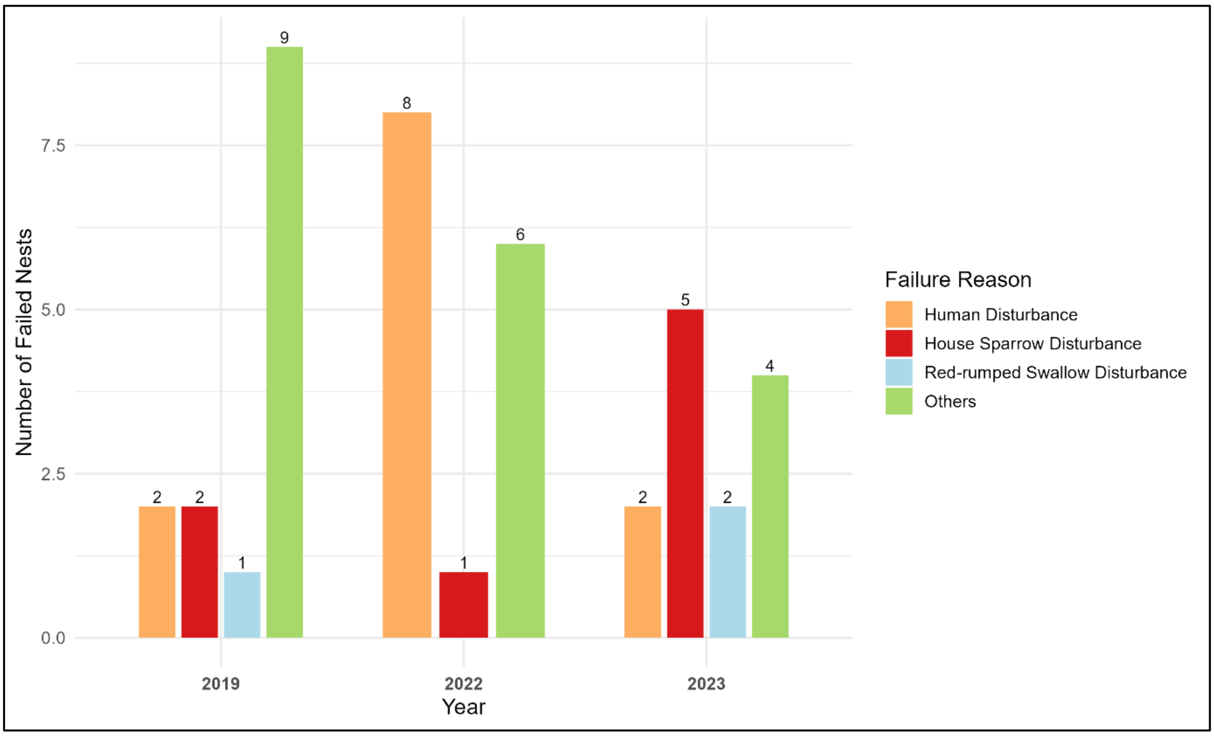

Fig 4.15 Number of nests of Barn Swallow that failed due to reasons such as interference by other commensal species – House Sparrow and Red-rumped Swallow and anthropogenic disturbances across years in Kempty, Uttarakhand.

Dietary analysis

Barn Swallow in the Uttarakhand Himalaya exhibited a diverse diet during the breeding season, with notable preference for Coleoptera and Hymenoptera, remains of which occurred in 96.7% and 75% of total pellets examined, respectively. Other insect orders – Hemiptera, Diptera, Isoptera and Odonata occurred in only few pellets. Although this study provides the first dietary assessment of Barn Swallows from its southernmost extent of global breeding range in the Himalaya, the findings are consistent with of those conducted in temperate breeding regions

(Turner, 1982, 2006). The presence of large-bodied insect prey: Coleoptera and Hymenoptera in the diet indicates prey selectivity by Barn Swallows linked to prey size and the prey's flying ability (Orłowski & Karg, 2011, 2013a) consistent with optimal foraging theory (Turner, 2006).

At temperate breeding grounds in Europe and America, Barn Swallows primarily nests in barns where livestock husbandry is more common and thereby abundance of Coleoptera and Diptera prey which is also associated with higher reproductive success (Ambrosini et al., 2002; Orłowski & Karg, 2013b; Teglhøj, 2017). On the contrary, at our study sites nesting predominantly occurred within human habitations such as houses and shops and at sites where livestock husbandry is almost negligible. We suggest that this likely explain the lower occurrence of Diptera which is typically associated with livestock farming (Ambrosini et al., 2002; Teglhøj, 2017) and relatively higher presence of Hymenoptera in the diet. A similar pattern was also observed by (Glowacki, 1977) at rural sites in Poland lacking animal husbandry, where Diptera constituted only minor proportion in the diet of Barn Swallows, while Hymenoptera accounted for more than 70%.

The site-specific dietary differences are governed by multiple factors such as local prey availability, land-use patterns driving the occurrence of prey and human activities (Turner, 1982; Henderson et al., 2007; Orłowski & Karg, 2011). The differences in diet between rural and urban settlements highlights the influence of local habitat and seasonal weather conditions influencing the insect prey availability. At the urban site, Nainital the higher occurrence of Diptera likely is due to habitat characteristics such as nest sites located in markets with presence of organic waste. The smaller occurrence of Isoptera (termites) and Odonata in the diet also indicate the presence of habitat specific seasonal swarming. It would be interesting to record the influence of such seasonal swarming events on the reproductive success of Barn Swallows. For instance, flying termites and flying ants have been recorded as important prey for Barn Swallows populations wintering in Africa (Turner, 1982), even though the presence of the insect groups is dependent on the swarming events.

The comparison of prey sampling with the dietary composition of Barn Swallows revealed a degree of prey selection by the swallows. The insect sampling at study sites revealed Diptera as the most frequently encountered insect order, yet this group was underrepresented in the diet. This could likely be due to different digestion processes of chitin parts of different prey groups where faecal samples tend to preserve chitin-rich prey like beetles while softer-bodied prey such as dipterans dismembers. However, studies report that, in general, swallows during breeding often select for larger prey (Turner, 1982; Mengelkoch et al., 2004), relative to their abundance in the habitat, compared with smaller prey items (McClenaghan et al., 2019).

Our study relied on faecal sample analysis which has been employed in many previous studies (Bryant, 1973; Waugh, 1978; Turner, 1982, 1983; Orłowski & Karg, 2011, 2013b) and is reported to yield a reliable picture of diet of insectivorous birds (Poulsen & Aebischer, 1995; Orłowski & Karg, 2011, 2013b). While this method has limitations - particularly the underrepresentation of soft-bodied insects like Diptera due to digestion-related biases - it remains a practical and cost-effective tool for large-scale dietary studies. In our case, the uniform application of this method across all sites ensured consistency in data collection and enabled valid comparisons of dietary composition. It is important to note that dietary outcomes can vary across methodologies: faecal analysis tends to highlight hard-bodied prey such as Coleoptera and Hymenoptera, whereas DNA metabarcoding may overrepresent soft-bodied groups like Diptera due to primer biases (Pompanon et al., 2011). Therefore, these methodological differences require careful interpretation and underscore the importance of comparative approaches to capture dietary diversity fully.

Conservation implications and future directions

The findings of this chapter demonstrate that the breeding distribution and nesting ecology of Barn Swallows in the Uttarakhand Himalaya are governed by a complex interaction between elevation, climate, and human-modified habitats. Although the species exhibits considerable behavioural flexibility, its strong reliance on indoor nesting and specific building types renders it particularly vulnerable to rapid changes in construction practices, building renovation, and urban expansion. The progressive replacement of traditional architecture with sealed, modern structures is likely to reduce nesting opportunities and may contribute to local population declines, a pattern that has been documented across the species' range. Conservation strategies in the Himalayan region should therefore prioritise the retention of nest-friendly architectural features, promote community awareness, and integrate bird-sensitive guidelines into rural development and urban planning initiatives.

Beyond nest-site availability, the sustainability of Barn Swallow populations is closely linked to the availability and quality of aerial insect prey. Understanding dietary flexibility and foraging habitat use across both breeding and non-breeding periods is increasingly critical in the context of widespread insect declines and rapidly changing agricultural landscapes. Recent studies have demonstrated significant reductions in aerial insect biomass, particularly of nutritionally important taxa, driven by land-use intensification and pesticide use (Hallmann et al., 2017; Bowler et al., 2019). Importantly, declining insect populations may reduce prey quality rather than absolute prey quantity, with negative consequences for nestling growth, fledging condition, and post-fledging survival (Twining et al., 2016; Zhao et al., 2022). At the Himalayan breeding sites examined in this study, systematic assessment of foraging habitats and insect prey composition will therefore be essential for interpreting long-term patterns in reproductive success.

These concerns are particularly acute in the Indian Himalaya, a climatically sensitive region undergoing rapid socio-economic transformation. Accelerating urbanisation, expansion of road networks, tourism pressure, and rural outmigration are collectively reshaping settlement patterns and land-use practices (Pathak et al., 2017). Although Barn Swallows readily nest in human-dominated landscapes, insufficient or degraded foraging habitats may create urban ecological traps, wherein apparently suitable nesting sites are embedded within landscapes that fail to support adequate food resources (Teglhøj, 2017). Long-term monitoring at our study sites has already revealed a steady increase in building modernisation accompanied by a decline in suitable nesting structures. When coupled with reduced insect availability, such changes may result in breeding habitats that support nest initiation but yield poor reproductive outcomes.

As aerial insectivores and flagship farmland species, Barn Swallows play an important ecological role by contributing to natural pest regulation in agricultural systems (Jedlicka et al., 2011; Crisol-Martínez et al., 2016). Declines in insect prey can therefore have cascading effects, limiting population survival at both breeding (Grüebler & Naef-Daenzer, 2008) and wintering grounds (Sicurella et al., 2015). In light of the global decline in aerial insects (Wagner, 2020; Wagner et al., 2021), long-term, integrative monitoring of insect abundance, nesting success, and habitat change—particularly within human-dominated landscapes—is essential to assess the long-term viability of Barn Swallow populations across their full annual cycle.

4.5 References

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Chapter 5
Evolutionary History and Population Variation of the Barn Swallow (*Hirundo rustica)* Breeding Across the Indian Himalayan Region

5.1 Introduction

The Barn Swallow is a member of the most species-rich genus *Hirundo*, in the swallow family Hirundinidae, comprising 14 described species (Turner, 2004). Among the members of genus *Hirundo,* the Barn Swallow is the only species having a broad Holarctic breeding distribution and has been studied extensively through molecular and phylogenetic research. Studies show *H. rustica* to have an African origin which is supported by their close affinity to African congeners such as *H. aethiopica* and *H. angolensis* (Carter et al., 2020; Dor et al., 2010). It is estimated that around 493 kya, divergence from these relatives occurred and the ancestral lineage emerged during Pleistocence (between 280 and 300 kya), a period of major climatic oscillations that likely facilitated dispersal out of Africa (Teglhøj, 2020; Lombardo et al., 2022). Phylogeographic studies reveal the role of glacial-interglacial periods in shaping the subspecies divergence supporting the hypothesis that subspecies differentiated primarily because of range expansions and contractions in response to climatic shifts (Turner & Rose, 2010).

Barn Swallow, a human-commensal is well known among the local people across its distribution range owing to its nature of building its cup-shaped mud nest in human-inhabited areas. Consequently, it is the most widespread and abundant swallow species in the world, breeding in Eurasia and North America and migrating long-distances to winter in south to tropical Africa, northern Australia, Central and South America. Globally, six subspecies have been recognized of which four are strict migrants and two are residents (Dor et al., 2010; Brown & Brown, 2020).

The Barn Swallow is described by its characteristic plumage features include shining metallic blue-black dorsal body with chestnut forehead, chin and throat patch, a distinctive dark blue breast-band and elongated outermost tail feathers which form a distinct V-shape (Møller & Gregersen, 1994; Turner, 2004). However, ventral coloration varies from buff-white to red-buff across different populations (Møller 1994). Morphologically, the subspecies (*described in Chapter 2, section 2.3*) vary in certain traits such as body size, ventral coloration, extent of breast band, and tail streamer length, and in life-history traits such as migration patterns (Turner & Rose, 1989; Turner, 2004, 2006; Winkler et al., 2017; Seifert et al., 2018; Turbek et al., 2022; Tian et al., 2024; Anisimova et al., 2025). The largest of all is the European *rustica* with white to pale buff ventral coloration and moderately broad and complete breast band while Asian subspecies *gutturalis* is small and buff-bellied with narrower, often broken breast band.

Siberian *tytleri* is characterized by intermediate body size and dark brown ventral colour with narrow and complete breast band (Scordato & Safran, 2014). American *erythrogaster* is similar to *gutturalis* with extensively rufous throat, broken breast band diffused with rufous throat, underparts rufous chestnut to orange. Two sedentary subspecies: Egyptian *savignii* is smaller and has rufous-chestnut underparts while Middle Eastern subspecies *transitiva* is similar to *rustica* but has broader breast band and much darker rufous-buff vent (Dor et al., 2011).

Studies carried out using mitochondrial DNA (mtDNA) confirm that Barn Swallow species complex is monophyletic and different subspecies forms two major phylogenetic clusters, possibly diverged ~100 kya and geographically correspond to Europe-Middle East clade and Asia-America clade (Dor et al., 2010; Zink et al., 2006; *see Fig 2.3*). European and West Asian populations differentiated around the onset of the Holocene (~11 kya), coinciding with post-glacial warming and the stabilization of breeding habitats (Smith et al., 2018). In contrast, East and South Asian lineages colonized independently during the late Pleistocene, while the colonization of the Americas, a relatively recent event likely within the past 20–50 kya and possibly facilitated by both natural dispersal across Beringia and subsequent human-mediated processes (Hobson et al., 2015; Scordato et al., 2017; Lombardo et al., 2022). There was also a secondary dispersal event occurred about 7 kya from North America back into the Asia (Zink et al., 2006) suggested by the close phylogenetic relationship between Asian *tytleri* and American *erythrogaster*. Further, (Dor et al., 2010) using mtDNA also suggest intermingling of nominate *rustica* (migratory) with the resident *transitiva* in Israel.

The dynamic demographic history of Barn Swallows reflects a series of founder effects, bottlenecks, and secondary expansions linked to past climate fluctuations. Studies carried out using mitogenomic data show distinct haplogroups corresponding to isolated refugia, while at the same time multiple studies also revealed repeated episodes of secondary contact particularly across Eurasia resulting into formation of subspecies and hybrid zone (Santure et al., 2010; Scandolara et al., 2014; Lombardo et al., 2022). Nuclear genomic evidence further emphasizes species to have traits of high connectivity and adaptability that likely facilitated survival through repeated climatic oscillations (Safran et al., 2016; Liu et al., 2020).

In the Indian subcontinent, three out of six subspecies are reported to occur (*Fig 5.1*), where two subspecies, *H. r. rustica* and *H. r. gutturalis* breed in the Himalayas and winter in more or less throughout the subcontinent while the third subspecies, *H. r. tytleri* is a winter visitor in Northeast India (Ali & Ripley, 1987). Given varying morphometric variations among different subspecies, the occurrence of the known subspecies and their breeding distributional range is speculative. Further, there is no knowledge on the evolutionary history of the populations breeding in the Himalayan region as to when the species colonized India and how glacial events in the Himalayas have shaped its distribution in the region. Given, it is particularly interesting to determine the history of populations breeding in Manipur that have adapted to become a sedentary population unlike the migratory populations of the Himalayan region. This study fills this gap by determining the phylogeography of Barn Swallow populations breeding in the Indian Himalayan Region. The Barn Swallow populations breeding across the world have been extensively studied and therefore we included the populations breeding in India to gain deeper insights into their evolutionary history and relationships among the swallow populations.

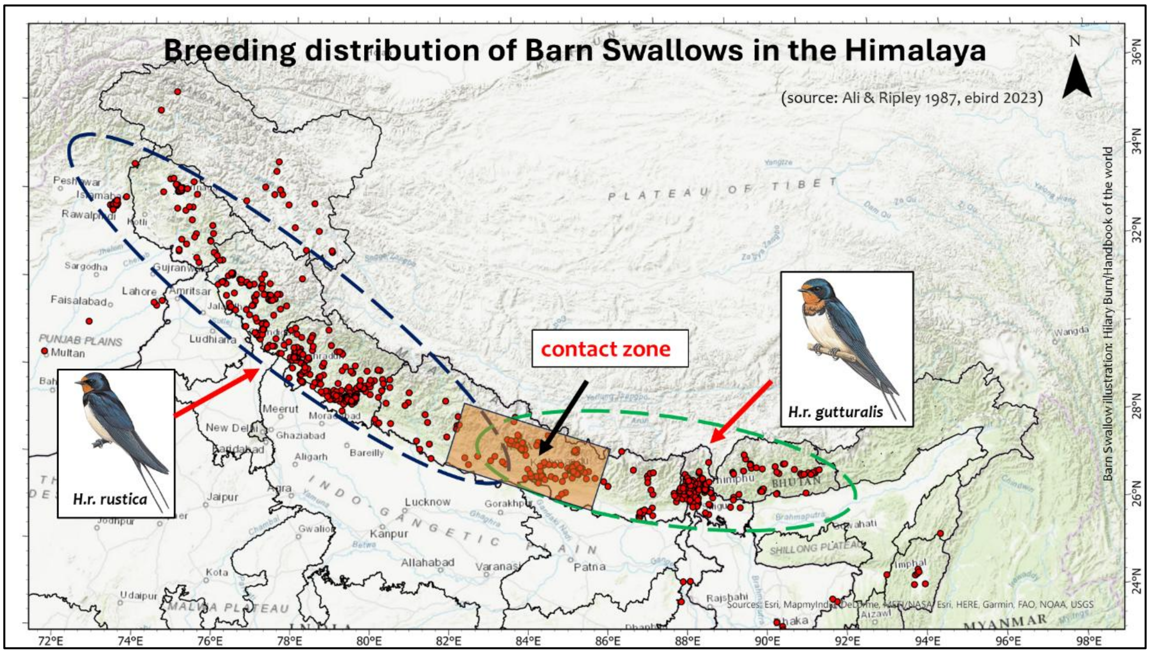

Fig 5.1 Barn Swallow subspecies distribution (in blue and green ovals) with a speculation of hybrid zone in the Central Himalayan Region as described by Ali & Ripley (1987). eBird locations filtered for the breeding period of Barn Swallows (in red) are also plotted to visualise the overall occurrence.

5.2 Methodology

Bird capture and sampling

For morphometric analysis, adult Barn Swallows were captured across sites across breeding range in Kashmir, Uttarakhand, North Bengal and Manipur. Birds were captured near their nests using nylon mist-nets (mesh size: 16*16 mm, length: 3 m and 12 m) and customized butterfly net made of muslin cloth. This prevented any damage to the wings of the captured birds. Upon capture birds were taken out of the net and placed in a paper bag to measure weight (in g) using Pesola Balance. Thereafter, set of other morphometric data including head length, tarsus length, bill length & bill width, wing length, tail inner length, and tail outer (streamer) length (all in mm) were measured using digital vernier callipers. Adults were banded using two rings, one numbered aluminium ring on right tarsus and a colour band on the left tarsus. A small amount of blood sample was extracted from the branchial vein of the adults for the genetic analysis. No sample was extracted from the juvenile swallows.

Morphometry data analysis

To visualize the populations' morphometric traits in space, Principal Component Analysis (PCA) was carried out using wing length, tarsus length, head length, bill length & bill width. Wing length was taken as a measure of body size following (James, 1970), and differences in populations was examined using one-way ANOVA, followed by a post-hoc test. Since sites differed in latitudes, Kashmir being at higher latitude, Uttarakhand and North Bengal mid-latitude, and Manipur at the lowest latitude, a linear regression was also carried out to check for latitudinal variations in body size and other morphometric traits. The sexually dimorphic trait- tail streamer length was analysed separately for males and females.

Molecular Phylogeography

Sampling and DNA preservation

Blood samples were obtained from breeding populations of Barn Swallows across the Himalayan region and Northeast India; Kashmir (n = 28), Uttarakhand (n = 25), North Bengal (n = 20), and Manipur (n = 35) (*Table 5.1*). Immediately after collection, blood samples were stored under sterile conditions in centrifuge tubes containing RNAlater stabilization solution (Thermo Fisher Scientific) to preserve nucleic acids. Samples were subsequently stored at −20 °C to prevent DNA degradation.

DNA extraction

Genomic DNA was extracted from blood samples using the DNeasy Blood & Tissue Kit (Qiagen, Hilden, Germany), following the standard protocol. The quality and integrity of extracted DNA were assessed by electrophoresis on a 0.8% agarose gel stained with nucleic acid dye and visualized under UV illumination.

Table 5.1 Number of samples collected across Barn Swallow breeding sites in India and number of samples sequenced for ND2 and Cytb genes.

Region	Samples		
	Collected	**Sequenced for ND2**	**Sequenced for Cytb**
Kashmir	28	15	06
Uttarakhand	25	12	14
North Bengal	20	09	10
Manipur	35	21	15

PCR amplification and sequencing

Two mitochondrial genes were selected for this study: the complete Cytochrome *b* (Cyt *b*) gene and a partial fragment of the NADH dehydrogenase subunit 2 (ND2) gene. Following (Dor et al., 2010), the Cyt *b* gene was amplified using the forward primer ProgND5F (5′-CACTCTGGCCTAATCAAGTCCTAC-3′) and the reverse primer ProgCBR (5′-GGCAGTCTTCAATCTTTGGC-3′). The ND2 gene fragment was amplified using primers METb (5′-CGAAAATGATGGTTTAACCCCTTCC-3′) and TRPc (5′-CGGACTTTAGCAGAAACTAAGAG-3′) following (Hunt et al., 2001).

Polymerase chain reactions (PCRs) were performed in 20 µl reaction volumes containing 10–20 ng of genomic DNA, 1× PCR buffer (Applied Biosystems), 2.5 mM $MgCl_2$, 0.2 mM of each dNTP, 5 pmol of each primer, and 5 units of Taq DNA polymerase (Thermo Scientific). PCR cycling conditions consisted of an initial denaturation at 95 °C for 5 min, followed by 35 cycles of denaturation at 95 °C for 40 s, annealing at 54–56 °C for 40 s, and extension at 72 °C for 50 s, with a final extension at 72 °C for 15 min. Negative controls were included to monitor contamination and amplification reliability.

PCR products were examined on a 2% agarose gel and visualized under UV light following staining with nucleic acid dye. Successful amplicons were purified using Exonuclease I and Shrimp Alkaline Phosphatase (USB, Cleveland, OH), incubated for 15 min at 37 °C followed by enzyme inactivation at 80 °C. Purified PCR products were sequenced bidirectionally using BigDye Terminator v3.1 chemistry on an ABI 3500XL Genetic Analyzer (Applied Biosystems, Carlsbad, CA, USA).

Data analysis

A total of 60 complete Cyt *b* and partial ND2 sequences of Barn Swallows from four Indian states were generated. Forward and reverse sequences were edited and assembled using Sequencher® v4.9 (Gene Codes Corporation, Ann Arbor, MI, USA). Gene boundaries were verified by manual inspection and alignment with homologous sequences available in GenBank to ensure correct annotation.

Additionally, sequences representing six subspecies of Barn Swallows (*H. r. rustica*, *H. r. erythrogaster*, *H. r. transitiva*, *H. r. savignii*, *H. r. tytleri*, and *H. r. gutturalis*) were retrieved from GenBank to cover the global distribution range. All sequences were aligned using CLUSTAL X v1.8 and manually inspected for alignment accuracy. DnaSP v5 was used to estimate haplotype diversity (h) and nucleotide diversity.

Phylogeographic analysis

Phylogenetic analyses were conducted using BEAST v1.7 (Drummond et al., 2012). The Ethiopian Swallow (*Hirundo aethiopica*) was used as an outgroup to infer phylogenetic relationships, with accession numbers provided in Additional file 1. A Yule speciation prior and the HKY + I + G nucleotide substitution models were applied for tree reconstruction. Two independent Markov Chain Monte Carlo (MCMC) analyses were run for 10 million generations, sampling every 1,000 generations.

Convergence and effective sample sizes were assessed using Tracer v1.6 (Rambaut et al., 2014), and the first 10% of trees from each run were discarded as burn-in. Maximum clade credibility trees were generated using TreeAnnotator (implemented in the BEAST v1.7 package) and visualized using FigTree v1.4.4. The spatial distribution of haplotypes was visualized using a median-joining network constructed in PopART software (Leigh et al., 2015). Genetic distances among lineages were calculated using the Tamura–Nei (TN92 + G) model with a discrete gamma distribution, selected based on the lowest Bayesian Information Criterion (BIC) value in MEGA X (Kumar et al., 2018).

5.3 Results

5.3.1 Plumage variations

Across sites of capture, Barn Swallow populations exhibited variations in overall plumage colouration and extent of breast band (*Fig 5.2*). While Swallows captured from Uttarakhand and North Bengal predominantly exhibited buff-bellied colouration with broken as well as broad breast band. Birds from Kashmir with complete breast band had white as well as rufous belly. However, swallows captured in Manipur were largely rufous to chestnut orange with broken as well as complete breast band.

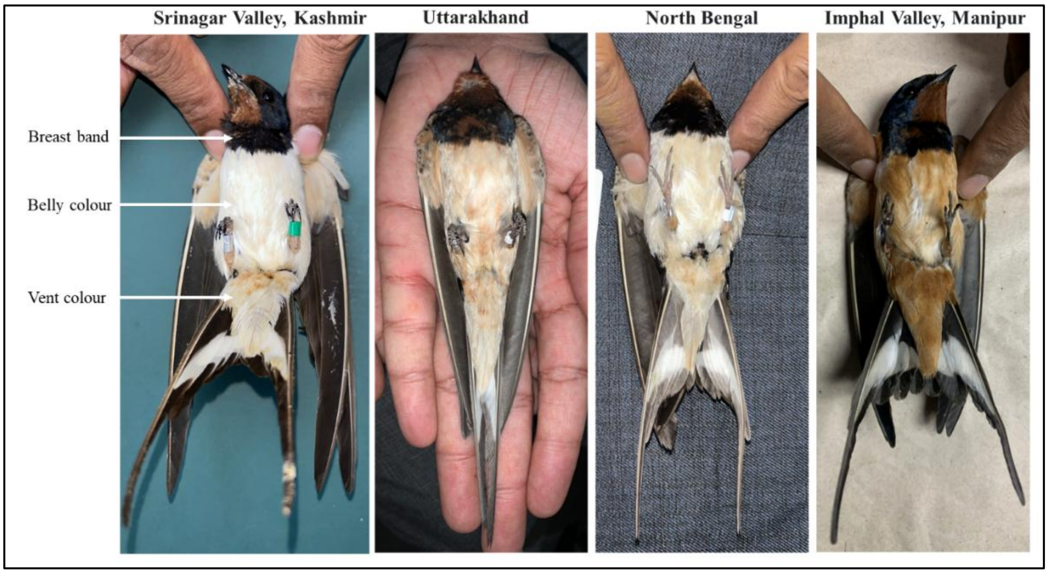

Fig 5.2 Plumage variations in Barn Swallow populations sampled from across the Indian Himalayan Region and Manipur. The characters – breast band extent, belly colour and ventral colour shown in the image are generally used as reference for subspecies delineation, although these characters are less useful in the zones of hybridisation.

5.3.2 Morphometric variations

A total of 215 Barn Swallows were captured of which traits of 158 adults (81 males & 77 females) were examined for the morphometric analysis. Based on PCA, the first axis PC1 representing a general body size axis, with strong positive loadings from head length, wing length, and tarsus length while PC2 represents bill morphology axis, dominated by high positive loadings of bill length and bill width. The first two principal components together explained 58.6% of the total variation, with PC1 accounting for 34.6% and PC2 for 24.0% of the variance (*Table 5.2*). Based on the morphometric measures, PCA revealed clear morphological structuring among populations across regions (*Fig 5.3*).

Populations from the Srinagar valley were strongly associated with positive PC1 scores, indicating relatively larger body size, whereas individuals from the Imphal valley clustered towards negative PC1 values, suggesting comparatively smaller body size. The Himalayan population: individuals from Uttarakhand and North Bengal spanned a broad range along PC1, overlapping with both valleys but centred near intermediate values. The Himalayan population showed higher dispersion along PC2, with many individuals scoring positively, indicating greater variability in bill morphology. In contrast, both Srinagar and Imphal valley populations were more tightly clustered around the PC2 origin, suggesting relatively conserved bill traits.

Table 5.2 Loadings of morphological variables on the first two principal components. PC1 represents a general body size axis, with strong positive loadings from head length, wing length, and tarsus length. PC2 represents a bill morphology axis, dominated by high positive loadings of bill length and bill width. The first two components together explain 58.64% of the total morphological variation.

Characters	PC1 (body size)	PC 2 (bill morphology)
Head Length	0.82	-0.21
Wing Length	0.64	-0.21
Tarsus Length	0.61	-0.19
Bill Length	0.50	0.62
Bill Width	0.13	0.83
Eigen Values	1.73	1.20
Cumulative Variance	34.60	**58.64**

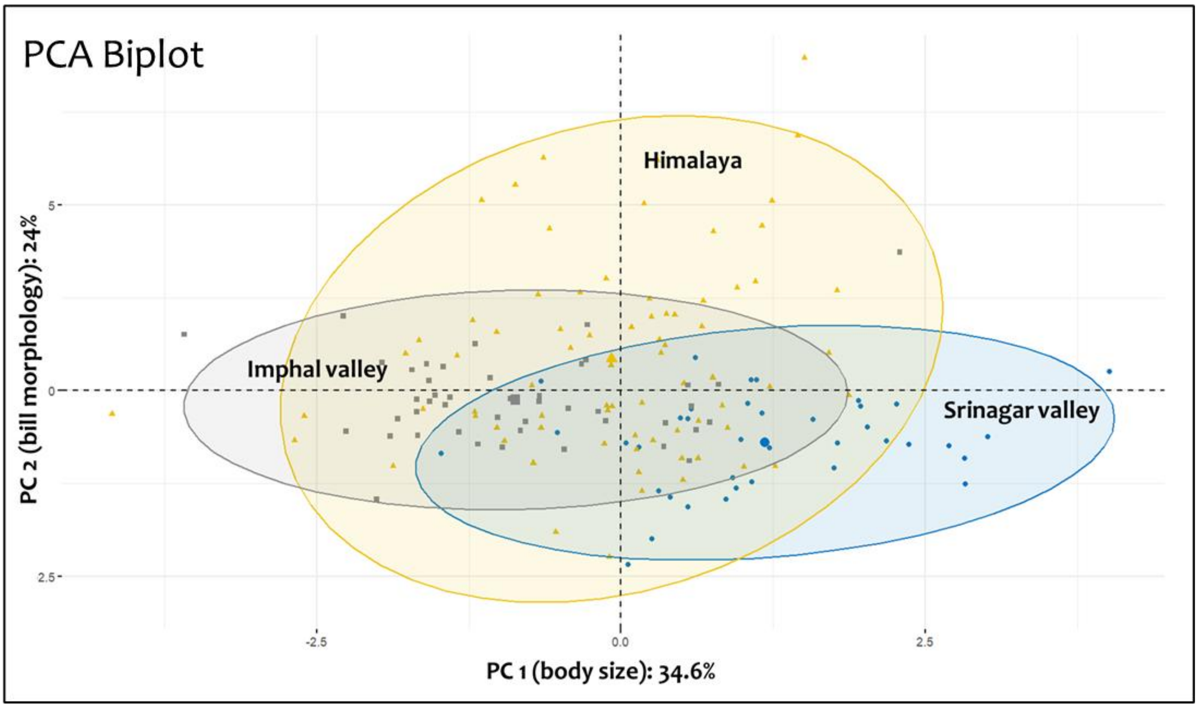

Fig 5.3 PCA biplot depicting traits of Barn Swallows from three regions, Srinagar valley, Kashmir (in blue), Uttarakhand and North Bengal as part of central Himalayan region (in yellow), and Imphal valley, Manipur in east (in grey). The two PC axis explained for 58.64% variation among the populations. PC 1 which represents body size highlights the Kashmir birds to be larger in body size compared to birds of Uttarakhand, North Bengal and Manipur region.

Morphometric variations within populations

Barn Swallows captured from the breeding range varied in their morphometric characters (*Table 5.3)*. Specifically, the representative of body size, wing length, was greatest in birds from the Srinagar Valley, Kashmir (120.6 ± 3.8 mm, range: 112–128 mm) and was significantly longer than that of Himalayan (117.7 ± 3.6 mm, range: 104–126 mm) and Imphal Valley birds (116.5 ± 3.2 mm, range: 111–123 mm) (one-way ANOVA: $F_{2, 86.46} = 13.88$, $p < 0.05$, n = 158, *Fig 5.4*).

Table 5.3 Morphometric measurements of adult Barn Swallows captured in Srinagar valley in Kashmir, central Himalayan region (Uttarakhand and North Bengal) and Imphal Valley in Manipur. Note: Tail streamer is the difference between outer and inner tail length and is a sexually selected trait with males having longer tail streamers than females.

Morphological trait	**Srinagar Valley** (n = 38)	**Himalayan Region (Uttarakhand and North Bengal)** (n = 75)	**Imphal Valley** (n = 45)
	Average ± SD (Range)	**Average ± SD (Range)**	**Average ± SD (Range)**
Body weight (g)	17.9 ± 1.4 (14.5 – 21.5)	17.2 ± 1.6 (11 – 20.5)	15.5 ± 0.8 (14 – 18)
Tarsus length (mm)	11.5 ± 0.4 (10.7 – 12.4)	11.1 ± 0.4 (10.3 – 12.0)	11.0 ± 0.5 (8.5 – 12)
Head length (mm)	30.1 ± 0.7 (28.4 – 31.7)	29.3 ± 0.6 (27.3 – 30.6)	29.0 ± 0.6 (27.6 – 31.1)
Bill length (mm)	11.7 ± 0.6 (10.4 – 13.2)	11.9 ± 0.6 (9.8 – 13.3)	11.5 ± 0.4 (10.3 – 12.3)
Bill width (mm)	5.4 ± 0.1 (5.3 – 5.7)	5.5 ± 0.3 (4.8 – 6.8)	5.4 ± 0.2 (5.2 – 6.1)
Bill depth (mm)	3.3 ± 0.1 (3.1 – 3.4)	3.3 ± 0.1 (2.8 – 3.6)	3.2 ± 0.1 (2.9 – 3.4)
Wing length (mm)	120.6 ± 3.8 (112 – 128)	117.7 ± 3.6 (104 – 126)	116.5 ± 3.2 (111 – 123)
Outer tail length (mm)	95.3 ± 10.9 (73 – 115)	86.9 ± 8.6 (71 – 107)	87.8 ± 10.1 (65 – 118)
Inner tail length (mm)	47.1 ± 1.4 (44 – 50)	45.9 ± 1.9 (42 – 55)	45.7 ± 1.3 (43 – 48)
Tail streamer length (mm)	48.2 ± 10.8 (25 – 68)	41.1 ± 8.5 (26 – 63)	42.1 ± 10.1 (20 – 71)

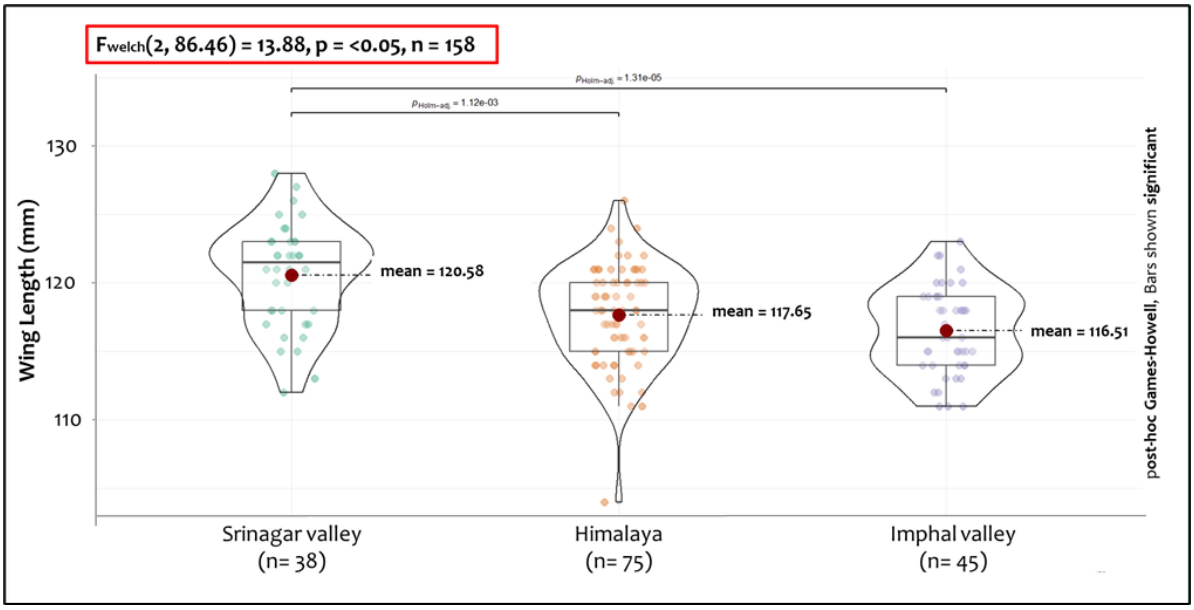

Fig 5.4 Variations in wing length of Barn Swallow populations breeding across Srinagar valley, Kashmir, Himalayan region in Uttarakhand and North Bengal, and Imphal valley, Manipur. Swallows of Srinagar valley were significantly larger in body size than that of other regions.

Sexually-selected trait – outer tail length

The length of outer-most tail feather of male Barn Swallows was found to be longer than the females across all sites (*Fig 5.5)*. Furthermore, males of Srinagar valley had significantly longer outer tail (102.9 ± 7.2 mm) than of males of the Himalayan region (93.1 ± 8.4 mm) and Imphal valley (92.2 ± 10.1 mm) (one-way ANOVA: $F_{2, 48.46} = 13.10$, $p < 0.05$, n = 81, *Fig 5.6*). Females of Kashmir also had longer outer tail (85.9 ± 6.4 mm) than of Himalayan region (81.8 ± 4.5 mm) and Imphal valley (81.7 ± 6.4 mm, *Table 5.4*).

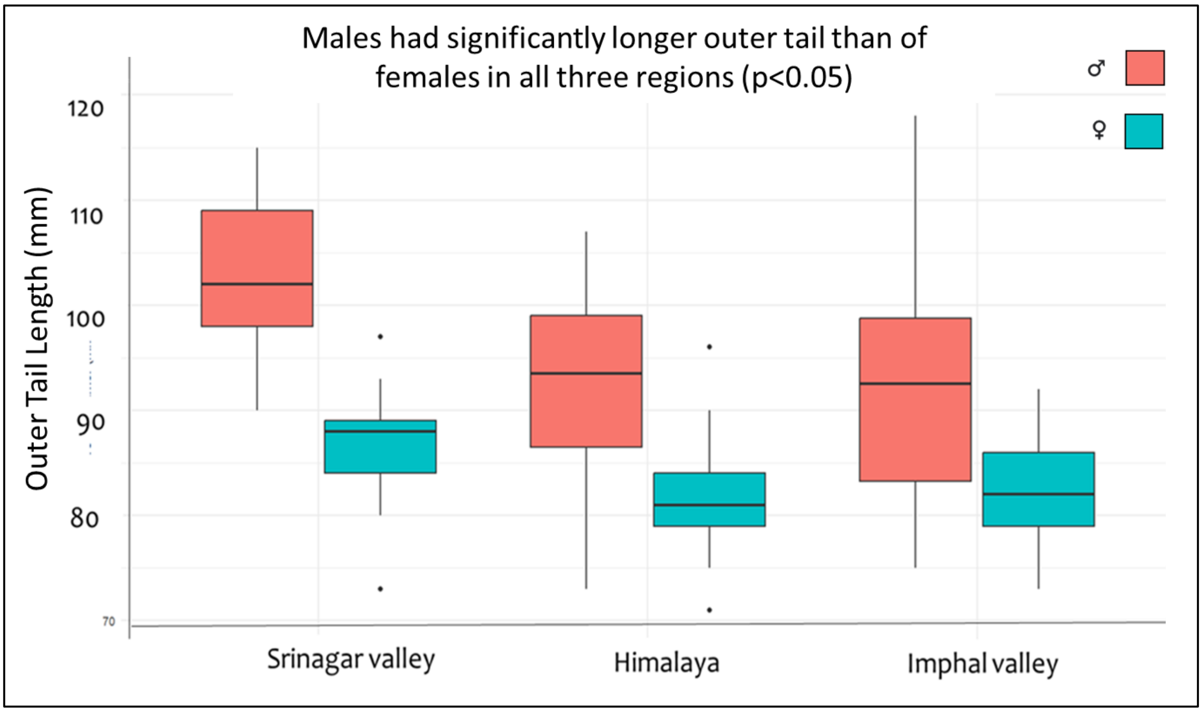

Fig 5.5 Length of outermost tail feather in Barn Swallow populations across sampled regions wherein males (red) had significantly longer outer tail than females (blue).

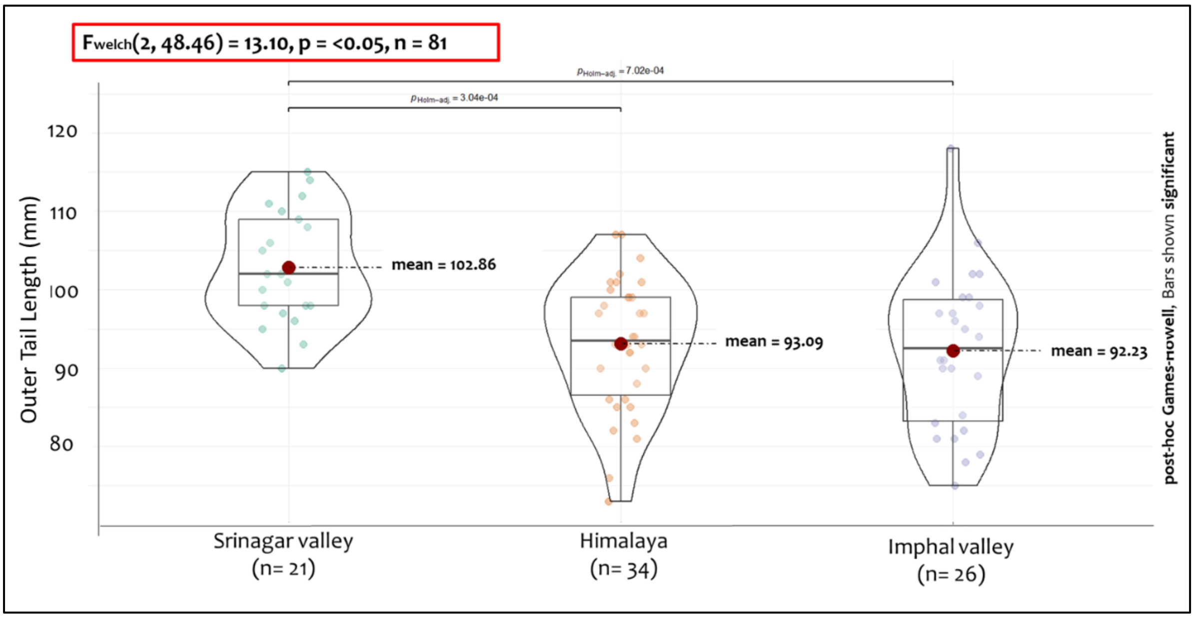

Fig 5.6 Comparison of outer tail length in male Barn Swallows across sites, figure depicting males of Srinagar valley to have significantly longer outer tail than that of Himalayan and Imphal valley males.

Table 5.4 Morphometric measurements of male versus female Barn Swallows captured in Srinagar valley in Kashmir, central Himalayan region (Uttarakhand and North Bengal) and Imphal Valley in Manipur. Note: Tail streamer or the difference between outer tail length and inner tail length was longer in males across all sampled regions.

Morphological trait	**Srinagar Valley**		**Himalayan Region (Uttarakhand and North Bengal)**		**Imphal Valley**	
	Male (n = 21)	**Female (n = 17)**	**Male (n = 34)**	**Female (n = 41)**	**Male (n = 26)**	**Female (n = 19)**
Body weight (g)	17.6 ± 0.9	18.4 ± 1.7	16.9 ± 1.6	17.5 ± 1.5	15.7 ± 0.8	15.2 ± 0.8
Tarsus length (mm)	11.5 ± 0.5	11.5 ± 0.3	11.1 ± 0.3	11.2 ± 0.4	11.0 ± 0.6	11.1 ± 0.3
Head length (mm)	30.4 ± 0.7	29.9 ± 0.6	29.5 ± 0.5	29.2 ± 0.7	29.1 ± 0.7	29.0 ± 0.5
Bill length (mm)	11.8 ± 0.6	11.7 ± 0.5	12.0 ± 0.5	11.8 ± 0.6	11.5 ± 0.4	11.6 ± 0.3
Bill width (mm)	5.4 ± 0.1	5.4 ± 0.1	5.6 ± 0.3	5.5 ± 0.4	5.4 ± 0.2	5.4 ± 0.1
Bill depth (mm)	3.3 ± 0.1	3.3 ± 0.1	3.3 ± 0.2	3.3 ± 0.1	3.2 ± 0.2	3.2 ± 0.1
Wing length (mm)	122.4 ± 3.1	118.4 ± 3.4	118.5 ± 3.9	117.0 ± 3.3	117.5 ± 3.2	115.2 ± 2.7
Outer tail length (mm)	102.9 ± 7.2	85.9 ± 6.4	93.1 ± 8.4	81.8 ± 4.5	92.2 ± 10.1	81.7 ± 6.4
Inner tail length (mm)	47.0 ± 1.4	47.2 ± 1.4	45.4 ± 1.7	46.2 ± 2.0	45.9 ± 1.1	45.6 ± 1.4
Tail streamer length (mm)	55.9 ± 6.9	38.7 ± 6.3	47.7 ± 8.0	35.6 ± 3.8	46.4 ± 10.2	36.2 ± 6.2

Latitudinal trend

Morphological traits showed consistent positive relationships with latitude (*Table 5.5*). Wing length increased significantly with latitude ($\beta = 0.40 \pm 0.08$ mm per degree, $P < 0.001$), with latitude explaining 13.8% of the variation (*Fig 5.7*). Similarly, tarsus length increased with latitude ($\beta = 0.04 \pm 0.01$ mm, $P < 0.001$; Adjusted $R^2 = 0.11$). Body mass exhibited the strongest latitudinal pattern, increasing by 0.21 ± 0.03 g per degree latitude ($P < 0.001$) and showing the highest explanatory power (Adjusted $R^2 = 0.22$). Head length also increased significantly with latitude ($\beta = 0.09 \pm 0.02$ mm per degree, $P < 0.001$; Adjusted $R^2 = 0.18$).

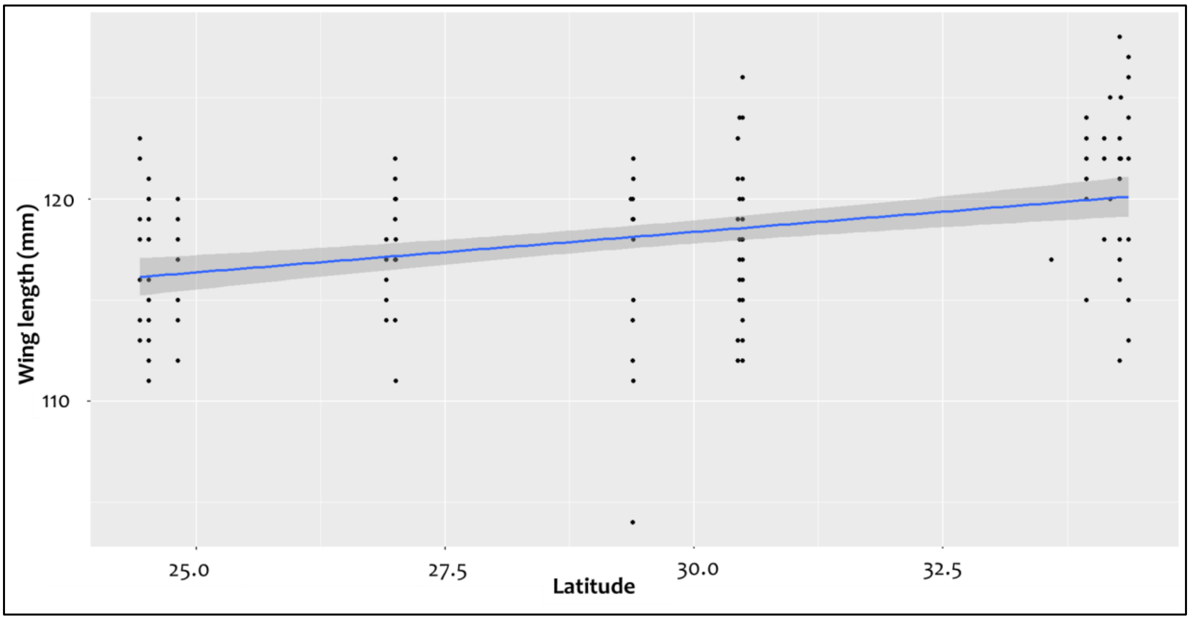

Fig 5.7 Trend in wing length of Barn Swallow populations across the latitude. At higher latitudes, birds of Srinagar valley had longer wing length while at the lowest latitude in Imphal valley, wing length is the smallest.

Table 5.5 Linear regression results showing the relationship between latitude and morphological traits. Estimates represent change in trait value per one-degree increase in latitude.

Trait	Intercept (Estimate ± SE)	Latitude slope (Estimate ± SE)	*t* value	*P* value	Adjusted R^2
Wing length	106.39 ± 2.29	0.40 ± 0.08	5.12	8.98×10^{-7} ***	0.138
Tarsus length	9.93 ± 0.28	0.04 ± 0.01	4.50	1.33×10^{-5} ***	0.109
Body weight	10.67 ± 0.94	0.21 ± 0.03	6.69	3.82×10^{-10} ***	0.218
Head length	26.86 ± 0.44	0.09 ± 0.02	5.86	2.69×10^{-8} ***	0.180

5.3.3 Phylogeography of Barn Swallows

The Bayesian consensus tree based on both Cyt *b* and ND2 genes revealed that Barn Swallow sequences from Indian populations clustered into two major clades (*Fig 5.8*, *Fig **5.9***). A distinct Himalayan clade was recovered, comprising all samples from Kashmir, Uttarakhand, and North Bengal. In contrast, samples from Manipur with only two samples from Uttarakhand clustered within the Asian subspecies clade, *H. r. gutturalis*.

Both phylogenetic reconstruction and median-joining network analyses (*Fig 5.10*) consistently indicated the presence of two genetically distinct clusters of Barn Swallows within India. The Himalayan clade exhibited a unique genetic signature, clearly differentiated from other recognized subspecies of Barn Swallows.

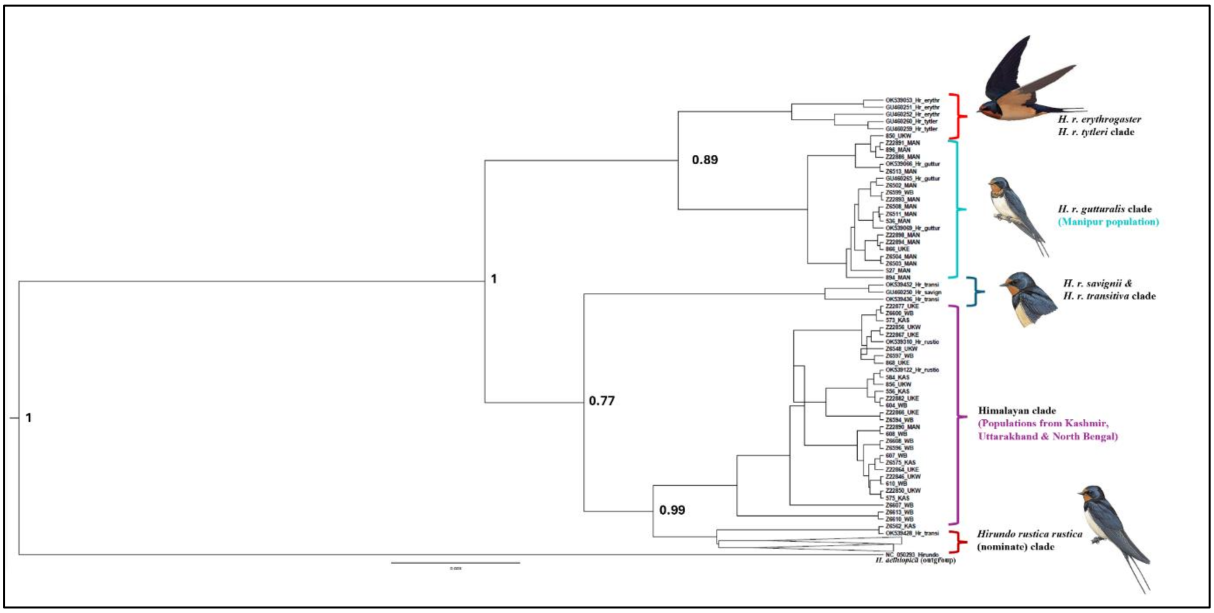

Fig 5.8 Bayesian phylogenetic relationships of Indian Barn Swallow populations inferred from mitochondrial Cytochrome b (Cyt b) gene sequences. The phylogenetic tree revealing a distinct Himalayan clade of Barn Swallows composing birds from Kashmir, Uttarakhand and North Bengal and is more closely related to the nominate *Hirundo rustica rustica*. While the Manipur populations formed part of the Asian *H. r. gutturalis* clade and more closely related to the Siberian *H. r. tytleri* and American *H. r. erythrogaster*.

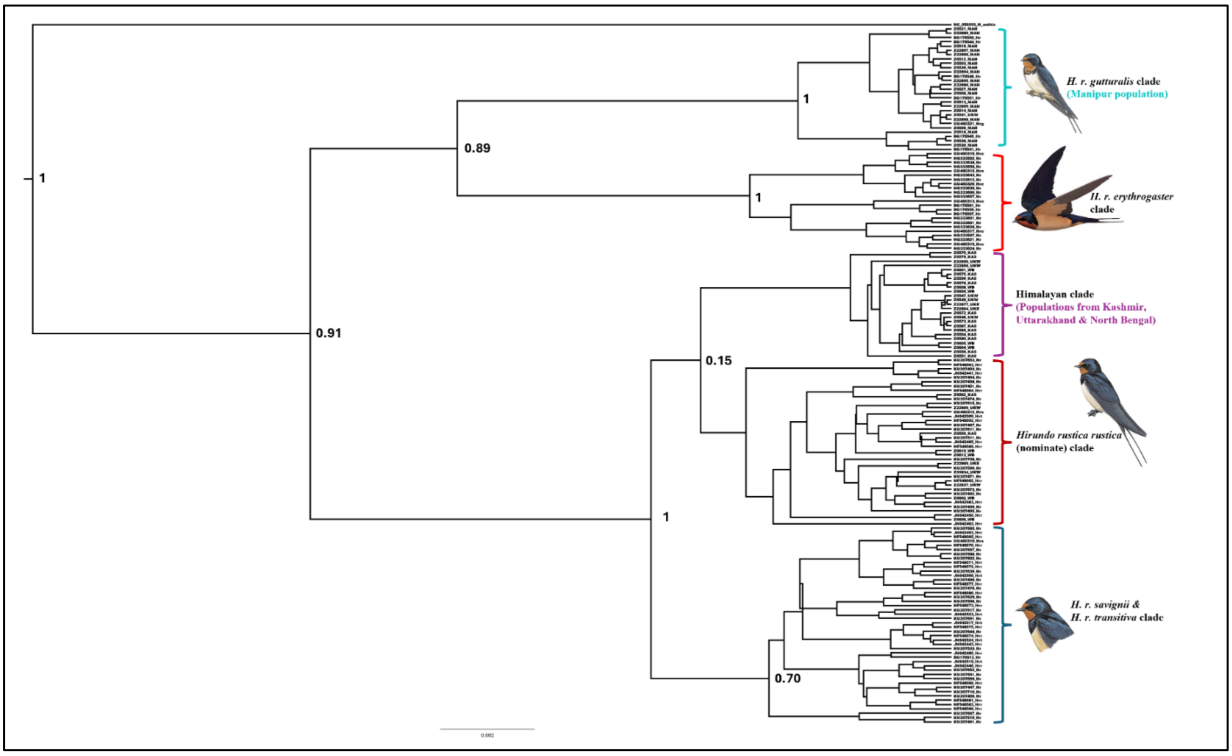

Fig 5.9 Bayesian phylogenetic relationships of Indian Barn Swallow populations inferred from mitochondrial ND2 gene sequences. Similar to the Cytb gene phylogenetic relationship, ND2 tree also revealed a distinct Himalayan clade of Barn Swallows composing birds from Kashmir, Uttarakhand and North Bengal and is more closely related to the nominate *Hirundo rustica rustica*. While the Manipur populations formed part of the Asian *H. r. gutturalis* clade and more closely related to the American *H. r. erythrogaster*.

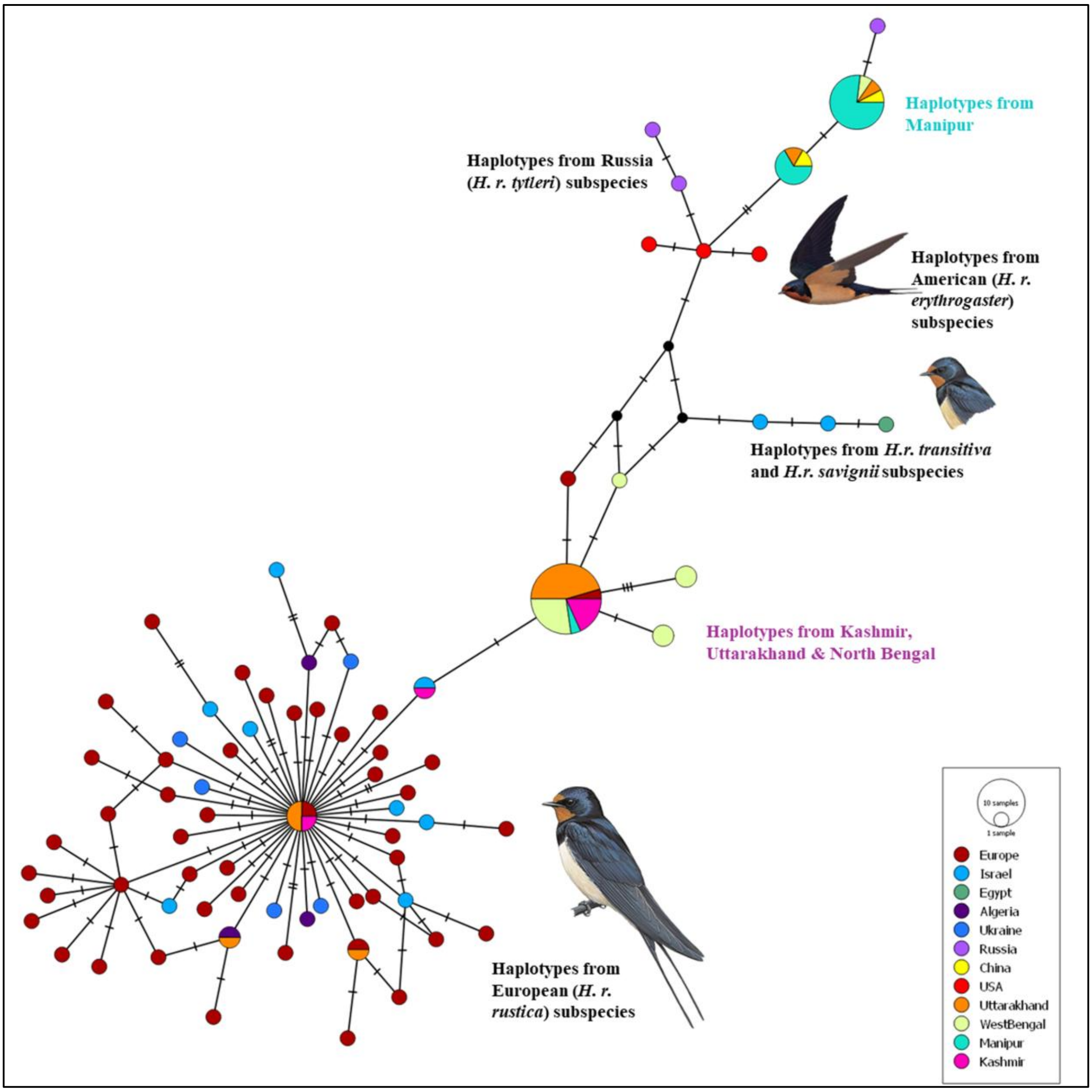

Fig 5.10 ND2 haplotype network showing genetic differentiation of Himalayan and non-Himalayan (Manipur) Barn Swallows, and their shared haplotype with populations of European (*H. r. rustica*), and sedentary (*H. r. transitiva* and *H. r. savignii*), American (*H. r. erythrogaster*) and Siberian (*H. r. tytleri*) populations.

5.4 Discussion

Variation in overall morphology along the Himalayan gradient

The present study reveals pronounced geographic variation in morphometric traits of Barn Swallows breeding across the Himalayan region and Northeast India, highlighting the role of latitude, ecology, and potential geographic barriers in shaping phenotypic differentiation. Birds breeding at higher latitudes in the Srinagar Valley exhibited significantly larger body size and longer wings compared to populations from the central Himalaya (Uttarakhand and North Bengal) and Northeast India (Manipur). This pattern conforms to the general rule of latitudinal size variation within species (James, 1970), whereby individuals at higher latitudes tend to be larger, potentially as an adaptation to colder climates, aerodynamic efficiency, or migratory demands.

The PCA further resolved three morphometric clusters, with Kashmir birds forming a distinct group characterized by overall larger body size. Wing length showed a strong positive relationship with latitude, reinforcing the influence of geographic gradients on morphological traits. Similar latitudinal and regional variation in wing morphology has been documented in Barn Swallows across Eurasia and East Asia, where differences in wing length and shape are often associated with migration distance and flight performance (Liu et al., 2020; Scordato et al., 2017).

Sexual dimorphism in tail streamer length was evident across all populations, with males consistently exhibiting longer outer tail feathers than females, a well-documented sexually selected trait in Barn Swallows. Notably, males from the Srinagar Valley possessed significantly longer tail streamers than males from the central Himalayan region and Imphal Valley. Geographic variation in the expression of sexually selected traits has been reported previously in Barn Swallows and is thought to reflect spatial variation in sexual selection intensity, ecological constraints, or mating systems (Safran et al., 2016). A broader meta-analysis across subspecies further indicates that the strength of sexual selection acting on tail streamer length varies geographically and seasonally, potentially contributing to regional divergence in male ornamentation.

The relative morphometric similarity among Himalayan populations, combined with the distinctiveness of Kashmir birds, suggests partial phenotypic cohesion along the Himalayan axis, with possible restriction of westward dispersal by major geographic barriers such as the

Pir Panjal range. Whether additional ecological or topographic barriers operate further east along the Himalayan breeding range remains unknown. These findings raise the possibility that Barn Swallows breeding across different parts of the Himalaya may follow distinct migratory strategies or experience different selective regimes, a hypothesis that warrants further investigation through migratory tracking and ecological studies.

This study, for the first time recorded the presence of a resident breeding population in Imphal Valley, Manipur. Interestingly, when compared with other swallow populations breeding in the Himalayan region, breeding birds in Manipur exhibited varying overall plumage colour (*Fig 5.2*). This variation was also prominent within and among populations across sampled sites (). Further, the morphological characteristics, the average body size (represented by wing length) and outer tail length when compared with the measurements of museum specimens of *H. r. rustica, H. r. gutturalis* and *H. r. tytleri* presented by Ali & Ripley, (1987) (*Table 5.6*) do not permit confident subspecies identification of the breeding populations. Moreover, the plumage colouration indicates Manipur birds to be likely an intermediate between the American subspecies *H. r. erythrogaster* and the Siberian *H. r. tytleri.* This challenges existing assumptions about subspecies distributions in South and Southeast Asia and suggests a more complex biogeographic history than previously recognised.

Interestingly, populations also intermix and form hybrid zones (Scordato et al., 2017, 2020) and these then exhibit diverse migratory strategies. Birds from the *rustica – gutturalis* hybrid zone in western China migrate either westward to Africa or south across the Tibetan Plateau into India (Turbek et al., 2022), and populations breeding in Amur contact zone winter in Southeast Asia (Heim et al., 2020). However, still important uncertainties remain, particularly in Asia where subspecies and hybrid populations exhibit diverse and poorly resolved migratory strategies. For instance, migration of Siberian *H. r. tytleri* is poorly known, with only one geolocator-tracked individual suggesting a direct route into Southeast Asia (Anisimova et al., 2025). These contrasting patterns highlight significant knowledge gaps in the migratory connectivity of Asian Barn Swallow populations, particularly those moving into or wintering within the Indian subcontinent.

Table 5.6 Morphometric measurement of traits - wing length and outer tail length reported by Ali & Ripley (1987) of museum specimens of *H. r. rustica, H. r. gutturalis* and *H. r. tytleri* compared with birds sampled in the present study from Srinagar valley, Kashmir, Uttarakhand, North Bengal and Imphal Valley, Manipur.

Subspecies/ Populations	Wing length (mm)		Outer Tail length (mm)	
	♂	♀	♂	♀
H. r. rustica	120 – 129	116 – 128	93 – 122	76 – 102
H. r. gutturalis	110 – 123	108 – 113	72 – 96	67 – 73
H. r. tytleri	115 – 124	NA	74 – 79	NA
Srinagar valley	115 – 128	111 – 124	90 – 115	73 – 97
Uttarakhand	104 – 124	111 – 126	73 – 107	75 – 96
North Bengal	114 – 121	111 – 122	76 – 99	71 – 83
Imphal valley	111 – 123	111 – 122	75 – 118	65 – 92

Phylogeographic structure of Indian Barn Swallow populations

Phylogeographic analyses based on mitochondrial Cyt *b* and ND2 genes revealed clear genetic structuring among Barn Swallow populations within India. Both Bayesian phylogenetic reconstruction and median-joining haplotype network analyses consistently recovered two major genetic clusters. A distinct Himalayan clade encompassed all samples from Kashmir, Uttarakhand, and North Bengal, whereas all samples from Manipur and a small subset from Uttarakhand clustered within the Asian subspecies clade, *H. r. gutturalis*. The concordance between phylogenetic and network-based approaches strengthens the inference of genuine population structure rather than methodological artifacts.

These results are particularly informative when interpreted in the context of the comprehensive phylogeny presented by Dor et al. (2010) of the genus *Hirundo* and the Barn Swallow subspecies complex. Dor et al. (2010) demonstrated that while several recognized subspecies of Barn Swallows show relatively shallow mitochondrial divergence, geographically structured lineages can still be detected, reflecting recent expansion, localized isolation, and differential gene flow. The distinct Himalayan clade identified in the present study suggests that populations breeding along the Himalayan axis may represent a regionally differentiated lineage that has not been fully resolved in broader-scale phylogenetic analyses.

Recent advances using complete mitochondrial genomes further support the existence of geographically structured haplogroups across the global range of Barn Swallows, with subspecies often corresponding to distinct matrilineal lineages (Lombardo et al., 2022). Although mitochondrial markers alone cannot capture the full complexity of population history, the unique genetic signature of the Himalayan clade detected here indicates either long-term partial isolation or restricted maternal gene flow relative to neighbouring Asian populations. Further, the placement of a small number of Uttarakhand samples within the *H. r. gutturalis* clade suggests the presence of a potential contact zone or secondary admixture between Himalayan and eastern Asian lineages. Similar patterns of incomplete lineage sorting and introgression have been documented in Barn Swallow hybrid zones elsewhere, where genetically distinct subspecies meet and interbreed while maintaining phenotypic differentiation (Scordato et al., 2017).

Barn Swallows are known for their exceptional dispersal ability and for repeatedly colonising new regions through both natural movements and human-mediated habitat expansion (Hobson et al., 2015; Scordato et al., 2017). Phylogenetic studies indicate that the *H. rustica* complex is monophyletic and structured into two major clades: a Europe–Middle East clade and an Asia–America clade (Zink et al., 2006; Dor et al., 2010). European and West Asian populations differentiated around the onset of the Holocene (Smith et al., 2018). The East and South Asian lineages colonized independently during the late Pleistocene, while the colonization of the Americas, a relatively recent event likely occurred at least 50 thousand years ago (kya; Lombardo et al., 2022).

Notably, a secondary dispersal event from North America back into Asia approximately 27 kya has been proposed, explaining the close genetic affinity between *tytleri* and *erythrogaster* (Zink et al. 2006). Against this backdrop, we propose two non-mutually exclusive hypotheses to explain the Manipur population, first secondary colonisation and admixture – where the breeding population in Manipur might have an origin from *H. r. tytleri*, with historical introgression from *erythrogaster* following back-colonisation into Asia, resulting in the observed intermediate phenotype (*Fig 5.11*). And second, shift in historical migratory strategy

- the wintering *tytleri* populations in Northeast India might have abandoned long-distance migration and became sedentary, similar to historical shifts documented in North American Barn Swallows (Winkler et al., 2017) that began breeding within their former wintering range in South America during the 19th century. This adaptation of breeding in Imphal valley could have further facilitated by the tolerable climatic regime as well as availability of nest sites in the region. Either scenario represents a significant range and behavioural shift and underscores the Barn Swallow's capacity for rapid ecological and evolutionary responses. Moreover, whether these breeding populations are joined with migratory subspecies *tytleri* as reported by Ali & Ripley, (1987) is yet to be studied.

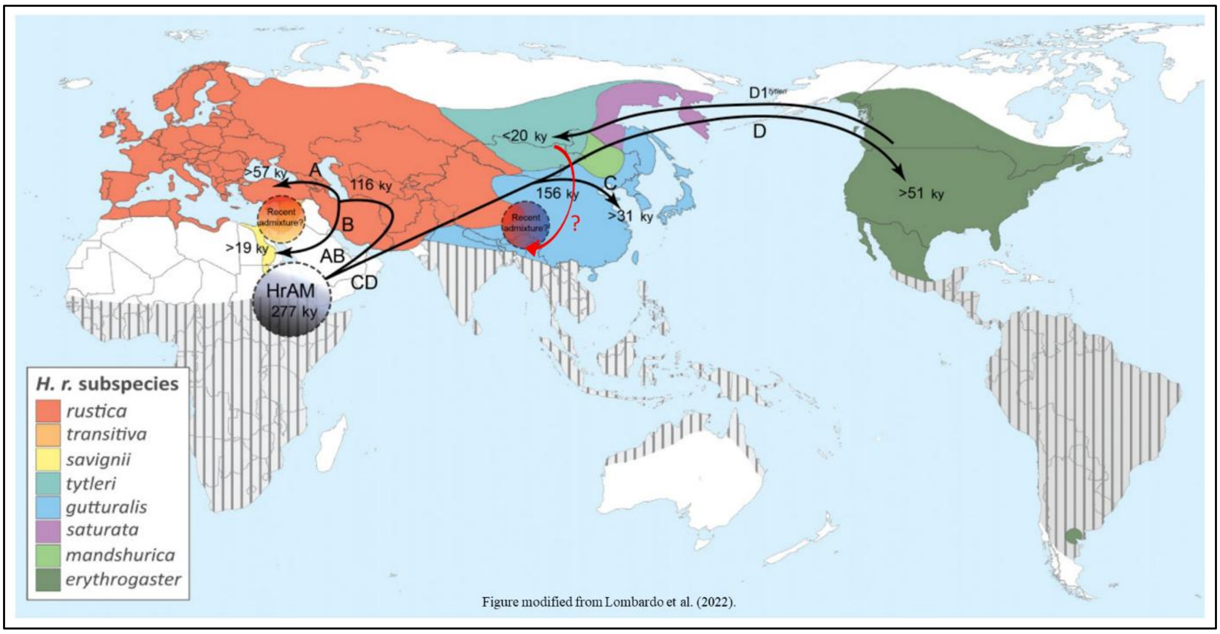

Fig 5.11 The geographical and temporal distribution of Barn Swallow subspecies. Colours indicate the breeding ranges of different subspecies and striped areas indicate wintering ranges. The dashed grey circle indicates the possible ancestral region of the *Hirundo rustica*, while the other dashed circles indicate zones where two haplogroups are currently found, possibly indicating recent admixture between subspecies. Similar is postulated for the populations breeding in Imphal valley which could likely a result of secondary colonisation and recent admixture (in red arrow). Figure modified from Lombardo et al. (2022).

Concordance between morphology and genetics: implications for subspecies differentiation

The integration of morphometric and phylogeographic evidence in this study reveals a notable concordance between phenotypic differentiation and mitochondrial genetic structure. The distinct Himalayan genetic clade broadly corresponds with populations exhibiting similar morphometric traits, particularly in wing length and overall body size, suggesting that geographic isolation and local adaptation may be acting in concert to shape divergence along the Himalayan axis.

Comparative studies from other parts of the Barn Swallow's range have shown that subspecies such as *H. r. rustica*, *H. r. gutturalis*, and *H. r. mandschurica* differ consistently in morphometric and plumage traits, even when genetic differentiation is modest (Dor et al., 2010; Liu et al., 2020). Furthermore, genomic analyses across hybrid zones indicate that phenotypic traits associated with migration and sexual selection can remain differentiated despite ongoing gene flow, supporting the idea that selection can maintain population structure in highly mobile species (Scordato et al., 2017).

Sexual selection may play an additional role in reinforcing divergence among Himalayan populations. Geographic variation in tail streamer length, particularly the exaggerated traits observed in males from the Srinagar Valley, could reflect localized mate choice preferences or ecological constraints that differ from those operating in central Himalayan or northeastern populations (Scordato & Safran, 2014). Such differences may contribute to assortative mating and reduced gene flow over evolutionary time.

Despite these patterns, caution is warranted in assigning formal subspecies status to Himalayan Barn Swallows based solely on mitochondrial DNA and morphology. As emphasized by Dor et al. (2010), the Barn Swallow subspecies complex represents a continuum of divergence shaped by recent expansion, high dispersal ability, and variable selection pressures. The Himalayan lineage identified here may therefore represent an incipient evolutionary unit or management unit rather than a fully differentiated subspecies.

Future directions and broader implications

The present findings highlight the Himalaya as a potentially important axis of divergence within the Barn Swallow's Asian range. To fully resolve the evolutionary status of Himalayan populations, future studies should integrate genome-wide nuclear markers, detailed analyses of plumage coloration, and high-resolution tracking of migratory routes and wintering grounds. Such approaches will be critical for determining whether the observed genetic and morphometric differentiation reflects long-term isolation, divergent migratory strategies, or ongoing secondary contact.

Understanding population structure in Barn Swallows is particularly relevant in the context of rapid environmental change and widespread population declines reported in many parts of the species' range. Identifying distinct evolutionary or demographic units within the Himalaya may have important implications for conservation planning and for understanding how migratory birds respond to ecological barriers and climatic gradients across complex mountainous landscapes.

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Chapter 6
Nature-Culture Linkages: The Story of Co-Existence of People with Barn Swallows (*Hirundo rustica*) in the Himalayan Region

6.1 Introduction

Barn Swallows across the globe rely almost exclusively on human-made structures for nesting. However, this was not always the case, as reports from 19^{th} and early 20^{th} century documents sightings of Barn Swallows in caves, cliffs, and tree hollows (Baird et al., 1874; Speich et al., 1986), and in human settlements in Europe and North America (Frazer, 1891). Suckley & Cooper (1860) reported the earliest nesting by the species under the eaves of houses in North America, suggesting the shift to anthropogenic structures for nesting to be relatively recent (Zink et al., 2006). This is also evident by molecular analysis wherein the occurrence of low genetic differentiation among the *H. rustica* subspecies complex points towards recent global expansion of the species, likely to have occurred during the Holocene (Zink et al., 2006; Dor et al., 2010; Smith et al., 2018). The presence of human settlements enabled the species to exploit nesting space inside the properties which provided additional protection to the nest, regulated temperatures to raise the young, and availability of more localized food sources (Speich et al. 1986) which led the Barn swallow to be referred as a human-commensal species.

The commensal relationship of Barn Swallows with humans have fascinated people all around the world; a striking example of how an animal behaviour can have an influence on human culture and thoughts. In ancient literature, Barn Swallows are mentioned in European folklore, in Greek Mythology and in several texts in Christianity (*Fig 6.1*, Green, 2019; Enany, 2022). In Europe, the close associations of Barn Swallows with people are believed to have emerged due to two key factors: migration and commensal nesting. The species' returning to breeding areas in spring following the cold harsh winters was viewed as a symbol of harbinger of spring. While its behaviour of nesting within homes, barns and farm buildings ensured deeply rooted connections with people.

In Asian breeding range, presence of a Barn Swallow nest in or near personal residence is considered as sign of good luck and fortune (Kim et al., 2023). In China, Taiwan and Korea Barn Swallows are commonly seen nesting in corridors of buildings, over people's doorways, inside houses, etc., and residents take active measures in supporting the nest structures by providing ledges under the nest and placing paper or cardboard below the nest to collect droppings and maintain cleanliness (Fachon, 2021; Kim et al., 2023) Across the breeding range of Barn Swallows, several cultures revere the species and believe that disturbing the nest can bring unfortune upon them.

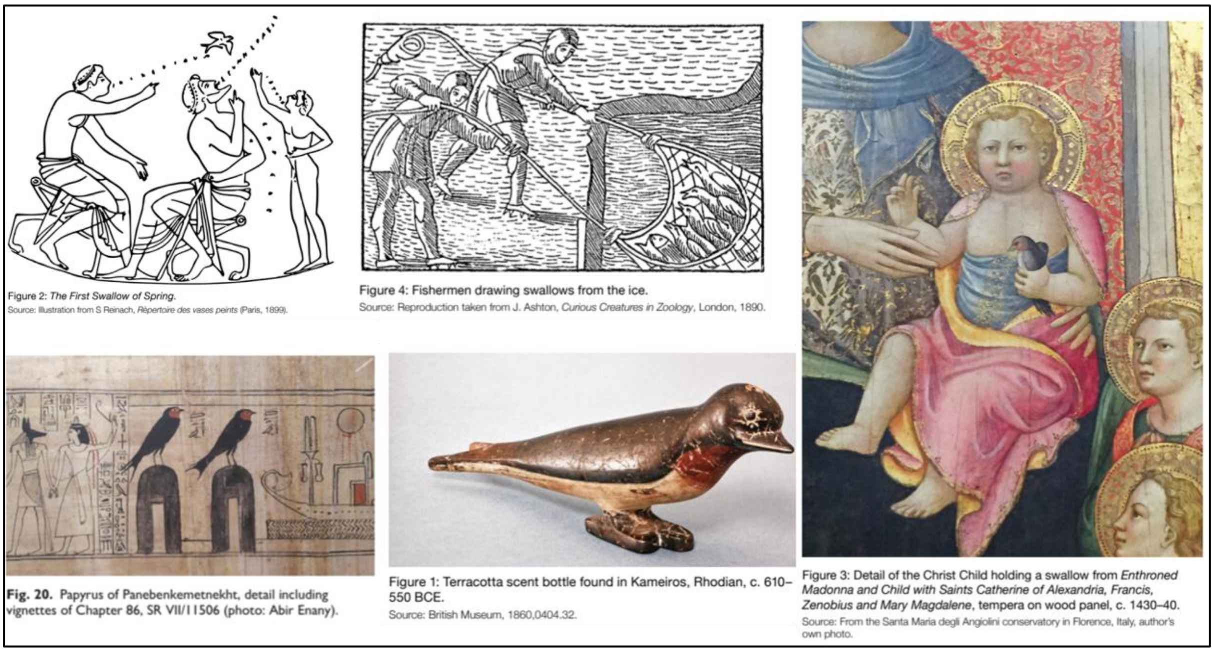

Fig 6.1 Significance of Barn Swallows in historical and cultural records from across the globe (Source: Green, 2019; Enany, 2022).

In the Himalaya, Barn Swallows are summer-breeding visitor and are distributed primarily between 1000 – 2000 m asl and nest in human dwellings largely in houses and shops (*see Chapter 4*). Unlike in other regions where Barn Swallows are reported in ancient literature and folklore, the relationship of Barn Swallows with humans in the Indian Himalayan region is not reported. While studying the nesting ecology and population variations of Barn Swallows across the Himalayan region, the importance of the cultural linkage of species with humans was observed. Therefore, with the aim of documenting the traditional knowledge and perception of residents of the Himalayan region towards the nesting of Barn Swallows this study was designed as part of the thesis.

6.2 Study Area and Methods

Across the Himalayan States, opportunistic surveys were carried out in Kashmir, Himachal Pradesh, Uttarakhand, Sikkim, North Bengal and in northeastern State, Manipur, to record the presence of nesting Barn Swallow populations in 2022 and 2023. The surveys were designed in such a way that the breeding range of the species across the geographical range (using eBird record) was covered. Following highways and major roads connecting to cities, towns and villages, intensive surveys particularly in Uttarakhand (*Fig 6.2*) were carried out, recording responses of 466 property owners.

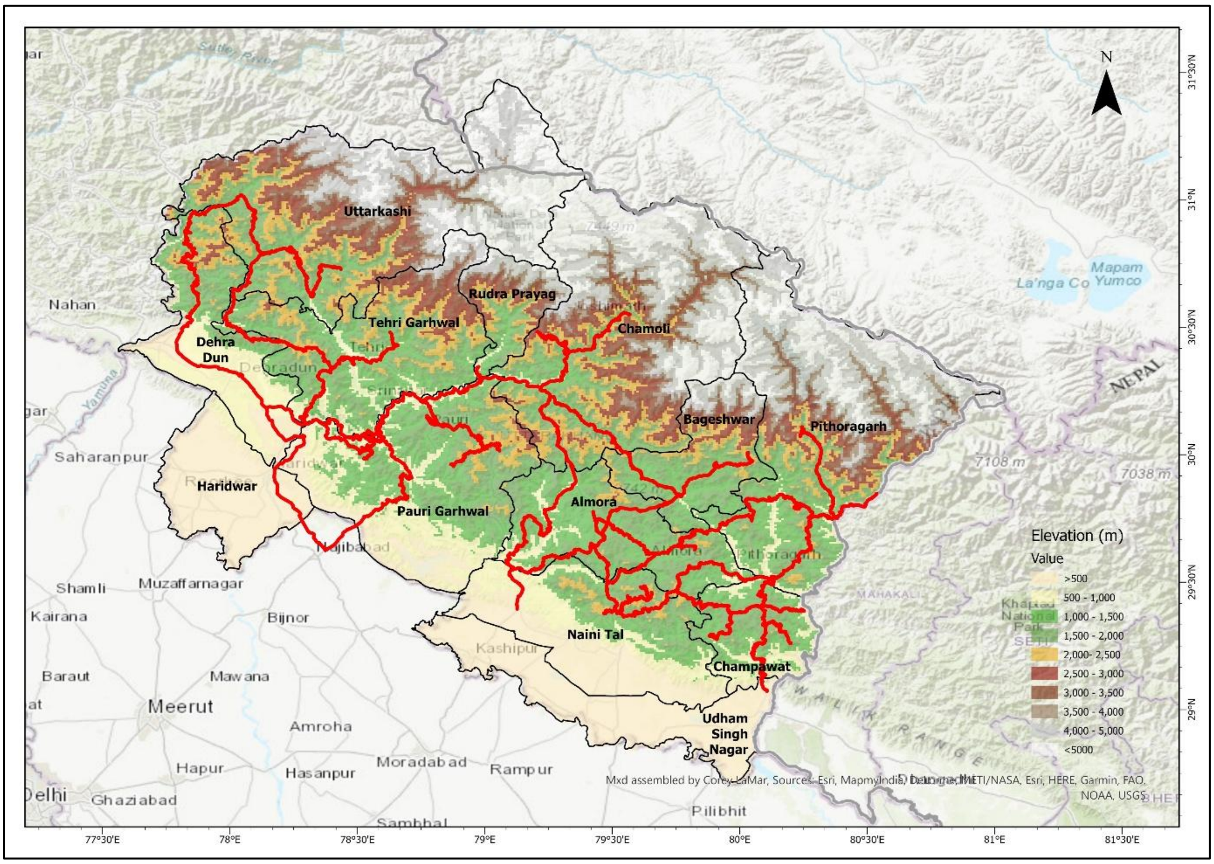

Fig 6.2 Survey routes (in red) that were followed to locate the presence of Barn Swallow nests across the breeding range in Uttarakhand

On sighting a Barn Swallow nest in or around a property, the resident/owner of the property was inquired on the nesting employing open-ended questionnaire survey. A set of 10 questions were asked focusing largely on the history of nesting, breeding periodicity, local name of Barn Swallow, reasons for nest loss, etc. Since the survey period overlapped with COVID-19 associated lockdowns in the country, the impact of closure of properties on nesting of Barn Swallows was also assessed.

6.3 Results & Discussion

In the Himalaya, Barn Swallows share a unique relationship with the people of hills owing to their nature of nesting predominantly in shops and houses. The nesting ecology chapter further details on the building preferences for Barn Swallows across their breeding range in India from largely nesting in shops in Himachal Pradesh, Uttarakhand and North Bengal to almost exclusively nesting in traditional houses in Kashmir and Manipur (*see Chapter 4*). Across the region, local people consider the nesting of swallows– a sign of good fortune. This was evident as across the region people have different names for the Barn Swallow such as *Katij* (Kaur, 2024a)*, Dev Chidiya, Dhan Chidiya, Gotayi* (Kaur, 2024)*, Sambraang*, etc., signifying importance of these human-commensal in their cultures (*Table 6.1*).

Table 6.1 Vernacular names of Barn Swallows and their meaning recorded during the study across its breeding distribution in the Indian Himalayan Region and Northeast India.

State	Local Name	Meaning/Significance
Kashmir	*Katij, Ababeel*	"Bird of the gods"
Himachal Pradesh	*Ram Chidi*	"God bird"
Uttarakhand	*Dev Chidiya, Dhan Chidiya, Gautayi, Gautada*	"God bird/ bird of the land of gods (Devboomi)", "bird of prosperity", "Bird of the country"
North Bengal & Sikkim	*Gauthali*	"Bird of the house"
Manipur	*Sam-braang*	"Bird of the house" which guides humans in how and where to build their houses

Barn Swallows and People of Uttarakhand:

Of 466 respondents, nearly 50% respondents had been staying in the same property for last 40 to 60 years and therefore had a deeper knowledge on Barn Swallows. Residents reported the nesting as old as 50 to over 100 years (*Fig 6.3*). Across sites, Barn Swallows showed high affinity (79%) to nest in old and traditional buildings and surveys revealed that they show high nest-site fidelity by returning to the same nest in consecutive years.

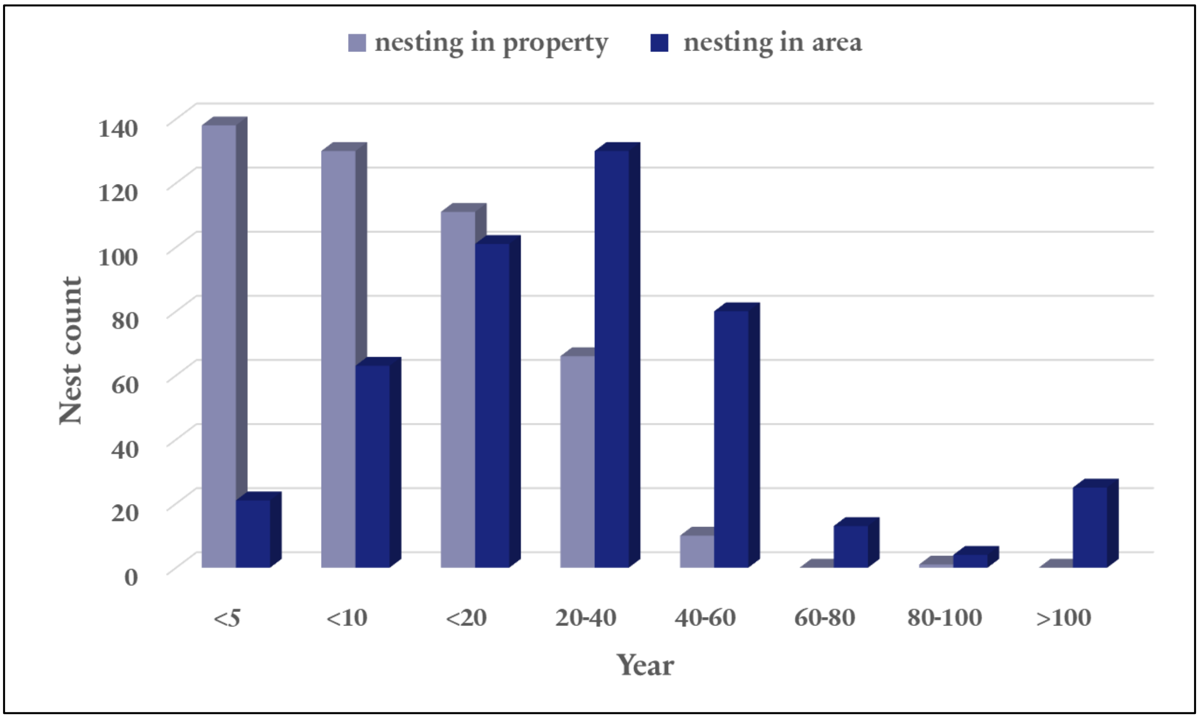

Fig 6.3 Nesting history of Barn Swallows across sites in Uttarakhand. At some sites nesting was reported to be more than 100 years old, however, due to modifications of buildings Barn Swallows are increasingly shifting to modified buildings given there is an accessibility. This can be seen in the figure with large number of nests with only 5 or less years of history in the properties.

People reported that generally Barn Swallows lay two broods per season (~ 50%). Because of the nest re-use by the swallows (82% of old nests), old nests are left undisturbed and intact (reported by 93% respondents). The nest survey data across the Uttarakhand region implied that Barn Swallows show strong preference for nesting inside human structures rather than outside (86%, n=1400). Respondents indicated several threats to a Barn Swallow nest predominantly due to disturbance by another commensal species, House Sparrows, followed by incidents of chicks falling out of the nest, hit by ceiling fans, nest predation by domestic cats, etc. (*Fig 6.4*).

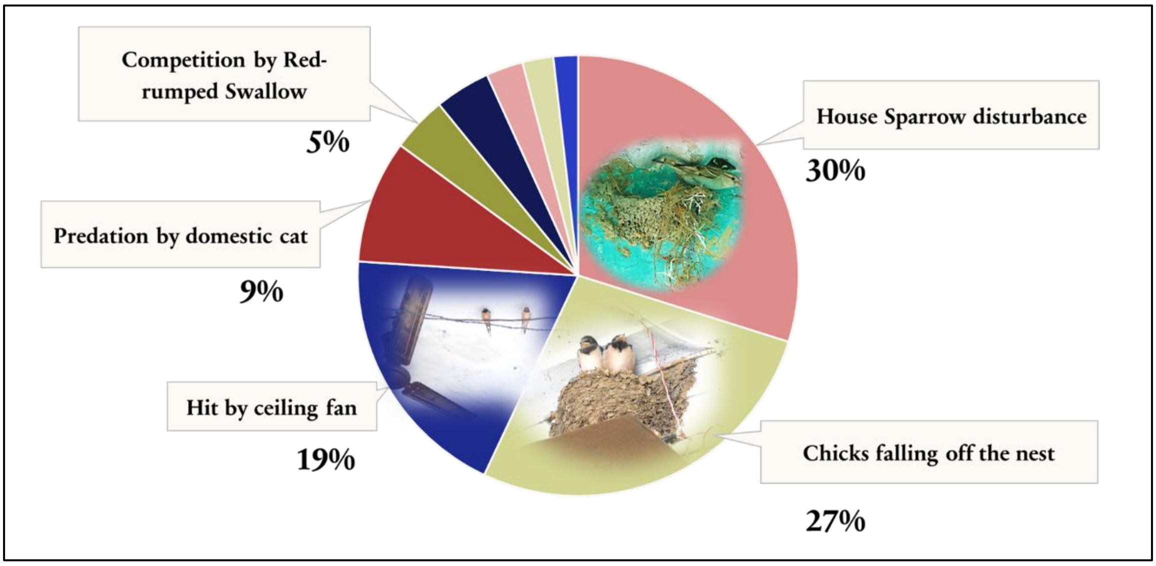

Fig 6.4 Reasons of Barn Swallow nest failure reported by people across the sites in Uttarakhand. Competition with other human-commensals - House Sparrow and Red-rumped Swallow is the predominant reason (35%) behind the loss of nests. Other reasons for nest loss included chicks falling out of the nests, hit by ceiling fans, predation by domestic cats, etc.

Barn Swallows during COVID-19 lockdown

As nesting occurred exclusively in human properties, data from 400 property owners were filtered to assess the impact of the lockdown on nesting; 96% were shop owners and 4% were house owners. These properties were classified as commercial stores providing essential services (e.g. medical stores and police stations) that remained open throughout the lockdown (n = 14), and non-essential service shops, such as shopping stores, that remained closed (n = 371; *Table 6.2* Properties hosting Barn Swallow nests and impact of lockdown on nesting in 2020 and 2021 in Uttarakhand.

The questionnaire survey revealed that during the COVID-19 lockdown, nesting by Barn Swallows was continued in houses and in shops providing essential services, whereas nests built inside non-essential shops were abandoned due to property closure (28.8%, n = 107). Despite the temporary closure of shops, no nest failure was reported in 71.2% of cases (n = 264; *Table 6.2*, *Fig 6.5*A). This persistence was attributed to several factors, including the presence of alternative entry points to the interiors of premises, such as small openings above shop shutters or gaps in windows and doors (*Fig 6.5*B).

In 45% of cases, access for swallows was deliberately provided by shopkeepers, a practice that existed prior to the COVID-19 lockdown to facilitate nesting within their properties (*Fig 6.6*).

During the lockdown, active nest protection measures were taken by some shopkeepers, with 16% reporting that shutters were kept partially open (with permission from authorities), and 11% indicating that small openings were created in shutters to allow free movement of swallows (*Fig 6.7*). In a few instances, nests were relocated by swallows (12.5%) to areas just outside the premises due to restricted access during closures. In rural areas, less stringent lockdown measures allowed birds to nest without disturbance (15%).

Table 6.2 Properties hosting Barn Swallow nests and impact of lockdown on nesting in 2020 and 2021 in Uttarakhand

Property Type & No. of Nests	Impact (Yes/No)
House (15 nests)	No
Essential shop (14 nests)	No
Non-essential shop (371 nests)	Yes (n = 107) No (n = 264)

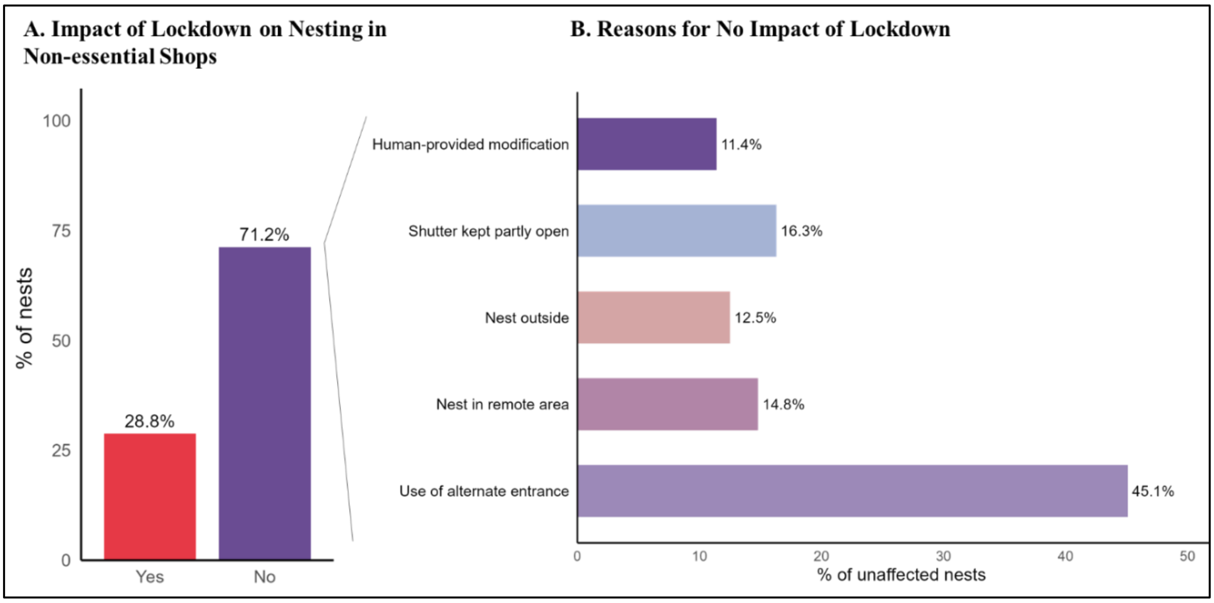

Fig 6.5 Impact of Covid-19 Lockdown on Barn Swallow nesting in non-essential properties (shops) in Uttarakhand (A); Graph showing reasons for no impact of lockdown on nesting in non-essential shops (B).

Fig 6.6 Availability of alternate entrances in shops that were closed during the lockdown, the image below depicts small entrance above the shop shutter being utilised by a nesting pair.

Fig 6.7 Active human interventions, images of shop entrances that were cut by property owners to let swallows continue nest inside their property during the lockdown.

6.4. Conclusions

Barn Swallows as Cultural Commensals: Deep Historical Roots

The findings from the Indian Himalayan region aligns with the global knowledge on Barn Swallow as a human-commensal, exploiting human structures for nesting by closely associating with daily routines of people. The strong preference of Barn Swallow nesting inside houses and shops highlights tolerance of local people towards species' nesting. While some also actively encourage nesting by providing nesting substrates and place cardboards under the nest for cleanliness and for protecting chicks accidentally falling out of the nest. Barn Swallows find their mention in many ancient literatures, (Frazer's (1891) interpretation of ancient Greek texts describes swallows freely entering homes with open shutters, nesting among rafters, and synchronising their movements with daily human routines. Such descriptions closely resemble present-day observations from the Indian Himalayan Region, where swallows access their nest freely during the day through open shop shutters and roost safely inside at night.

Globally, the near absence of Barn Swallows from natural nesting substrates today, coupled with their almost exclusive reliance on anthropogenic structures such as bridges, barns, porches, doorways, sheds, and culverts (Zink et al., 2006), suggests a strong evolutionary shift toward human-associated habitats. Genetic studies further indicate low differentiation across global populations, supporting a relatively recent global expansion during the Holocene that coincides with the spread of permanent human settlements and agriculture (Zink et al., 2006; Dor et al., 2010; Smith et al., 2018). This transition is thought to confer multiple adaptive advantages, including enhanced protection from predators, improved nest adhesion, stable thermal environments, and proximity to predictable food resources (Speich et al., 1986; Møller, 2001). Collectively, this evidence positions the Barn Swallow as one of the most evolutionarily successful avian commensals.

Human–Swallow Coexistence in a Global Context

The coexistence patterns observed in the Himalayas closely parallel accounts from other parts of the world, indicating that positive perceptions of Barn Swallows are strongest in regions where the species breeds in close association with people. Across many Asian societies, Barn Swallows are regarded as harbingers of good fortune and seasonal renewal (*Table 6.3*a). The Mandarin term *jia yan* ("house swallow") explicitly reflects this intimate association between the species and human dwellings. Comparable beliefs are recorded across Europe and Russia, where swallows symbolize fortune but are also associated with cautionary narratives - such as misfortune befalling those who harm nests (Fachon, 2021). These narratives likely function as indirect means of conservation mechanisms working across regions and across generations. Similar to the breeding regions in the Himalaya, naming conventions in other regions emphasize that breeding proximity to humans is central to shaping cultural relationships. Further, it is to note that perceptions of Barn Swallows tend to be neutral in overwintering or non-breeding regions where swallows do not nest within human structures (*Table 6.3*b). This pattern was further supported by surveys in Manipur, where communities in the hill regions had no awareness on Barn Swallow nesting. The absence of cultural associations in these areas likely reflects the species' absence in the hill habitats of Northeast India, reinforcing the idea that human–swallow relationships are most strongly developed in regions where breeding occurs near human habitations.

Table 6.3 Barn Swallow associations (positive, neutral and negative) with the people across the world, information adapted from Fachon, (2021).

a. Positive Associations		
Country/Region	**Belief/Perception**	**Remarks**
China (urban)	Symbol of luck and good fortune	Residents actively facilitate nesting; daily routines adjusted to allow birds access
Taiwan	Symbol of fortune and seasonal change	Nests repaired using tape and sticks; newspapers placed below nests; strong emotional attachment
Russia (rural)	Symbol of fortune	Swallows welcomed in courtyards, sheds, animal structures, above doorways
Taiwan (Taipei City)	Swallows perceived almost as pets	Residents may oppose scientific research due to fear of harming birds
Czech Republic	High concern for swallow welfare	Landowners monitor nests themselves to ensure no population decline
USA (Colorado)	Valued for pest control, Emotional loss when birds die	Recognized for reducing mosquitoes and disease risk in horse farms, Landowners' express grief after extreme weather events
USA (Tennessee, Kentucky)	Emotional attachment, friendship	Individuals name swallows, protect them from predators

Romania	Cultural presence in folklore	Appears in bedtime fairy tales
Mexico	Cultural symbolism	Children sing songs about swallows
b. **Neutral Associations**		
Country / Region	**Belief / Perception**	**Remarks**
Venezuela	Neutral; no cultural association	Swallows overwinter; not associated with buildings
Belize	Neutral	Migratory species; minimal interaction with people
Mexico (non-breeding regions)	Fewer cultural associations	Cultural tales stronger in breeding regions than overwintering areas
Mongolia	Indifference	Nomadic lifestyle of Mongolians; swallows nest under bridges or sheds
c. **Negative Associations**		
Country / Region	**Belief / Perception**	**Remarks**
China (urban regions)	Nests associated with dirtiness	Increased wealth leads to cleaner houses and window screens, excluding swallows
China	Harm to nest - misfortune	Belief that damaging nests causes hair loss
USA (Colorado)	Fear of aggressive behaviour	Homeowners avoid entrances due to defensive adults
Russia	Harm leads to destruction	Belief that disturbed swallows may burn barns
Czech Republic	Considered hygiene risk	Veterinary regulations lead to nest removal
Industrial farming regions (general)	Viewed as disease vectors	Nest removal common in industrialized agriculture

Regional Perceptions Across the Indian Himalayas

Across the Himalayan breeding range, consistently positive perceptions of Barn Swallows, though expressed through distinct regional and cultural frameworks was distinctive. In Kashmir, where the species is locally known as *Ababeel or Katij*, swallows hold religious significance due to their mention in the holy book Quran and are widely regarded as sacred birds. Despite this reverence, nesting is now largely restricted to rural areas where traditional housing still provides suitable indoor nesting opportunities. Local communities across Kashmir reported a marked decline in swallow sightings, attributing this trend to increasing urbanisation and changing attitudes toward wildlife in urban centres (Kaur, 2024a).

In the Central Himalayan region including Himachal Pradesh, Uttarakhand, North Bengal, and Sikkim Barn Swallows are widely perceived as symbols of prosperity and good fortune and are commonly associated with Goddess Laxmi due to prevalence of Hindu religion. Such beliefs translate into strong nest protection practices, with many households actively avoiding disturbance due to fears of bad omens. Similar patterns have been reported in other parts of Asia, where swallows are culturally protected and welcomed into human dwellings (Osawa, 2015; Zhao et al., 2022). In several Himalayan households, I encountered residents to be reluctant to allow close inspection of nests, which reflects their deep emotional attachment and widespread belief that touching a nest would cause permanent abandonment.

In Manipur, Barn Swallows showed a distinct ecological pattern, nesting at relatively low elevations (~700 m) and forming resident populations within the Imphal Valley. Similar to Kashmir, swallows primarily occupied older traditional houses in rural areas of Imphal. Among the Meitei community, the presence of a swallow nest is widely considered auspicious and symbolic of divine blessing, closely paralleling beliefs reported from other Hindu-dominated regions of South Asia.

A case of strong cultural association during COVID-19 lockdown

The striking finding of the study was the continued nesting of Barn Swallows that occurred even during the lockdown. The active measures taken by property owners during the COVID-19 pandemic to help swallows nest demonstrate the strong cultural ties between humans and swallows. The belief that these birds have nested alongside them for many years and therefore have an equal right to nest in their houses or shops is deeply rooted in culture. These cultural values, especially for Barn Swallow in the Himalayan region, which has fully adapted to human infrastructure, are vital for their survival.

Shifting Perceptions, Urbanisation, and Emerging Threats

In the last few decades, the widespread population decline of Barn Swallows across much of their global range is concerning (Lee, 2009; Ambrosini et al., 2012; Vickery et al., 2013; PECBMS, 2024). These declines are primarily attributed to the loss of traditional nesting structures and reductions in aerial insect prey driven by agricultural intensification and land-use change (Teglhøj, 2017; Imlay & Leonard, 2019; Michel et al., 2021). Currently, many people protect Barn Swallow nests by placing materials such as cardboard beneath them, which serves a dual purpose: maintaining cleanliness and preventing nestlings from dying after accidentally falling out of the nest (*Fig 6.8*A–C). With ongoing modernisation, many households are modifying their properties; however, some residents intentionally leave small spaces intact to allow swallows to continue nesting (*Fig 6.8*D). Further, with changing climatic conditions and increasingly warmer summers, the use of ceiling fans has become more common, and this has emerged as a major cause of nestling mortality. In response, some households have adapted by switching to table fans, thereby reducing the risk of swallow deaths (*Fig 6.8*E–F).

These initial findings suggest that, in the Himalayas, positive perceptions toward Barn Swallows remain deeply rooted. However, rapidly changing lifestyles and increasing tourism pressure appear to be contributing to a rise in negative perceptions at certain sites. Consequently, Barn Swallow populations nesting in such areas may become increasingly vulnerable to socio-economic change in the future. This along with other threats in the climatically sensitive Himalayan region - rapid urbanisation, expanding road networks, tourism development, and rural outmigration (IHCAP, 2016; Pathak et al., 2017) may cause severe loss of nest-site availability to the swallows. The replacement of traditional housing with concrete structures, increasing use of window screens, heightened concerns about hygiene, and stricter building regulations may reduce nesting opportunities and weaken human tolerance toward swallows, trends already observed in parts of East Asia (Fachon, 2021).

Fig 6.8 Adaptations by local people to protect Barn Swallow nests in the Indian Himalayan Region. Measures include placing pieces of cardboard beneath nests to maintain cleanliness and prevent chicks from falling (A–C). Some property owners retain nesting space even after modifying their buildings by leaving small areas intact to allow swallows to continue nesting (D), while others have replaced ceiling fans with modified or table fans to reduce the risk of swallow mortality (E–F).

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Synthesis

This work presents a multi-scale and integrative examination of the ecology, evolution, and human dimensions of the Barn Swallow (*Hirundo rustica*) breeding in the Indian subcontinent, with a particular emphasis on the Himalayan region. It represents the first comprehensive effort to establish ecological, migratory, and evolutionary baselines for Barn Swallow populations breeding in India and provides a critical foundation for future research on aerial insectivores in the region. By combining citizen-science–derived migration data, intensive field-based studies of breeding ecology, morphometric and phylogeographic analyses, and socio-cultural investigations, this work moves beyond single-discipline approaches. It demonstrates how large-scale biogeographic processes, local ecological conditions, evolutionary history, and human practices interact to shape population structure, migratory strategies, and long-term persistence in one of the world's most widespread and well-known human-commensal migratory birds.

At the broadest spatial scale, analyses of five years of eBird data establish the first quantitative description of Barn Swallow migration within the Indian subcontinent. These analyses reveal consistent latitudinal segregation between breeding in the Himalaya and wintering in southern India, accompanied by substantial interannual variation in migration timing, speed, and distance. The detection of weak but directional northward shifts in breeding and migratory centroids suggests early responses to climatic change, positioning the Indian subcontinent as a key region for understanding future reorganization of Asian migratory systems. In a country where long-term, standardized bird monitoring programs remain limited, this approach demonstrates the value of citizen science for reconstructing migration dynamics at large spatial scales. The analytical framework applied here is readily transferable to other migratory species and, when integrated with climate and weather data, has strong potential for predicting species responses to habitat alteration and climate change. Future work can build on this foundation by incorporating atmospheric conditions, monsoon dynamics, and long-term climatic trends, as well as by identifying critical wintering areas and evaluating how habitat quality at these sites influences survival, migration timing, and subsequent breeding success.

At regional and local scales, systematic surveys and intensive nest monitoring across the Indian Himalaya reveal that Barn Swallows are widespread and regular breeders across a broad elevational range yet are almost entirely dependent on human-made structures for nesting. Spatial variation in breeding success, phenology, and reproductive output reflects differences in regional climate, settlement structure, and local habitat quality. The observed advancement of breeding phenology over recent years mirrors global trends in migratory birds and underscores the sensitivity of Himalayan breeding populations to environmental change. Dietary analyses demonstrate selective foraging on large-bodied insects and clear differentiation between rural and urban prey use, highlighting the vulnerability of this aerial insectivore to declining insect populations and land-use change despite its apparent behavioural flexibility. While this study provides the first detailed understanding of Barn Swallow nesting ecology in the Indian Himalaya, future research should explicitly integrate fine-scale weather data—particularly rainfall patterns during the breeding season—to assess their effects on foraging activity, nestling provisioning, and nest success. Given that prolonged rainfall can severely limit aerial insect availability, understanding weather-mediated constraints on breeding is likely to be critical. Additionally, documenting habitat characteristics, prey availability, and diet composition at wintering grounds remains an important research priority, as conditions during the non-breeding season can strongly influence migration timing, arrival condition, and reproductive performance at breeding sites.

At an evolutionary scale, the integration of morphometric and mitochondrial genetic data reveals pronounced geographic structuring among Barn Swallow populations within India. A genetically distinct Himalayan lineage encompassing Kashmir, Uttarakhand, and North Bengal broadly corresponds with morphometric differentiation along latitudinal gradients, suggesting the combined influence of historical isolation, local adaptation, and selective pressures associated with migration and sexual selection. In contrast, the newly documented resident breeding population in Manipur exhibits distinct plumage characteristics, smaller body size, and genetic affinity with *H. r. gutturalis*, challenging traditional subspecies assignments and pointing to a more complex biogeographic history involving secondary colonization, admixture, or shifts from migratory to sedentary breeding strategies. Together, these findings highlight the Himalaya as an underappreciated centre of diversification within the *H. rustica* complex and suggest that Himalayan populations may represent an incipient evolutionary or management unit rather than a fully differentiated subspecies. Resolving these patterns will require future studies integrating genome-wide nuclear markers to estimate divergence times, identify hybridization zones, and clarify subspecies boundaries, which is essential for understanding population connectivity, evolutionary trajectories, and conservation priorities.

Crucially, this thesis demonstrates that the ecology of Barn Swallows in the Himalaya cannot be fully understood without accounting for their deep and enduring entanglement with human societies. Ethnographic-style surveys reveal that cultural tolerance, religious symbolism, and long-standing nest protection practices have historically buffered breeding populations against disturbance, effectively functioning as an informal yet powerful conservation mechanism. However, rapid urbanisation, architectural modernization, expanding tourism, and changing hygiene norms threaten both nesting opportunities and cultural acceptance. Given the species' near-total dependence on human structures for breeding in the region, Barn Swallows are uniquely vulnerable to socio-economic change, even in landscapes that remain ecologically suitable. Long-term monitoring of these changes along with breeding sites of Barn Swallows should be a research priority in the Himalayan region.

Taken together, the synthesis of ecological, evolutionary, and cultural evidence underscores a central conclusion of this thesis: the persistence of Barn Swallows in the Indian Himalaya is shaped as much by human values and behaviours as by climate, geography, and biological processes. The Himalaya emerges not only as a migratory corridor and breeding stronghold, but also as a dynamic socio-ecological system where evolutionary divergence, migratory connectivity, and cultural coexistence intersect. By establishing foundational baselines and revealing previously undocumented patterns, this thesis provides a robust framework for future research integrating genome-wide genomics, fine-scale movement tracking, and long-term socio-ecological monitoring, and offers clear guidance for conservation strategies that recognize both ecological processes and the cultural landscapes within which this iconic migratory bird continues to breed.

Annexure 1

Publications (peer-reviewed)

Kaur, A., Chauhan, H., and Kumar, R. S. (2026). Prey composition in the diet of an avian aerial insectivore – the Barn Swallow (*Hirundo rustica*) in the Indian Himalaya. *Avian Conservation and Ecology* (**accepted for publication**).

Avian Conservation and Ecology ISSN: 1712-6568

28/01/2026, 11:33 Roundcube Webmail :: Fwd: ACE-ECO-2026-3055; Editorial Decision

Fwd: ACE-ECO-2026-3055; Editorial Decision

From Suresh Kumar <suresh@wii.gov.in>
To Amarjeet Kaur Scientist C <amarjeet@wii.gov.in>
Date 2026-01-28 11:22

Manuscript #ACE-ECO-2026-3055, Version: 3

Title: Prey composition in the diet of an avian aerial insectivore – the Barn Swallow (*Hirundo rustica*) in the Indian Himalaya

Manuscript type: Research Paper
Word count: 6182

Authors: Amarjeet Kaur, Harsh Chauhan, Suresh Kumar

Dear Suresh Kumar:

We have completed reviews of your article submitted to Avian Conservation and Ecology and are happy to inform you that it has been accepted for publication.

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jlavers@csu.edu.au

Decision submitted by Jennifer Lavers

Editorial Decision: Accept

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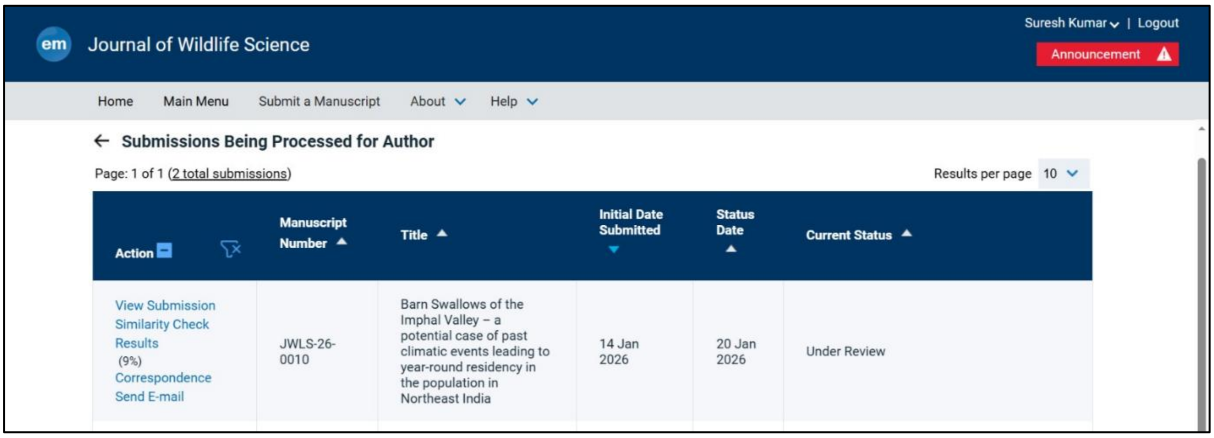
Page 1 of 1

Article code	Title	Section	Submitted	Status
ACE-ECO-2026-3055	Prey composition in the diet of an avian aerial insectivore – the Barn Swallow (*Hirundo rustica*) in the Indian Himalaya (*Version 3*)	Research Paper	2026-01-23	**Accepted**

Kaur, A., and Kumar, R. S. (2026). Barn Swallows of the Imphal Valley – a potential case of past climatic events leading to year-round residency in the population in Northeast India submitted in the *Journal of Wildlife Science* (**in review**)

Journal of Wildlife Science ISSN (Online): 3048-7803



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Announcement

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Submissions Being Processed for Author

Page: 1 of 1 (2 total submissions)

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Action	Manuscript Number	Title	Initial Date Submitted	Status Date	Current Status
View Submission Similarity Check Results (9%) Correspondence Send E-mail	JWLS-26-0010	Barn Swallows of the Imphal Valley – a potential case of past climatic events leading to year-round residency in the population in Northeast India	14 Jan 2026	20 Jan 2026	Under Review

Annexure 2

Popular articles

Kaur, A. (2024). Barn Swallow: A tale of homecoming. WII Newsletter, Vol. 31(1): 30–31.

Return of swallow, return of spring: A Barn Swallow individual that was captured and ringed in Nainital with both a metal (uniquely coded) and a colour ring in 2022, was subsequently re-sighted in 2023 at the same nest, thereby demonstrating site-fidelity in the population

BARN SWALLOW: A tale of homecoming

- AMARJEET KAUR

Each year after her long absence in the warm lands of the south she comes to us with the sunshine and the flowers, and she tells us with her merry chatter that spring is on the way.
- Dr. Giuseppe Pitrè

Cultural and traditional beliefs, such as not disturbing a bird's nest in one's house or viewing nesting as a sign of good fortune, have fostered a close relationship between Barn Swallows and humans in Uttarakhand. Often, if comfortable, the Barn Swallow family befriends their human hosts and allows physical approach. In this image, a lady 'greets' swallow fledglings, who will soon embark on a southward journey with their parents.

30 WII newsletter - Spring 2024

In this transitional season, the sun shares the lingering soft warmth of winter, while the wind carries the fragrant promise of new life. Afternoons are hot, yet nights remain cool. Life announces its grandiose rebirth as the Palash (*Butea monosperma*), Silk cotton tree (*Bombax ceiba*), and Purple orchid tree (*Bauhinia purpurea*) burst forth with vibrant colours through their showy flowers. The ceaseless serenades of the Asian Koel (*Eudynamys scolopaceus*) and Common Hawk-Cuckoo (*Hierococcyx varius*) collectively announce the arrival of spring on the WII campus.

Amidst this awakening, a small yet resilient long-distance migrant, the Barn Swallow (*Hirundo rustica*), embarks on its homeward journey to the human settlements of the Himalaya. Known by various names such as "Dev chidiya", "Dhan chidiya" or "Gotayi" this bird is welcomed as the harbinger of spring in the hills of Uttarakhand. Revered as a symbol of Goddess Lakshmi, the Dev chidiya returns to its nest, diligently repairing it with nearby damp mud and grass in preparation for raising a new family.

Soon, life bursts forth anew as four or five baby swallows announce their arrival with constant begging calls for food. The adult swallows tirelessly hunt for aerial insects, making a series of rounds throughout the day to feed their hungry chicks, until dusk sets in. The setting sun signals the busy parents to finally call it a day and return to rest alongside their chicks within the safe confines of human dwellings. With the dawn of the next day, the cycle repeats itself until the chicks can fend for themselves.

As dark, moisture-laden clouds start hovering above, June-end onwards, threatening monsoonal downpours, barn swallow families begin preparing for their journey southwards. They bid a temporary farewell to their human hosts, promising to return the next spring! They leave in the hope that their human hosts will welcome them back with open doors, windows, and most importantly, warm hearts.

About the Author

Amarjeet began her career as a professional ornithologist with the Wildlife Institute of India in the Amur Falcon research project, tracking the bird's migration in remote villages of Nagaland and Manipur. She later enrolled into the Institute's PhD program (affiliated with Saurashtra University) in 2019, focusing on Barn Swallow ecology in the Indian Himalaya Region. Her research navigates the intersection of wildlife ecology and sociology, including documenting local narratives and perceptions about the species.

Email : 10amarjeetkkaur@gmail.com

Barn swallow pairs often build nests near each other in available spaces within the same property, this combined presence helps to more successfully warn against and deter away predators. In this bustling Nainital vegetable shop, two Barn Swallows guard their respective nests, ready to start their new families.

Once cave-nesters, Barn Swallows now rely completely on human habitats for nesting. They seek safe spaces in architecturally appropriate shops and houses, having become completely dependent on the warmth and protection offered by their human hosts.

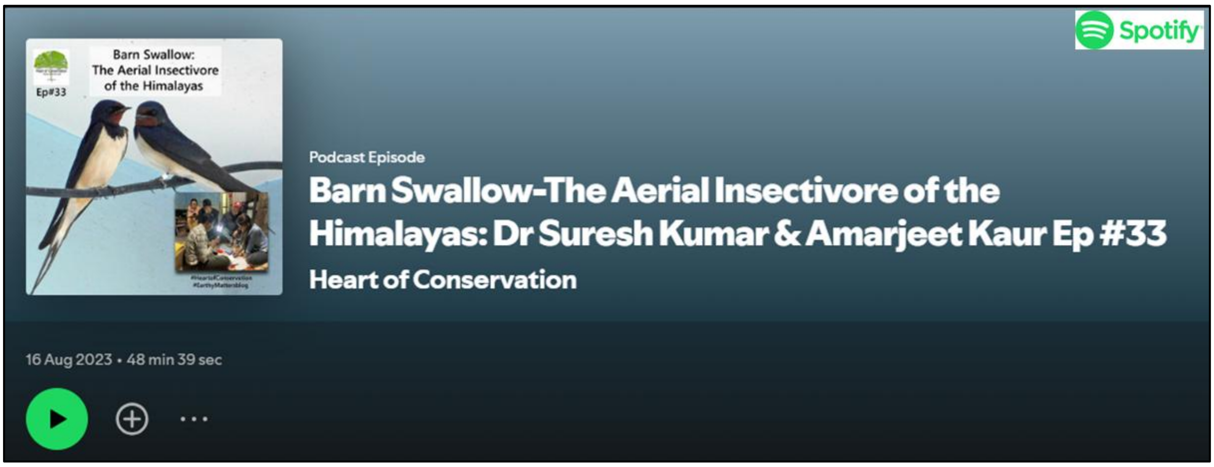
As the season progresses, swallow chicks fill the room with their constant calls, announcing their hatching. Here, a human host has kindly placed a cardboard beneath the Barn Swallow nest to protect it and prevent chicks from falling. The parent swallows appear to appreciate this gesture, using the cardboard as a perch while feeding and guarding their chicks.

Popular articles

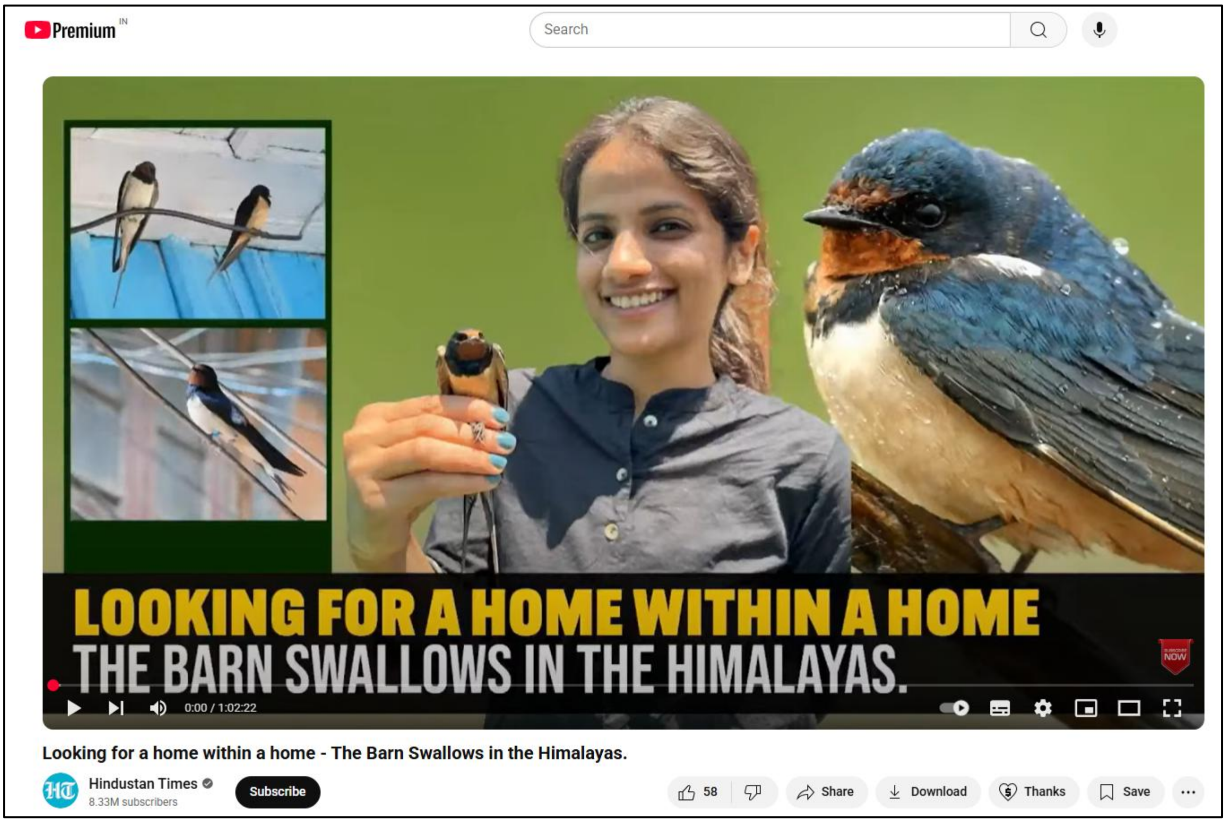
Kaur, A. (2024). The Beloved *Katij* of Kashmir. Nature inFocus.

Popular talks

Kumar, R. S. and **Kaur, A**. (2023). Barn Swallow – the aerial insectivore of the Himalayas. Podcast episode no. 33. Heart of Conservation. https://open.spotify.com/episode/5xGdSTrE14Gix0FtVeGfuk?si=7v0qbSUpTxKQ00mE-3RnlQ



Kaur, A. (2025). Looking for a home within a home – the Barn Swallows in the Himalayas. Live Webinar. Hindustan Times. https://www.youtube.com/watch?v=9IST36u37FQ



Annexure 3

National Conferences

Kaur, A., and Kumar, R.S (2021). Poster presentation titled "Common birds in a changing world: Monitoring Barn Swallow populations in the Himalaya" held on 26th – 27th March 2021 (online mode) at Bird Monitoring Symposium 2021.

CERTIFICATE

OF PARTICIPATION

THIS CERTIFICATE IS PRESENTED TO

Amarjeet Kaur

FOR PRESENTING HER WORK AS A POSTER AT THE BIRD MONITORING IN INDIA SYMPOSIUM 2021.
THE SYMPOSIUM WAS AN ONLINE EVENT HELD ON 26 - 27 MARCH 2021.
WE APPRECIATE HER ACTIVE PARTICIPATION AT THE EVENT.

27.03.2021

DATE

SIGNATURE

Priti Bangal

On behalf of the Organising Committee 2021
(Ghazala Shahabuddin, Rajah Jayapal,
Suhel Quader and Priti Bangal)

birdmonitoring.in

Kaur, A., and Kumar, R.S (2025). Oral presentation titled “Common Birds in a Changing World: Nesting Ecology of Barn Swallow in the Himalayas” held on 5th – 6th September 2025 (online mode) at Bird Monitoring Symposium 2025.


CERTIFICATE

OF PARTICIPATION

THIS CERTIFICATE IS PRESENTED TO

Amarjeet Kaur

FOR PRESENTING HER WORK AT THE BIRD MONITORING IN INDIA SYMPOSIUM 2025.
THE SYMPOSIUM WAS AN ONLINE EVENT HELD ON 5 - 6 SEPTEMBER 2025.
WE APPRECIATE HER ACTIVE PARTICIPATION AT THE EVENT.

6.09.2025

DATE

SIGNATURE

Priti Bangal

On behalf of the Organising Committee
(Monica Kaushik, Parveen Shaikh, Priti Bangal,
Tarun Menon, Suhel Quader, and Ankita G)

birdmonitoring.in

International Conference

Kaur, A., and Kumar, R.S (2023). Oral presentation titled "A Close-Knitted Relationship: Barn Swallows (*Hirundo rustica*) and the Humans of the Himalaya" in the session Nature and Humans - Human-wildlife interactions at the British Ecology Society Annual Meeting 2023, Belfast, United Kingdom.

BRITISH ECOLOGICAL SOCIETY

BES Annual Meeting:
12-15 December 2023, Belfast, UK

This certificate confirms that

Amarjeet Kaur

Attended BES2023 in Belfast, UK, and delivered an in-person ***ORAL*** presentation in the session ***S46: Nature and Humans - Human-wildlife interactions*** titled:

" A Close-Knitted Relationship: Barn Swallows (Hirundo rustica) and the Humans of the Himalaya."

Co-Author: Suresh Kumar

Rachel Kudlick

Events Manager
British Ecological Society

British Ecological Society

42 Wharf Road, London, N1 7GS, UK
Tel: +44 (0) 20 3994 8241