FROM TROPICAL SHORES TO HIGH-ALTITUDE LAKES: PRELIMINARY ASSESSMENT OF TRANS-HIMALAYAN MIGRATION OF BROWN-HEADED GULLS *CHROICOCEPHALUS BRUNNICEPHALUS* BETWEEN SRI LANKA AND THE TIBETAN PLATEAU

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ABSTRACT

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The Brown-headed Gull (BHGU) *Chroicocephalus brunnicephalus* is a common non-breeding migrant to Sri Lanka's coasts. However, its migration across the Central Asian Flyway—traversing numerous geographic barriers such as the Himalayas and the Tibetan Plateau to reach the southern Indian peninsula and Sri Lanka—has not been studied. We GPS-tracked two BHGUs between Sri Lanka and their breeding grounds on the Tibetan Plateau from 2021 to 2023, documenting four migrations in total—three northward and one southward. During northward migration (25 April–20 May), the gulls covered 2,786.7 ± 168.0 km in 6.8 ± 1.05 d without any stopovers, although they made several rest stops (< 48 h each), including along the Ganges River in northern India. BHGU1 remained on the Tibetan Plateau for 157 d; BHGU2's duration of stay is unknown due to a temporary device failure. Southward migration occurred between 06 October and 19 December, with BHGU2's migration taking > 31 d, including two stopovers totaling 13 d along India's west coast. Notably, both gulls followed India's east coast during northward migration, whereas BHGU2 followed the west coast southward, indicating a loop migration pattern. The gulls crossed the Himalayas at ground elevations of 3,568–6,003 m above sea level, navigating three main regions: Annapurna, Khumbu/Everest, and Kanchenjunga. They often used valleys and gorges such as the Marsyangdi Valley, Kali Gandaki Gorge, and Dudh Koshi River, although they also occasionally flew over or near the main Himalayan peaks. Our findings reveal new insights into the extreme altitudes reached by migrating BHGUs, both while crossing the Himalayas and flying over inland India, even in the absence of topographic constraints. Further tagging of this non-breeding population is needed to explore potential age- or sex-related variation in migratory strategies, and to understand how this relatively small species (372.5 ± 53.0 g) manages high-altitude migration—a trait previously studied primarily in larger birds.

Key words: Central Asian Flyway, GPS-GSM transmitters, Himalayan crossing, Mannar, migration, seabirds

INTRODUCTION

The Central Asian Flyway (CAF) is one of the nine major globally recognized migratory flyways where birds breeding in the arctic and temperate regions of Russia and Central Asia migrate to the South Asian tropics during the boreal winter (Mundkur et al., 2023). The CAF poses a series of geographic and ecological barriers for migratory birds (Dixon et al., 2017), most notably the formidable Himalayan mountain range. This range separates the northern breeding grounds from the Indian subcontinent, which constitutes the major non-breeding area within the CAF (Newton, 2008; Prins & Namgail, 2017). The Himalayan range rises to an average elevation of 6,100 m above mean sea level (AMSL) with its highest peaks reaching 8,000 m AMSL. Even the mountain passes and valleys that cut through this barrier are typically situated at elevations of 4,000–6,000 m AMSL (Prins & Namgail, 2017).

Adding to this challenge, the Tibetan Plateau—situated in China, immediately north of the Himalayan range and known as the 'Roof of the World'—covers over 2.5 million km^2 and has an average elevation of 4,500 m AMSL (Dixon et al., 2017).

Despite this challenging barrier, increasing evidence indicates that various species of birds from breeding grounds north of the Himalayas in central and northern Asia, such as geese, ducks, cranes, raptors, waders, and passerines, overfly the Himalayas during their annual migrations (Batbayar & Lee, 2017; Delany et al., 2017a,b; Dixon et al., 2017; Higuchi & Minton, 2017; Juhant & Bildstein, 2017; Literák et al., 2022; Namgail et al., 2017; Takekawa et al., 2017; Turbek et al., 2022).

The Brown-headed Gull (BHGU) *Chroicocephalus brunnicephalus* is a widely distributed species, commonly observed as a boreal winter migrant to Nepal, the coasts of India, northern Sri Lanka, and Southeast Asia. It also occasionally spends the non-breeding period westward up to the Arabian Peninsula. Breeding of the BHGU occurs in the mountains of south-central Asia (up to 4,500 m AMSL), encompassing regions from Turkestan in the west, southwest Gansu in China in the east, and the Pamirs and Tibet in the south, including Ladakh in northern India (Fig. 1; BirdLife International, 2024; Burger et al., 2020; del Hoyo et al., 1996; Global Register of Migratory Species, 2004; Harrison et al., 2021; Liu & Chen, 2021). Accordingly, its migration between breeding and non-breeding grounds is challenged by the world's tallest physical barriers for a migratory bird: the Himalayas and the Tibetan Plateau. Furthermore, as its breeding range is exclusively confined to the poorly studied CAF, its migration within this flyway, despite these geographic barriers, remains an area of limited knowledge.

The global population of the BHGU was estimated to be between 100,000 and 200,000 individuals in 2006 (Wetlands International, 2024). However, recent counts at several important coastal sites for the species in India and Sri Lanka alone totaled 200,000 individuals (S. Balachandran, unpubl. data, June 2024). Between 2010 and 2015, the annual Asian Waterbird Census reported an annual average of 15,586 (1,288–51,441) BHGUs spending the non-breeding season in Sri Lanka (Mundkur et al., 2017). Although currently classified as Least Concern (BirdLife International, 2024), BHGUs show a decreasing population trend based on a range-wide assessment in South and Southeast Asia (Mundkur & Langendoen, 2022; State of India's Birds [SoIB], 2023).

Little is known about the precise annual migratory strategies and movements of BHGU, especially within the CAF. While Ratanakorn et al. (2012) and Yu et al. (2024) used satellite telemetry

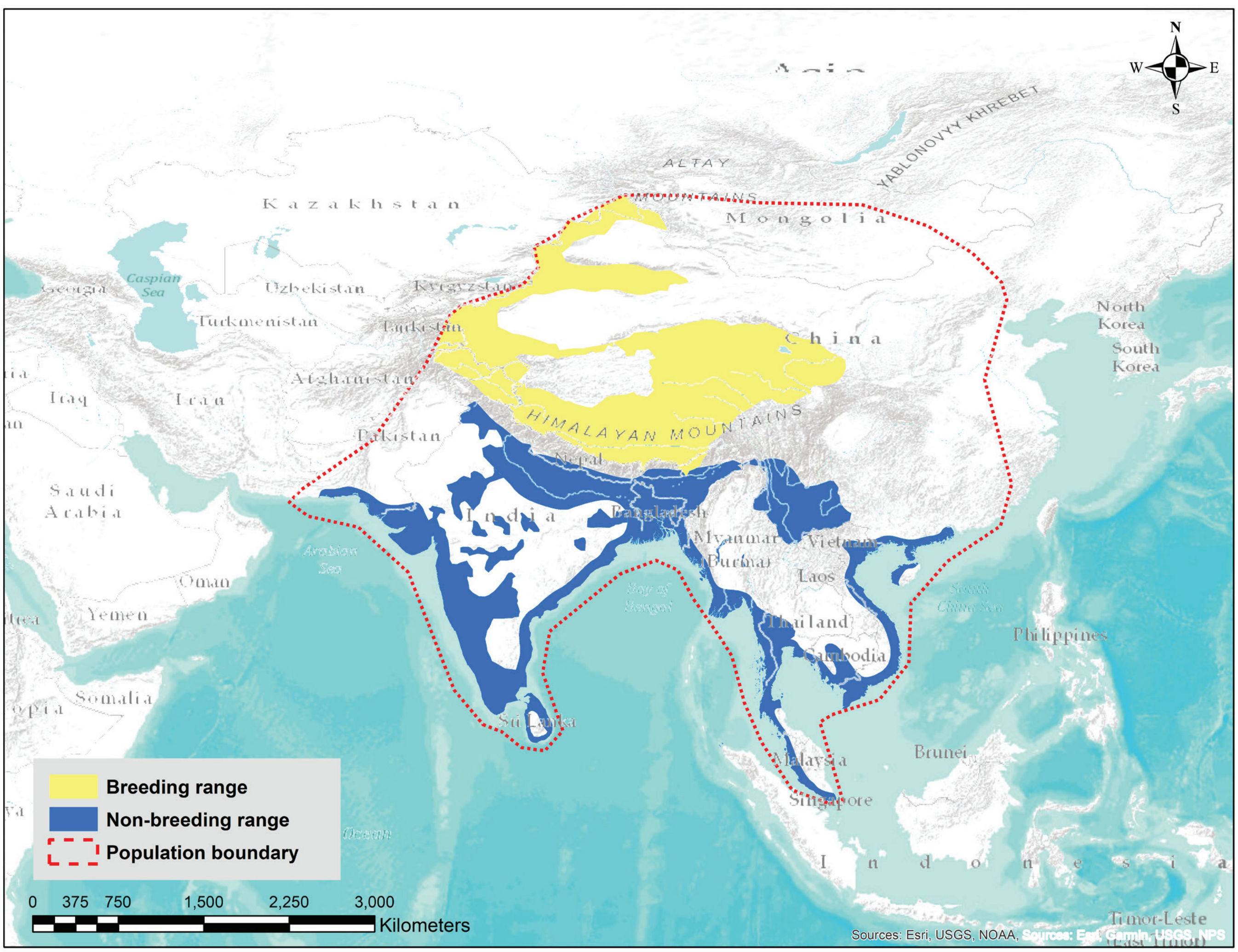

Fig. 1. Distribution map of Brown-headed Gull *Chroicocephalus brunnicephalus*, showing their breeding range (yellow), non-breeding range (blue), and population boundary (red dashed line). Based on Liu & Chen (2021), BirdLife International (2024), and Wetlands International (2024).

to assess the movements of more easterly populations migrating to Southeast Asia—primarily to understand their potential role in spreading Highly Pathogenic Avian Influenza (HPAI)—no other studies have investigated the migration patterns of this species.

Our study aimed to address these knowledge gaps through the following objectives: (i) delineate the northward and southward migration routes and identify the stopover sites across the CAF of Sri Lankan non-breeding BHGUs; (ii) assess the local movements of BHGUs at both their breeding and non-breeding grounds; and (iii) understand how BHGUs react to and overcome the mountain barriers and extreme elevations during migration.

METHODS

Bird capture and deployment of GPS-GSM transmitters

During late March–early April 2021/22, just before their northward departure, four BHGUs were captured at their non-breeding site in Taleimannar, Mannar Island, northwestern Sri Lanka (9°3′31″N, 79°49′7″E). The gulls were captured near the coastline using a locally adapted baited trapping method under relevant permits. In 2021, three gulls were captured, but due to limited device availability, only one adult (BHGU1; 410 g) was tagged. In 2022, another sub-adult (2CY) (BHGU2; 335 g) was captured and tagged. BHGU1 was fitted with a HQBG2009P transmitter (9.1 g; Hunan Global Messenger Tech, China) and BHGU2 was fitted with a Debut Mini transmitter (6.4 g; Druid Tech, China; Fig. 2; Table 1). Both were solar-powered GPS-GSM transmitters.

Transmitters were attached as backpacks using a permanent harness made of durable nylon string inserted into Teflon ribbon (~1–2 g), ensuring the total weight remained below 3% of the bird's body mass (Table 1). All birds were measured and ringed (using uniquely numbered metal rings and two green-colored leg flags) and immediately released after processing. All bird handling was conducted by two trained and experienced bird banders (GP and SS).

The transmitters were programmed to record location (positioning accuracy ± 5–10 m), flying altitude, and instantaneous speed (accuracy ± 0.1 m/s) every 1 min–2 h, depending on battery conditions and transmitter type. When GPS positioning was disturbed, backup positioning using Base Station Service (BSS),

Fig 2. The tagged Brown-headed Gulls *Chroicocephalus brunnicephalus* (left: BHGU1, adult; right: BHGU2, sub-adult) from Mannar, Sri Lanka, during 2021–2022. SS is holding the bird in both photos. Photos by GP.

TABLE 1
Summary of tracking data from two Brown-headed Gulls *Chroicocephalus brunnicephalus* tagged at their non-breeding grounds in Mannar Island, northwestern Sri Lanka, during the 2021–2023 migration period

Individual	Age	Sex	Weight (g)		Capture period	Start date	End date	No. of days tracked	No. of filtered GPS points	Total track (km)	No. of trips	
			Bird	Device							Northward	Southward
BHGU1	Adult	Female	410	9.1	2021 non-breeding season	04 Apr 2021	10 Oct 2021	189	2,202	8,057	1	0[a]
BHGU2	Sub-adult (2CY)	Female	335	6.4	2022 non-breeding season	30 Mar 2022	04 May 2023	400	10,223	13,202	2[b]	1[c]

[a] BHGU1 initiated its southward migration, but transmission ceased shortly afterward while it was still north of the Himalayas.

[b] The second northward migration track of BHGU2 in 2023 was incomplete due to inconsistent data collection, resulting in sparse and limited GPS fixes during this period. As a result, the inferred track may not represent the exact path taken by the bird. Additionally, transmission ceased altogether after the bird had completed approximately five-sixths of the journey, just south of the Himalayas.

[c] The southward migration track of BHGU2 in 2022 was incomplete; transmission began only as the bird was crossing the Himalayas, resulting in a data gap between its breeding/post-breeding ground and the Himalayas, spanning 30 June–18 November.

which obtains location data from terrestrial base stations instead of satellites, was enabled (positioning accuracy ± 50–2,000 m).

Molecular sexing of tagged birds

We collected 20 μL of blood from the brachial vein of the wing and preserved it in Queen's lysis buffer for analyses (Seutin et al., 1991). From these blood samples, we extracted DNA using the cetyltrimethylammonium bromide (CTAB) method (Bogožalec Košir et al., 2023). We then performed PCR-based molecular sexing using the P2/P8 primer pair to amplify fragments of the CHD-W and CHD-Z sex chromosomes (Fridolfsson & Ellegren, 1999). This resulted in two distinct bands in females, indicating the presence of both Z and W chromosomes, as females are heterogametic.

Segmentation of movement bouts to identify migration/stopover periods and sites

The movements of the two tagged birds were monitored from April 2021 to May 2023. BHGU1 was tracked from April to October 2021 (189 days), and BHGU2 from March 2022 to May 2023 (400 days; Table 1). During this period, we collected a total of 17,863 GPS positions. The dataset was filtered by removing failed location attempts (i.e., latitude and longitude set to 0/0) and duplicate positions (n = 5,438). After filtering, 12,425 GPS positions remained and were used in the analysis.

We then classified segments of filtered movement tracks into periods of direct migratory flight and periods of relative quiescence (i.e., stopover sites, and non-breeding and breeding areas, where birds may still fly between feeding and roosting sites but do not engage in long directional movements that contribute to migration) (Deng et al., 2019; Wang et al., 2018b). This classification was performed using the modified first passage time method (Edelhoff et al., 2016).

This segmentation allowed us to identify and categorize the movement tracks into four stages representing the annual cycle of the gulls: non-breeding period, northward migration, breeding and post-breeding period, and southward migration. We further isolated stopover periods and sites from other periods of a migration episode.

A stopover site was defined as a site where birds remained for at least 48 h during migration, with movements confined within a cluster whose maximum pairwise distance did not exceed 50 km (~25 km radius). Previous studies applied slightly different thresholds, using 30 km (Van Wijk et al., 2012; Kölzsch et al., 2016) or 20 km (Guo-Gang et al., 2014) radii, reflecting the maximum distances birds typically travel between roosting and foraging areas at non-breeding sites. In our study, however, the tagged gulls regularly commuted up to 50 km between roosting and feeding sites during the non-breeding period. To avoid over-segmenting stopovers, we therefore adopted a 50 km maximum pairwise distance threshold. We assumed that those clusters lasting > 48 h contributed significantly to migratory fattening (Guo-Gang et al., 2014; Muzaffar et al., 2008) and rest.

Brief stops that did not meet the stopover criteria—lasting less than 48 h and primarily associated with resting between successive migratory flights, with little to no refueling value—were defined as rest stops, which are considered part of active migration (Bayly et al., 2018). Rest stops were identified only for tracks with high-resolution temporal data (1–2 h fix intervals), as sparser datasets may not reliably detect such brief pauses (Bouten et al., 2013).

The departure from a non-breeding or breeding area was defined as the first point in time when the individual left the site after a prolonged period of occupancy. Conversely, the arrival at a non-breeding or breeding area was marked by the first point in time when the bird reached the site prior to a subsequent prolonged stay (Gu et al., 2019).

Calculation of migration parameters

Having identified the periods of migration, we then defined and calculated the following migration parameters, based primarily on the definitions provided by Gu et al. (2019):

(1) Migration duration: The amount of time the birds took to travel (including stopovers) between the non-breeding site and the breeding site (on northward migration) or between the breeding site and the non-breeding site (on southward migration).

(2) Stopover duration: The sum of all stopover durations spent by a bird at all stopover sites during a migration episode.

(3) Travel days: Total migration duration minus stopover duration.

(4) Migration distance: The sum of all migratory legs during a migration season. A migratory leg is the distance connecting two successive stopover, non-breeding, or breeding sites, measured as the orthodromic distance between the two points. Migration distance excludes the distances traveled during stopovers but includes the short distances traveled within rest stops (Gudmundsson & Alerstam, 1998; Gu et al., 2019).

(5) Total fly number: The number of migration legs.

(6) Migration speed: Migration distance divided by migration duration (Gu et al., 2019; Nilsson et al., 2013).

(7) Daily travel speed: Migration distance divided by travel days (Gu et al., 2019; Nilsson et al., 2013).

(8) Step length: Migration distance divided by the number of migratory legs from non-breeding/stopover site to the next stopover/breeding site.

(9) Number of stopovers.

(10) Straightness index: A measure of path tortuosity of migration. It is a number constrained between 0 and 1 and is calculated by dividing the straight-line (great-circle) distance between the starting and ending points of the migration route by the actual distance covered along the observed route. A value closer to 1 indicates a more direct, straighter path, while values closer to 0 reflect a more tortuous, or winding, route (Benhamou, 2004; Wang et al., 2018a).

Analysis of altitudes during migration and diel migration pattern

To better understand the migration strategies of this possible trans-Himalayan migrant, we studied the ground elevation over which the birds flew, their flying altitudes, and the distances traveled during day and night. Due to the uncertainty associated with GPS-measured altitude data, we calculated weighted moving averages from the raw altitude values, which reduced noise and helped identify general patterns in flying altitude (Banerjee & Bansal, 2017). The respective ground elevations for each GPS fix were derived from the 30-arc second DEM of Asia (U.S. Geological Survey's Center for Earth Resources Observation and Science [USGS EROS], 1996), using ArcMap 10.8. We then analyzed changes in ground elevation and flying altitude across latitudes, considering only the GPS fixes collected in flight by excluding those with instantaneous speeds < 10 km/h, which predominantly include occasions of sitting, walking, or floating on water (Klaassen et al., 2012; Shamoun-Baranes et al., 2011).

To evaluate whether the birds were traveling during the day or night, we computed sunrise and sunset times for each GPS fix using the *getSunlightTimes* function from the "suncalc" package in R (McDuie et al., 2019; Thieurmel et al., 2019). Based on these times, we categorized each GPS fix as either day or night and then calculated the distances traveled during each period.

All the analysis and visualization were conducted using R 4.2.2 (R Core Team, 2023), ArcMap 10.8, and Google Earth Pro 7.3.6.9345.

RESULTS

From April 2021 to May 2023, the tagged BHGUs generated movement tracks covering a cumulative distance of 21,259 km. These included two complete (both northward) and two incomplete (one northward and one southward) migration tracks (Table 1). Specifically, BHGU2 completed more than one annual cycle, undertaking two northward migrations (one complete, one incomplete) and one incomplete southward migration. The departure date for the latter was unknown due to a data gap. BHGU1 completed one northward migration and initiated its southward migration, but transmission ceased shortly afterward (Fig. 3). Therefore, only the two complete northward migrations were used to calculate migration parameters (Table 2).

The northward migration

The gulls departed Sri Lanka on 25 April (BHGU1) and 14 May (BHGU2) and arrived at their breeding grounds on the Tibetan Plateau on 03 May (BHGU1) and 20 May (BHGU2), respectively. During this northward migration, they covered a distance of 2,786.73 ± 168.02 km (mean ± standard deviation [SD]) in 6.84 ± 1.05 d, without any stopovers. Therefore, the number of travel days was equivalent to the total migration duration for both birds. Consequently, the northward migration speed and daily travel speed were the same, averaging 414.54 ± 88.48 km/d. The straightness index of their northward migration route was 0.80 ± 0.18 (Table 2).

During the three observed northward migrations, both birds initially flew northward along the eastern coast of India, reaching the state of Andhra Pradesh before veering inland between 15°48′N and 16°18′N. The two complete tracks revealed that the birds briefly rested at the Ganges River in either Uttar Pradesh or Bihar, northern India (between 25°N and 26°N), for 32–42 h, although these pauses did not meet our criteria for a stopover. BHGU2 flew over inland India (from the coast of Andhra Pradesh to the Ganges River) in 34 h (2022), covering 1,560 km non-stop at an average speed of 45.88 km/h. In contrast, BHGU1 took 52 h (2021) to travel 1,112 km with multiple brief stops along the way, moving at an average speed of 21.38 km/h.

After departing from the Ganges, the birds flew directly toward the Himalayas, traversing central to eastern Nepal. Subsequently, they crossed the Himalayas and arrived on the Tibetan Plateau in China, where they spent the boreal summer. The incomplete northward track of BHGU2 in 2023 suggested a more direct route from Andhra Pradesh to Nepal, with minimal or no rest at the Ganges, before reaching eastern Nepal, where signal transmission ceased (Fig. 3).

Although our gulls did not stop over during their northward migration, they did make successive rest stops en route (lasting 6–42 h), primarily during the day, before and after crossing the Himalayas. BHGU1 made four rest stops at: (i) Point Calimere Ramsar Site, Tamil Nadu (10°17′45″N, 79°48′56″E; 8 h), (ii) Ganrel Reservoir, Chhattisgarh (20°34′12″N, 81°32′23″E; 10 h), (iii) the Ganges River, Varanasi, Uttar Pradesh (25°22′49″N, 83°10′44″E; 42 h) in India, and (iv) Pozi Co Lake, Shigatse, Tibet (30°30′13″N, 86°7′13″E; 6 h). BHGU2 made five rest stops at: (i) the Godavari River mouth, Andhra Pradesh (16°37′24″N, 81°51′25″E; 8 h), (ii) the Ganges River, Munger, Bihar (25°20′29″N, 86°34′9″E; 15 h), (iii) the Ganges River, Patna, Bihar (25°42′40″N, 84°51′57″E; 17 h), India, (iv) the Yarlung Zangbo River, Shigatse, Tibet (29°20′45″N, 88°8′8″E; 6 h), and (v) a small glacial lake in Nagqu, Tibet (30°23′23″N, 89°25′1″E; 15 h). In both gulls, the longest of these stops was made at the Ganges River (Fig. 3; Table A1 in Appendix, available on the website).

The birds mainly traveled at night, covering 70% of the migration distance during this time. They covered 304 ± 197 km at night (maximum: 675 km) and 147 ± 186 km during day (maximum: 658 km).

Breeding and post-breeding period

Both birds utilized high-altitude lakes (~4,700 m AMSL) in the Nagqu District of the Tibetan Plateau, China, during the boreal summer.

BHGU1 spent the early summer (04 May–12 July) at Angzicuo Lake (31°0′0″N, 86°58′22″E) and nearby Dongbucuo Lake (31°20′36″N, 87°12′49″E). Based on the extent and timing of movements, we assumed that BHGU1 was nesting in Dongbucuo, though its breeding success is unknown due to lack of direct observation. Later, it traveled 267 km northwest, utilizing seven other large lakes within the Changtang Plateau Important Bird Area (IBA), including Lake Yibug Caka (32°54′27″N, 86°39′43″E), where it remained for 45 consecutive days (31 July–14 September), likely for molting. It then returned to Dongbucuo on 19 September, where it stayed for 17 more days before beginning its southward migration on 06 October. In total, BHGU1 spent 5.2 mo (156.5 d; 03 May–06 October) on the Tibetan Plateau (Fig. 4).

BHGU2 arrived at Gerencuo Lake, part of the Tibet Selincuo Wetlands Ramsar Site (31°0′28″N, 88°29′35″E; located 80 km east of Angzicuo), on 20 May. Like BHGU1, BHGU2 also reached Lake Yibug Caka via Jiongmocuo Lake (32°17′38″"N, 86°34′13″E). However, frequent transmission gaps during this period prevented detailed study of its summer movements. On 30 June, while at Yibug Caka, the bird's GPS positioning completely stopped, resulting in a data gap of approximately 4.5 mo (from 30 June to 18 November).

The southward migration

BHGU1 commenced its southward migration on 06 October from Angzicuo Lake, taking a more easterly route (~280 km east of its

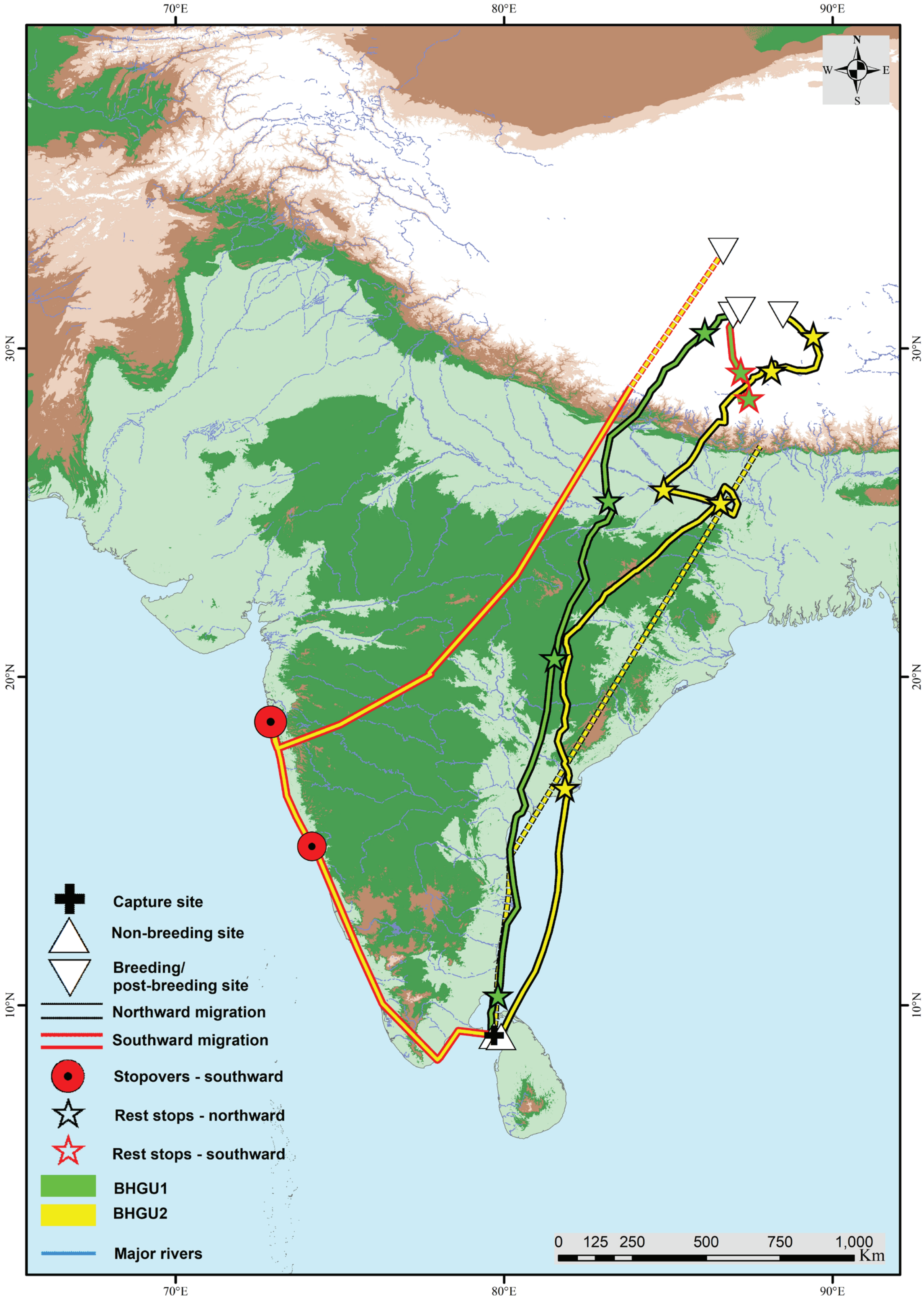

Fig. 3. Northward and southward migration routes of two successfully tracked Brown-headed Gulls *Chroicocephalus brunnicephalus* using GPS-GSM transmitters from non-breeding grounds in Mannar, Sri Lanka, to breeding grounds in the Tibetan Plateau, China, during 2021–2023. The black-bordered lines represent northward migration and the red-bordered lines denote southward migration. Thin-bordered dashed lines directly connect two consecutive GPS fixes across a data gap and indicate inferred segments that may not represent the exact path taken. Upward triangles denote non-breeding sites; downward triangles denote breeding and post-breeding sites. The red circles show stopover sites during southward migration, and their size corresponds to stopover duration. There were no stopover sites during northward migration. The black-bordered stars represent rest stops during northward migration, while the red-bordered stars indicate rest stops during southward migration (note that rest stops were not identified for BHGU2's southward migration due to limited temporal resolution of the data). Details of each stopover site and rest stop are provided in the Table A1 (Appendix, available on the website).

TABLE 2
Key migration parameters calculated for two complete northward migration tracks generated from two tagged Brown-headed Gulls *Chroicocephalus brunnicephalus*, BHGU1 and BHGU2, marked in the non-breeding period in Sri Lanka and followed over two years

Bird	Year	Departure date	Arrival date	Migration duration (d)	Stopover duration (d)	Travel days (d)	Migration distance (km)	Total fly no.	Migration speed (km/d)	Daily travel speed (km/d)	Step length (km)	No. of stopovers	Straightness index
BHGU1	2021	25 Apr 2021	03 May 2021	7.6	0	7.6	2,667.9	1	352	352	2,667.9	0	0.9
BHGU2	2022	14 May 2022	20 Ma 2022	6.1	0	6.1	2,905.5	1	477	477	2,905.5	0	0.7
Mean				6.8	0	6.8	2,786.7	1	415	415	2,786.7	0	0.8
Standard deviation				1.1	0	1.1	168.0	0	88	88	168.0	0	0.2

northward Himalayan crossing). It made two rest stops lasting 14–40 h before entering the Himalayan range (see Table A1 for details). However, its transmission stopped on 10 October when it was 50 km north of the Himalayas (Fig. 3).

Following the failure of GPS positioning, BHGU2 did not resume data collection until 18 November, when backup positioning was activated. Consequently, the timing of its southward departure could not be recorded. Nevertheless, we were able to track the remainder of its southward migration. BHGU2 took a more westerly route compared to BHGU1, crossing the Himalayas ~280 km west of its northward Himalayan crossing. Thereafter, it flew through northern and central India, arriving on the coast of Maharashtra in western India. There, it stopped over for eight days (24 November–02 December) near Alibag Beach (18°36′49″N, 72°52′51″E) before flying south to its next stopover in the Kali River estuary (14°50′34″N, 74°8′36″E) in Karnataka, where it stayed for five days (10–15 December). It then continued to follow the coastline, arriving on the Tamil Nadu coast and then crossing Rama's Bridge Island chain to reach its non-breeding ground on Mannar Island, Sri Lanka, on 19 December (Fig. 3).

Accordingly, the reported segment of BHGU2's southward migration lasted 31 d, mostly along India's west coast, resulting in an anticlockwise loop migration (Fig. 3). Although detailed migration parameters could not be calculated (due to the unknown departure date), this journey was evidently slower than the northward migration, taking > 31 d with a stopover duration of 13 d, compared to an average migration duration of 6.8 d with no stopovers during the northward journey.

Furthermore, another gull that we ringed in 2021 (without a transmitter) was resighted at Azhikkal Beach, Kerala, India (11°49′5″N, 75°20′15″E) on 01 December 2023 (P. Sathiyaselvam, personal communication, May 07, 2024). This individual was possibly on a southward migration along India's west coast, similar to BHGU2, who also passed through Kerala in mid-December.

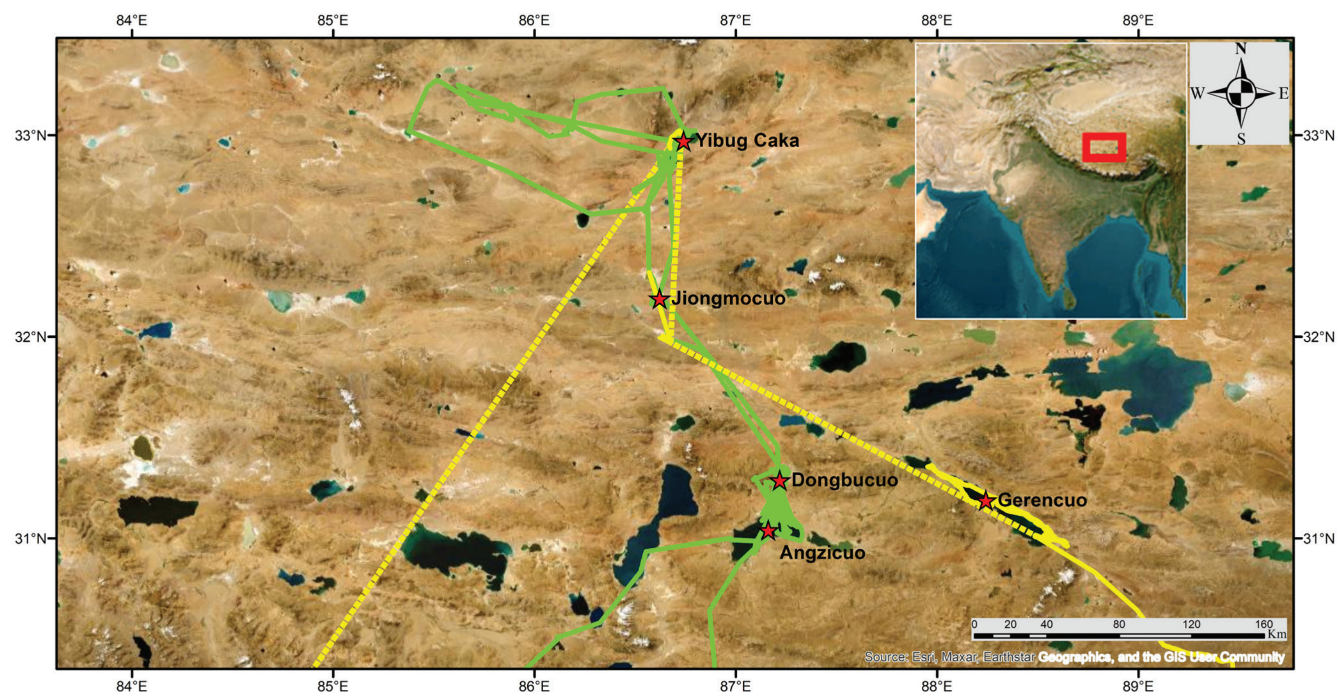

Fig. 4. The local movements of two tagged Brown-headed Gulls *Chroicocephalus brunnicephalus*, BHGU1 (green) and BHGU2 (yellow), during the 2021/22 boreal summer in the Tibetan Plateau, China. The dashed lines directly connect two consecutive GPS fixes across a data gap.

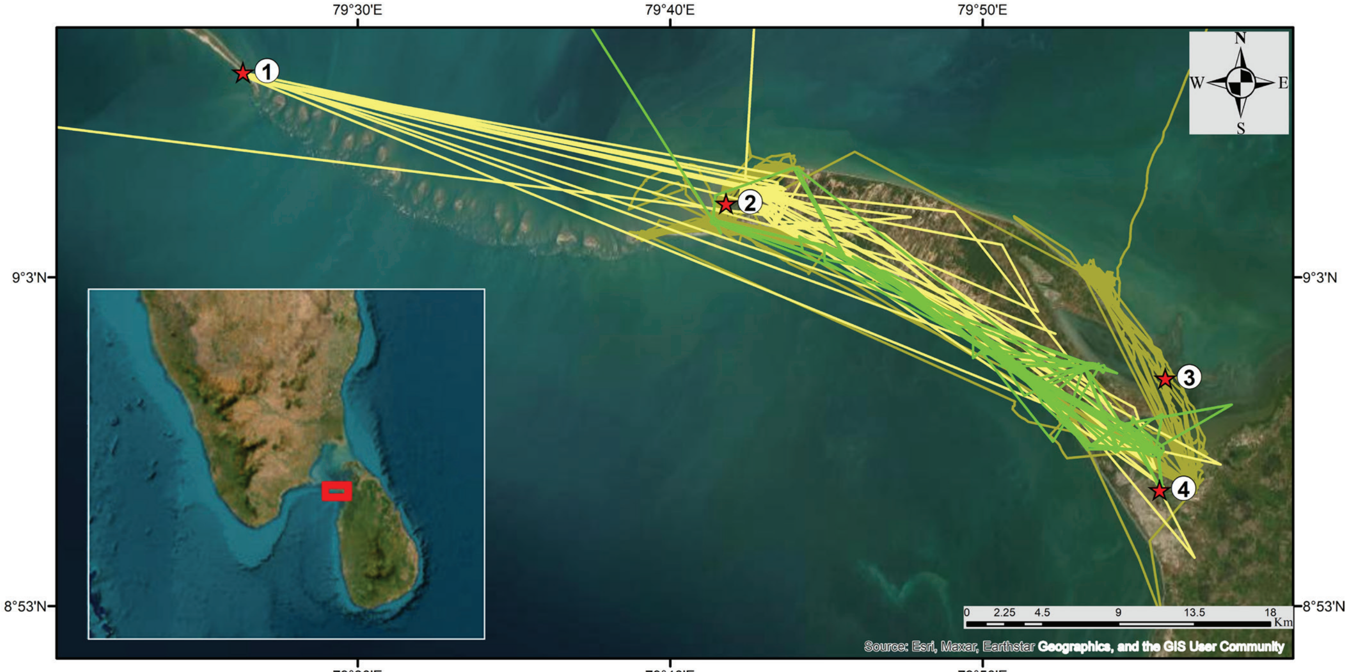

Fig. 5. The local movements of two tagged Brown-headed Gulls *Chroicocephalus brunnicephalus*, BHGU1 (green) and BHGU2 (light yellow, March 2021–May 2022; and bright yellow, December 2021–April 2023), during two successive non-breeding seasons from 2021–2023. Key sites are: (1) Dhanushkodi, India, (2) Adam's Bridge Marine National Park, (3) Vidataltivu Nature Reserve, and (4) Vankalei Sanctuary in Sri Lanka.

The non-breeding period

We monitored the movements of BHGU2 on Mannar Island over two successive non-breeding seasons (March–April 2022 and December 2022–April 2023) and of BHGU1 for one month (April 2022). The gulls primarily used the western and eastern seaboards of Mannar Island, as well as its southern coast. They regularly moved among Adam's Bridge Marine National

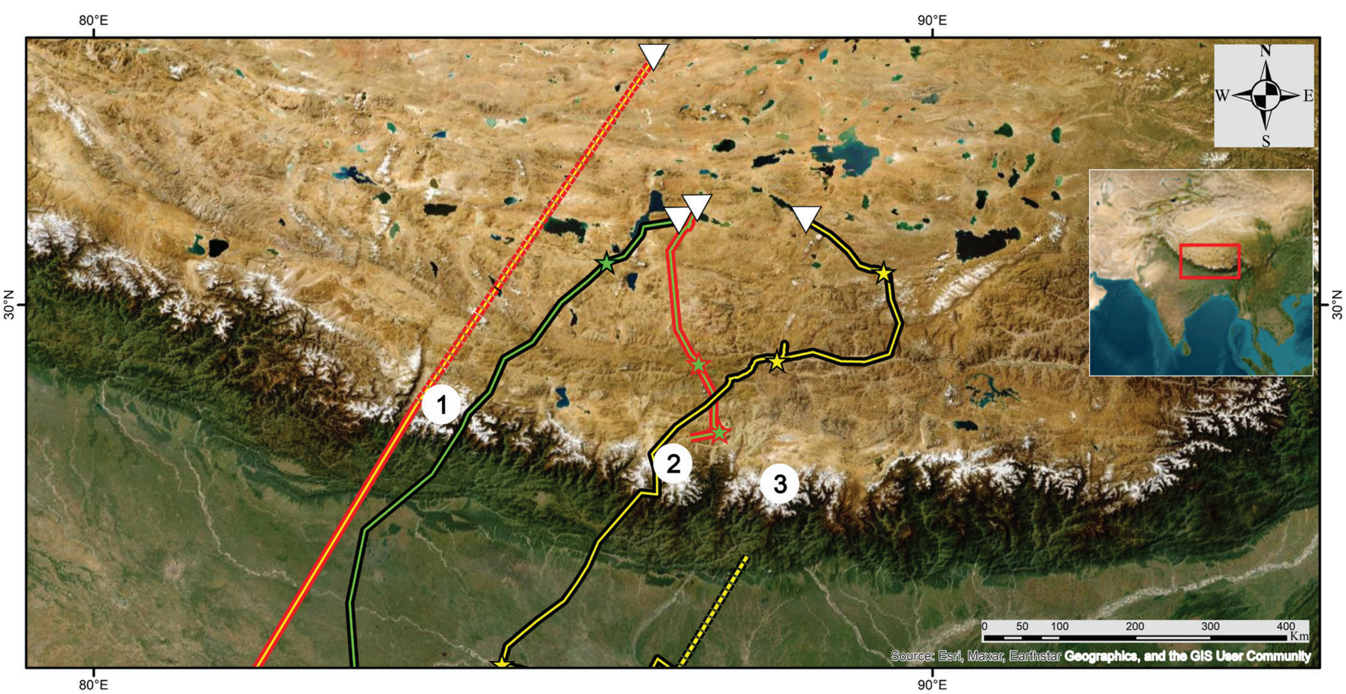

Fig. 6. Four migration tracks (including two incomplete tracks) and the initiation of a fifth, recorded from two tagged Brown-headed Gulls *Chroicocephalus brunnicephalus*, BHGU1 (green) and BHGU2 (yellow)—between 2021 and 2023, showing Himalayan crossing locations situated in the (1) Annapurna, (2) Khumbu/Everest, and (3) Kanchenjunga regions of Nepal. The third crossing location is inferred from the preceding flight trajectory and regional topography due to the absence of detailed GPS positions.

TABLE 3
Time schedules of Brown-headed Gull *Chroicocephalus brunnicephalus* defining the four main stages of the annual cycle, based on criteria described in the text, derived from tracked movements of two tagged individuals

Individual	Non-breeding			Northward migration			Breeding and post-breeding			Southward migration		
	Start	End	Duration	Start	End	Duration	Start	End	Duration	Start	End	Duration
BHGU1	–	05 Apr 2021	–	25 Apr 2021	03 May 2021	7.6	03 May 2021	06 Oct 2021	156.6	06 Oct 2021	–	–
BHGU2	–	14 May 2022	–	14 May 2022	20 May 2022	6.1	20 May 2022	–	–	–	19 Dec 2022	–
	19 Dec 2022	30 Apr 2023	131.7	30 Apr 2023	[a]	–	–	–	–	–	–	–

[a] BHGU2 stopped transmission on 04 May 2023 while it was in eastern Nepal (~80 km south to Himalayas), preventing determination of the end date of its northward migration in 2023.

Park (9°4′15″N, 79°37′42″E), Vankalei Sanctuary Ramsar Site (8°56′0″N, 79°55′0″E), and Vidataltivu Nature Reserve (8°58′52″N, 79°57′46″E), and frequently visited fishing harbors and beaches on the island. BHGU2 occasionally visited Dhanushkodi, India, via Rama's Bridge, utilizing India's Gulf of Mannar Marine National Park (9°8′15″N, 79°28′21″E). Compared to their movements during the post-breeding period on the Tibetan Plateau, the gulls utilized a relatively smaller area during the non-breeding period in Mannar Island, with their movements largely restricted to a circular area approximately 70 km in diameter (Fig. 5).

The Himalayan crossing

Of the four migration tracks generated, three provided detailed GPS positions as the birds traversed the Himalayas. On two other occasions, transmission ceased approximately 50–80 km from the mountain range; however, based on the preceding flight trajectory and topography of the region (i.e., the most likely and feasible crossing points), we were still able to infer the general areas where the birds likely crossed. Consequently, the identified crossing locations were situated within the Annapurna, Khumbu/Everest, and Kanchenjunga regions of the Himalayas, where the gulls mostly made use of the valleys and gorges to cross over (Fig. 6). The two complete northward migration tracks indicated that the tagged gulls crossed the Himalayas at an average ground elevation of 5,350 m (4,697–6,003 m) AMSL.

Within the Annapurna region, our observations identified two passages that appeared to be utilized by these gulls for navigating across the Himalayan barrier, namely the Marsyangdi Valley and the Kali Gandaki Gorge. The northward migration track of BHGU1 lay next to Mount Panbari Himal, yet it is likely that the bird avoided the peak (6,887 m AMSL) by utilizing a relatively lower passage adjacent to it. The maximum ground elevation reached by BHGU1 during this crossing was 4,697 m AMSL. Another crossing route identified in the same region was through the Kali Gandaki Gorge, used by BHGU2 during its southward migration in 2022. Base station data indicated a location at 3,568 m AMSL, near which the crossing likely occurred. This point lies only 600 m from the Gandhaki River.

In the Khumbu/Everest region, we identified another high-elevation passage utilized by the gulls, as BHGU2 flew over Mount Cho Oyu during its northward migration in 2022. The maximum ground elevation crossed at this passage was 6,003 m AMSL. This crossing point is situated 37 km northwest of Mount Everest. The bird entered the Himalayan range through river valleys, including the Dudh Koshi River, which flows through the Khumbu Valley. However, it later changed course toward Cho Oyu and crossed the mountain, without seeking lower-elevation alternatives. The southward migration initiated by BHGU1 in 2021 also indicated a trajectory leading toward the Khumbu Valley.

A possible third corridor across the Himalayas is inferred from the incomplete track of BHGU2 during its northward migration in 2023 (Fig. 6). Based on the bird's trajectory prior to signal loss, it likely intended to cross the Himalayas through the Kanchenjunga Valley (4,000–5,000 m AMSL).

DISCUSSION

To help fill knowledge gaps in the migration phenology of South Asian BHGUs, we document the first detailed movement patterns of two tagged BHGUs from Mannar, Sri Lanka, tracked over three successive years and covering four migrations—three northward and one southward—across the Central Asian Flyway. We infer how the BHGU tackles the high-altitudes of the Himalayas during its trans-Himalayan migration. While we recognize that a larger sample size, incorporating both sexes and different age classes, would have provided more comprehensive insights, the current gaps in knowledge and the lower variance in our dataset indicate that our findings offer a valuable initial opportunity to understand the migration strategies of this poorly studied species.

Despite the small sample size, the migration distance, duration, and speeds of tagged BHGUs were comparable to those of BHGUs migrating to non-breeding grounds further east, up to Southeast Asia (Table 2; Ratanakorn et al., 2012; Yu et al., 2024), suggesting broadly similar migration patterns across distinct non-breeding populations.

Our findings suggest that South Asian non-breeding BHGUs may exhibit loop migration patterns: BHGU2 followed an anticlockwise loop, and the southward trajectory initiated by BHGU1 also indicates the possibility of loop migration (Fig. 3). Similar anticlockwise loops have been observed in non-breeding populations further east, which migrate along the eastern Qinghai-Tibetan Plateau during northward migration and take higher-elevation westerly routes during southward migration (Ratanakorn et al., 2012; Yu et al., 2024). Loop migration, adopted by many bird species (Dixon et al., 2017; Galtbalt et al., 2022; Klvaňa et al., 2018; Liu et al., 2018) may arise as a consequence of seasonal changes in weather conditions and/or food supply along the route, leading to differences in optimal northward and southward migration routes (Klaassen et al., 2010; Klvaňa et al., 2018). It highlights the flexibility and resilience of migratory strategies—traits that may be critical in the face of climate change (Newton, 2008). However, loop migrants may be exposed to a broader array of anthropogenic threats due to greater spatial coverage. It may also lead to greater mixing of populations across flyways, potentially increasing the risk of disease transmission (Fourment et al., 2017).

Our two tagged gulls followed coastal or marine routes for approximately half of their overall migratory flights (48%): 30% during northward migration (based on both BHGU1 and BHGU2) and 66% during southward migration (based on BHGU2, the only individual with southward data). This pattern suggests a seasonal shift in route preference—favoring more direct, inland routes during the faster, stopover-free northward migration, and more coastal routes during the slower southward migration, which included extended stopovers. Gulls may favor coastlines during the latter because these habitats presumably offer more predictable and plentiful food sources and allow fly-and-forage migration (Klaassen et al., 2012). The longest sea crossing reported in the study spanned 735 km over 11 h, as BHGU2 traveled from northern Sri Lanka to Andhra Pradesh in 2022 (Fig. 3).

However, it should be acknowledged that our findings may not capture the full range of migratory strategies within the population, which can vary due to differential migration—variation in timing, route, or distance linked to age, sex, or body size (Baert et al., 2018; Newton, 2011). For example, Baert et al. (2018) reported sex-specific differences in duration and habitat use during southward migration in Lesser Black-backed Gulls *Larus fuscus*, although no such differences were observed during northward migration. Age-related differences in gulls include juveniles migrating farther and using different routes or non-breeding areas compared to adults (Marques et al., 2009, 2010). Additionally, younger breeders tend to arrive at breeding sites later than adults (Newton, 2011), consistent with our observations: the 2CY BHGU2 arrived on the Tibetan Plateau later in 2022.

The Himalayan crossing

En route to their breeding grounds, South Asian BHGUs fly over the Himalayas rather than circumnavigating them, unlike Heuglin's Gulls *L. heuglini* tracked from Sri Lanka to the Russian Arctic (Panagoda et al., 2025). Southeast Asian BHGUs have also been observed crossing the Himalayas, though farther east, where elevations are relatively lower than those in the central Himalayas crossed by our birds (Ratanakorn et al., 2012; Yu et al., 2024). These findings suggest that migrating BHGUs may cross the Himalayas at multiple locations, potentially along the entire mountain range. However, our results further showed that BHGUs tend to follow valleys and gorges that cut through the Himalayas, providing routes with substantially lower terrain. This ground-hugging strategy—following low-elevation terrain whenever available while crossing a mountain range—is used by many species, including the Bar-headed Goose *Anser indicus* (Bishop et al., 2015; Hawkes et al., 2013), Demoiselle Crane *Grus virgo* (Higuchi & Minton, 2017), raptors (Bijlsma, 1991; Chettri et al., 2006; Higuchi & Minton, 2017; Juhant & Bildstein, 2017), and passerines (Delany et al., 2017a).

Among the passages utilized by the tagged BHGUs to cross over the Himalayas, the Kali Gandaki Gorge is already recognized as an important bird migration corridor in the Himalayas (Bijlsma, 1991; Chettri et al., 2006; Delany et al., 2017a; Higuchi & Minton, 2017; Inskipp & Inskipp, 1991; Javed et al., 2000; Juhant & Bildstein, 2017). By flying through this gorge, BHGU2 traversed the Himalayan barrier at a relatively low ground elevation of ~2,800 m AMSL, which would otherwise have been twice as high (> 5,500 m AMSL).

By keeping to steep gorges, the gulls could have made use of the (orographic) updrafts and katabatic winds (Hawkes et al., 2013; Higuchi & Minton, 2017; Scott et al., 2015), conserving energy through gliding or flapping sparingly instead of continuously flapping. Soaring or updraft-assisted non-flapping flight is an energetically efficient form of flight, used by many long-distance migrants, especially raptors (Bildstein, 2006; Juhant & Bildstein, 2017; Kerlinger, 1989). As flight-style generalists—mastering various strategies including flapping, thermal soaring, ridge soaring, and dynamic soaring (Klaassen et al., 2012; Rayner, 1988; Shamoun-Baranes et al., 2006)—the gulls could have taken advantage of the varied topography, engaging in soaring flight where possible. The low-lying gorges and valleys took them further through an atmosphere with higher partial oxygen pressure (PO_2) (Parr, 2019).

Although our BHGUs generally followed valleys and gorges during their Himalayan crossing, they were also capable of crossing higher elevations: BHGU2 crossed Mount Cho Oyu (8,201 m AMSL), the world's sixth-highest mountain, at a location where the ground elevation was 6,003 m AMSL. Overall, the gulls in our study crossed the Himalayas at ground elevations between 3,568 and 6,003 m AMSL, with an average maximum ground elevation of 5,703 m AMSL during migration (Fig. 7A). Calculated average flying altitudes indicate that migrating BHGUs flew even higher, with the maximum average flying altitude reaching 6,547 m AMSL. However, due to the uncertainties associated with GPS-derived altitude data, we refrained from making further inferences about their exact flying altitudes.

Overcoming the challenges of high-altitude Himalayan overflight

Birds flying at extreme elevations face numerous challenges (Parr, 2019). At 5,000–6,000 m, the PO_2 is about half that at sea level, severely limiting aerobic metabolism necessary for sustained flight (Scott et al., 2015). Freezing temperatures year-round in the high Himalayas increase thermoregulatory demands (Scott et al., 2015; Yang et al., 2011), while dry air heightens the risk of dehydration, potentially constraining flight duration (Engel et al., 2006; Scott et al., 2015). Reduced air density at high altitudes makes lift generation increasingly difficult, and high atmospheric turbulence further complicates flight (Barry, 2008; Kerlinger, 1989; Scott et al., 2015).

In spite of challenges, numerous bird species reach extreme altitudes to cross the Himalayan barrier during migration. Several species have been recorded flying over the Tibetan Plateau and

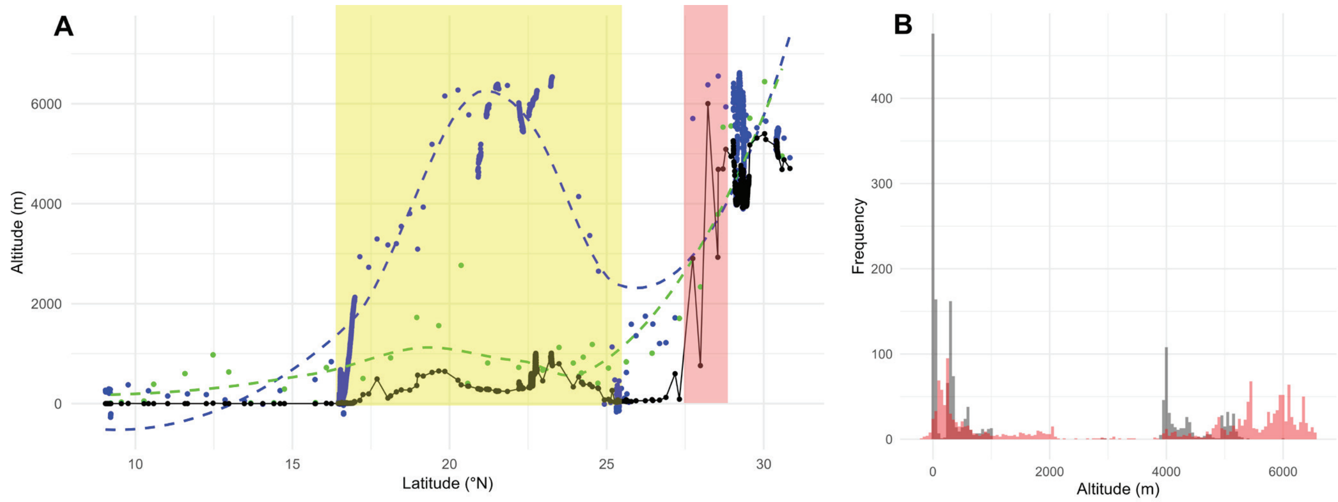

Fig. 7. Ground elevations and average flying altitudes of northward-migrating Brown-headed Gulls *Chroicocephalus brunnicephalus* (*n* = 2) from Sri Lanka to the Tibetan Plateau, China. (A) Plot showing ground elevation (black line) and average flight altitudes across latitudes for two gulls: BHGU1 (green) and BHGU2 (blue). Trend lines illustrate how flight altitude varies with latitude for each bird. The yellow shaded region indicates the inland segment across India, from the Andhra Pradesh coast to rest stops along the Ganges River. The pink shaded region denotes the Himalayan mountain range. (B) Histogram showing the frequency distribution of ground elevations and average flying altitudes encountered by migrating Brown-headed Gulls during migration. Black bars represent ground elevation; pink bars represent average flying altitude.

Himalayas at altitudes surpassing 7,000–8,000 m: Himalayan Vulture *Gyps himalayensis*, Demoiselle Crane, Black-necked Crane *Grus nigricollis*, Bar-headed Goose (Parr, 2019), and Steppe Eagle *Aquila nipalensis* (Batbayar & Lee, 2017; Table 4). However, it should be noted that this evidence does not support a general paradigm of sustained high-altitude migration. Instead, the birds rarely reached altitudes exceeding 6,000 m, and when they did, it was only for short periods (Hawkes et al., 2013; Parr, 2019).

Birds adopt various strategies to succeed in high-altitude migration. While some species trade off distance for altitude (Groen & Prins, 2017), others have evolved morphological, behavioral, and physiological adaptations (Hawkes et al., 2017; Namgail et al., 2017), which have been particularly well-studied in Bar-headed Geese (Hawkes et al., 2011; Scott et al., 2015) and, to a lesser extent, Ruddy Shelducks *Tadorna ferruginea* (Parr, 2019). The Bar-headed Goose shows specialized traits such as high ventilation rates, efficient gas exchange, larger lungs, high blood-oxygen affinity, and dense, mitochondria-rich flight muscle capillarization (Scott et al., 2015). Similarly, Ruddy Shelducks exhibit elevated mitochondrial oxidative capacity in their flight muscles and enhanced capacity of the heart to oxidize lactate under hypoxia (Parr, 2019).

Most species that have been documented to fly at extreme altitudes are large-bodied (> 2,000 g; Table 4), likely reflecting both the physiological advantages of larger body size in such conditions and a tracking bias, as larger birds are more frequently tagged and studied. While the aforementioned mechanisms may also apply to BHGU, which weighs only 450–714 g (Burger et al., 2020; 372.5 ± 53.0 g in our study), it offers a compelling opportunity to investigate how smaller-bodied birds cope with the same challenges. Future studies using devices capable of recording precise altitude and physiological data, such as heart rate, could yield valuable insights into such adaptations.

In all instances, our BHGUs crossed the Himalayas at dawn, similar to Bar-headed Geese, which start their ascent to high altitudes during the night or early morning (Hawkes et al., 2013; Scott et al., 2015). Although ascending to high altitudes at night likely incurs a greater metabolic cost (due to the need for more flapping in the absence of daytime updrafts), the cooler, denser night air may offer advantages once cruising altitude is reached. Denser air provides more lift and higher PO_2, potentially reducing the energetic cost of maintaining flight (Hawkes et al., 2011; Parr, 2019), even if climbing to those altitudes is initially demanding (Scott et al., 2015).

The energetically expensive feat of crossing the Himalayas (Groen & Prins, 2017) might have been made possible for the gulls largely due to the availability of wetlands on either side of the mountain range: the Gangetic floodplain wetlands to the south and numerous glacial lakes in the Tibetan Plateau to the north (Namgail et al., 2017). The gulls made brief stops (< 48 h) at these sites immediately before and after crossing this barrier (Fig. 3; Table A1). Migrant ducks have also been found to utilize a similar strategy (Dutta & Konwar, 2013; Jun et al., 2004; Namgail et al., 2017; Prins et al., 2017). The importance of these wetlands may increase when they are located near major ecological barriers, such as the Himalayas in this case.

High-altitude flying of gulls in absence of topographic barriers

While it is expected that BHGUs must reach extreme altitudes to overfly the Himalayas, it was unexpected to observe them flying to such heights over inland India, specifically the stretch from the Andhra Pradesh coast to the Ganges River, where the average ground elevation is only 305 m AMSL. Although some uncertainty remains regarding the average flying altitudes, the general trend of high-altitude flight was clear. Both gulls reached considerable altitudes over this stretch, particularly BHGU2, which exceeded 6,000 m AMSL (Fig. 7A).

TABLE 4
Maximum altitudes recorded by telemetry devices on birds during migration across the Tibetan Plateau and Himalayas[a]

Species	Number of birds tracked (*n*)	Weight of bird (g)	Maximum altitude recorded (m AMSL)	Reference
Himalayan Griffon *Gyps himalayensis*	18	8,000–12,000	8,426	Parr, 2019
Demoiselle Crane *Grus virgo*	15	2,000–3,000	7,365	Parr, 2019
Black-necked Crane *Grus nigricollis*	4	5,000–7,000	7,353	Parr, 2019
Bar-headed Goose *Anser indicus*	38	2,000–3,000 (2,260)	7,290	Bishop et al., 2015; Hawkes et al., 2011; Hawkes et al., 2013; Hawkes et al., 2017; Parr, 2019
Steppe Eagle *Aquila nipalensis*	1	2,000–4,900 (3,500)	7,200	Batbayar & Lee, 2017
Garganey *Spatula querquedula*	3	240–585	6,930*	Namgail et al., 2017
Northern Shoveler *Spatula clypeata*	2	410–1,100	6,830*	Namgail et al., 2017
Ruddy Shelduck *Tadorna ferruginea*	15	970–1,725 (1,300)	6,800	Parr, 2019
Black-eared Kite *Milvus migrans lineatus*	19	630–1,080	6,500	Kumar et al., 2020; Literák et al., 2022
Brown-headed Gull *Chroicocephalus brunnicephalus*	2	450–714 (372.5)	6,003*	This study
Short-toed Snake Eagle *Circaetus gallicus*	3	1,200–2,300	6,076	Parr, 2019
Whimbrel *Numenius phaeopus*	1	270–493	6,000*	Li et al., 2020
Common Redshank *Tringa totanus*	10	85–155	5,800*	Li et al., 2020
Grey Plover *Pluvialis squatarola*	1	165–395 (295)	5,546*	G. Panagoda, unpubl. data
Pallas's Gull *Larus ichthyaetus*	4	900–2,000	5,000–6,000*	Guo-Gang et al., 2014
Hen Harrier *Circus cyaneus*	2	300–708	5,125	Parr, 2019
Eurasian Wigeon *Mareca penelope*	3	600–1,000	4,310*	Namgail et al., 2017
Gadwall *Mareca strepera*	2	550–1,000	4,310*	Namgail et al., 2017

[a] Studies lacking in-flight measurements of the actual altitude of birds during migration are marked by an asterisk, and the maximum ground elevations likely reached are provided. *n* = the number of birds successfully tracked across the Tibetan Plateau and Himalayas. The weight of the bird is as given in Birds of the World (2024), with the average weight of tagged birds in parentheses, if provided in the cited literature.

The high-altitude flight likely allowed BHGU2 to complete this inland stretch much faster (see Results) and with less energy expenditure. While the records refer to different years, BHGU2's inland flight occurred 18 d later in the spring (mid-May 2022) compared to BHGU1's inland flight in late April 2021. The ambient temperature tends to rise daily during this time of year in inland India, which may have prompted BHGU2 to ascend even higher to avoid the warmer land temperatures, while also taking advantage of thermal uplift that increases daily in spring with rising ambient temperatures (Galtbalt et al., 2022). When flying in high-temperature air columns, birds experience heat stress and increased water loss. By reaching higher altitudes, they could more efficiently use their energy and water reserves, benefiting from the strong tailwinds that occur at these altitudes while minimizing water expenditure in the relatively cold and humid air (Schmaljohann et al., 2008).

Fig. 7B shows that while the gulls flew over ground elevations of 4,000 m AMSL only 21% of the time, they reached flying altitudes above 4,000 m AMSL on 57% of occasions. This indicates that gulls tend to fly at extreme altitudes even in the absence of topographic barriers. This behaviour is consistent with findings from other studies, which suggest that high-altitude migration may help avoid high temperatures, reduce water loss, and exploit favorable winds (Alerstam & Gudmundsson, 1999; Liechti & Schaller, 1999; Parr, 2019; Schmaljohann et al., 2008; Senner et al., 2018).

Gulls, as feeding generalists, may exhibit greater migratory flexibility than many waterbirds (Klaassen et al., 2012), and no specific threats have been identified for BHGUs (BirdLife International, 2024). However, among the identified stopovers and rest stops, only Point Calimere is protected as a Ramsar Site. Some sites (e.g., the Godavari Estuary, and areas near Munger and Patna; see Results) partially overlap with or are adjacent to IBAs, but their legal protection status is uncertain. Many of these locations are also used by a diverse array of migrants, including ducks and shorebirds (Namgail et al., 2017; GP, unpubl. data), which are often less resilient to habitat degradation. Broader site assessments and protection of key sites would thus benefit a wider range of migratory waterbirds in the CAF.

Many migrants of the CAF navigate annually across the Himalayas and the Tibetan Plateau, together forming the world's tallest physical barrier for migratory birds (Prins & Namgail, 2017). The corridors used to traverse this barrier, along with the wetlands that provide crucial resting and refueling sites, are necessary to enable this extraordinary journey. However, the Himalayan landscape is undergoing rapid change (Humbert-Droz, 2017; Rasool & Johari, 2021), with major infrastructure development occurring along the river valleys and at high-altitude lakes (Humbert-Droz, 2017), posing serious threats to migration systems that have persisted for millions of years. Higuchi & Minton (2017) reported a decline in the number of Demoiselle Cranes using the Kali Gandaki Gorge in recent years, attributed to large-scale development that has altered habitats along the river. Identifying, properly managing, and conserving these critical migratory bottlenecks in the Himalayas—which may be few and far between—are essential to ensure that important trans-Himalayan migration routes remain viable for birds in the future.

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All authors declare that they have no conflicts of interest.

ETHICAL STATEMENT

This work was carried out under permits from the Department of Wildlife Conservation, Sri Lanka (Permit Nos. WL/3/2/25/20 and WL/3/2/37/19), the Ministry of Defence, Sri Lanka (Permit No. MOD/MLO/02/01 A-3 (27)), and the Telecommunications Regulatory Commission of Sri Lanka (Permit Nos. TRC/SM/SS/0024/00/20/048(C/1507) and TRC/SM/SS/0024/00/20/049(I/1167)).

AUTHOR CONTRIBUTIONS

GP: Conceptualization, methodology, formal analysis, investigation, data curation, writing—original draft, writing—review & editing, visualization, project administration. IW: Software, formal analysis, writing—original draft, writing—review & editing, visualization. BZ: Methodology, software, data curation. FM: Resources, project administration, funding acquisition. YC: Software, data curation. SK: Conceptualization, resources, writing—review & editing, supervision, project administration, funding acquisition. TM: Conceptualization, methodology, validation, resources, writing—original draft, writing—review & editing, and supervision. SB: Conceptualization, validation, resources, writing—original draft, writing—review & editing, and supervision. LC: Conceptualization, methodology, resources, supervision, writing—review & editing, funding acquisition. SS: Conceptualization, methodology, validation, investigation, resources, writing—original draft, writing—review & editing, supervision, project administration, funding acquisition.

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