國立臺灣大學國際學院生物多樣性國際學程

碩士學位

Master's Program in Biodiversity

International College

National Taiwan University

Master Thesis

小燕鷗(Sternula albifrons)在台灣的繁殖族群之遷徙路徑研究

Migration Routes of Little terns (*Sternula albifrons*) Breeding in Taiwan

Ashanti Marie Mckoy

指導教授：袁孝維 博士

Advisor: Hsiao-Wei Yuan, Ph.D.

中華民國 112 年 8 月

August, 2023

doi:10.6342/NTU202303015

Contents

doi:10.6342/NTU202303015

Acknowledgements

This thesis has been an all-consuming project, and it has also been the most challenging undertaking that I have had the honor to complete. However, it would have been significantly more difficult had it not been for the numerous individuals who offered their time and assistance. Hence, I would like to thank those who acted as beacons of guidance and encouragement while I had to leave my comfort zone to complete this degree. To Professor Yuan, thank you for welcoming me into your lab, entrusting me with such an interesting project, and for believing that I was up for the challenge. To Han-Po (張瀚柏), Yun-Xuan (林昀萱),Ben and all my lab mates, thank you for answering all my coding questions, I am very grateful for the patience you extended to me. To my family in Taiwan, my biodiversity classmates, thank you for always being friendly faces during the most difficult time of my life, as well as for being my companions as we figured out how to navigate through grad school. Many thanks to Rajatanan, Carina, and Euchie for offering support whenever I felt I was going to give up, you made this journey feel a bit less draining every day. A special thanks to Joneli Pinelo for continuously being a safe space after my long days of writing and coding, always listening to me freak out about my presentations, and following me to the library when I needed to work on my draft at all hours of the day. To my parents, brother, and grandmother for always allowing me to follow my own path, even if it took me far away from home. Lastly, to Meghan and the other assistants of the International College, thank you for always assisting me throughout my time here at The International College at National Taiwan University.

doi:10.6342/NTU202303015

Abstract

The Little tern is a migratory sea bird with a wide range, and populations found on every continent except for Antarctica and the continental Americas. Recently these populations have been experiencing a decline due to habitat degradation and human disturbance. To implement more comprehensive approaches to retain stable populations, dynamic conservation tactics must be employed. The prerequisite for this is detailed knowledge of a bird's annual cycle, to ensure protection at all stages. The movement of the Taiwanese population of the Little tern has previously been estimated solely based on banding data. For this reason, this project aimed to obtain a more detailed understanding of the movement of the Taiwanese breeding population of the Little tern over its yearly cycle. This was executed by utilizing geolocator tracking data from 5 individuals from 2 breeding grounds in the northeastern breeding site in Yilan County, Taiwan during the 2013 and 2016 breeding periods. This allowed for the elucidation of their southbound and northbound migration routes, as well as the identification of stopover locations used. Results obtained were then confirmed with banded bird sightings from the projected regions and were then compared with routes of the previously tracked population in Chiba, Tokyo and Okinawa, Japan.

All tracked birds used the East-Asian Australasian Flyaway from the breeding grounds in Taiwan to arrive to non-breeding grounds in Western and South-Eastern Australia. Along the route, The Philippines and Eastern Indonesia were utilized as stopover sites, with the southbound movement lasting longer than the northbound movement. This is the first geolocator study to describe the routes for Taiwanese Little terns. The routes employed by the terns are used by a wide range of sea birds, and therefore the findings from this study can be used to identify conservation gaps in regions along the flyway.

doi:10.6342/NTU202303015

Keywords

Little tern, migration, light level geolocator, migration phenology, migratory routes, conservation, Taiwan

doi:10.6342/NTU202303015

List of Figures

doi:10.6342/NTU202303015

doi:10.6342/NTU202303015

List of Tables

doi:10.6342/NTU202303015

Introduction

1.1 Animal migration

The phenomenon of migration can be defined as the seasonal, round trip, movement of organisms between locations, this is a ubiquitous occurrence in the animal kingdom (Shaw, 2020). This behavior can be observed in countless genera across the globe, and is found in every category of ecosystem, as well as across all major vertebrate lineages (birds, fish, mammals, reptiles, amphibians), as well as many invertebrates (Shaw, 2016) (Hobson & Ryan Norris, 2008). When the earliest studies of migratory organisms occurred over a century ago, it was believed that migration served to remove excess individuals from a population (Peters et al., 2017). Only in the past has migration been viewed, as David Lack describes, as “a product of natural selection,” expected to occur when the benefits of movement out of an area outweigh the costs (Lack, 1968). This movement between locations, results in migratory species being dependent on a suite of interconnected sites. Although categorized generally by the common need to move, migration is actually a broad term which may be categorized into different concepts (Hobson & Ryan Norris, 2008), the two most known are: (1) a seasonal to-and-fro movement of populations between regions, which pertains to instances whereby conditions are alternately temporally favorable or unfavorable (Shaw, 2020), (2) round trip migration, also referred to as loop migration (Dingle & Drake, 2007)is a variation of this whereby animals return to a general breeding area from which they originated but may stage their movements through a succession of nonbreeding areas, and perhaps follow different paths on the outward and return journeys. Another widely observed form is one-way migration; this involves animals moving from a location where they were produced to another where they breed and produce the next generation before dying (Dingle & Drake, 2007), however this form is mainly observed in insects and marine larvae (Bauer & Hoye, 2014)

doi:10.6342/NTU202303015

1.2 Migratory species conservation

As the basis for their movement involves a need for favorable sustenance, temperature or satisfactory breeding conditions (Bauer & Hoye, 2014), migratory species often have large geographical ranges. Although this extensive movement has been identified as an evolutionary trait developed for individual or species survival, the movements of these animals have also been advantageous for other species in their shared environment. For instance, Migratory species serve as nutrient transport, and biomass transfer within ecosystems in which they occur (Runge *et al*., 2015). In addition to this, these animals are vital bioindicators and their movements and pressures allow for the assessment and observation of changes along major flyways and habitats. (Zöckler, 2005). In recent years, migratory bird species in particular have often been used as gauges for landscape health, as these migrants are capable of altering their route in a short time, depending on the productivity of the site (Tankersley, 2004).

The dependence on more than one geographic site, has resulted in the management and conservation of migrants to be particularly arduous (Runge *et al*., 2014). This is due to the planning and action in circumstances such as these, requiring implementation at several locales which may be separated, geographically or even politically. Hence, mechanisms to conserve these species require dynamic and proactive approaches between nations to prove to be effective. Dynamic conservation strategies that tailor the delivery of habitat to when and where it is most needed can be critical for the persistence of species especially those with diverse and dispersed habitat requirements, as is witnessed in many migrant populations (Reynolds et al., 2017). The implementation of dynamic conservation strategies are imperative for the maintenance of migrant groups, which is necessary, as migratory populations have been displaying declining trends over the past decade (Singh & Milner-Gulland, 2011). Of this decline, seabirds and forest birds have

doi:10.6342/NTU202303015

had the most severe declines, especially in Southeast Asia (Butchart et al., 2005). The root of this global decline varies among case studies; however, the foundation of the issues tends to be anthropogenic in nature, with the leading issues being habitat loss, degradation and fragmentation (Lascelles et al., 2014). The previously mentioned factors synergized with contributing factors specifically, inadequate protection and climate change, has led to the decline of more than half of the migratory bird species across all major flyways in the last 30 years (Runge et al., 2015).

In terms of current conservation action, it has been observed that only 9% of 1451 migratory bird species are adequately covered by protected areas across all stages of their annual cycle (Runge et al., 2015). On that account, Reynolds (2017) has stated that conservationists need to surmount at least three substantive challenges. They must be able to (i) predict where the species will be over the course of their annual cycle, (ii) identify areas that are suitable for the species or that can be modified to make them suitable, and (iii) create cost-effective mechanisms to ensure that the habitat will be there when the species arrive (Reynolds et al., 2017). This demonstrates that a comprehensive knowledge of a species and its whereabouts is a prerequisite in order to effectively improve its conservation, as the limited knowledge of the distribution, abundance, and habitat associations of migratory species hinders effective conservation actions (Runge et al., 2015).

Although efforts to amass these key details of a specie's life cycle has presented complications due to their dynamic movement, it is especially difficult to elucidate in marine migratory species as theirs is more enigmatic in nature. Migratory marine species or "MMS" include organisms such as marine mammals, seabirds, turtles, sharks, and tuna, many of which are now among the most vulnerable due to the diverse range of pressures they encounter during their extensive movements (Lascelles et al., 2014).

doi:10.6342/NTU202303015

1.3 Tracking migratory seabirds

Tracking migratory animals has involved numerous tactics over the years, however, until very recently all approaches involved the use of externally placed passive markers (Hobson, 2008). These are applied to individuals with the objective of those same individuals being located elsewhere at a later period, or the use of recognized phenotypic traits that showed known geographic variation (Hobson & Ryan Norris, 2008). For birds, geographic variation in plumage and other morphological traits have been used to describe migratory connectivity, these however have been found to be ineffective in many bird species with wide ranges and can lead to biased conjectural routes (Bairlein, 2001).

In contrast, active extrinsic markers are those that send out signals that can be intercepted with a suitable receiver device (Viljoen et al., 2016). Advances in tracking technology have allowed the placement of devices on migratory animals to be more widely applied. This is because any signal-transmitting tracking tool on an animal must be small enough that the animal can carry it without difficulty while also performing the same task as larger trackers, this requires an immense amount of power. Different tracking technologies can be classified either by the way they derive location data or by the way in which we obtain the data (Bridge et al., 2011).

The progression of modern miniaturized data loggers has revolutionized the study of seabirds when away from their breeding colonies (Robertson et al., 2012). Currently, the smallest devices capable of detecting and logging position information are geolocators, which use changes in ambient light levels to estimate the times of sunrise and sunset, from which latitude and longitude can be calculated (Burger & Shaffer, 2008). The development of geolocators weighing only 2.0g - 1.5 g allowed their use for the first time on seabirds as small as terns (Egevang et al., 2010). Kürten (2019) has demonstrated that geolocators can be used to study migratory behavior on small

doi:10.6342/NTU202303015

seabirds without causing problems or introducing bias. This has allowed for researchers to generate information about connectivity between frequented areas (breeding, stopover and nonbreeding grounds), which can then guide future conservation interventions, especially regional populations (Faaborg et al., 2010).

1.4 Little tern (*Sternula albifrons*)

The Little tern (*Sternula albifrons*) is the only member from Laridae family currently found in Taiwan (Lin & Pursner, 2021), it is a colonially breeding seabird with an extensive range (Medeiros et al., 2007). Deterred by vegetation, these birds nest in open sand and gravel habitats; particularly near coastal regions and along riverbanks when found inland (Noreikiene et al., 2012). They are also common estuarine birds, and are known to forage in closer proximity to the breeding colony in comparison to other terns (Catry et al., 2006). Due to the preferred habitats used by the species, they are subject to risks caused by rising sea levels due to climate change (Noreikiene et al., 2012).

There are currently four main subspecies: *S.albirfons albifrons, S. albirfons guineae, S. albirfons placens, and S. albirfons sinensis* (*Avibase*, 2023)*,* with the subspecies *S. albifrons sinensis* found in Eastern Asia and Australia (BirdLife International, 2023). Although listed as of 'Least Concern' according to the IUCN Red List (BirdLife International, 2018), due to the worldwide issue of decreasing coastal areas, which serve as the birds' habitat, the number of individuals has been dwindling year by year (Pakanen et al., 2014) (BirdLife International, 2018). This has led to the species currently being categorized as 'Endangered' in New South Wales, Australia (*Biodiversity Conservation Act*, 2023) and Critically Endangered in Victoria, Australia (*Flora and Fauna Guarantee Act Threatened List*, 2023). In Taiwan, where some populations reside along the coast for their breeding period, they are listed as 'Near Threatened', along with a

doi:10.6342/NTU202303015

declining population trend (Lin & Pursner, 2021). The Taiwanese breeding populations are found in the coastal counties of Yilan, Hualien, Taoyuan, Hsinchu, Zhanghua, and Jiayi as well as the offshore islands of Matsu and Penghu (NTU Biodiversity Center, 2020). At the northeastern breeding site in Yilan, Taiwan the current population had a maximum count of 88 individuals in 2021 and 753 individuals in 2022 between April and July collectively among the estuaries of Lanyang, Xincheng, and Nanou (NTU Forest Department, 2023). In a genetic analyses conducted by Kong (2023) it was found that there is a high level of connectivity between individuals of the Taiwanese Little terns, with little to no population structure. It was also revealed that there was not significant genetic variation between the western and eastern sides of the country (Kong, 2023), which suggests that the migratory routes and nonbreeding grounds utilized by the Little terns along the eastern coast is also used by the individuals along the western coasts.

As conservation approaches for managing migratory species are becoming more dynamic (Reynolds et al., 2017), in order to properly conserve this marine bird more needs to be understood about its whereabouts throughout its annual cycle. Currently, studies on the annual cycle of the Little tern have mainly been conducted on the breeding populations in Japan. Fujii (2016) reported that individuals of the Tokyo, Chiba and Okinawa breeding population migrate to Australia, using Taiwan, Papua New Guinea, Indonesia, and the Philippines as stopover sites. It has been recently found that the Okinawa population shows a closer relation to the Taiwanese population than other Japanese populations, suggesting the gene flow may be due to a shared nonbreeding ground (Kong, 2023). However, there is currently little information known about the migratory routes of the Taiwanese breeding population of the Little Tern.

doi:10.6342/NTU202303015

Research Objectives

Overall, this study aims to elucidate the migration routes of Little tern individuals breeding in Taiwan and to describe their migration behavior in order to expand upon previously acquired knowledge of their annual cycle. This involves: (1) to map the southbound and northbound migration routes of the tagged Little terns by modelling movement data from ambient light-level readings collected by geolocator loggers, and (2) to describe the phenological migratory behavior of the tagged Little tern (*Sternula albifrons*) individuals.

I hypothesized that (1) individuals would utilize coastlines and use Australia as the primary nonbreeding grounds, as was observed in the previously studied East-Asian individuals in Japan, and (2) there would not be much variation in phenological migratory behavior between the tagged Little tern (*Sternula albifrons*) individuals.

doi:10.6342/NTU202303015

Methodology

2.1 Field Methods

Geolocator attachment and retrieval

The field work aspect of the study was performed in the northeastern region of Taiwan by project collaborators during the summer breeding period (June and July) over the course of the 2012 and 2016 breeding seasons. Bird capture and banding occurred at two study sites: the Lanyang Estuary (24.7021°N, 121.7378’E) and Xincheng Estuary (24.631762°N, 121.849314’E) in Yilan County of New Taipei City (Figure 1). Both sites were chosen due to having been previously recorded as regularly used breeding sites of individuals of the species.

Captures were performed with tent spring traps using active nests, whereby the track is triggered when the parents return and sit on the nest. A total of 18 birds were trapped, weighed and ringed, then fitted with light-level geolocators (MK5090, Bio track Ltd. and Intigeo-P65, Migrate Technology Ltd.). The tracking apparatus included a metal ring ID which was fitted unto the tarsus of each bird along with an engraved flag and geolocator (Figure 2), the total mass of each assembled apparatus was within a range of 0.9g-1.0g, which is in accordance with international guidelines stating that the mass should not exceed 3% of the bird’s body mass (Weiser, 2016). Two types of geolocators were used: Bio track and Migrate Technology.

Although collectively 18 birds were deployed with geolocators, only 6 geolocators were retrieved (33% of tagged birds), only 5 of which recorded comprehensive annual flight data (27% of tagged birds). Of the data retrieved, one data set was acquired from the 2012-2013 flight cycle (G01), while four were acquired from the 2016-2017 cycle (V409, V410, V412, V413).

doi:10.6342/NTU202303015

2.2 Data Analysis

After the data loggers were retrieved, the data was downloaded, the Bio Track model MK5090 and Migrate Technology model Intigeo-P65 geolocators, recorded light intensity every two minutes and every five minutes, respectively. Five out of six of the recovered geolocators contained usable light recordings for analysis, one individual from the 2013 period and four from the 2016 period. The light level data obtained was analyzed by employing the “Threshold” Method (Figure 3), which is the most widely used light analyses methods for light level migratory analyses (Lisovski et al., 2012, 2020), using R version 4.2.2 (*R: The R Project for Statistical Computing*, 2023). This approach allows for different datatypes to be analyzed based on individually designated thresholds (Lindström et al., 2015).

This process commenced with the defining of twilight events, which is the time whereby light levels pass a predetermined threshold that divides day time from night time (Bråthen et al., 2021; Lisovski et al., 2020). In this case, there was a period of inspection to determine potential “false twilights”, which would interfere with the subsequent processes. These “false twilights” can be produced by shading due to the environmental factors or perching during the day, causing a false night time reading or exposure to bright artificial light during the night time which may produce a false day time reading (Bindoff et al., 2018; Lindström et al., 2015). This was followed by extracting the times of sunset and sunrise by using a light level threshold of 2 (Figure 4). Once obtained, these sunset and sunrise periods are equated to the duration of one day, then a blunt position estimation is produced based on the location where the bird was during this change in light intensity (Lisovski et al., 2020).

A median sun elevation angle was obtained by executing a calibration procedure, based on the light intensity recordings when located at the release and re-capture site (Lisovski et al., 2020).

doi:10.6342/NTU202303015

This was followed by an estimation of locations using the “GeoLight” package (Lisovski et al., 2020), in order to understand the general movements which were made. Near the autumn and spring equinoxes (March 20th-22nd, September 21st- 24th), the positions were assessed individually as these time periods are known to produce error, due to the change in designated sun angles (Ekstrom, 2004).

The Hill-Ekstrom calibration was then conducted, this allows for the identification of the stationary periods by using the reference sun elevations produces in the previous calibration period (Lisovski et al., 2012). With these generalities understood, the movement analysis was performed, this is done by employing the “changeLight” function (Lisovski et al., 2020). This function allows for the definition of stationary periods, in this case a minimum of 3 days was equated to a stopover period, this allowed for movement and residency phases to be distinguished. The “mergeSite” tool is then used to merge consecutive sites that may be have been separated by twilight errors, to do this it employs a maximum likelihood fit (Lisovski et al., 2012), this allowed for the production of rudimentary maps.

Following the elucidation of the potential routes, including the stopover and nonbreeding grounds, the likelihood of these locations was confirmed using citizen science websites such as ebird.com which established the occurrence of migrating individuals in Indonesia and the Philippines (Fink et al., 2022); 10000birds.com which reported Taiwanese banded individuals on the shores of Southern Australia (Clare, 2015), and inaturalist.org which confirmed the occurrence on the Eastern Philippine coasts and Indonesian Islands (iNaturalist, 2023). This was done to ensure that the species had been observed in the projected locations. Next, local news reports of bird sightings were used such as The Taipei Times (The Taipei Times, 2012) and Focus Taiwan

doi:10.6342/NTU202303015

(Focus Taiwan, 2012), which stated that the Taiwanese banded birds were found in the projected nonbreeding grounds.

The Victoria Wader Study Group through personal communication which has stated on their database sightings and recordings of Taiwanese Little terns near their coast. This was followed by confirming sightings of banded individuals using their website database "BirdMark", which uses banding data to visualize the frequented locations of marked birds (Deakin University, Australia, 2022). This enabled a confirmation of the utilization of the coast of Eastern and Western regions of Australia as non-breeding grounds for individuals from the Northern Taiwan region (Deakin University, Australia, 2022). After the estimations were confirmed, the primary maps developed using R software and the generated coordinates were used to developed more comprehensive maps for better data visualization to portray the movement of the terns by using QGIS Software version 3.30.3 (QGIS Development Team, 2023).

doi:10.6342/NTU202303015

Results

Previous researchers recovered six out of eighteen deployed trackers, which allowed for the documentation of a full one-year migration cycle of each post-breeding bird. Complete migratory schedule and routes were obtained for five individuals, the details of the geolocators tags and attachment information of the retrieved individuals are archived in Table 1.

3.1 Migration Phenology

Loggers recovered recorded data for an average of ± 342 days for all birds. All individuals departed the breeding grounds during the summer in late June, July, or August, as seen in Figure 31. The mean duration of migration to the nonbreeding grounds was ± 48 days, with an average ±18 day observed as the stopover period for the individuals (Table 2). For the northbound migration the return began in March and April for most birds, while V412 began in early January (Figure 32). The mean duration of migration to the breeding grounds was less than that of the previous migratory movement, at only ± 34 days, with an average ± 11 days observed as the stopover period for the individuals (Table 2).

3.2 Migratory routes

All five Little terns traveled along the East Asian-Australasian Flyaway (Figure 25). The routes used by birds from Xincheng Estuary and Lanyang Estuary were similar in pattern for both the individual tracked in 2013-2014 period and the individuals tracked in the 2016-2017 period (Figure 25). For the southbound migration the terns flew over the Pacific Ocean and utilized Southeast Asian coasts until the arrival at the Australian coasts. All birds had stopovers in either the coasts of The Philippines or an Indonesian island (Figure 25). Although the birds were all located in similar sites in Taiwan during the breeding season, they did not all arrive in the same region of the nonbreeding grounds. Instead, the birds used two main routes; V409 (Figure17) and

doi:10.6342/NTU202303015

V410 (Figure 19), which were breeding pairs in the 2016 breeding season, stayed in Eastern Australia near the state of Victoria, about 4437 miles from the breeding grounds. Meanwhile, G1 (Figure 15), V412 (Figure 21) and V413 (Figure 23) used along the coasts of northern and eastern Western Australia, an estimated 3,547 km from the breeding grounds. The birds were all observed to mainly utilize coasts during the migratory journey, however there were brief stages over land throughout the passage, with brief stationary periods near inland waterbodies. Along the journey, the birds flew to stopover locations along the coasts of Indonesia and the Philippines, which is about 2,800 miles and 1,925 miles from the nonbreeding grounds respectively.

For the northbound migration, all birds returned to the initial breeding grounds. Along the route the individuals used a similar directional movement, utilizing the same stopover locations, the Philippines and Indonesia. As displayed in Figure 29, the birds mainly visited the Philippine coasts, especially in the northern and western regions. In Indonesia the birds displayed a widespread range, with the most frequented areas being near West Papua and the Maluku Islands (Figure 30).

doi:10.6342/NTU202303015

Discussion

The results of this study display the annual cycle of the geolocator tagged Little terns from the breeding grounds in northeastern Taiwan to their non-breeding grounds in Australia. It reports that the birds utilize the East Asian-Australian Flyaway from Taiwan to Australia, flying mainly along the coasts. Along the route, the birds had stopover periods in Indonesia and The Philippines for both stages of the migration. Pertaining to the southbound migration, many of the Little terns left the breeding grounds in July and August, then arrived at the non-breeding grounds in September and October, ending the northbound migration. Meanwhile for the northbound migration, the depart began on average in March and April, ending in April and May in Taiwan once again. In terms of the duration of both voyages, the southbound flight took longer to complete, and had shorter stopover periods.

4.1 Stopover Behavior

The birds in this study and previous eastern Pacific Little terns were all observed to use stopovers between the breeding and non-breeding grounds. The stopover sites are locales which serve as refueling, resting sites for the birds during their migratory excursion (Warnock, 2010) (Schmaljohann & Eikenaar, 2017). This may occur because the individuals do not possess sufficient storage of energy to cover the long distances, this behavior is particularly common after a large ecological barrier is crossed (Bounas et al., 2023). Studies have also found that stopovers can also serve as physiological recovery period for migratory birds, to heal from injuries or conditions suffered along the course of the previous flight namely organ recovery, muscle repair, etc. (Guglielmo et al., 2001)(Schmaljohann et al., 2022).

The Philippines and Indonesia served as the stopover locations for the tracked Little terns in both study periods (2013-2014, 2016-2017) included in this research, and was also utilized in

doi:10.6342/NTU202303015

some capacity by both the mainland and Okinawa Japanese individuals (Fujii et al., 2016). Both jurisdictions act as major stopover locations as a part of the East-Asian Australasian Flyaway, with the Philippines receiving about 500,000 waterbirds annually (Biodiversity Management Bureau Staff, 2021) and Indonesia receiving about 20,000 waterbirds annually, although literature is lacking in Indonesia in terms distributional records (Mundkur, 2007) (Crossland et al., 2006) and in the Philippines the literature is limited (Putra et al., 2017) .

4.2 Migration Strategy Variations

There was variation observed in the timing of commencement and conclusion for the migration (Table 2). An early departure from the non-breeding grounds was observed in V412, which was about 32 days prior to the departure of the remainder of the tracked individuals. Previous studies have reported that migratory males with higher quality phenotypic traits tend to be the earliest arrivals (Velmala et al., 2015). However, due to the lack of sex identification of the tagged birds, this cannot be assumed as a contributing factor for this early departure of V412. In addition , recent developments in migration phenology research has discovered that an advancement in migration timing is a recent reoccurring trend in migratory populations over the last decade, this involves an early arrival at the breeding grounds and an early departure from the non-breeding grounds, due to changing climate which allow the breeding grounds to have optimal conditions earlier (Gill et al., 2014)(Lawrence et al., 2022)(Zimova et al., 2021)(Chambers et al., 2014)(Miller-Rushing et al., 2008). However, currently there is lack of evidence to definitively conclude the cause of this early departure.

It was also observed that the duration of the southbound migration from breeding grounds to nonbreeding grounds was longer in comparison to the northbound migration from non-breeding grounds to breeding grounds. This is a commonly observed behavioral pattern among migratory

doi:10.6342/NTU202303015

seabirds (Bayly & Gómez, 2011)(Carneiro et al., 2019)(Schmaljohann, 2018), and is hypothesized to be due to the lower pressure required for site selection upon arrival at the non-breeding grounds. Meanwhile, the site selection process following the arrival at the breeding grounds entails a greater level of discernment between quality spots, as a higher quality breeding grounds has been documented to increase the breeding success (Morrison et al., 2019).

4.3 Drivers of route choice

The migratory route or network choice can have severe implications on an individual's fitness (Sawyer et al., 2019), this had led researchers to infer about the factors which an individual relies on over the course of the route selection process. In the study conducted, the birds utilized two regions of Australia: namely, Western Australia and Victoria. All five tracked terns displayed a preference for the same route for both journeys. According to, recent studies the route choice is mainly due favorable environmental conditions along the corridor, as this has been observed in various species (Purcell & Brodin, 2007)(Sawyer et al., 2019)(Goodenough & Patton, 2019). The key environmental factors viewed as most significant are ocean surface winds and temperature, which functions as a critical variables in the timing of the flight (Carneiro et al., 2020)(Hensz, 2015)(Felicísimo et al., 2008).

The southbound migratory terminal is the nonbreeding grounds, Australia. This choice has been found to be influenced by food resources available and upwellings in the area (Hensz, 2015) (Raymond et al., 2010). Little terns have a diet similar to most terns, namely small fish, crustaceans and insects (Brenninkmeijer et al., 2002)(Catry et al., 2006)(Cramp, 1985). The Australian states of Western Australia and Victoria which the birds utilized act as nonbreeding grounds for about 16 species of migratory shorebirds (Surman & Nicholson, 2009) and more than 30 species (State Government of Victoria, 2019) respectively. Landscape surveys have shown that the seagrass and

doi:10.6342/NTU202303015

algae beds as well as high rates of tidal exchange in these areas, especially near sandflats serve as suitable habitats for small sized fish and crustaceans, which are the preferred diet of the species (Chafer & Brandis, 2006).

As for the Little terns not included in the study, as well as the 12 individuals that were not able to be recaptured, it is likely that Australia is also used as a nonbreeding site, as there is no distinct population division (Kong, 2023). However as displayed in Figure 33, Little terns of the East Asian Australasian region may also use Papua New Guinea, Indonesia, Singapore, and Malaysia as nonbreeding sites (BirdLife International, 2023).

4.4 East Asian Australasian Flyway and Conservation Implications

The East Japanese population was found to migrate to southeastern Asia and southeastern Australia, while the Okinawa population was found to migrate to northwestern Australia and northeastern Australia. This similarity between both populations strongly suggests that this may be the main migration routes used by this sub-species of the Eastern Pacific region. During the voyage, the birds all utilize the East-Asian Australasian Flyway, this encompasses the region from Russia to New Zealand, and incorporates over 37 countries (Yong et al., 2018), this pathway serves as one of the major flyways used by migratory birds. More specifically, it is used by 500 million migratory waterbirds (*Eaaflyway*, n.d.) and has more than a notable 400 sites of importance (Bamford et al., 2008). Amongst the birds utilizing this path, is the recently studied Japanese breeding population of the Little tern (Fujii, 2016). The observance of individuals of both East Asian populations across this flyaway renders the species vulnerable to potential environmental changes in locales along this route, as any disturbance along the migratory pathway may cause an effect on the individual (Goodenough & Patton, 2019)(Schuster et al., 2019). Although highly employed, this ecological corridor also faces a deal of threats, the most prominent of which is

doi:10.6342/NTU202303015

habitat loss and degradation (Yong et al., 2018). While conservation efforts have been increasing in the East-Asian region, namely Japan, Korea, and Taiwan, in response to higher rates of population decline of bird species, there has been conservation gaps, knowledge gaps and a lack of coastal governance and management in the South-East Asian region, which the terns frequent as stopover sites along their migration (Szabo & Mundkur, 2017)(Yong et al., 2022). These jurisdictions are critical for the management of the species, as they utilize these locations when they require sufficient energy in a short period, while avoiding conflict due to predators and competition with other species (Moore et al., 2005)(Schmaljohann et al., 2022).

Therefore while the current conservation efforts have been constructive, researchers have discovered that 91% of migratory birds are not receiving adequate coverage of their range, which increases their exposure to potential threats in a portion of their annual cycle; which in turn affects population dynamics (Runge et al., 2015)(Conklin et al., 2021). Evidence of the cost to population was described by Studds (2017) whereby birds dependent on Yellow Sea tidal mudflats as a stopover declined up to 8 percent per year as the habitat experienced threats. This displays the need for an increase in enforcement in more jurisdictions along an avian migratory route. In the case of the tracked terns in this study, the wide range visited in Australia poses an issue since wider ranges are more difficult to manage; however, the East Asian Australasian flyaway currently has objectives to conserve on a wider ecosystem scale (*Eaaflyway*, n.d.). In order for this wide scale protection to be achieved, there needs to be a strengthening of participation in order to establish collective commitments to the conservation targets for the conservation of migratory species and allow for better organizing by increasing multilateral agreements and international collaboration (Szabo et al., 2016)(Hays et al., 2019)(Rueda-Uribe et al., 2021).

doi:10.6342/NTU202303015

4.5 Concerns and Future Research

Whilst the routes and stopover areas have been successfully described, this study is to serve as a foundational elucidation of the migration routes of the Taiwanese Little tern (*Sternula albifrons*) individuals. This is because the geolocators employed to document the migration of the Little tern possesses a spatial accuracy of ~200 km (Halpin et al., 2021). For this reason, geolocator tracking allows for blunt, less precise location data in comparison to more sophisticated tracking devices, such as satellite markers and GPS trackers (Kralj et al., 2020). This results in the findings of geolocator studies to be subject to uncertainty (Lisovski et al., 2018).

Additionally, while geolocators have been found to have minimal effects on study specimen (Bridge et al., 2011), it has been found that geolocator attachment affects return rate (Taff et al., 2018). This contributes to the recapture difficulty common in geolocator studies, this study similarly to other geolocator based studies only represents a small portion of the overall Little tern population of Taiwan. As a result concerns of inadequate sample size must be noted, which in turn causes aspects of the migration ecology such as site fidelity, individual response and migration tactics not being able to be comprehensively described. Subsequent studies should also be performed with a prerequisite sex identification to identify the dependence of sex on route choice and phenology. This study was not able to display migratory route fidelity, due to the short study period. However migratory route fidelity is a previously observed trait in the *Sternula* genus, such as in the Least tern (Atwood & Massey, 1988) and in larger terns of the greater Laridae family, such as the Gull-billed tern (Goodenough & Patton, 2019). There was also consistency seen in the stopover sites used among the individuals, which is observed as a common trait in avian migrants (Merkel et al., 2021).This is regarded as a successful migratory behavior as a level of consistency

doi:10.6342/NTU202303015

in route choice can enhance survival, migration efficiency and avoided risk (Cantos & Tellería, 1994).

doi:10.6342/NTU202303015

Conclusion

In summary, the primary goals of this thesis were to identify the migration routes used by individuals of the Little tern (*Sternula albifrons*) breeding population in Taiwan and to describe variation in migration behavior, in order to contribute towards a greater comprehensive understanding of their migration ecology. Specifically, it displayed how members of the breeding population, similarly to individuals of the Japanese population journey to Australia for its non-breeding period. In doing so, they utilized the coasts of the Philippines and Indonesia as major stopover sites for feeding and rest. In addition to this, it displayed that although the birds share the same breeding grounds, they conclude the southbound migration at different regions of the nonbreeding grounds, estimated to be the coasts of the Australian states: Western Australia and Victoria.

Previous migration studies of this species had only tracked individuals of the Japanese mainland and Okinawa populations. This study serves as one of the first records of the migratory ecology of the only member of the Laridae family which possesses a breeding population in Taiwan. This thesis has demonstrated how modern tracking technology allows necessary insight into the migratory movements of migrants in previously inaccessible environments.

doi:10.6342/NTU202303015

Literature Cited

Atwood, J. L., & Massey, B. W. (1988). Site Fidelity of Least Terns in California. *The Condor*, *90*(2), 389–394. https://doi.org/10.2307/1368567

Bairlein, F. (2001). Results of bird ringing in the study of migration routes. *Ardea*, *89*, 7–19.

Bamford, M., Watkins, D., Bancroft, W., Tischler, G., & Wahl, J. (2008). Migratory shorebirds of the East Asian-Australasian Flyway: Population estimates and internationally important sites. *Wetlands International*, *1*, 1–240.

Bauer, S., & Hoye, B. (2014). Migratory Animals Couple Biodiversity and Ecosystem Functioning Worldwide. *Science*, *344*(6179). https://doi.org/DOI: 10.1126/science.1242552

Bayly, N. J., & Gómez, C. (2011). Comparison of autumn and spring migration strategies of Neotropical migratory landbirds in northeast Belize. *Journal of Field Ornithology*, *82*(2), 117–131. https://doi.org/10.1111/j.1557-9263.2011.00314.x

Bindoff, A. D., Wotherspoon, S. J., Guinet, C., & Hindell, M. A. (2018). Twilight-free geolocation from noisy light data. *Methods in Ecology and Evolution*, *9*(5), 1190–1198. https://doi.org/10.1111/2041-210X.12953

Biodiversity Conservation Act 2016 No 63—NSW Legislation. (2023, April 28). https://legislation.nsw.gov.au/view/html/inforce/current/act-2016-063

Biodiversity Management Bureau staff. (2021). *Rare migrant spotted in Tanza marine tree park*. Republic of the Philippines Department of Envoronment and Natural Resources Biodiversity Management Bureau. https://www.bmb.gov.ph/index.php/resources/news-and-events/202-rare-migrant-spotted-in-tanza-marine-tree-

doi:10.6342/NTU202303015

park#:~:text=The%20Philippines%20is%20part%20of,January%20of%20the%20following%20year.

BirdLife International. (2023). *Species factsheet: Sternula albifrons*. BirdLife International. http://datazone.birdlife.org/species/factsheet/little-tern-sternula-albifrons

BirdLife International, B. I. (BirdLife I. (2018). IUCN Red List of Threatened Species: Sternula albifrons. *IUCN Red List of Threatened Species*. https://www.iucnredlist.org/en

Bounas, A., Komini, C., Talioura, A., Toli, E.-A., Sotiropoulos, K., & Barboutis, C. (2023). Adaptive Regulation of Stopover Refueling during Bird Migration: Insights from Whole Blood Transcriptomics. *Genome Biology and Evolution*, *15*(4). https://doi.org/10.1093/gbe/evad061

Bråthen, V., Moe, B., Amélineau, F., Ekker, M., Helgason, H., Johansen, M., Merkel, B., Tarroux, A., Åström, J., & Strøm, H. (2021). *An automated procedure (v2.0) to obtain positions from light-level geolocators in large- scale tracking of seabirds A method description for the SEATRACK project*.

Brenninkmeijer, A., Stienen, E., Klaassen, M., & Kersten, M. (2002). Feeding ecology of wintering terns in Guinea-Bissau. *Ibis, v.144, 602-613 (2002)*, *144*. https://doi.org/10.1046/j.1474-919X.2002.00100.x

Bridge, E. S., Thorup, K., Bowlin, M. S., Chilson, P. B., Diehl, R. H., Fléron, R. W., Hartl, P., Kays, R., Kelly, J. F., Robinson, W. D., & Wikelski, M. (2011). Technology on the Move: Recent and Forthcoming Innovations for Tracking Migratory Birds. *BioScience*, *61*(9), 689–698. https://doi.org/10.1525/bio.2011.61.9.7

doi:10.6342/NTU202303015

Burger, A. E., & Shaffer, S. A. (2008). Perspectives in Ornithology Application of Tracking and Data-Logging Technology in Research and Conservation of Seabirds. *The Auk*, *125*(2), 253–264. https://doi.org/10.1525/auk.2008.1408

Butchart, S., Stattersfield, A., Bennun, L., Shutes, S., Akcakaya, H. R., Baillie, J., Stuart, S., & Hilton-Taylor, C. (2005). Measuring Global Trends in the Status of Biodiversity: Red List Indices for Birds. *PLoS Biology*, *2*, e383. https://doi.org/10.1371/journal.pbio.0020383

Cantos, F. J., & Tellería, J. L. (1994). Stopover Site Fidelity of Four Migrant Warblers in the Iberian Peninsula. *Journal of Avian Biology*, *25*(2), 131–134. https://doi.org/10.2307/3677031

Carneiro, C., Gunnarsson, T. G., & Alves, J. A. (2019). Faster migration in autumn than in spring: Seasonal migration patterns and non-breeding distribution of Icelandic whimbrels Numenius phaeopus islandicus. *Journal of Avian Biology*, *50*(1). https://doi.org/10.1111/jav.01938

Carneiro, C., Gunnarsson, T. G., & Alves, J. A. (2020). Linking Weather and Phenology to Stopover Dynamics of a Long-Distance Migrant. *Frontiers in Ecology and Evolution*, *8*, 145. https://doi.org/10.3389/fevo.2020.00145

Catry, T., Ramos, J. A., Paiva, V. H., Martins, J., Almeida, A., Palma, J., Andrade, P. J., Peste, F., Trigo, S., & LuÍs, A. (2006). Intercolony and Annual Differences in the Diet and Feeding Ecology of Little Tern Adults and Chicks in Portugal. *The Condor*, *108*(2), 366–376. https://doi.org/10.1093/condor/108.2.366

Chafer, C., & Brandis, C. (2006). Changes in the waterbird community of the Lake Illawarra estuary: 20 years of research. *Wetlands Australia*, *21*. https://doi.org/10.31646/wa.271

doi:10.6342/NTU202303015

Chambers, L. E., Dann, P., Cannell, B., & Woehler, E. J. (2014). Climate as a driver of phenological change in southern seabirds. *International Journal of Biometeorology*, *58*(4), 603–612. https://doi.org/10.1007/s00484-013-0711-6

Clare, M. (2015, December 20). *A Little Tern flagged in Taiwan visits Australia – 10,000 Birds*. 10000 Birds. https://www.10000birds.com/a-little-tern-flagged-in-taiwan-visits-australia.htm

Conklin, J. R., Lisovski, S., & Battley, P. F. (2021). Advancement in long-distance bird migration through individual plasticity in departure. *Nature Communications*, *12*(1), Article 1. https://doi.org/10.1038/s41467-021-25022-7

Cramp, S. (1985). The Birds of the Western Palearctic. Vol. IV. Terns to Woodpeckers. In *Handbook of the Birds of Europe, the Middle East, and North Africa: The Birds of the Western Palearctic Volume IV: Terns to Woodpeckers*. Oxford University Press.

Crossland, A., Sinambela, S., & Sitorus, A. (2006). An overview of the status and abundance of migratory waders in Sumatra, Indonesia. *Stilt*, *50*.

Deakin University, Australia. (2022). *BirdMark*. BirdMark.Net. https://www.birdmark.net/bm_overviewPlainFlags.php

Dingle, H., & Drake, V. A. (2007). What Is Migration? *BioScience*, *57*(2), 113–121. https://doi.org/10.1641/B570206

Egevang, C., Stenhouse, I. J., Phillips, R. A., Petersen, A., Fox, J. W., & Silk, J. R. D. (2010). Tracking of Arctic terns *Sterna paradisaea* reveals longest animal migration. *Proceedings of the National Academy of Sciences*, *107*(5), 2078–2081. https://doi.org/10.1073/pnas.0909493107

doi:10.6342/NTU202303015

Ekstrom, P. (2004). An advance in geolocation by light. *Memoirs of National Institute of Polar Research. Special Issue*. https://www.semanticscholar.org/paper/An-advance-in-geolocation-by-light-Ekstrom/4f088db4afb9f5d0c05976b537134413b6df7564

Faaborg, J., Holmes, R. T., Anders, A. D., Bildstein, K. L., Dugger, K. M., Gauthreaux, S. A., Heglund, P., Hobson, K. A., Jahn, A. E., Johnson, D. H., Latta, S. C., Levey, D. J., Marra, P. P., Merkord, C. L., Nol, E., Rothstein, S. I., Sherry, T. W., Sillett, T. S., Thompson, F. R., & Warnock, N. (2010). Recent advances in understanding migration systems of New World land birds. *Ecological Monographs*, *80*(1), 3–48.

Felicísimo, Á. M., Muñoz, J., & González-Solis, J. (2008). Ocean Surface Winds Drive Dynamics of Transoceanic Aerial Movements. *PLOS ONE*, *3*(8), e2928. https://doi.org/10.1371/journal.pone.0002928

Fink, D., Auer, T., Johnston, A., Strimas-Mackey, M., Ligocki, S., Robinson, O., Hochachka, W., Jaromczyk, L., & Davies, I. (2022). *Little Tern—Abundance map—EBird Status and Trends*. EBird Status and Trends. https://science.ebird.org/status-and-trends/species/litter1/abundance-map

Flora and Fauna Guarantee Act Threatened List. (2023, June). https://www.environment.vic.gov.au/conserving-threatened-species/threatened-list

Focus Taiwan. (2012, November 17). *Bird species tagged in Taiwan spotted in Australia for first time*. Focus Taiwan. https://focustaiwan.tw/society/201211170015

Fujii, T., Kitamura, W., Murofushi, A., Kanazawa, S., & Moriyama, A. (2016). *An Explanation of Migration Routes of Little Terns breeding in Okinawa*. https://kaken.nii.ac.jp/grant/KAKENHI-PROJECT-15K06935/

doi:10.6342/NTU202303015

Gill, J. A., Alves, J. A., Sutherland, W. J., Appleton, G. F., Potts, P. M., & Gunnarsson, T. G. (2014). Why is timing of bird migration advancing when individuals are not? *Proceedings of the Royal Society B: Biological Sciences*, *281*(1774), 20132161. https://doi.org/10.1098/rspb.2013.2161

Goodenough, K. S., & Patton, R. T. (2019). Satellite Telemetry Reveals Strong Fidelity to Migration Routes and Wintering Grounds for the Gull-Billed Tern (Gelochelidon nilotica). *Waterbirds*, *42*(4), 400–410. https://doi.org/10.1675/063.042.0405

Guglielmo, C. G., Piersma, T., & Williams, T. D. (2001). A sport-physiological perspective on bird migration: Evidence for flight-induced muscle damage. *Journal of Experimental Biology*, *204*(15), 2683–2690. https://doi.org/10.1242/jeb.204.15.2683

Halpin, L. R., Ross, J. D., Ramos, R., Mott, R., Carlile, N., Golding, N., Reyes-González, J. M., Militão, T., De Felipe, F., Zajková, Z., Cruz-Flores, M., Saldanha, S., Morera-Pujol, V., Navarro-Herrero, L., Zango, L., González-Solís, J., & Clarke, R. H. (2021). Double-tagging scores of seabirds reveals that light-level geolocator accuracy is limited by species idiosyncrasies and equatorial solar profiles. *Methods in Ecology and Evolution*, *12*(11), 2243–2255. https://doi.org/10.1111/2041-210X.13698

Hays, G. C., Bailey, H., Bograd, S. J., Bowen, W. D., Campagna, C., Carmichael, R. H., Casale, P., Chiaradia, A., Costa, D. P., Cuevas, E., Nico de Bruyn, P. J., Dias, M. P., Duarte, C. M., Dunn, D. C., Dutton, P. H., Esteban, N., Friedlaender, A., Goetz, K. T., Godley, B. J., … Sequeira, A. M. M. (2019). Translating Marine Animal Tracking Data into Conservation Policy and Management. *Trends in Ecology & Evolution*, *34*(5), 459–473. https://doi.org/10.1016/j.tree.2019.01.009

doi:10.6342/NTU202303015

Hensz, C. M. (2015). Environmental factors in migratory route decisions: A case study on Greenlandic Arctic Terns (Sterna paradisaea). *Animal Migration*, *2*(1), 76–85. https://doi.org/10.1515/ami-2015-0004

Hobson, K. A. (2008). Using endogenous and exogenous markers in bird conservation. *Bird Conservation International*, *18*(S1), S174–S199. https://doi.org/10.1017/S0959270908000361

Hobson, K. A., & Ryan Norris, D. (2008). Animal Migration: A Context for Using New Techniques and Approaches. In *Terrestrial Ecology* (Vol. 2, pp. 1–19). Elsevier. https://doi.org/10.1016/S1936-7961(07)00001-2

Home—Eaaflyway. (n.d.). Retrieved April 17, 2023, from https://www.eaaflyway.net/

iNaturalist. (2023). *Little Tern Sternula albifrons*. INaturalist. https://www.inaturalist.org/taxa/144529-Sternula-albifrons

Kong, M.-S. (2023). *Exploring genetic diversity and population structure of the Little Tern (Sternula albifrons) in Taiwan based on mtDNA and ddRAD sequencing data* [Master's Thesis, National Taiwan University]. doi:10.6342/NTU202300368

Kralj, J., Martinović, M., Jurinović, L., Szinai, P., Sütő, S., & Preiszner, B. (2020). Geolocator study reveals east African migration route of Central European Common Terns. *Avian Research*, *11*(1), 6. https://doi.org/10.1186/s40657-020-00191-z

Kürten, N., Vedder, O., González-Solís, J., Schmaljohann, H., & Bouwhuis, S. (2019). No detectable effect of light-level geolocators on the behaviour and fitness of a long-distance migratory seabird. *Journal of Ornithology*, *160*, 1087–1095. https://doi.org/10.1007/s10336-019-01686-3

doi:10.6342/NTU202303015

Lack, D. (1968). Bird Migration and Natural Selection. *Oikos*, *19*(1), 1–9. https://doi.org/10.2307/3564725

Lascelles, B., Notarbartolo Di Sciara, G., Agardy, T., Cuttelod, A., Eckert, S., Glowka, L., Hoyt, E., Llewellyn, F., Louzao, M., Ridoux, V., & Tetley, M. J. (2014). Migratory marine species: Their status, threats and conservation management needs. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *24*(S2), 111–127. https://doi.org/10.1002/aqc.2512

Lawrence, K. B., Barlow, C. R., Bensusan, K., Perez, C., & Willis, S. G. (2022). Phenological trends in the pre- and post-breeding migration of long-distance migratory birds. *Global Change Biology*, *28*(2), 375–389. https://doi.org/10.1111/gcb.15916

Lin, D.-L., & Pursner, S. (2021). *The State of Taiwan's Birds*. Endemic Species Research Institute, Taiwan Wild Bird Federation, Taiwan. https://www.bird.org.tw/report/2020/english

Lindström, Å., Alerstam, T., Bahlenberg, P., Ekblom, R., Fox, J., Råghall, J., & Klaassen, R. (2015). The migration of the great snipe Gallinago media: Intriguing variations on a grand theme. *Journal of Avian Biology*, *47*, n/a-n/a. https://doi.org/10.1111/jav.00829

Lisovski, S., Bauer, S., Briedis, M., Davidson, S. C., Dhanjal-Adams, K. L., Hallworth, M. T., Karagicheva, J., Meier, C. M., Merkel, B., Ouwehand, J., Pedersen, L., Rakhimberdiev, E., Roberto-Charron, A., Seavy, N. E., Sumner, M. D., Taylor, C. M., Wotherspoon, S. J., & Bridge, E. S. (2020). Light-level geolocator analyses: A user's guide. *Journal of Animal Ecology*, *89*(1), 221–236. https://doi.org/10.1111/1365-2656.13036

Lisovski, S., Hewson, C. M., Klaassen, R. H. G., Korner-Nievergelt, F., Kristensen, M. W., & Hahn, S. (2012). Geolocation by light: Accuracy and precision affected by environmental

doi:10.6342/NTU202303015

factors. *Methods in Ecology and Evolution*, *3*(3), 603–612. https://doi.org/10.1111/j.2041-210X.2012.00185.x

Lisovski, S., Schmaljohann, H., Bridge, E., Bauer, S., Farnsworth, A., Gauthreaux, S., Hahn, S., Hallworth, M., Hewson, C., Kelly, J., Liechti, F., Marra, P., Rakhimberdiev, E., Ross, J., Seavy, N., Sumner, M., Taylor, C., Winkler, D., Wotherspoon, S., & Wunder, M. (2018). Current Biology: Inherent limits of light-level geolocation may lead to over-interpretation. *Current Biology*, *28*, 89–102. https://doi.org/10.1016/j.cub.2017.11.072

Medeiros, R., Ramos, J. A., Paiva, V. H., Almeida, A., Pedro, P., & Antunes, S. (2007). Signage reduces the impact of human disturbance on little tern nesting success in Portugal. *Biological Conservation*, *135*(1), 99–106. https://doi.org/10.1016/j.biocon.2006.10.001

Merkel, B., Descamps, S., Yoccoz, N. G., Grémillet, D., Daunt, F., Erikstad, K. E., Ezhov, A. V., Harris, M. P., Gavrilo, M., Lorentsen, S.-H., Reiertsen, T. K., Steen, H., Systad, G. H., Þórarinsson, Þ. L., Wanless, S., & Strøm, H. (2021). Individual migration strategy fidelity but no habitat specialization in two congeneric seabirds. *Journal of Biogeography*, *48*(2), 263–275. https://doi.org/10.1111/jbi.13883

Miller-Rushing, A. J., Lloyd-Evans, T., Primack, R. B., & Satzinger, P. (2008). Bird migration times, climate change, and changing population sizes. *Global Change Biology*, *14*(9), 1959–1972. https://doi.org/10.1111/j.1365-2486.2008.01619.x

Moore, F., Woodrey, M., Buler, J., Woltmann, S., & Simons, T. (2005). *Understanding the Stopover of Migratory Birds: A Scale Dependent Approach*.

Morrison, C. A., Alves, J. A., Gunnarsson, T. G., Þórisson, B., & Gill, J. A. (2019). Why do earlier-arriving migratory birds have better breeding success? *Ecology and Evolution*, *9*(15), 8856–8864. https://doi.org/10.1002/ece3.5441

doi:10.6342/NTU202303015

Mundkur, T. (2007). *Status of Waterbirds in Asia*. Wetlands International. https://www.wetlands.org/publications/status-of-waterbirds-in-asia-2/

Noreikiene, K., Berthelsen, U. M., & Gienapp, P. (2012). The first microsatellite markers for little terns (Sternula albifrons). *Conservation Genetics Resources*, *4*(2), 447–450. https://doi.org/10.1007/s12686-011-9570-9

NTU Biodiversity Center. (2020). *Report of the ecological survey and data collection on Taiwan seabird population 2020*. National Taiwan Univeristy.

NTU Forest Department. (2023). *111 Annual Seabird Population Survey (Unpublished)*. National Taiwan University.

Pakanen, V.-M., Hongell, H., Aikio, S., & Koivula, K. (2014). Little tern breeding success in artificial and natural habitats: Modelling population growth under uncertain vital rates. *Population Ecology*, *56*(4), 581–591. https://doi.org/10.1007/s10144-014-0446-1

Peters, W., Hebblewhite, M., Mysterud, A., Spitz, D., Focardi, S., Urbano, F., Morellet, N., Heurich, M., Kjellander, P., Linnell, J. D. C., & Cagnacci, F. (2017). Migration in geographic and ecological space by a large herbivore. *Ecological Monographs*, *87*(2), 297–320.

Purcell, J., & Brodin, A. (2007). Factors influencing route choice by avian migrants: A dynamic programming model of Pacific brant migration. *Journal of Theoretical Biology*, *249*(4), 804–816. https://doi.org/10.1016/j.jtbi.2007.08.028

Putra, C. A., Perwitasari-Farajallah, D., & Mulyani, Y. A. (2017). Habitat Use of Migratory Shorebirds on the Coastline of Deli Serdang Regency, North Sumatra Province. *HAYATI Journal of Biosciences*, *24*(1), 16–21. https://doi.org/10.1016/j.hjb.2017.04.003

doi:10.6342/NTU202303015

QGIS Development Team. (2023, May). *A Free and Open Source Geographic Information System*. QGIS: A Free and Open Source Geographic Information System. https://qgis.org/en/site/

R: The R Project for Statistical Computing. (2023, June). https://www.r-project.org/

Raymond, B., Shaffer, S. A., Sokolov, S., Woehler, E. J., Costa, D. P., Einoder, L., Hindell, M., Hosie, G., Pinkerton, M., Sagar, P. M., Scott, D., Smith, A., Thompson, D. R., Vertigan, C., & Weimerskirch, H. (2010). Shearwater Foraging in the Southern Ocean: The Roles of Prey Availability and Winds. *PLOS ONE*, *5*(6), e10960. https://doi.org/10.1371/journal.pone.0010960

Reynolds, M. D., Sullivan, B. L., Hallstein, E., Matsumoto, S., Kelling, S., Merrifield, M., Fink, D., Johnston, A., Hochachka, W. M., Bruns, N. E., Reiter, M. E., Veloz, S., Hickey, C., Elliott, N., Martin, L., Fitzpatrick, J. W., Spraycar, P., Golet, G. H., McColl, C., … Morrison, S. A. (2017). Dynamic conservation for migratory species. *Science Advances*, *3*(8), e1700707. https://doi.org/10.1126/sciadv.1700707

Robertson, G., Fifield, D., Montevecchi, W., Gaston, A., Burke, C., Byrne, R., Elliott, K., Gjerdrum, C., Gilchrist, H., Hedd, A., Mallory, M., McFarlane Tranquilla, L., Regular, P., Ryan, P., Smith, P., & Wilhelm, S. (2012). Miniaturized data loggers and computer programming improve seabird risk and damage assessments for marine oil spills in Atlantic Canada. *Journal of Ocean Technology*, *7*, 41–58.

Rueda-Uribe, C., Lötberg, U., Ericsson, M., Tesson, S. V. M., & Åkesson, S. (2021). First tracking of declining Caspian terns Hydroprogne caspia breeding in the Baltic Sea reveals high migratory dispersion and disjunct annual ranges as obstacles to effective conservation. *Journal of Avian Biology*, *52*(9). https://doi.org/10.1111/jav.02743

doi:10.6342/NTU202303015

Runge, C. A., Watson, J. E. M., Butchart, S. H. M., Hanson, J. O., Possingham, H. P., & Fuller, R. A. (2015). Protected areas and global conservation of migratory birds. *Science (New York, N.Y.)*, *350*(6265), 1255–1258. https://doi.org/10.1126/science.aac9180

Runge, C., Martin, T., Possingham, H., Willis, S., & Fuller, R. (2014). Conserving mobile species. *Frontiers in Ecology and the Environment*, *12*(7), 395–402. https://doi.org/10.1890/130237

Sawyer, H., LeBeau, C. W., McDonald, T. L., Xu, W., & Middleton, A. D. (2019). All routes are not created equal: An ungulate's choice of migration route can influence its survival. *Journal of Applied Ecology*, *56*(8), 1860–1869. https://doi.org/10.1111/1365-2664.13445

Schmaljohann, H. (2018). Proximate mechanisms affecting seasonal differences in migration speed of avian species. *Scientific Reports*, *8*(1), Article 1. https://doi.org/10.1038/s41598-018-22421-7

Schmaljohann, H., & Eikenaar, C. (2017). How do energy stores and changes in these affect departure decisions by migratory birds? A critical view on stopover ecology studies and some future perspectives. *Journal of Comparative Physiology A*, *203*(6), 411–429. https://doi.org/10.1007/s00359-017-1166-8

Schmaljohann, H., Eikenaar, C., & Sapir, N. (2022). Understanding the ecological and evolutionary function of stopover in migrating birds. *Biological Reviews*, *97*(4), 1231–1252. https://doi.org/10.1111/brv.12839

Schuster, R., Wilson, S., Rodewald, A. D., Arcese, P., Fink, D., Auer, T., & Bennett, Joseph. R. (2019). Optimizing the conservation of migratory species over their full annual cycle. *Nature Communications*, *10*(1), 1754. https://doi.org/10.1038/s41467-019-09723-8

doi:10.6342/NTU202303015

Shaw, A. K. (2016). Drivers of animal migration and implications in changing environments. *Evolutionary Ecology*, *30*(6), 991–1007. https://doi.org/10.1007/s10682-016-9860-5

Shaw, A. K. (2020). Causes and consequences of individual variation in animal movement. *Movement Ecology*, *8*(1), 12. https://doi.org/10.1186/s40462-020-0197-x

Singh, N. J., & Milner-Gulland, E. J. (2011). Conserving a moving target: Planning protection for a migratory species as its distribution changes. *Journal of Applied Ecology*, *48*(1), 35–46. https://doi.org/10.1111/j.1365-2664.2010.01905.x

State Government of Victoria. (2019, September 17). *Waterways and catchments*. Victoria State Government. https://www.water.vic.gov.au/waterways-and-catchments/our-waterways/wetlands/migratory-shorebirds

Sternula albifrons (Little Tern)—Avibase. (2023, June). https://avibase.bsc-eoc.org/species.jsp?avibaseid=17310BF0FE9BAC8A

Studds, C. E., Kendall, B. E., Murray, N. J., Wilson, H. B., Rogers, D. I., Clemens, R. S., Gosbell, K., Hassell, C. J., Jessop, R., Melville, D. S., Milton, D. A., Minton, C. D. T., Possingham, H. P., Riegen, A. C., Straw, P., Woehler, E. J., & Fuller, R. A. (2017). Rapid population decline in migratory shorebirds relying on Yellow Sea tidal mudflats as stopover sites. *Nature Communications*, *8*(1), Article 1. https://doi.org/10.1038/ncomms14895

Surman, C., & Nicholson, L. W. (2009). A survey of the breeding seabirds and migratory shorebirds of the Houtman Abrolhos, Western Australia. *Corella*, *33*, 81–98.

Szabo, J. K., Choi, C.-Y., Clemens, R. S., & Hansen, B. (2016). Conservation without borders—Solutions to declines of migratory shorebirds in the East Asian—Australasian Flyway. *Emu - Austral Ornithology*, *116*(2), 215–221. https://doi.org/10.1071/MU15133

doi:10.6342/NTU202303015

Szabo, J. K., & Mundkur, T. (2017). *Conserving Wetlands for Migratory Waterbirds in South Asia* (B. A. K. Prusty, R. Chandra, & P. A. Azeez, Eds.; pp. 105–127). Springer India. https://doi.org/10.1007/978-81-322-3715-0_6

Taff, C. C., Freeman-Gallant, C. R., Streby, H. M., & Kramer, G. R. (2018). Geolocator deployment reduces return rate, alters selection, and impacts demography in a small songbird. *PloS One*, *13*(12), e0207783. https://doi.org/10.1371/journal.pone.0207783

Tankersley, R. D. (2004). Migration of birds as an indicator of broad-scale environmental condition. *Environmental Monitoring and Assessment*, *94*(1–3), 55–67.

The Taipei Times. (2012, November). *Bird from Taiwan spotted in Queensland, Australia*. The Taipei Times. https://www.taipeitimes.com/News/taiwan/archives/2012/11/18/2003547997

Velmala, W., Helle, S., Ahola, M. P., Klaassen, M., Lehikoinen, E., Rainio, K., Sirkiä, P. M., & Laaksonen, T. (2015). Natural selection for earlier male arrival to breeding grounds through direct and indirect effects in a migratory songbird. *Ecology and Evolution*, *5*(6), 1205–1213. https://doi.org/10.1002/ece3.1423

Viljoen, G. J., Luckins, A. G., & Naletoski, I. (2016). Animal Migration Tracking Methods. In G. J. Viljoen, A. G. Luckins, & I. Naletoski (Eds.), *Stable Isotopes to Trace Migratory Birds and to Identify Harmful Diseases: An Introductory Guide* (pp. 11–33). Springer International Publishing. https://doi.org/10.1007/978-3-319-28298-5_2

Warnock, N. (2010). Stopping vs. staging: The difference between a hop and a jump. *Journal of Avian Biology*, *41*, 621–626. https://doi.org/10.1111/j.1600-048X.2010.05155.x

Yong, D. L., Jain, A., Liu, Y., Iqbal, M., Choi, C.-Y., Crockford, N. J., Millington, S., & Provencher, J. (2018). Challenges and opportunities for transboundary conservation of

doi:10.6342/NTU202303015

migratory birds in the East Asian-Australasian flyway. *Conservation Biology*, *32*(3), 740–743. https://doi.org/10.1111/cobi.13041

Yong, D. L., Kee, J. Y., Aung, P. P., Jain, A., Yeap, C.-A., Au, N. J., Jearwattanakanok, A., Lim, K. K., Yu, Y.-T., Fu, V. W. K., Insua-Cao, P., Sawa, Y., Crosby, M., Chan, S., & Crockford, N. J. (2022). Conserving migratory waterbirds and the coastal zone: The future of South-east Asia's intertidal wetlands. *Oryx*, *56*(2), 176–183. Cambridge Core. https://doi.org/10.1017/S0030605320001374

Zimova, M., Willard, D. E., Winger, B. M., & Weeks, B. C. (2021). Widespread shifts in bird migration phenology are decoupled from parallel shifts in morphology. *Journal of Animal Ecology*, *90*(10), 2348–2361. https://doi.org/10.1111/1365-2656.13543

Zöckler, C. (2005). Migratory Bird Species as Indicators for the state of the environment. *Biodiversity*, *6*. https://doi.org/10.1080/14888386.2005.9712769

doi:10.6342/NTU202303015

Appendix

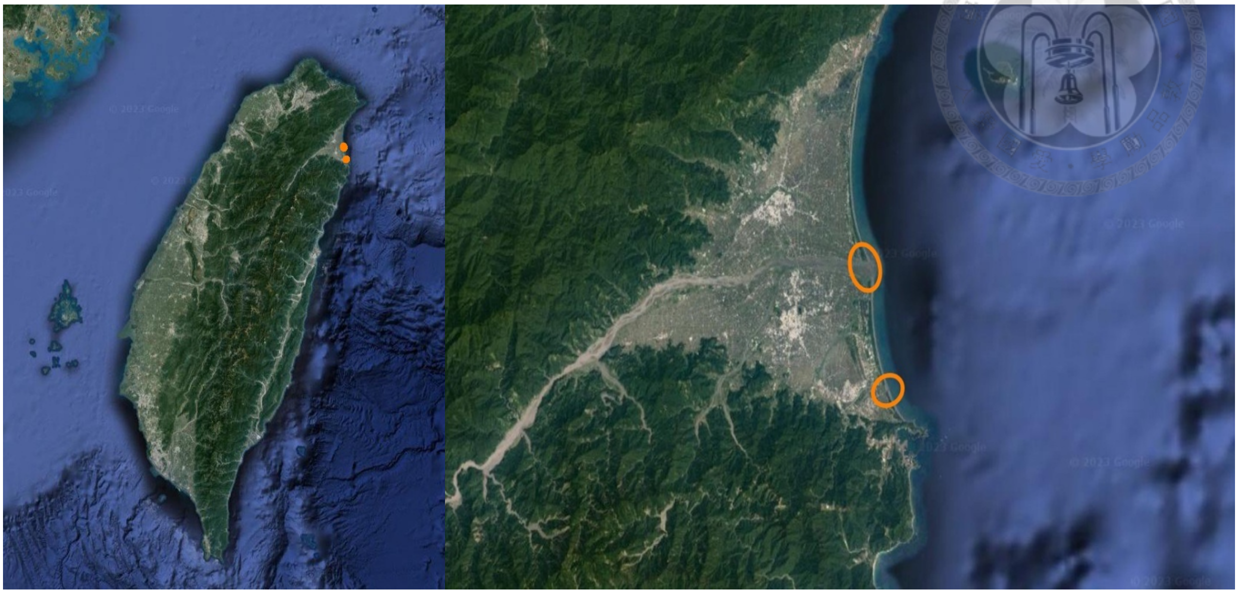

Figure 1. Map of Taiwan displaying two breeding grounds in Yilan County used as sampling locations for the 18 Little tern individuals that were trapped and tagged including: Lanyang Estuary (24.709970, 121.833073), and Xincheng Estuary (24.632,121.849314) created using QGIS v. 3.30.3.

doi:10.6342/NTU202303015

Table 1. Identification Numbers and Model Details of geolocator loggers recovered in Yilan county, along with dates of application and recovery.1 geolocator was recovered in the 2014 breeding period and 4 were recovered in the 2017 breeding period.

Logger ID	*Brand*	*Location*	*Model*	*Application Time*	*Retrieval Time*
G01	Bio track	Lanyang estuary	MK5090	2013-6-29	2014-06-07
V409	Migrate Technology	Xincheng estuary	Intigeo-P65	2016-06-21	2017-06-06
V410	Migrate Technology	Xincheng estuary	Intigeo-P65	2016-06-21	2017-06-06
V412	Migrate Technology	Lanyang estuary	Intigeo-P65	2016-07-03	2017-05-30
V413	Migrate Technology	Lanyang estuary	Intigeo-P65	2016-07-03	2017-05-30

doi:10.6342/NTU202303015

Figure 1. Retrieved geolocator V409. Picture on the left displays anterior view and picture on the right displays posterior view.

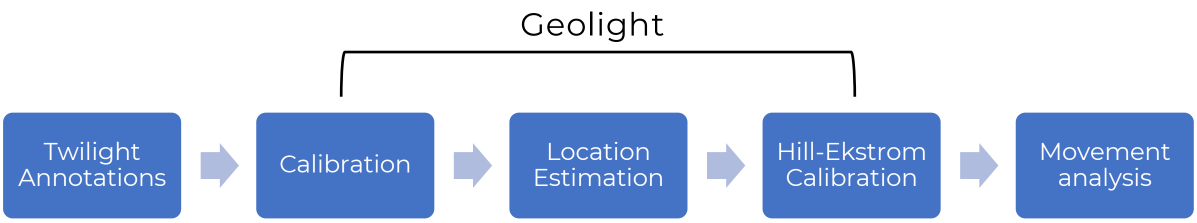

Figure 2. Flow chart displaying key steps in the methodology applied for the Threshold methods to analyze the light level data obtained from the geolocator loggers.

doi:10.6342/NTU202303015

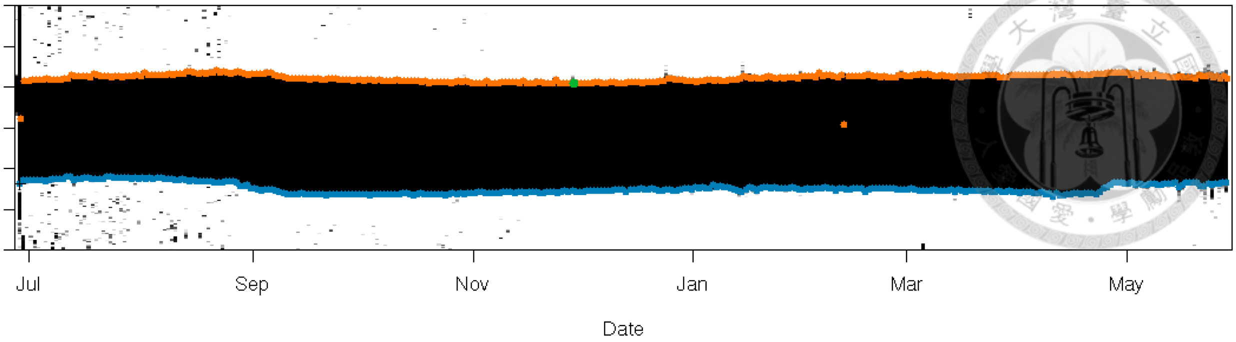

Figure 3. Twilight annotations after removing false twilights, displaying sunrises in orange and sunsets in blue over the course of eleven months in 2013 according to light level data obtained from G01 geolocator logger.

doi:10.6342/NTU202303015

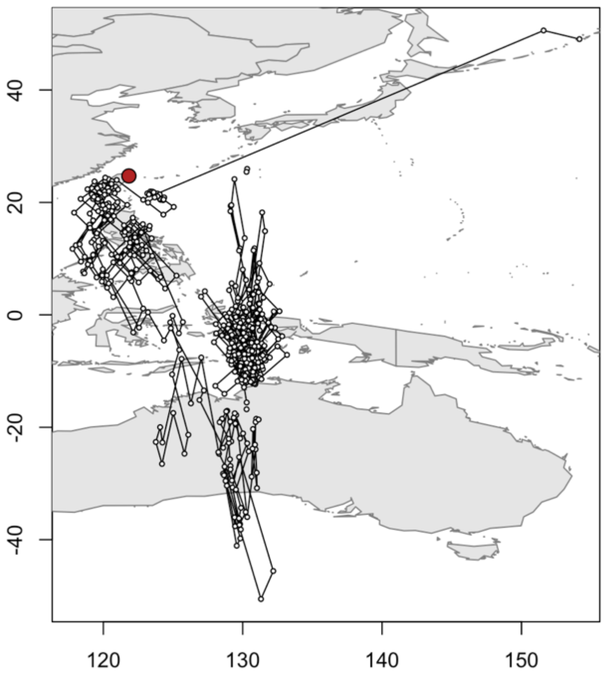

Figure 4. Estimated movement of G01 obtained following the execution of the twilight annotations *of light level data.*

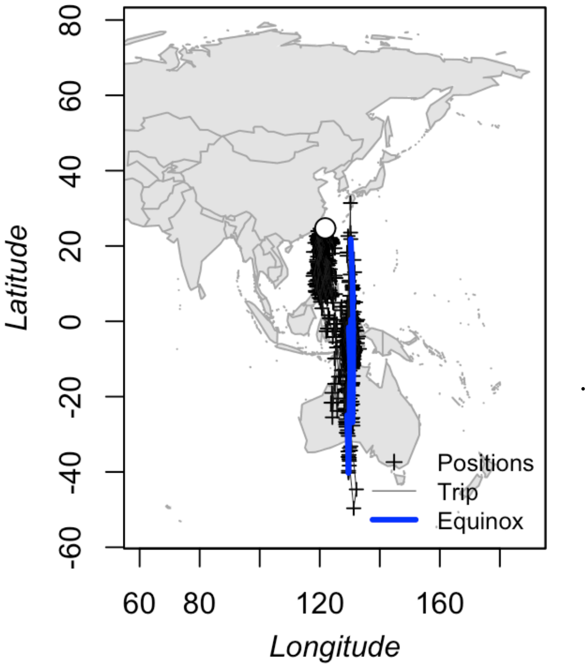

Figure 5. Estimated movement of G01 following the first round of calibrations and location estimations of light level data.

doi:10.6342/NTU202303015

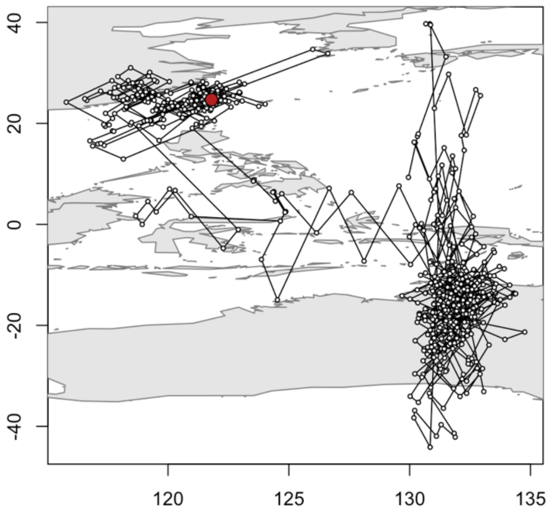

Figure 6. Estimated movement of V409 obtained following the execution of the twilight annotations of light level data.

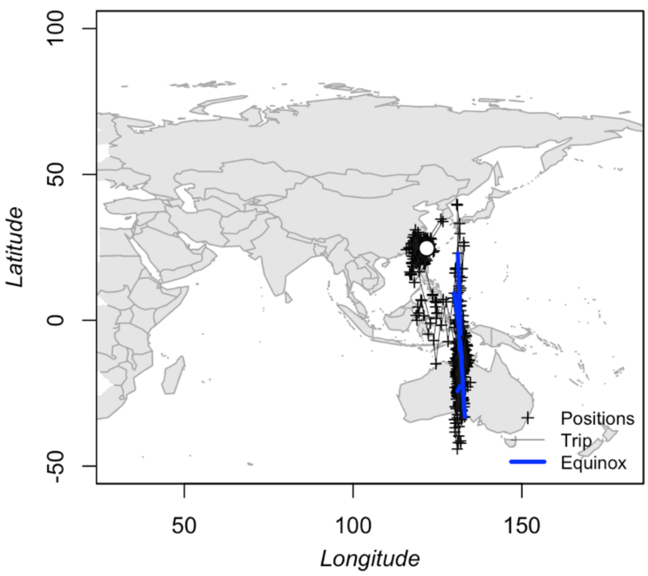

Figure 7. Estimated movement of V409 following the first round of calibrations and location estimations of light level data.

doi:10.6342/NTU202303015

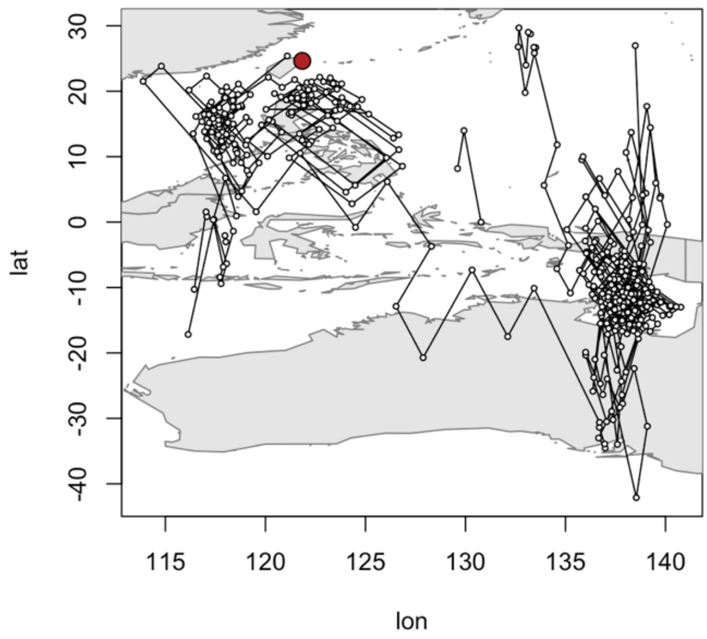

Figure 8. Estimated movement of V410 obtained following the execution of the twilight annotations of light level data.

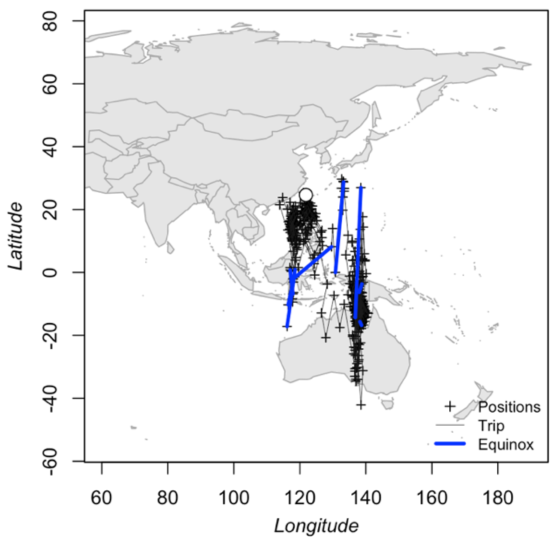

Figure 9. Estimated movement of V410 following the first round of calibrations and location estimations of light level data.

doi:10.6342/NTU202303015

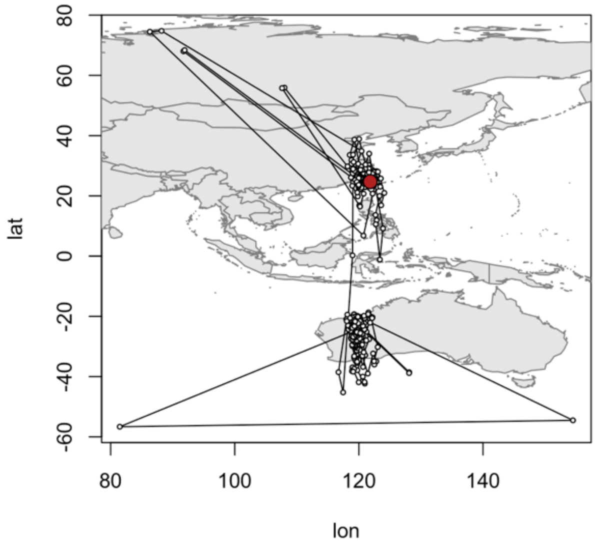

Figure 10. Estimated movement of V412 obtained following the execution of the twilight annotations of light level data.

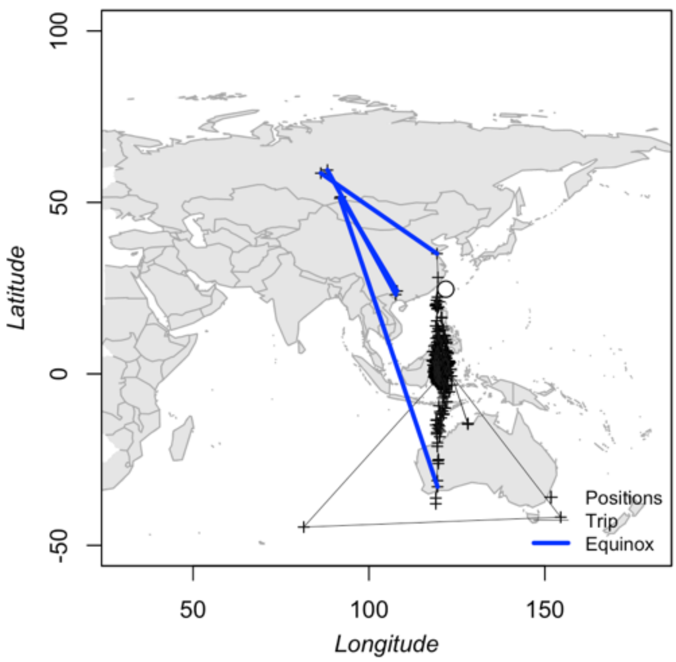

Figure 11. Estimated movement of V412 following the first round of calibrations and location estimations of light level data.

doi:10.6342/NTU202303015

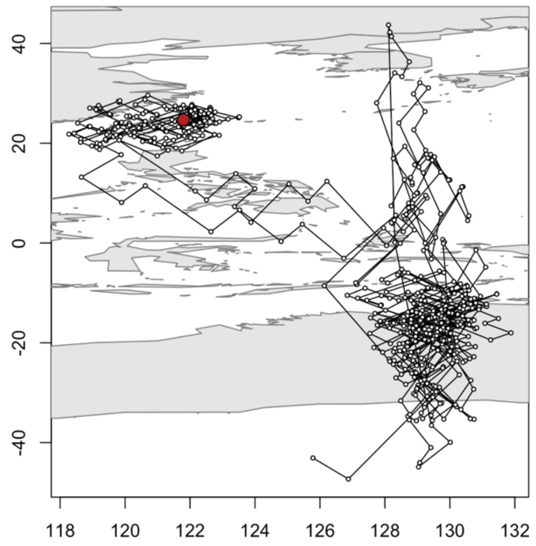

Figure 12. Estimated movement of V413 obtained following the execution of the twilight annotations of light level data.

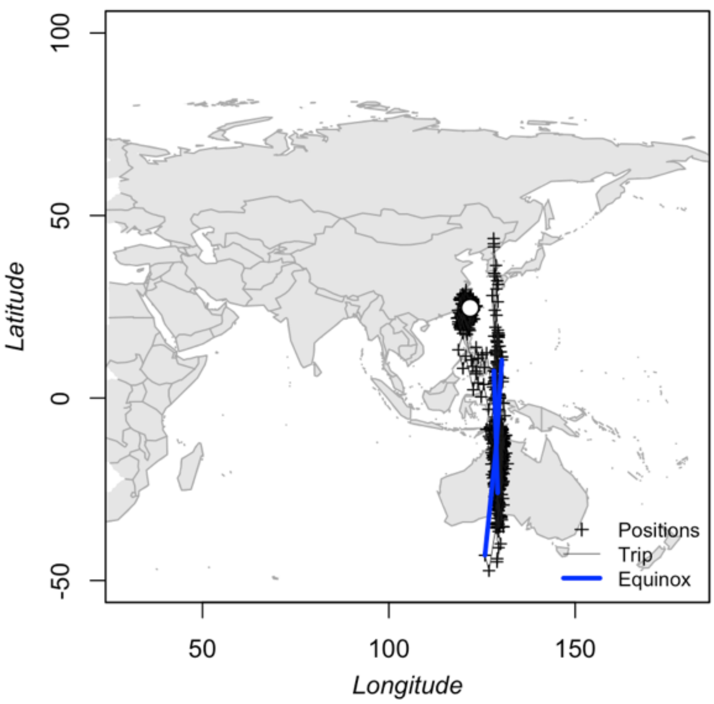

Figure 13. Estimated movement of V413 following the first round of calibrations and location estimations of light level data.

doi:10.6342/NTU202303015

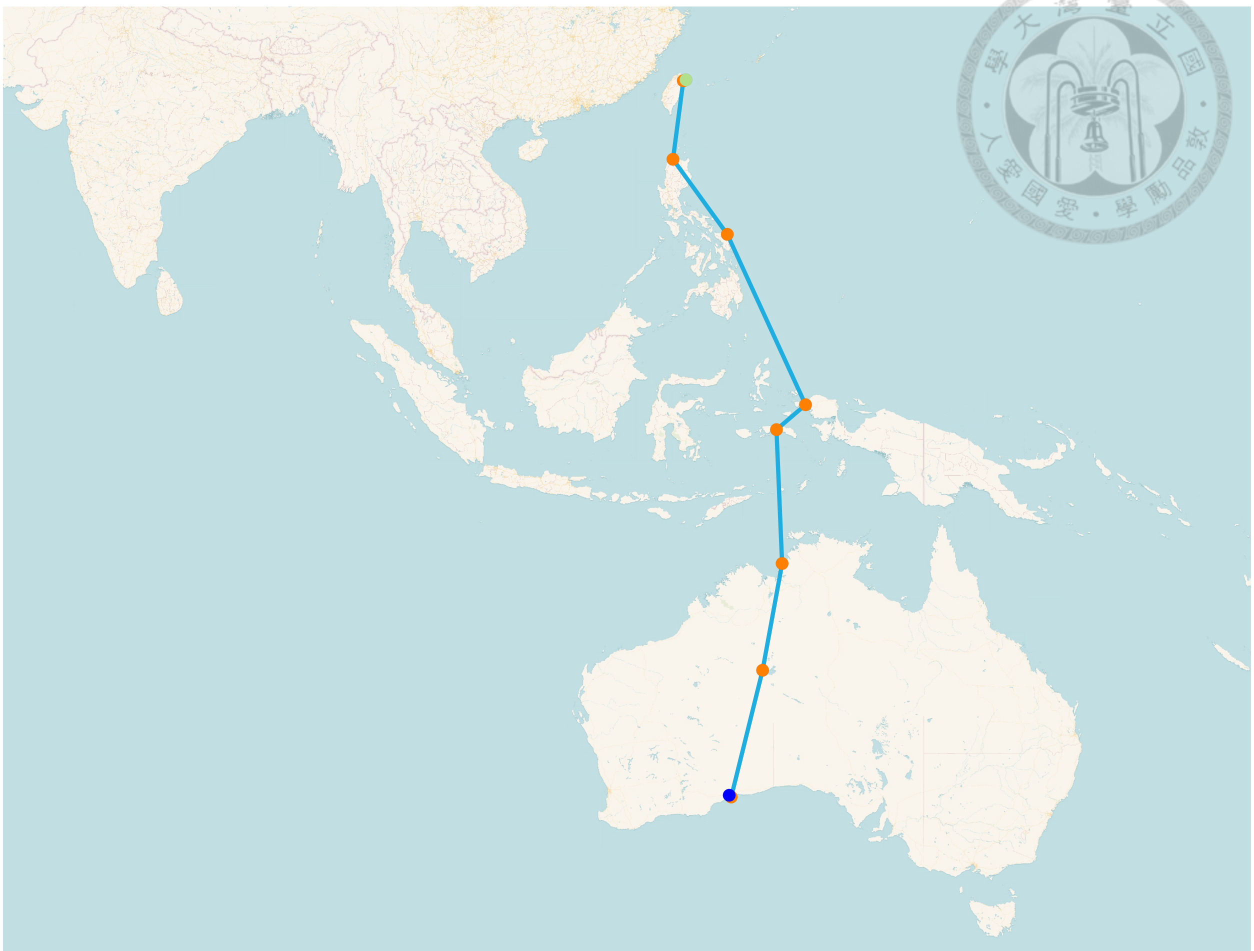

Figure 14. The southbound migration of the Little tern G01 displayed using the locations generated from the movement analysis. This movement commences in the breeding grounds in Taiwan and concludes in the nonbreeding grounds in Australia, according to analyzed light level geolocator data. The light green dot displays the breeding grounds, orange dots display stopover locations, and the blue dot displays the terminal stop at the nonbreeding grounds.

doi:10.6342/NTU202303015

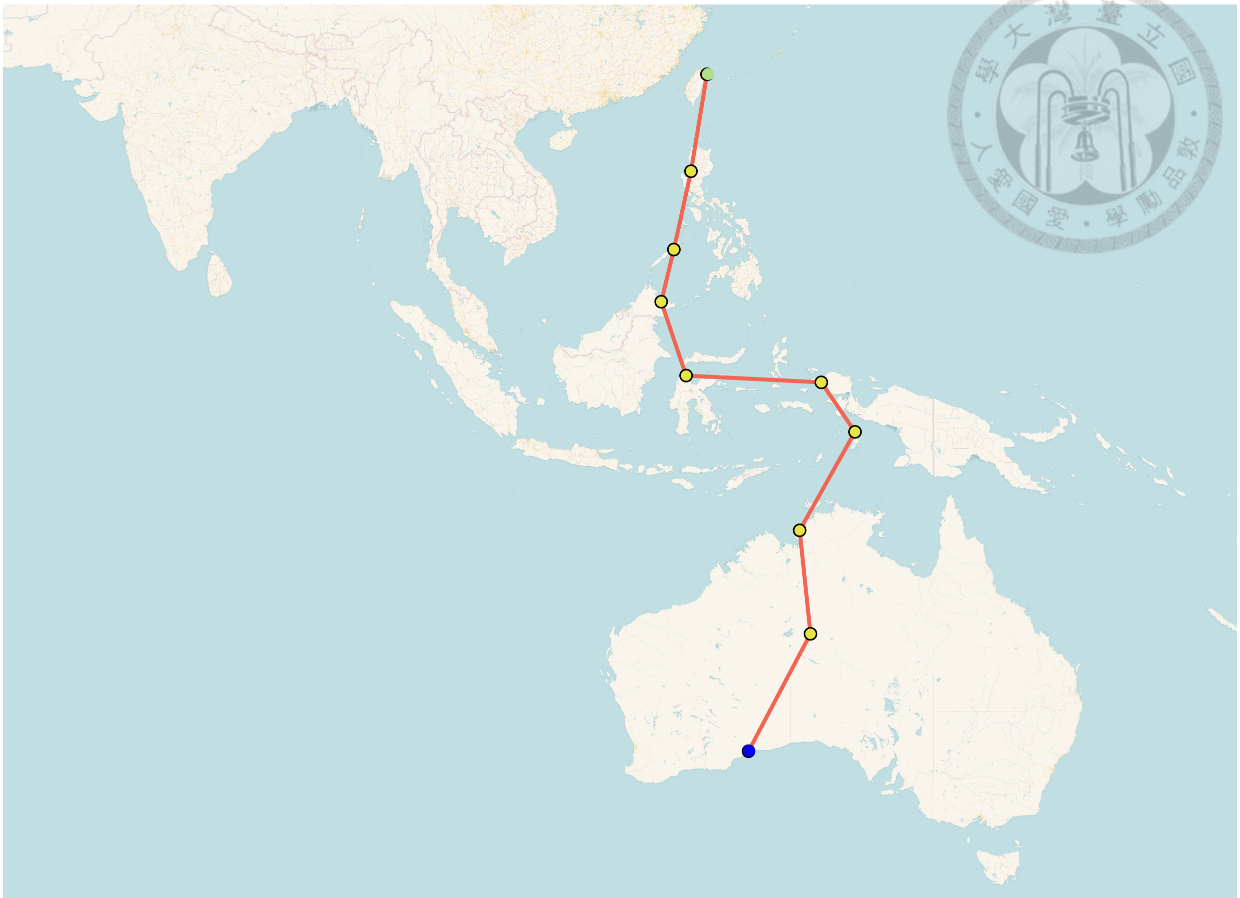

Figure 15. The northbound migration of the Little tern G01 displayed using the locations generated from the movement analysis. This movement commences nonbreeding grounds in Australia and concludes in the breeding grounds in Taiwan, according to analyzed light level geolocator data. The light green dot displays the breeding grounds, yellow dots display stopover locations, and blue dot displays the terminal stop at the breeding grounds.

doi:10.6342/NTU202303015

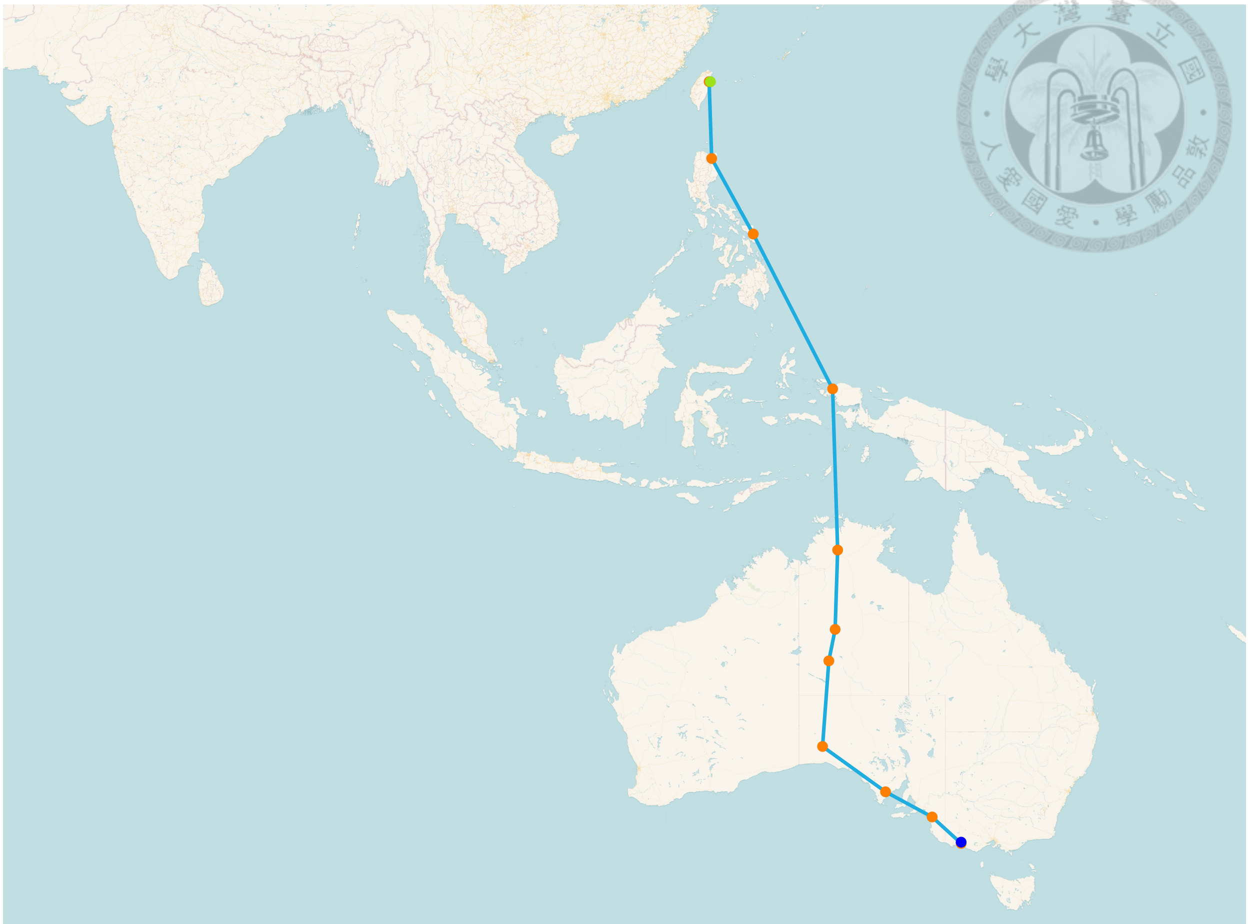

Figure 16. The southbound migration of the Little tern V409 displayed using the locations generated from the movement analysis. This movement commences in the breeding grounds in Taiwan and concludes in the nonbreeding grounds in Australia, according to analyzed light level geolocator data. The light green dot displays the breeding grounds, orange dots display stopover locations, and the blue dot displays the terminal stop at the nonbreeding grounds.

doi:10.6342/NTU202303015

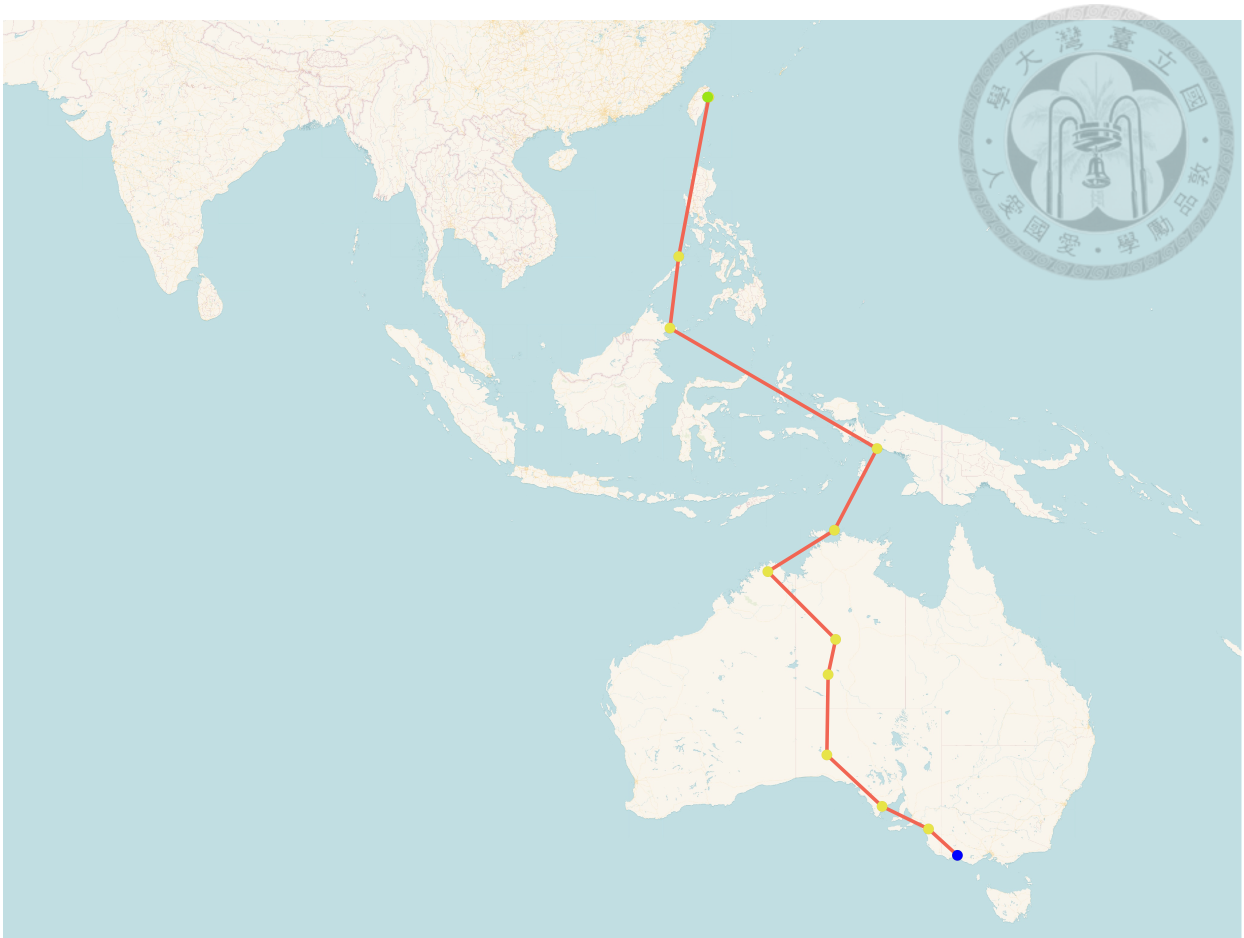

Figure 17. The northbound migration of the Little tern V409 displayed using the locations generated from the movement analysis. This movement commences nonbreeding grounds in Australia and concludes in the breeding grounds in Taiwan, according to analyzed light level geolocator data. The light green dot displays the breeding grounds, yellow dots display stopover locations, and blue dot displays the terminal stop at the breeding grounds.

doi:10.6342/NTU202303015

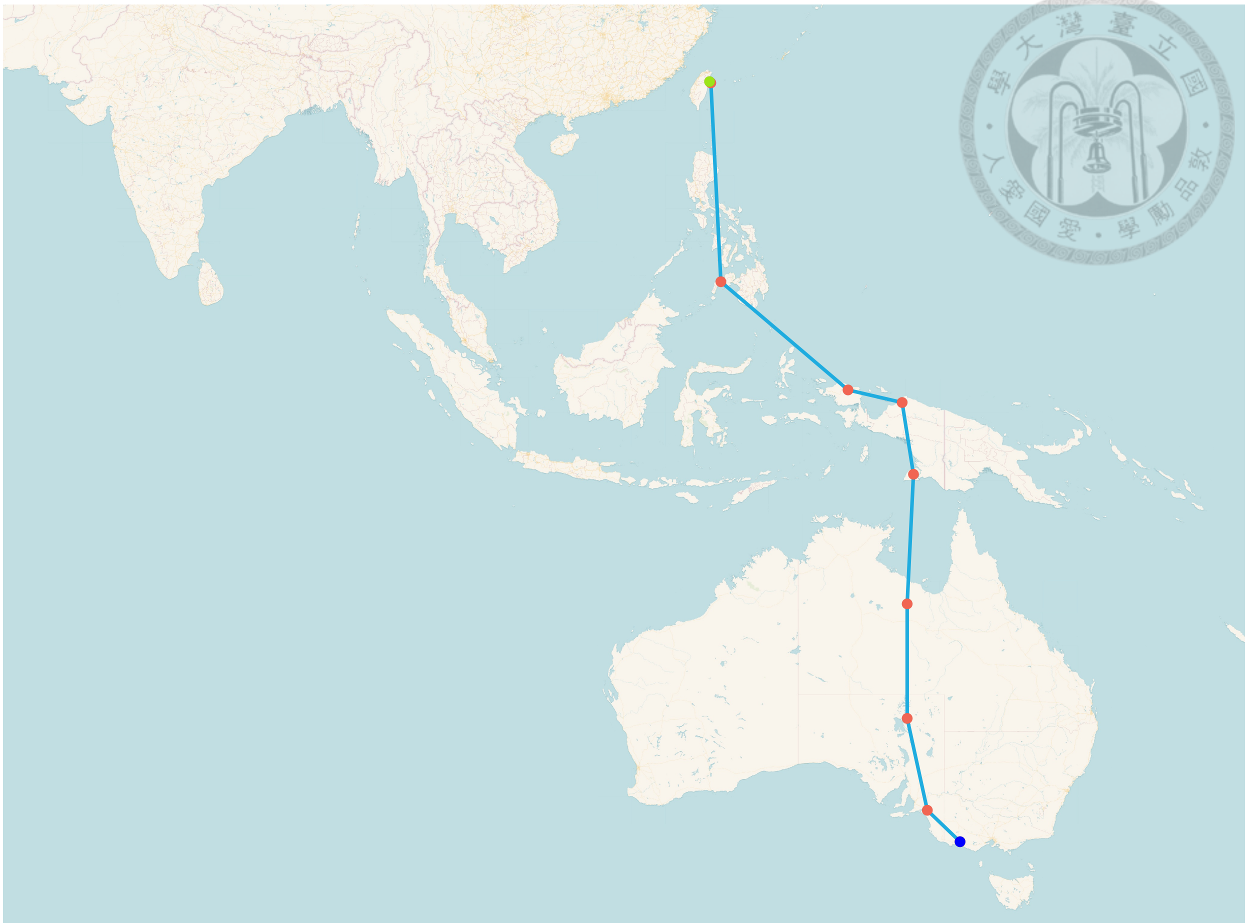

Figure 18. The southbound migration of the Little tern V410 displayed using the locations generated from the movement analysis. This movement commences in the breeding grounds in Taiwan and concludes in the nonbreeding grounds in Australia, according to analyzed light level geolocator data. The light green dot displays the breeding grounds, orange dots display stopover locations, and the blue dot displays the terminal stop at the nonbreeding grounds.

doi:10.6342/NTU202303015

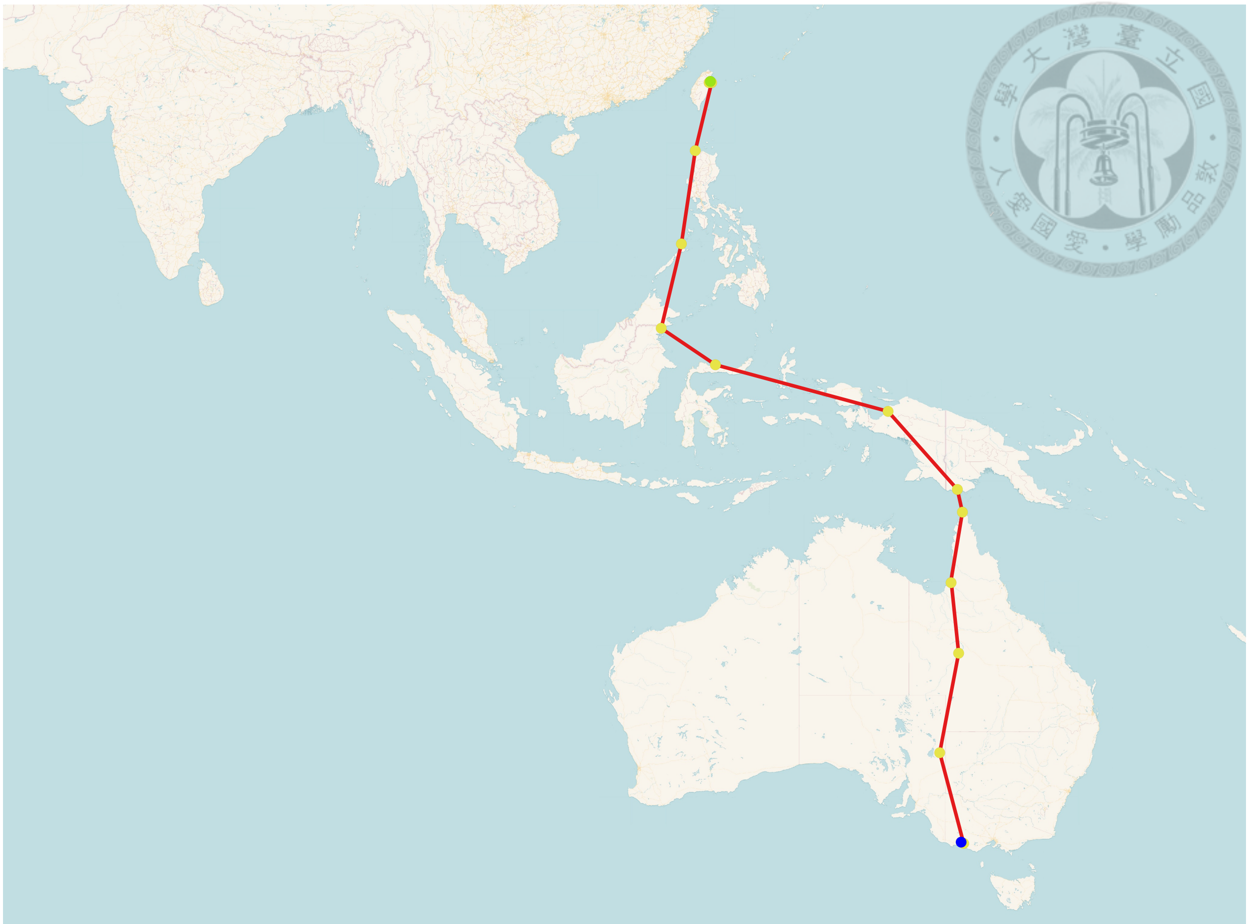

Figure 19. The northbound migration of the Little tern V410 displayed using the locations generated from the movement analysis. This movement commences nonbreeding grounds in Australia and concludes in the breeding grounds in Taiwan, according to analyzed light level geolocator data. The light green dot displays the breeding grounds, yellow dots display stopover locations, and blue dot displays the terminal stop at the breeding grounds.

doi:10.6342/NTU202303015

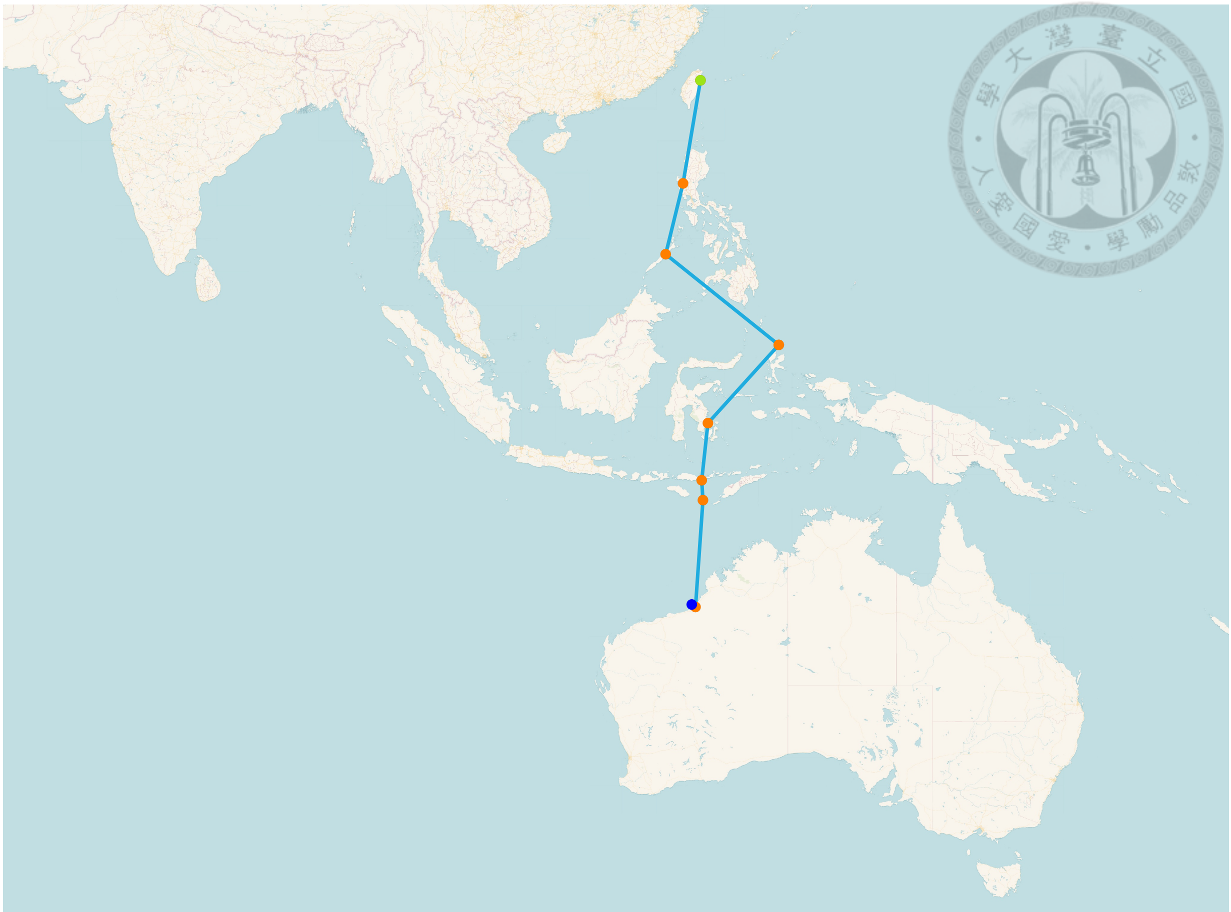

Figure 20. The southbound migration of the Little tern V412 displayed using the locations generated from the movement analysis. This movement commences in the breeding grounds in Taiwan and concludes in the nonbreeding grounds in Australia, according to analyzed light level geolocator data. The light green dot displays the breeding grounds, orange dots display stopover locations, and the blue dot displays the terminal stop at the nonbreeding grounds.

doi:10.6342/NTU202303015

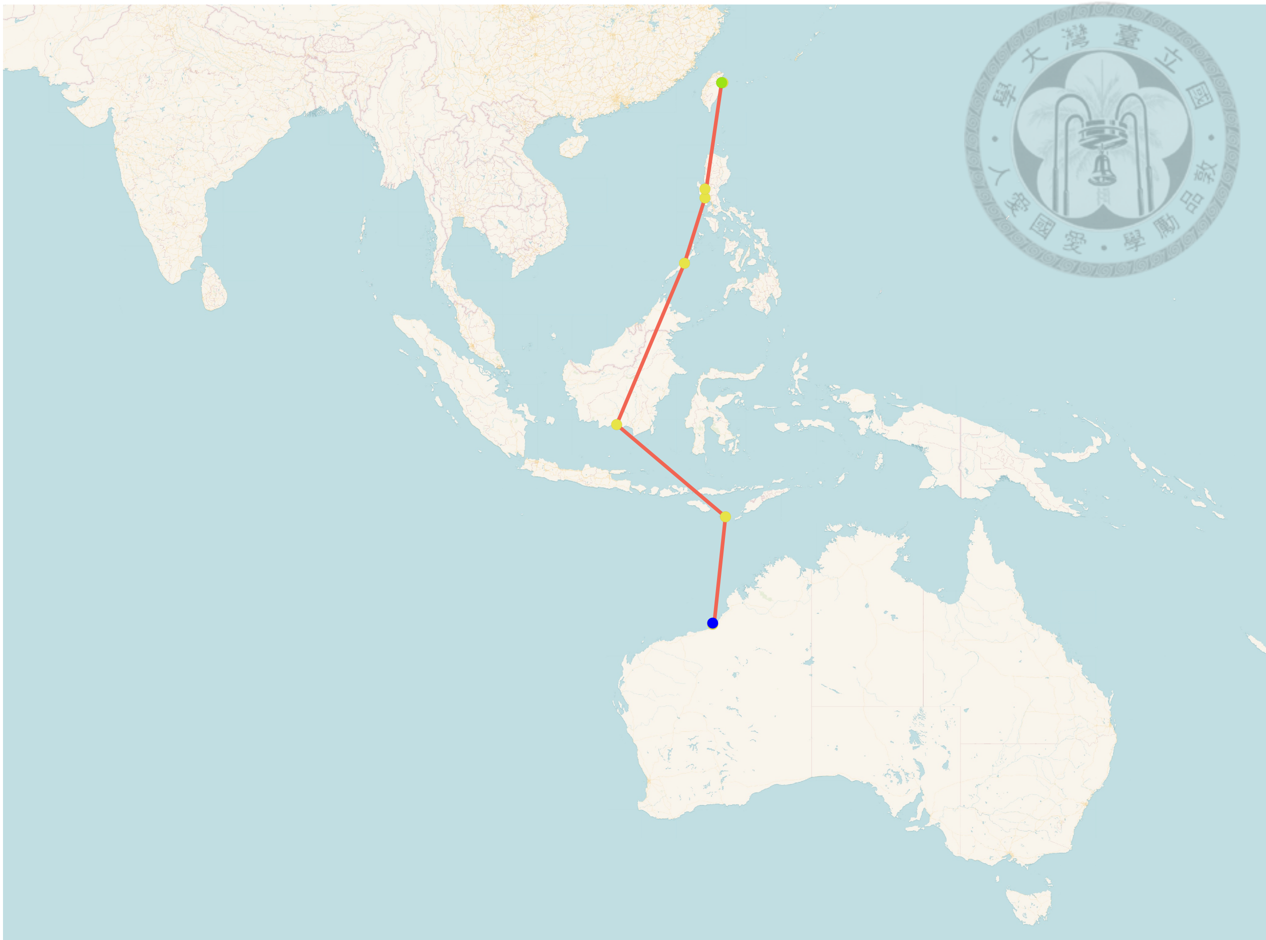

Figure 21. The northbound migration of the Little tern V412 displayed using the locations generated from the movement analysis. This movement commences nonbreeding grounds in Australia and concludes in the breeding grounds in Taiwan, according to analyzed light level geolocator data. The light green dot displays the breeding grounds, yellow dots display stopover locations, and blue dot displays the terminal stop at the breeding grounds.

doi:10.6342/NTU202303015

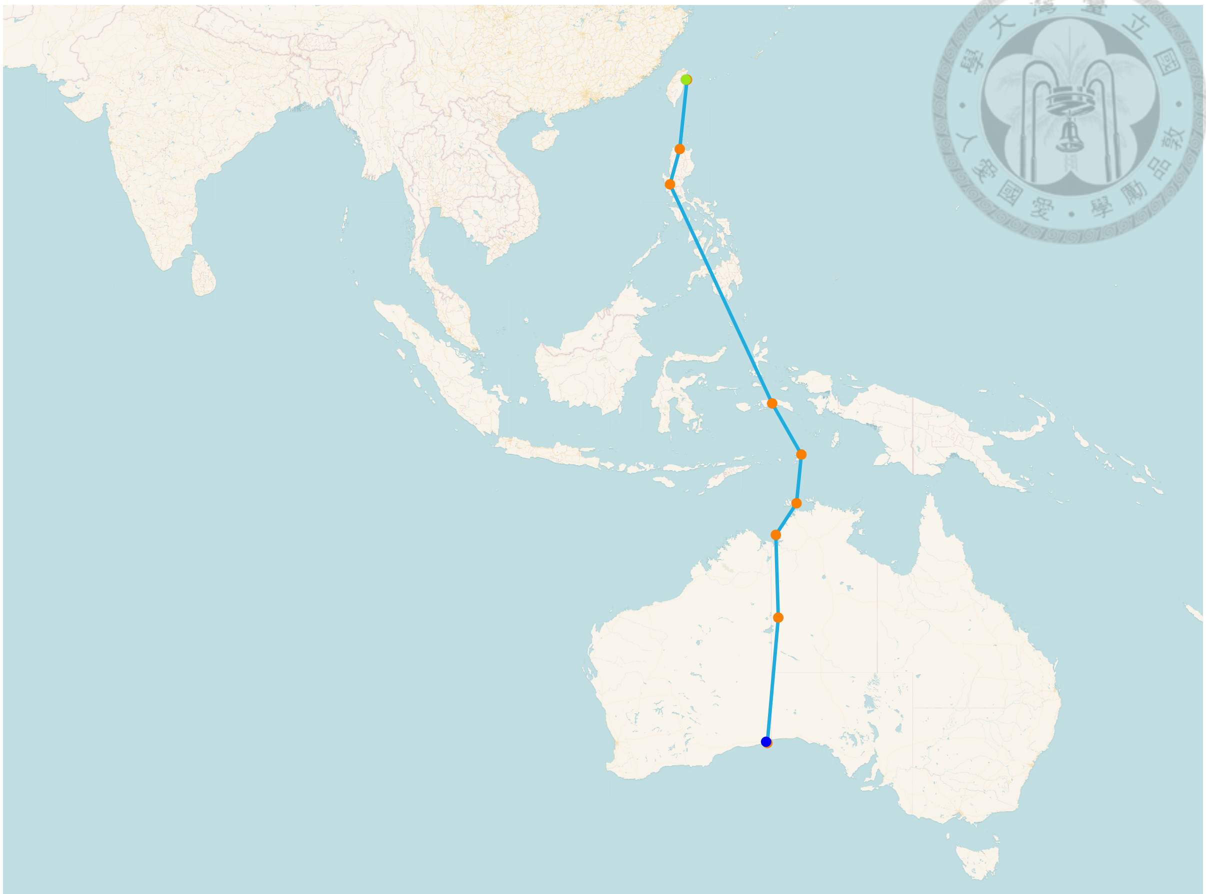

Figure 22. The southbound migration of the Little tern V413 displayed using the locations generated from the movement analysis. This movement commences in the breeding grounds in Taiwan and concludes in the nonbreeding grounds in Australia, according to analyzed light level geolocator data. The light green dot displays the breeding grounds, orange dots display stopover locations, and the blue dot displays the terminal stop at the nonbreeding grounds.

doi:10.6342/NTU202303015

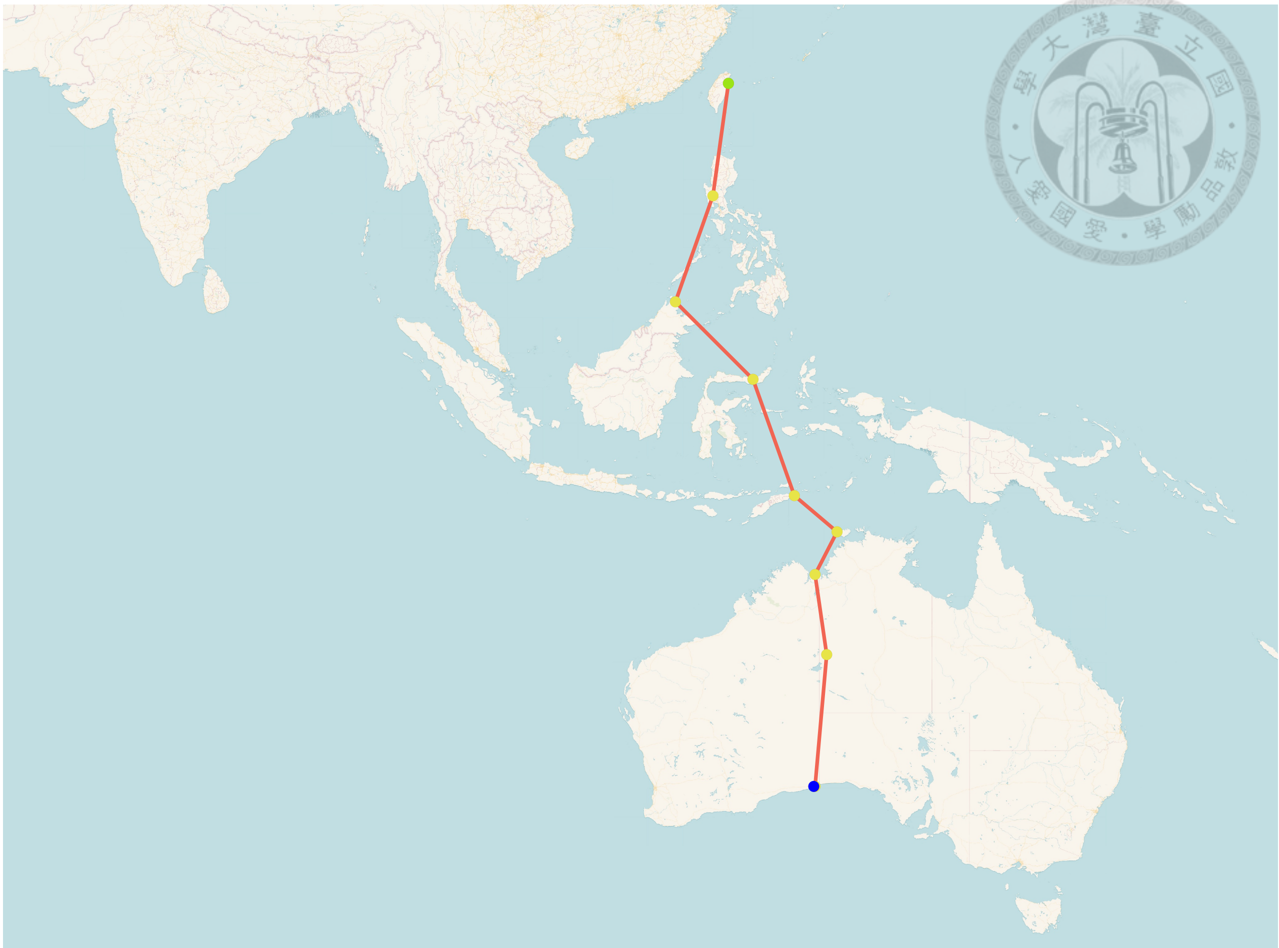

Figure 23. The northbound migration of the Little tern V413 displayed using the locations generated from the movement analysis. This movement commences nonbreeding grounds in Australia and concludes in the breeding grounds in Taiwan, according to analyzed light level geolocator data. The light green dot displays the breeding grounds, yellow dots display stopover locations, and blue dot displays the terminal stop at the breeding grounds.

doi:10.6342/NTU202303015

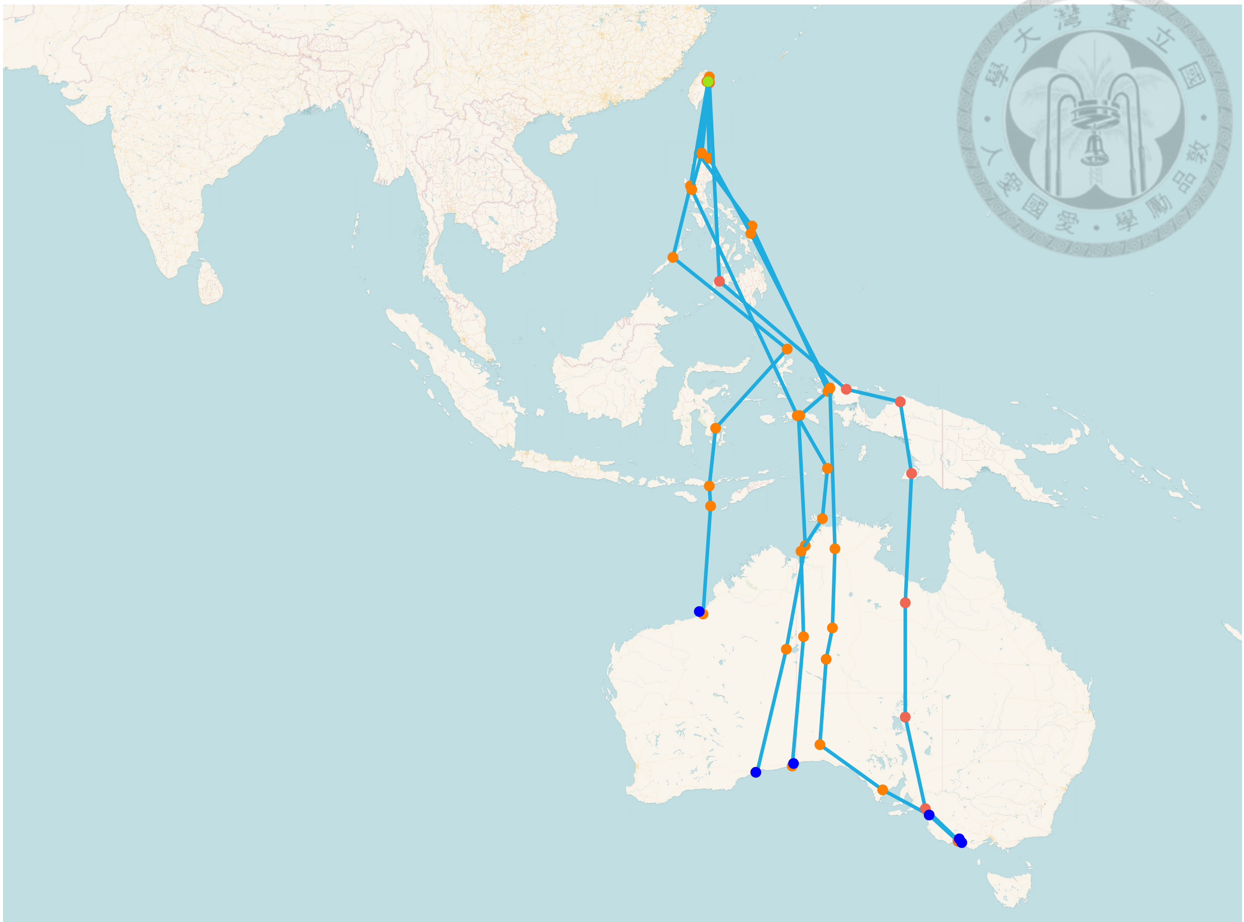

Figure 24. The southbound migration of the tagged Little terns (G01, V409, V410, V412, V413) traveling between the breeding grounds in Taiwan to the non-breeding grounds in Australia according to analyzed light level geolocator data. Green dots display the breeding area, orange dots display stopover locations in Southeast Asia and Northern Australia, and blue dots display nonbreeding grounds.

doi:10.6342/NTU202303015

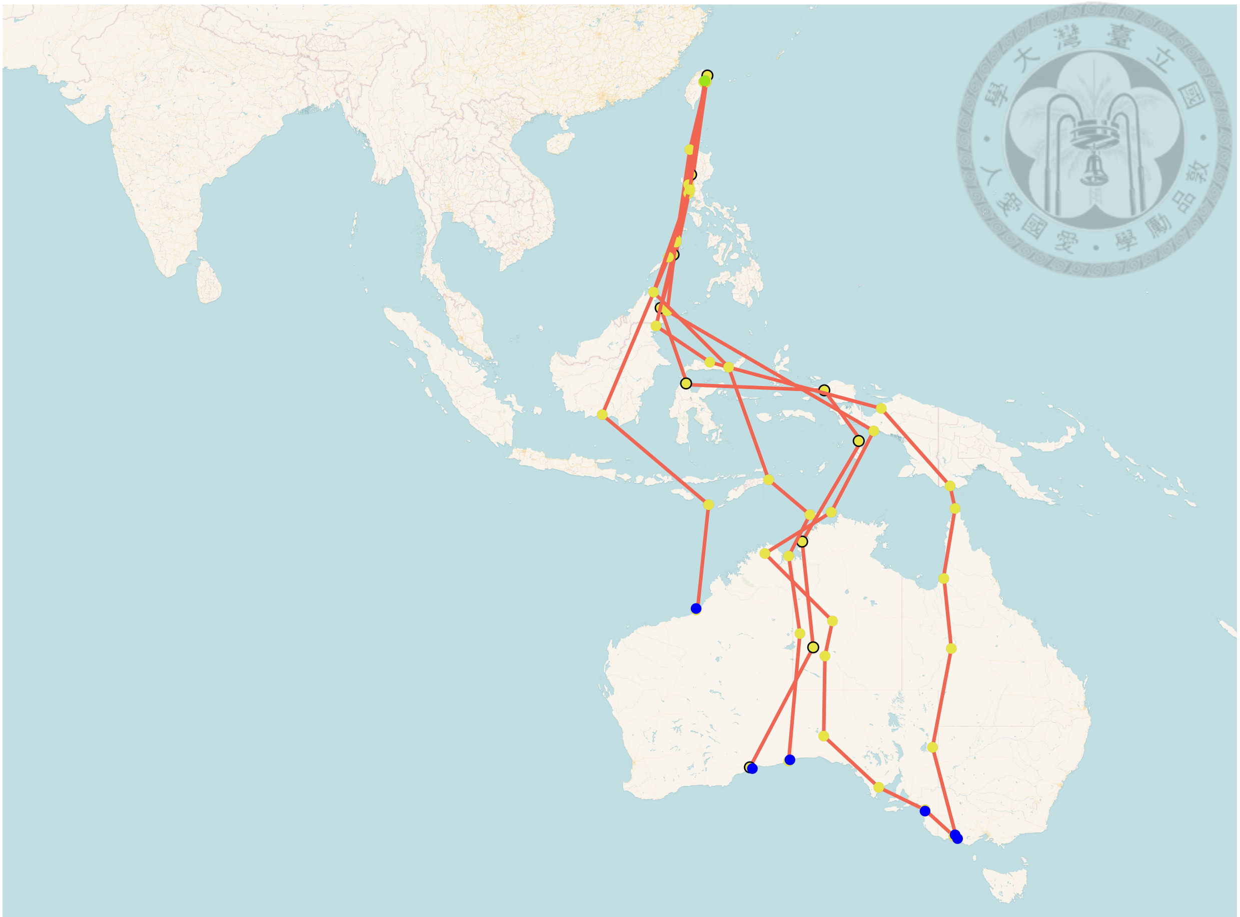

Figure 25. The northbound migration of the tagged Little terns *(G01, V409, V410, V412, V413) traveling* between the nonbreeding grounds in Australia to the breeding grounds in Taiwan according to analyzed light level geolocator data. Green dots display the breeding grounds, yellow dots display stopover locations in Southeast Asia and Northern Australia, and blue dots display nonbreeding grounds.

doi:10.6342/NTU202303015

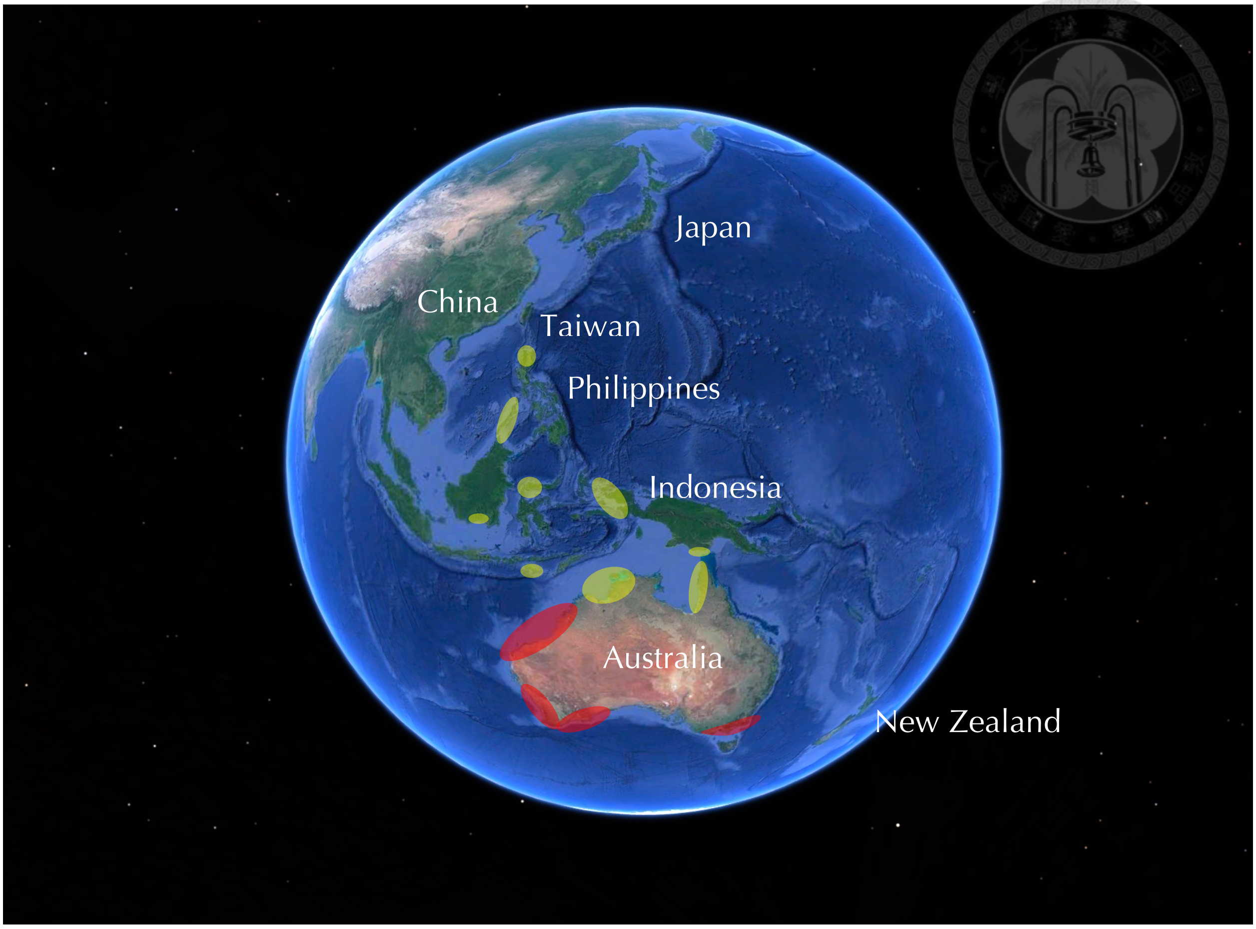

Figure 26. Map of the East-Asian Australasian region highlighting the major locations of interest for the five tracked Little tern individuals utilized during the annual cycles of 2013-2014 period (n = 1) and 2016-2017 period (n = 4). Yellow illustrates the stopover locations in The Philippines, Indonesia, and Northern Australia, and red illustrates the non-breeding grounds.

doi:10.6342/NTU202303015

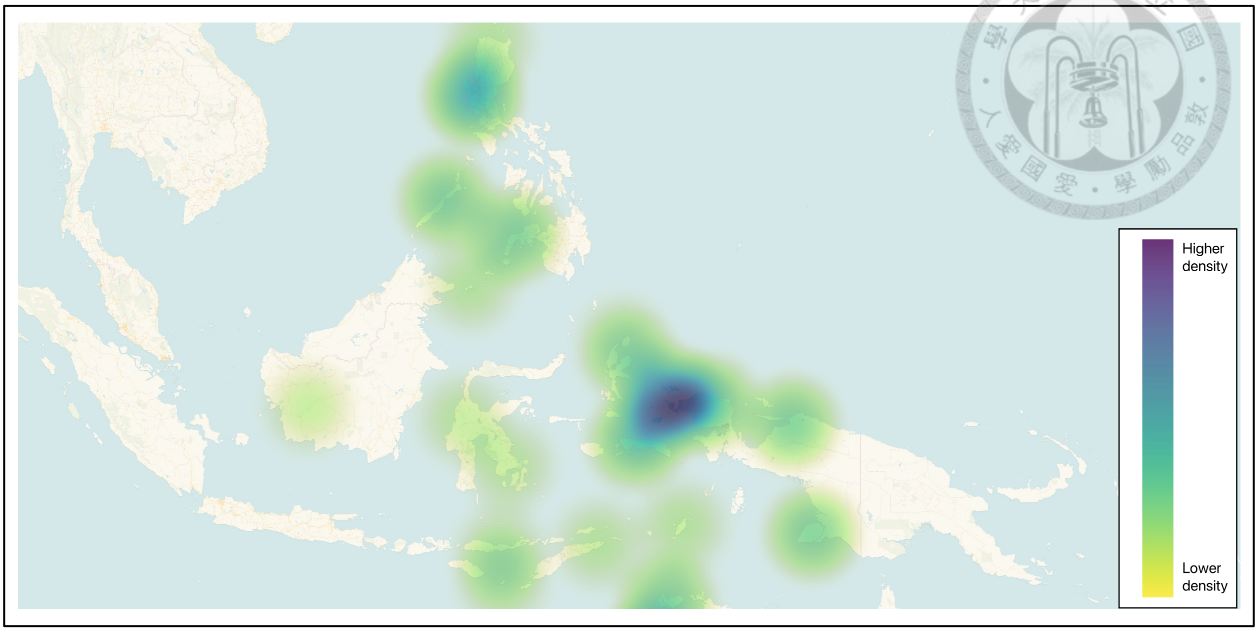

Figure 27. Regions of Southeast Asia utilized as stopover locations for the five tracked Little tern individuals utilized during the annual cycles of 2013-2014 period (n = 1) and 2016-2017 period (n = 4). The birds primarily visited the Philippines and Indonesia.

doi:10.6342/NTU202303015

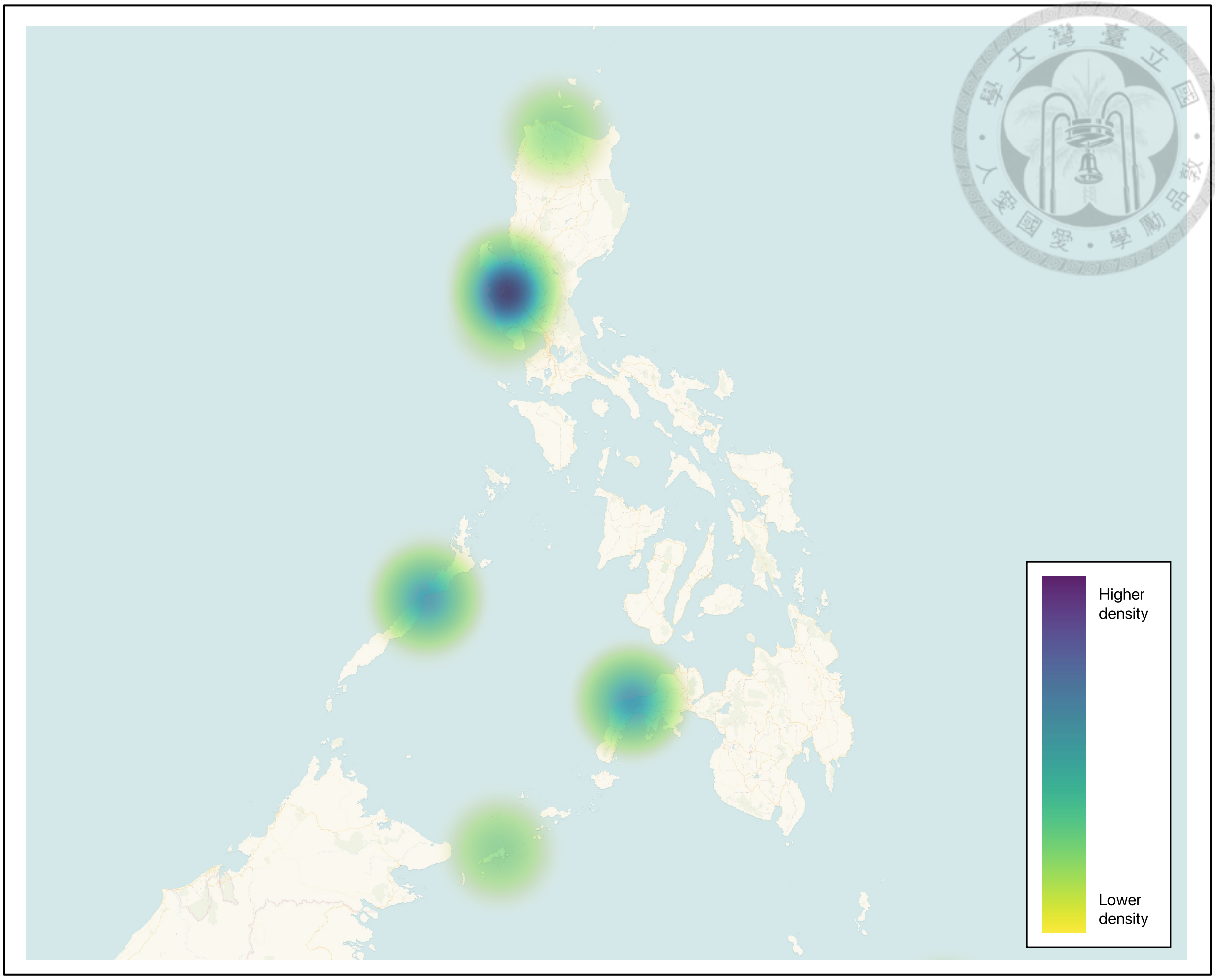

Figure 28. Regions of the Philippines utilized as stopover locations for the five tracked Little tern individuals utilized during the annual cycles of 2013-2014 period (n = 1) and 2016-2017 period (n = 4).

doi:10.6342/NTU202303015

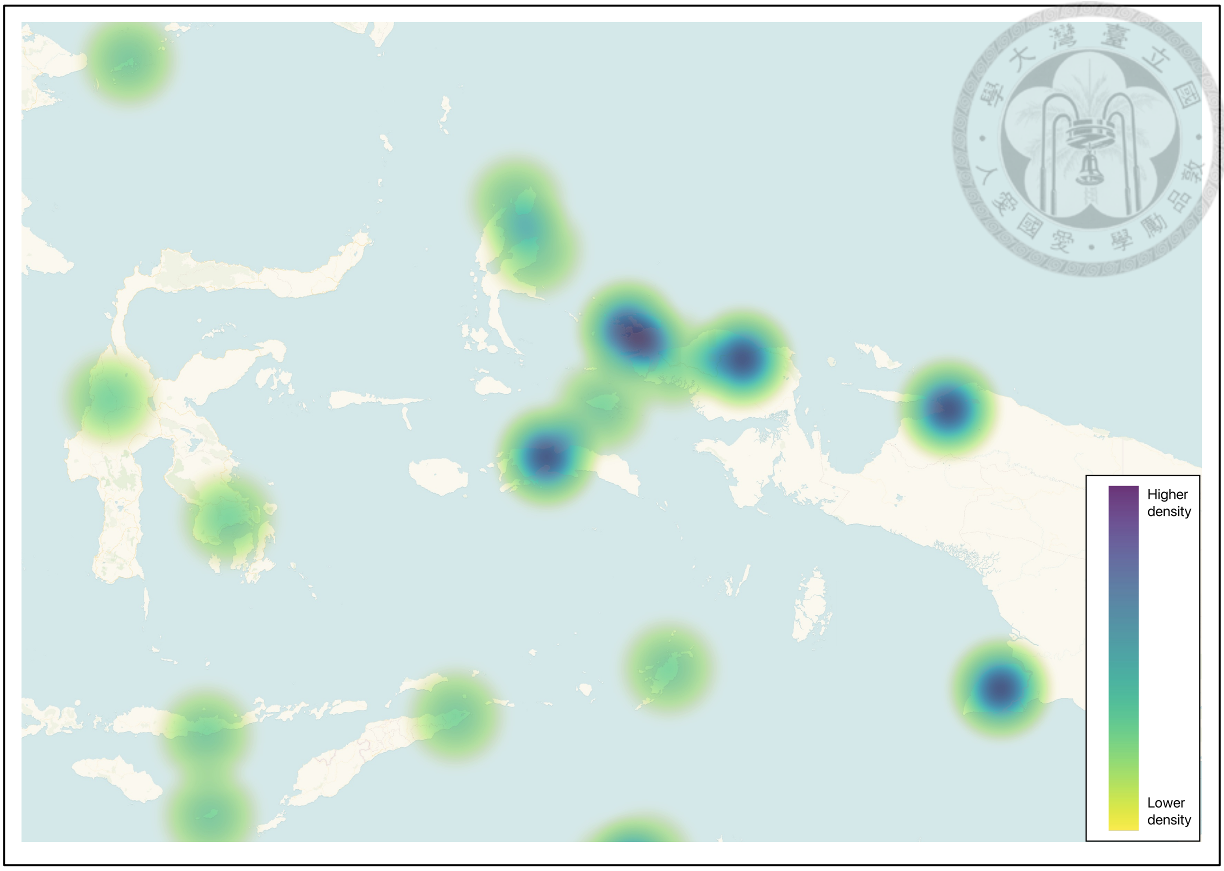

Figure 29. Regions of Indonesia utilized as stopover locations for the five tracked Little tern individuals utilized during the annual cycles of 2013-2014 period (n = 1) and 2016-2017 period (n = 4).

doi:10.6342/NTU202303015

Table 2. Migration phenology: mean timing of arrival at nonbreeding and breeding grounds, duration at nonbreeding grounds, and migration timing for the Little tern individuals from the breeding population in northeastern Taiwan in Yilan County along the *average* 5,614 km trajectory.

	Mean ±	Range
Commence south migration	August 4th	July 14th – August 25th
Duration of south migration	± 48 days	34 – 67 days
Stopover time	± 18 days	8 – 29 days
Arrive at non-breeding location	September 23rd	September 4th – October 13th
Duration at non-breeding location	± 170 days	91 – 212 days
Commence north migration	February 23rd	January 3rd- April 15th
Duration of north migration	± 34 days	28 – 45 days
Stopover time	± 11 days	4 – 22 days
Arrival at breeding grounds	March 23rd	February 2nd - May 12th

doi:10.6342/NTU202303015

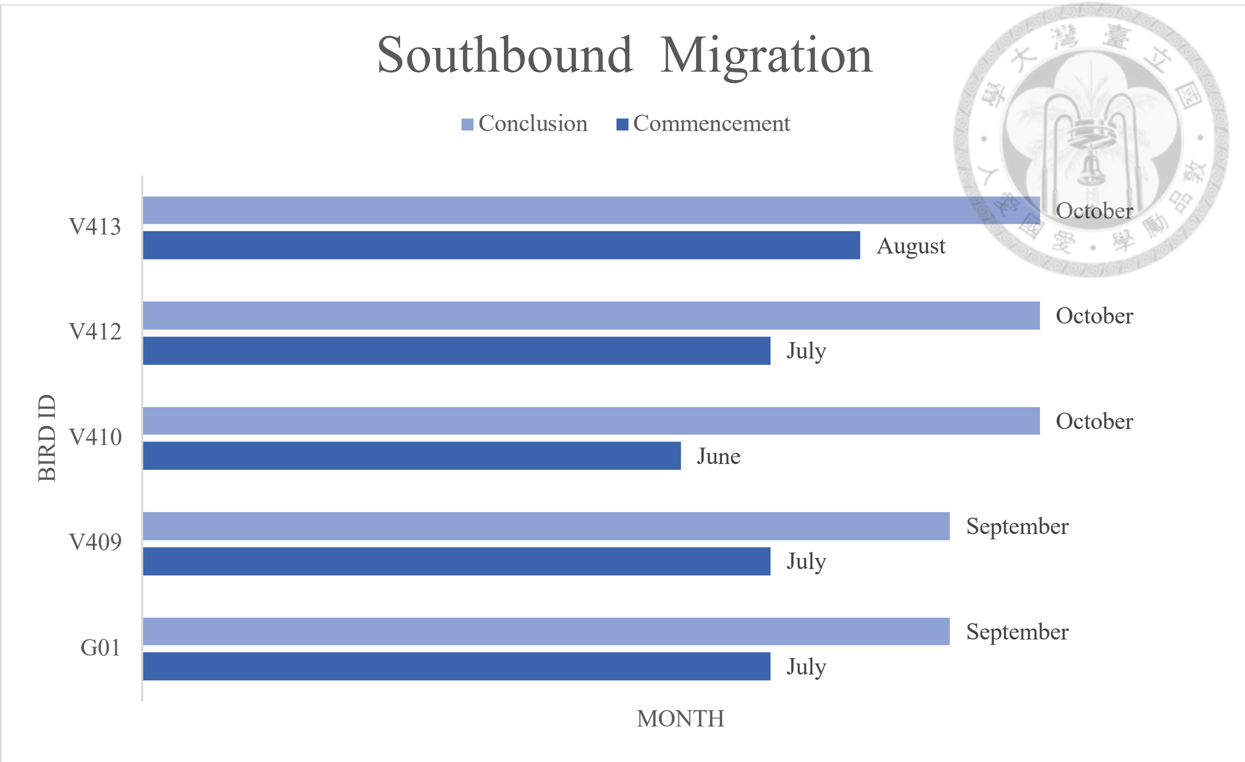

Figure 30. Month of migration commencement and conclusion for the southbound migration of the tagged Little terns. All terns commenced the southbound migration between June and August then concluded between September and October.

doi:10.6342/NTU202303015

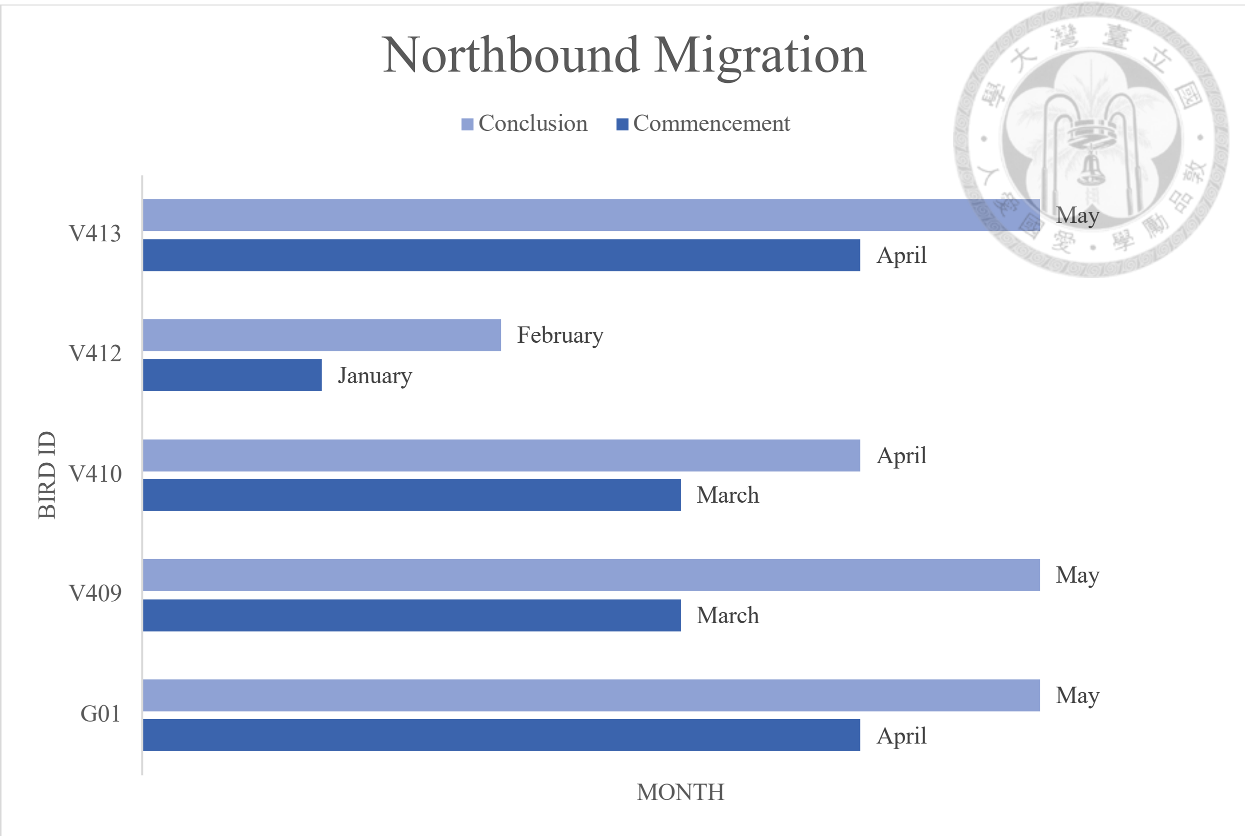

Figure 31. Month of migration commencement and conclusion for the northbound migration of the tagged Little terns. All terns commenced the northwards migration between January and April, then concluded between February and May.

doi:10.6342/NTU202303015

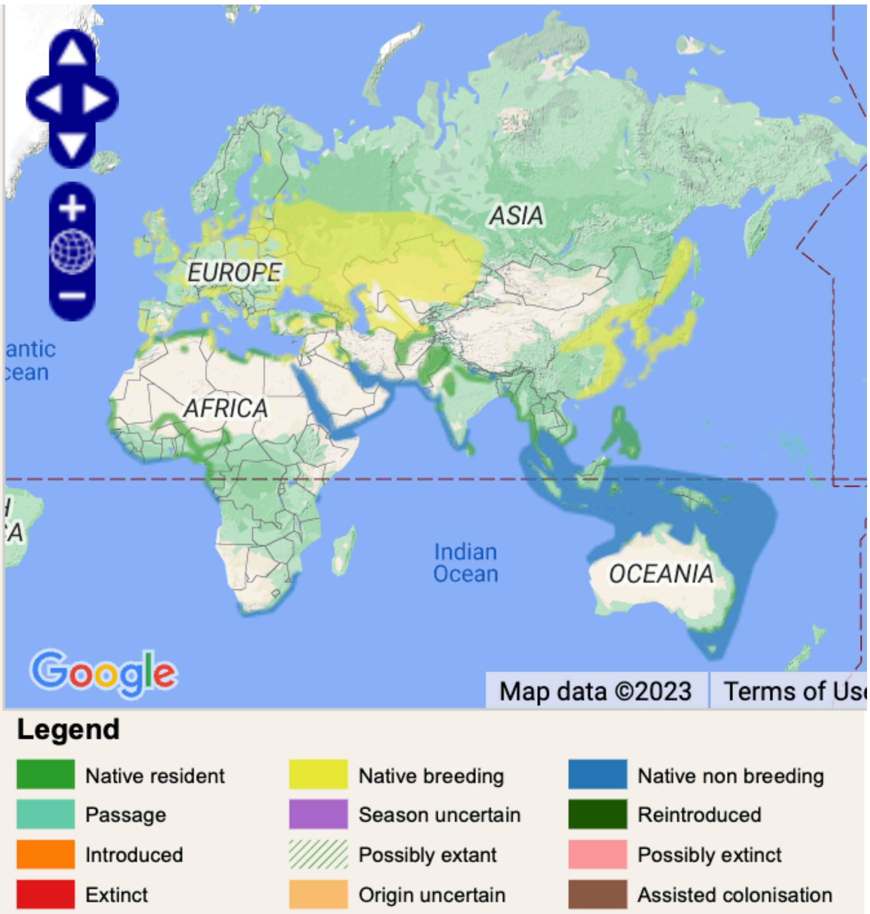

Figure 32. Little tern (*Sternula albifrons*) distribution map displaying regions of breeding, nonbreeding, and residency (source: BirdLife International, 2023)

doi:10.6342/NTU202303015