The Peruvian Tern *Sternula lorata* is an endangered seabird that nests asynchronously in different parts of its nesting range from northern Chile to Ecuador. Asynchronous nesting raises the possibility of counting individuals more than once during annual population censuses. We deployed 10 light-level archival tags (geolocators) to terns at the nesting ground in Mejillones, Chile, at the southern end of this species’ range during 06–11 September 2015, and we retrieved three the following year at the same location. Results showed that the tagged birds remained at the nesting grounds in Mejillones from July to December then migrated north, some in stages, to non-breeding areas along the coast of Peru and possibly Ecuador. Here they remained until early to mid-July 2016, although some movement among specific sites occurred between December 2015 and July 2016. They returned to their nesting areas more rapidly in early to mid-July. We detected no indications of additional nesting by these individuals away from Mejillones, Chile. Though sample size is small, these observations indicate at least that terns that breed in northern Chile likely do not nest again in Peru/Ecuador, though they may stay for extended periods. Therefore, we recommend that population estimates sum the counts of all nests and/or nesting pairs at all sites throughout the range each calendar year and count large roosting flocks separately. In addition, we suggest further studies to examine the possibility of geographically and temporally separated breeding populations.

**Key words:** Peruvian tern, *Sternula lorata*, migration, geolocator, asynchronous nesting

**INTRODUCTION**

Seabird populations in general are declining across the planet (Paleczny et al. 2015), but acquiring accurate population estimates by species can be difficult for those that have complex life histories, including large geographic movements (Schreiber & Burger 2001). Population estimates of migratory colonial nesting birds are further complicated when the timing of breeding is asynchronous (Nisbet & Drury 1972, Hébert & Barclay 1986, Hébert & McNeil 1999, Barré et al. 2012).

It is difficult to estimate numbers of the Peruvian Tern *Sternula lorata* due to its extensive geographic range, breeding asynchrony, and the potential for non-breeding birds to roost within or near nesting colonies. This leads to a potential overestimation of the population at both ends of their range. Peruvian Terns occur within the Humboldt Current Zone along the coast of western South America, from Salinas in southern Ecuador to La Península de Mejillones near Antofagasta in Chile (Zavalaga et al. 2009). In addition, they may occasionally occur along the Pacific coast of Colombia (Hilty & Brown 1986) and into the Gulf of Panama (Ridgely & Gwynne 1992). Within this range, they breed in Peru and northern Chile (Zavalaga et al. 2009). In northern Chile, the breeding season lasts from August until January, with the peak in October/November (Guerra-Correa et al. 2017). However, in
southern Peru and the northermost portion of Chile, nesting occurs from October to February, with a peak in November (del Hoyo et al. 1996, Vilina 1998, Zavalaga et al. 2008a, 2008b); in central Peru near Paracas, they nest from November until May (Amorós Kohn et al. 2010, Amorós Kohn & Saravia Guevara 2012). Asynchronous breeding occurs in other species of terns and larids (Nisbet & Drury 1972, Hébert & Barclay 1986, Hébert & McNeil 1999, Barré et al. 2012), but asynchronous breeding is typically noted within a geographic region and spans sequential months. The Peruvian Tern’s large spatial and temporal separation appears unique.

The asynchrony in nesting has led to difficulties estimating the population and allows for the possibility that two breeding populations along the South American Pacific coast are separated temporally. Researchers have assumed the terns nest once per year, with renesting in the same area if the nest fails. However, observations of large groups of up to several hundred apparently non-breeding terns roosting adjacent to nesting areas in northern Chile and Peru complicate population estimation, as they may be the breeding birds from the other end of the range (Guerra-Correa 2003, Zavalaga et al. 2009). An alternative theory is that the same birds may be breeding in July to December in Chile, then moving north to nest a second time in February to May in Peru. These large groups of non-breeding birds, therefore, may be composed of pre-or post-breeding individuals. The latter theory would lead to a far lower number of breeding adults than is currently estimated. Currently, migratory routes and non-breeding locations for the Peruvian Tern are poorly understood. It has been suggested that during the non-breeding season, they also occur offshore (Mackiernan et al. 2008a, 2008b), up to 200 km from the coast (Mackiernan et al. 2001), particularly during El Niño events (Zavalaga et al. 2008a). Therefore, to obtain an accurate population estimate, it is essential to resolve whether the same individuals breed in both locations.

Here we report results of a geolocator study of the Peruvian Tern’s annual movements, along with the location and number of nest attempts. Our goal was to provide relevant insights to researchers currently attempting to estimate the global population from population-based nest counts at colonies throughout their range. In addition, we tried to resolve whether there are two asynchronous nesting populations or if the same birds are nesting in both locations.

Answering these questions is important because the Peruvian Tern is classified as Endangered in Chile (MMA 2007) and Peru (D.S. N°004-2014-MINAGRI). Human development affects nesting locations adjacent to the Pan-American Highway through the coastal portions of the Atacama Desert in Peru and Chile. The highway bisects the coastal plains and provides access to numerous off-road trails for fishermen, algae harvesters, and off-road vehicle enthusiasts, which increase incursions into nesting areas. In addition, there has been increased residential and industrial development adjacent to port cities near the Peruvian Tern’s main nesting and foraging areas, particularly in the areas around Mejillones, Chile, and Paracas, Peru (Guerra-Correa 2003, Amorós Kohn et al. 2010). Threats associated with human development and presence include an increase in foxes Pseudalopex spp. and feral dogs near the highway and towns; increases in raptor populations due to irrigation, roadkill supplementing available food, and additional perches created by infrastructure development; and off-road vehicles that crush eggs and chicks near roads and population centers (Guerra-Correa et al. 2017). Foxes and aerial raptors are considered the main predators of Peruvian Terns and their eggs (Guerra-Correa et al. 2017). Additionally, Peruvian Tern populations also suffered from the 1972 stock collapse of Peruvian anchoveta Engraulis ringens, an important prey species (Guerra-Correa et al. 2017). The global population of Peruvian Terns appears to be decreasing; the current estimate is 600–1,700 individuals (Birdlife International 2021). This estimate could be far fewer if the same individuals are breeding twice, thus being counted twice by international census efforts.

**METHODS**

Our study was conducted in the pebble plains north of Mejillones, Segunda Región, Chile (23°03'S, 070°20'W). We captured 10 adult Peruvian Terns during 06–11 September 2015 using remotely triggered drop traps placed over nests during incubation, when parents are strongly attracted to the nest. Upon capture, we measured mass and wing chord, and we recorded the assigned nest number and location. Geolocators (Lotek mk20) were attached using 1-mm Kevlar thread, wrapped around a blank aluminum band (4 mm diameter) and sealed using marine epoxy. The total mass of the device and attachment weighed 0.75–0.80 g. The average body mass of the Peruvian Tern is 50 g, and the tag thus represents 1.6% of the tern’s total body mass, less than the 3% generally recommended (Kenward 2000). Persons acting as local colony monitors recorded nest outcomes.

The following season (31 August to 04 September 2016), we observed four terns that had returned with geolocators. Three were trapped as described previously, the geolocators were removed, and the birds were released. We sent the recovered geolocators to Lotek, who recovered the data. All three geolocators contained a full year of recordings and were still recording when removed from the birds (A. Marsh pers. comm.). The fourth bird that was observed with a geolocator was not associated with a nest and therefore was not captured.

Data were analyzed to determine sunrise and sunset times at each tern’s location throughout the year. From the sunrise/sunset data, the times of local noon and midnight were determined, and geographical coordinates of the tern’s approximate location were derived relative to noon and midnight Greenwich Mean Time (GMT). We used raw light data collected by the geolocators to estimate the geographic coordinates (latitude and longitude) using the Solar/Satellite Geolocation for Animal Tracking package (“SGAT”; Sumner et al. 2009, Wotherspoon et al. 2013) in program R (R Core Team 2017). We used an elevation threshold of 1° to derive the time of sunrise or sunset (twilight events) and determined the time of sunrise/sunset using the *findTwilights* function in the “TwGeos” package (Wotherspoon et al. 2013, https://github.com/slisovski/TwGeos.git). We set a minimum time between subsequent sunrise and sunsets to 6.5 h, which filtered out spurious sunrise/sunset times caused by shading of the geolocator or light pollution from human sources. We removed sunrise/sunset times using the *twilightEdit* function using the following two criteria: 1) the sunrise/sunset time had a time difference of 35 minutes or greater from sunrise/sunset times within two days on either side of the suspected outlier, and 2) the sunrise/sunset times of those four days (two days on either side) occurred within 25 minutes of one another.

Using Markov Chain Monte Carlo simulations in the “SGAT” package in R, we generated estimates of geographic locations while
incorporating the error inherent in light-level geolocation (shown in Figs. 3, 4, and 5 as “error clouds”). For each of the three terns, we specified one model that included the raw locations derived using the Threshold Method, which is a model that describes the error distribution between estimated and known sunrise and sunset times. We also specified a second behavioral model that described potential flight speeds. A distribution mask constrained stationary periods within a 1500-km buffer of the Peruvian Tern’s known distribution (Birdlife International 2021); this was selected to screen out outlier points with large deviations. We used the daily location estimates to generate migration schedules and locations using the \texttt{MigSchedules} function available in the “Llmig” package (https://github.com/MTHallworth/LLmig.git). The \texttt{MigSchedules} function uses natural breaks in latitude and longitude to assign stationary periods within the annual cycle. We used the resulting locations to determine where the three individuals spent the non-breeding season and their migratory routes. Finally, we removed locations and error distributions recorded within three weeks of the spring equinox (01 March to 15 April), along with those recorded within 3° of the Equator; these measurements showed a high degree of longitudinal error and were deemed unreliable.

In addition to using the light-level data to derive geographic locations, we used the data to determine when individuals may have been incubating nests. Because tags were affixed to leg bands, there are more “shading events” during incubation/brooding because the light sensor on the geolocator is obstructed by the bird’s body as it sits on the nest (see Verhoeven et al. 2020). We used the number of shading events (i.e., the number of times the light-level crossed the threshold value) as a proxy for daily incubation. Because a shading event must cross a threshold value, events in which light is reduced but not blocked do not typically trigger the threshold. Additionally, individual events can be eliminated by looking for sustained periods of shading that would indicate nesting rather than a single short event. For example, if two time periods of shading match the tern’s incubation and chick-brooding period, that would indicate that the tern nested twice.

**RESULTS**

**Light-level data**

Light levels indicated that terns 008 and 009 moved northward and remained near the same latitude (18°S) during early to mid-January (Fig. 1). Tern 010 appears to have moved northwards in two steps, the first in late December to early January and the second in mid-February. Southward movement took place in early July (Tern 008) and late July to early August (Terns 009 and 010).

![Fig. 1. Raw light-level data throughout the year for Peruvian Terns Sternula lorata 008, 009, and 010. Light areas in the figure indicate times when the geolocator recorded daylight, while dark areas indicate times when there was no light or the sensor was covered. Arrows indicate shifts in latitude over a short time; downward arrows indicate post-breeding migration north and upward arrows indicate pre-breeding migration south.](https://example.com/fig1.png)
Shading events

Tern 008 appeared to have continued incubation until 24 September 2015, then brooded the young until 13 October 2015 (Fig. 2). Colony monitors confirmed that this nest was successful. There is a second shadowing period between 21 November 2015 and 07 January 2016. This may have been a second nest attempt, but it consisted of fewer shading events (Fig. 2). There were a few minor shading events from 20 January to 20 May 2016. Beginning on 25 August 2016, many shading events were consistent with a second nest attempt in Mejillones, Chile.

Tern 009 appeared to have ceased incubating after capture on 12 September 2015. Monitors determined that this nest failed. A second period of shading consisted of fewer events between 23 November 2015 and 12 January 2016, while still in Mejillones, Chile (Fig. 2). Little to no shading was detected from 12 January to 29 August 2016, when it appears to have begun incubating again.

Tern 010 appeared to have stopped incubating, then made a second nesting attempt from 14 October to 10 November 2015 (Fig. 2). After that, there were occasional shading events from mid-November 2015 until late August 2016, but nothing consistent with another nesting attempt until the following year on approximately 25 August 2016 in Mejillones, Chile.

Movement and locations

Here we describe the paths taken by the terns, although the error is large particularly regarding latitude; this error worsens near the equinoxes. We assumed these terns are located near the middle of the error cloud and at locations where Peruvian Terns have been observed in the past. In these narratives, we also provide the nearest position on the coast, although they may also be offshore. All named locations should be considered approximate.

**Tern 008**

This tern was captured in Mejillones on 10 September 2015 at 09h10 (Chile Standard Time [CST], GMT−4) at nest N09 (UTM 360902, 7449812). We measured and marked it within five minutes, and it returned to the nest. The nest contained two eggs and was successful. It remained in the vicinity of Mejillones until 31 December 2015 (Fig. 3). It moved north to the vicinity of Iquique, Chile, between 31 December 2015 and 04 January 2016, then continued north to northern Peru near Paraiso during 04–09 January 2016, south to southern Peru near Ite 09–13 January 2016, then north to northern Peru/southern Ecuador between Paita, Peru, and Salinas, Ecuador, during 14 January to 13 July 2016 (Fig. 3). It began moving south along the coast, migrating from the Paita area on 13 July 2016, arriving back in Mejillones on 21 July 2016. It remained there until it was recaptured on a nest on 01 September 2016.

**Tern 009**

This tern was captured in Mejillones on 10 September 2015 at 10h10 CST at nest N10 (UTM 360996, 7449823). We measured and tagged the bird within five minutes. However, we did not observe whether it returned to the nest, which contained one egg that was subsequently depredated. Tern 009 remained in the

Fig. 2. Shading events for geolocators attached to Peruvian Terns *Sternula lorata* 008, 009, and 010 between September 2015 and September 2016.
vicinity of Mejillones until 31 December 2015, when it moved north to near Iquique, Chile, where it remained until 12 January 2016 (Fig. 4). It then moved further north into southern Ecuador, possibly near Salinas, from 15 January to 19 March 2016. It then moved south, to remain between Eten and Paraiso, Peru, from 19 March to 01 July 2016. Eventually it migrated back to Mejillones between 04 and 07 July 2016, remaining there until we recaptured it on a nest on 31 August 2016.

Tern 010

This tern was captured in Mejillones on 11 September 2015 at 08h00 CST at nest N05 (UTM 360735, 7450578). We measured and tagged it within 16 minutes, whereupon it returned to the nest. The nest contained two eggs but was subsequently abandoned. The tern remained in the vicinity of Mejillones until 31 December 2015, when it moved north to Paracas, Peru (Fig. 5). It remained there from 01 January to 19 February 2016. It then moved further north to San Pedro de Vice/Paita, where it remained from 19 February to 26 July 2016 (Fig. 5). Finally, it migrated back to Mejillones during 26–31 July 2016 and stayed there until it was recaptured on a nest on 04 September 2016 (Fig. 5).

Potential impacts of geolocator attachment

In 2015 we trapped and applied geolocators to terns at 10 nests. Pairs hatched eggs at five of these nests, three were abandoned, and two were depredated. In comparison, the hatching rate was 72% among the 385 nests in the region of Mejillones in the 2015/16 season; 12% were depredated and 11% were abandoned (Guerra-
Correa et al. 2017). However, due to our low sample of 10 nests at which geolocators were applied, we cannot determine if the hatch success rate of our subsample was representative.

We recovered three of ten geolocators one year after tagging, 2016. A fourth tern was observed with a geolocator in 2016, but it was never associated with a nest and we were unable to recapture it. Other than minor leg discoloration, we did not detect any leg injuries on any recovered terns.

**DISCUSSION**

The three individuals tracked in this study showed a similar movement pattern between breeding colonies in Mejillones and non-breeding areas in Peru and possibly southern Ecuador (Figs. 3–5). The three individuals nested in the vicinity of Mejillones between July and December 2015. One individual made a second nest attempt, and a second individual may have as well (Fig. 2). All three birds then migrated north in January 2016, spent the non-breeding season in Peru and Ecuador between January and July 2016, then migrated back to northern Chile in July 2016 (Figs. 3–5). On their northward migration, they stopped at intermediate sites. From January to July, some individuals moved among roosting areas, including returning south between February and March, but they remained in one location from March until they migrated back to the breeding sites in July (Figs. 3–5).

Based on shading events, the three terns captured near Mejillones nested between August and early January, and they did not nest in Ecuador or Peru between January and July. Therefore, we suggest that the Peruvian Terns counted as breeding individuals in northern Chile may be considered a distinct breeding population that nests there and is separate from those in central Peru to southern Ecuador. However, additional study is needed of populations nesting in southern Peru, as their nesting season overlaps with those nesting in northern Chile (del Hoyo et al. 1996, Vilina 1998, Zavala et al. 2008a). Therefore, to conduct population censuses for this species, nesting pairs in northern Chile should be considered different from those nesting from central to northern Peru.

On the breeding grounds in Chile and Peru, large groups of non-breeding terns congregate during the nesting season (Guerra-Correa 2003). Based on these data, we hypothesize that some terns roosting in Peru likely belong to the breeding population from northern Chile. Conversely, we also hypothesize that some of the terns roosting on nesting grounds in northern Chile may be from the breeding population in Peru.

Since the 2018 nesting season, Peruvian Tern chicks in both Peru and Chile have been marked with field-readable bands of different colors. As these individuals are recruited into breeding populations in their third to fourth years, re-sightings will begin to better inform this question of population separation. If these hypotheses prove true, then counts of nests, breeding individuals, and roosting (non-breeding) birds in the two populations should be separated when generating population estimates. Therefore, we recommend these populations be estimated by 1) using total nests or nesting pairs in both Chile and Peru/Ecuador, supported by 2) counts of roosting individuals in both Chile and Peru/Ecuador. Currently, non-breeding individuals at or near nesting colonies should be counted separately until further studies determine their population affiliations.

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**REFERENCES**


