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Contrasting migratory ecology of two threatened and allochronic storm-petrels breeding in the Mexican Pacific

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ABSTRACT: Migration is an essential life stage in many species, but is little understood in some groups, e.g. storm-petrels. Considering that storm-petrels reside in non-breeding areas for over half of their lifespan, identifying these areas is a priority for conservation efforts. Townsend's *Hydrobates socorroensis* and Ainley's storm-petrels *H. cheimomnestes* are 2 threatened sister species, breeding allochronically on Guadalupe Island (Mexican Pacific), for which migratory patterns are unknown. In this article, we describe the non-breeding areas of these 2 species, assess artificial light events recorded by geolocators, and describe the birds' daily activity patterns. We deployed geolocators from 2021 to 2023 and modeled migratory routes using SGAT. We successfully tracked 7 Townsend's and 4 Ainley's storm-petrels over their non-breeding period. Townsend's storm-petrels were found to travel to the south of the Baja California Peninsula and spent most of the time in Mexican waters, while Ainley's storm-petrels migrated toward Hawaii and spent most of the time on the high seas. For the Townsend's storm-petrels, 16.1% of their core areas are in protected waters, whereas for Ainley's storm-petrel, only 0.7% of the core areas are protected, and 0.8% of those areas are recognized as key biodiversity areas (KBAs). Further, our findings indicate that both species are mainly nocturnal, making them highly susceptible to the impacts of light pollution; we detected 6 artificial light events. Our findings also support the hypothesis that divergence in the migration patterns between allochronic populations could be a crucial factor in sympatric speciation, which seems likely in seasonal environments like the northern Pacific.

KEY WORDS: Hawaiian seabirds · Conservation · Exclusive economic zone · EEZ · Geolocators · GLS · Migration · Non-breeding areas · *Hydrobates leucorhous* · Leach's storm-petrel

1. INTRODUCTION

The migratory period is an essential life stage in most birds, as they leave their breeding grounds in search of suitable conditions for survival, recovery from the breeding season, and readiness for the next breeding attempt. Despite its relevance, migration is still little understood in some groups, such as small pelagic seabirds, because they spend most of their time far from human sight, covering vast distances in their non-breeding period (Warham 1992). Over the past 2 decades, our understanding of the non-breeding distribution of large and medium size pelagic seabirds has steadily expanded (Beal et al. 2021, Bernard et al. 2021). However, smaller storm-petrels remain among the least tracked species for which the non-

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breeding distribution remains largely elusive (Bernard et al. 2021). Tracking storm-petrels can provide valuable insights for regulating nocturnal threats in pelagic areas and the high seas, as these birds are primarily active at night and particularly sensitive to anthropogenic threats such as light pollution (Silva et al. 2020, Ryan et al. 2021, Collins et al. 2022). As storm-petrels can devote over half of their life to non-breeding areas, identifying their most critical areas during this period is a priority for conservation efforts.

In addition to their contributions to seabird conservation, tracking studies can also help in understanding ecological and evolutionary processes. Storm-petrels have played a crucial role as model species in understanding sympatric speciation through allochrony, i.e. when populations diverge by breeding at distinct times of the year (Taylor et al. 2019). A key question in this regard is whether the reproductive isolation associated with the divergence in the timing of breeding is the exclusive driving force leading to speciation or if this phenomenon is further enhanced by additional mechanisms, such as ecological differentiation through local adaptation to seasonal conditions (Dieckmann et al. 2004, Taylor & Friesen 2017). So far, the evidence shows that populations that have already undergone speciation exhibit greater levels of ecological divergence than those still in the process of speciation (Medrano et al. 2022, Wang et al. 2022). However, this evidence remains limited, especially concerning migratory patterns and non-breeding distribution, Therefore, it is important to expand the scope of research by conducting more studies involving a wider range of taxa.

Townsend's *Hydrobates socorroensis* and Ainley's storm-petrel *H. cheimomnestes* are 2 cryptic species of storm-petrels that are speciated by allochrony (Ainley 1980, Taylor et al. 2018). Townsend's storm-petrel breeds in summer, while Ainley's storm-petrel breeds in winter. The population size has been roughly estimated at 10 000 pairs per species. Both species breed uniquely on 3 islets (Morro Prieto, Islote Afuera, and Gargoyle Rock) next to Guadalupe Island off Baja California, Mexican Pacific (Kirwan et al. 2023, Medrano et al. 2023). Ainley's storm-petrel has been classified as Vulnerable (BirdLife International 2024a) and Townsend's storm-petrel as Endangered (BirdLife International 2024b) by the International Union for Conservation of Nature (IUCN). Due to the strong similarities in their plumages, and the potential confusion with Leach's storm-petrel *H. leucorhous*, the non-breeding movements of both species are poorly understood and are based on a handful of at-sea records (Kirwan et al. 2023, Medrano et al. 2023). In the case of Townsend's storm-petrel, the only information available shows that the species migrates towards the south of Guadalupe Island, reaching Socorro Island (where the species was described; Townsend 1890) and the high seas of 10° N (Crossin 1968). Ainley's storm-petrel is thought to also migrate towards the south, passing by Clarion Island and Revillagigedo Island until the Galapagos (Crossin 1968, Kirwan et al. 2014, Sieburth et al. 2023). To date, neither species has been tracked during the non-breeding period, partly due to the difficulty in deploying and recovering geolocators on these species, particularly in winter.

The goal of this study was to provide a first insight into the spatial ecology and pelagic behavior of Townsend's and Ainley's storm-petrels outside the breeding season, assess their spatial divergence, and explore the implications for both conservation and evolutionary understanding. Specifically, we aimed to (1) compare the migratory flyways and non-breeding areas between the 2 species, (2) assess the jurisdiction over the exclusive economic zones (EEZs) and the level of protection of the areas visited by the 2 storm-petrel species, and (3) compare the activity and nocturnal patterns across their non-breeding areas. To achieve these objectives, we deployed and recovered geolocators from 2021 to 2023 and modeled their migratory routes.

2. MATERIALS AND METHODS

2.1. Species and study area

Townsend's storm-petrel and Ainley's storm-petrel breed uniquely on 3 islets (Morro Prieto, Islote Afuera, and Gargoyle Rock) next to Guadalupe Island off Baja California. Our study was conducted on the Morro Prieto Islet (28.906° N, 118.289° W), where both species nest in large caves or in crevices in the rocks, and both parents incubate in alternating bouts (Kirwan et al. 2023, Medrano et al. 2023).

2.2. Fieldwork procedures

We worked with 97 nests of Townsend's storm-petrel and 89 nests of Ainley's storm-petrel in 2021–2022 and captured birds in their nests during the end of the incubation or early chick-rearing period. We deployed 10 W65A9-Sea Global Location Sensing (GLS) units built by Migrate Technology (here onwards: geolocators) (~0.8 g weight). In the case of

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Townsend's storm-petrel, the birds weighed an average (±SD) of 33.70 ± 4.07 g (N = 308). For Ainley's storm-petrel, we deployed 15 geolocators, and birds weighed 38.17 ± 13.25 g (N = 179). In both instances, the tags accounted for <3% of the bird's body weight. Geolocators were set to record maximum light levels every 5 min, which, after analyses, provide 2 locations with up to 400 km of spatial inaccuracy every day (Halpin et al. 2021). We analyzed the degree of inaccuracy considering the duration of the day within our dataset, referencing the methodology outlined in Halpin et al. (2021). Geolocators also recorded wet-dry data every 6 s and packed in 5 min intervals. We attached the tags to a metallic ring using a stainless-steel cable, and the ring was attached to the bird's tibia. Geolocators have been used in diverse species of storm-petrels, in some cases having an impact (Pollet et al. 2014), but with no impact in other cases (Medrano et al. 2024). In our study, when we recovered the geolocators, we decided to handle only the birds from the nests where we deployed geolocators, to avoid disturbing birds without geolocators. This fact prevented us from being able to assess for differences in return rates. However, no birds returned without tags or any signs of leg injuries.

2.3. Geolocator data pre-processing

To analyze the geolocator data, we calibrated the geolocators in the breeding colony (Morro Prieto), away from any artificial light sources, both before the deployment and after the recovery. After downloading the data, we processed the light data that was recorded by the geolocators every 5 min using the 'preprocessLight' function of the 'TwGeos' package in R (Lisovski & Hahn 2012). We used this function to estimate the hours of sunrise and sunset, examine the integrity of each day's light curve, and manually repair sunrise and sunset transitions with evident interferences. Then, we modeled the positions using the 'Solar/Satellite Geolocation for Animal Tracking (SGAT)' package (Lisovski et al. 2020), applying Markov chain Monte Carlo (MCMC) simulations to refine the locations of the individuals, especially near the equinoxes. Within this package, we used a tolerance on the sine of the solar declination (tol) value as small as possible (in most of the cases of 0.1), except in the case of 1 geolocator (CD255) which gave unrealistic values near the equinoxes, and we had to use a higher value (0.18). In all cases, we used a mean speed of 10 km h^{-1}, using reference values obtained from GPS tracking devices (F. Medrano et al. unpubl. data).

2.4. Non-breeding area characterization

We identified non-breeding areas creating kernel densities using the modeled positions of all the individuals. We calculated kernel contours using the 'kernelUD' and 'getverticeshr' functions of the 'adehabitatHR' package of R (Calenge 2006) and calculated the overlap between the species using the 'kerneloverlap' function of the same package at densities of 50% and 95%. For each species, we calculated the overlap between the contours at the core area (50% densities) with the currently designated key biodiversity areas (KBAs) (BirdLife International 2021) and marine protected areas (UNEP-WCMC & IUCN 2023). We also calculated the number of positions of each species within the EEZs. All layouts were made in Arcmap 10.7 (ESRI 2018).

Complementarily, to characterize whether birds visit areas with artificial light at night during the non-breeding season, we checked for light detections at night by the geolocators. Since we used Migrate Technology geolocators, we used a 20 lux threshold for natural light at night, as established for other species in the North Atlantic (Krüger et al. 2017).

2.5. Daily activity patterns

We assessed the changes in the daily proportion of time spent on the water (resting periods) during the non-breeding period based on wet-dry data collected in the geolocators every 6 s and packed in 5 min intervals. For each pack of information, we obtained the moon illumination, which can alter the activity of some storm-petrels (Medrano et al. 2024). For doing so, we used the 'calculateMoonlightIntensity' function from the 'moonlit' package from R (Śmielak 2023). With the activity data and the moon illumination, we built a set of candidate generalized additive mixed models (GAMMs), in which the explained variable was whether the bird was on the water or not, and the fixed factors were the interaction between the 2 continuous variables of time of day, day since the departure of the colony, and the smoothing factor of the moon index. The individual identity (ring) was added as a random intercept. We fitted our models with a binomial family using the function 'bam' from the package 'mgcv' (Wood 2001). We selected the best model explaining the data using the fewest parameters based on the lowest Akaike's information criterion (AIC).

To understand the relationship between the spatial and daily activity patterns, we built generalized linear mixed models (GLMMs) to compare the night flight

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index (NFI) between both species. The NFI is calculated with the difference between the proportions of time spent in flight during the night and daylight, divided by the maximum of the 2 values (Dias et al. 2012). We modeled the response variable NFI against a fixed factor for species and a random intercept of individual identity (ring). Complementarily, we built models summarizing the total amount of hours flying per day (grouping the proportion of that when the geolocator was dry). In this case, the response variable was the total hours flying per day, and the model again included a fixed factor for species, and a random intercept of individual identity (ring). In both models, we used the function 'lmer' from the package 'lme4' (Bates et al. 2015).

2.6. Ethics statement

All procedures involving animal manipulations comply with European and Mexican legislation. Deployment and recovery of geolocators and sampling procedures took <10 min per bird and did not have any visible detrimental effects on the animals. All work was carried out with permission from the Mexican Secretaría de Medio Ambiente y Recursos Naturales (SEMARNAT) (SGPA/DGVS/04050/20, SGPA/DGVS/04637/20, and SGPA/DGVS/06066/21).

3. RESULTS

We successfully tracked 7 Townsend's and 4 Ainley's storm-petrels (Fig. 1). The non-breeding areas of both species overlapped 0.5% in the core areas and 27% in the home range (Fig. 2). Specifically, Townsend's storm-petrel visited the equatorial waters of the Pacific Ocean, near Socorro Island and Revillagigedo Islands within the Mexican EEZ (72.79% of the fixes), Clipperton Island within the French EEZ (8.5% of the fixes), and Southern California within the US EEZ (2.63% of the fixes). Also, 3 birds traveled farther south to the high seas (16.06% of the fixes), reaching latitudes of 10° S. Ainley's storm-petrels visited mainly high seas waters (95.73% of the fixes), with some birds visiting the area in the north of Hawaii within the US EEZ (2.13% of the fixes; Fig. 2) and Mexican waters (2.13% of the fixes). Despite

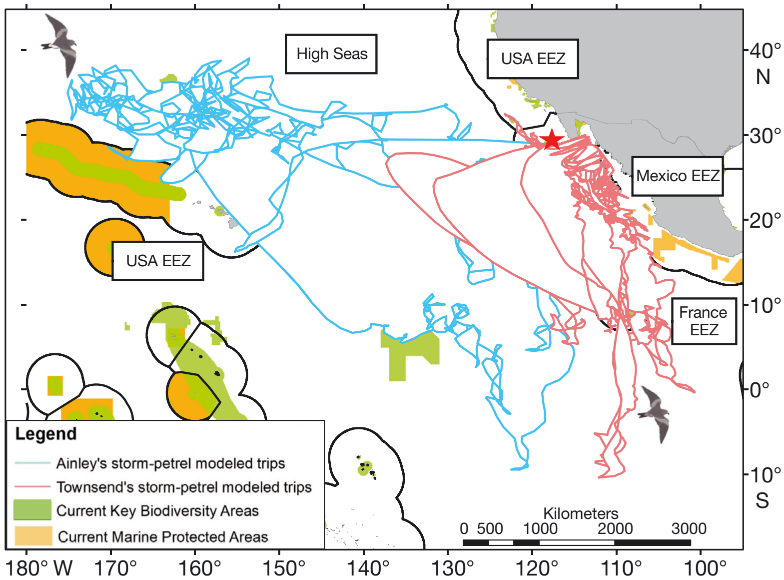

Fig. 1. Movements of Townsend's *Hydrobates socorroensis* and Ainley's storm-petrel *H. cheimomnestes* during the non-breeding period, tracked with light-level geolocators in 2021–2023 and after modeling the trajectories with Solar/Satellite Geolocation for Animal Tracking (SGAT). Current key biodiversity areas (BirdLife International 2021) and current marine protected areas (UNEP-WCMC & IUCN 2023) are indicated. Red star: Guadalupe Island. EEZ: exclusive economic zone

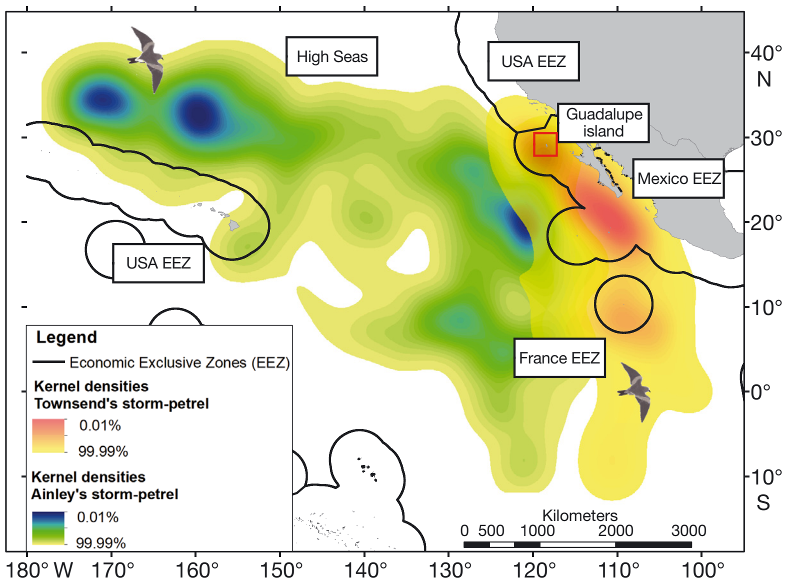

Fig. 2. Kernel density of the non-breeding distribution using all positions recorded by light-level geolocators and modeled with SGAT for Townsend's and Ainley's storm-petrels. EEZ: exclusive economic zone

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that we did not get absolute values, the estimated inaccuracy in the positions was 5.4% better than in tropics for Townsend's and 34.3% better for Ainley's storm-petrels.

Townsend's storm-petrels utilized protected waters for foraging within 16.1% of their core area, whereas Ainley's storm-petrels had only 0.7% of their foraging area under any form of protection. For Townsend's storm-petrels, 5.1% of the core area is currently designated as a KBA, whereas 0.8% of the core area used by Ainley's storm-petrels is KBA. Furthermore, in the non-breeding season, we detected 6 events of artificial light at night out of the astronomical twilight and dusk for Townsend's storm-petrel and none for Ainley's storm-petrel (Fig. 3). Light events occurred between 21:48 and 05:12 h.

Both species spent less time on the water at night than during daylight, except at the beginning and end of the migration (Fig. 4), when the birds flew from or to the breeding area also during daylight. Overall, during daylight, Townsend's storm-petrels were flying 31.3% of the time, while at night they were flying 72.7% of the time. In the case of Ainley's storm-petrel, during daylight, birds were flying 32.9% of the time, while at night they were flying 52% of the time. Activity patterns differed between species (GAMM estimate: -0.17, $t = -4.26$, $p < 0.05$), with Townsend's storm-petrel resting for shorter periods during the night than Ainley's storm-petrel. We also found that there is an increase in the probability of being active (i.e. with the geolocator dry) on brighter nights than on darker nights for both Townsend's (GAMM edf: 2.62, $F = 5.59$, $p < 0.05$) and Ainley's storm-petrel (GAMM edf: 5.24, $F = 3.94$, $p < 0.05$).

We found no differences in the NFI (mean ± SD) between Townsend's (0.57 ± 0.32) and Ainley's storm-petrels (0.32 ± 0.44) (LME df: 8, $t = 1.14$, $p = 0.28$). Both species were mostly nocturnal throughout space, but in some areas (especially near the colony), birds were also diurnal (Fig. 5). Also, we found no differences (LME df: 8, $t = 1.61$, $p = 0.14$) in the total of flight hours per day between Townsend's (mean ± SD: 12.7 ± 3.56 h) and Ainley's storm-petrels (9.88 ± 4.2 h). We found that birds of both species spent more time flying near the colony than farther away from it (Fig. 6).

4. DISCUSSION

This study provides new insights into the migratory movements and daily activity patterns of Townsend's and Ainley's storm-petrels. Both species barely over-

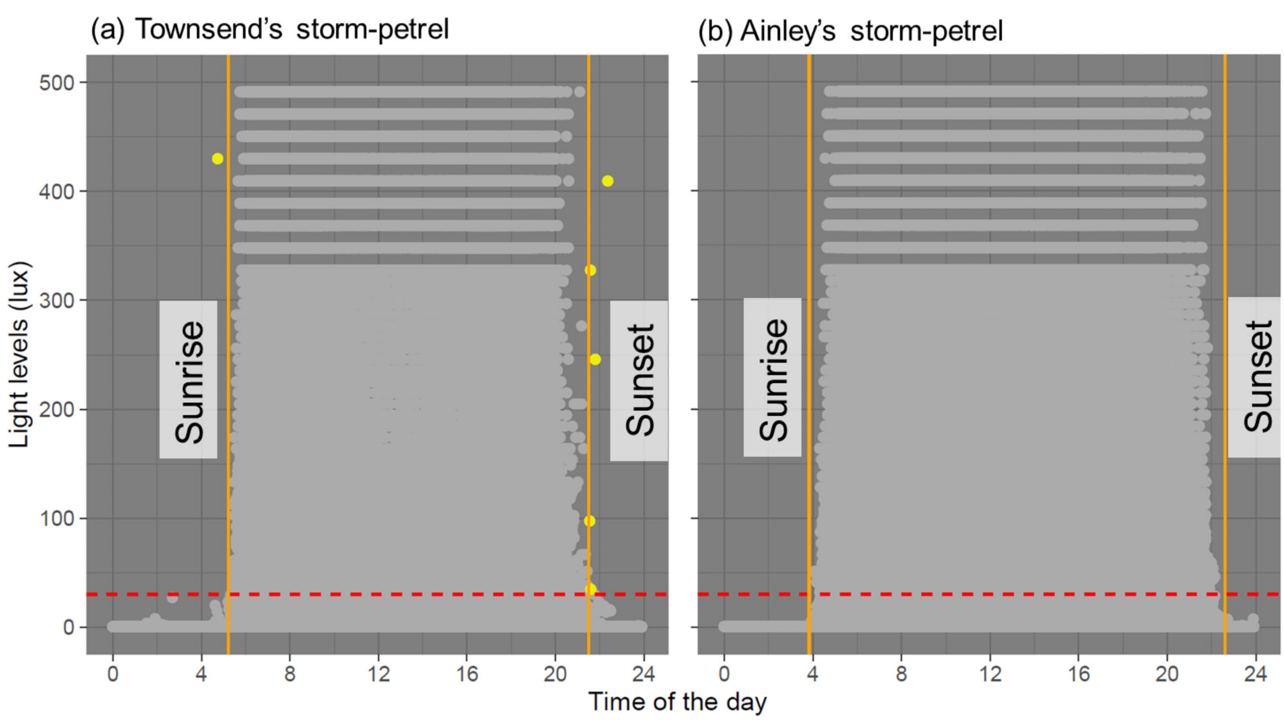

Fig. 3. Light levels detected by geolocators at each time of the day (truncated at 500 lux) deployed in (a) Townsend's and (b) Ainley's storm-petrels. Yellow dots: light events at night; orange vertical lines: minimum twilight time and maximum dusk time obtained with the geolocators; red dashed horizontal line: threshold of natural light at night, established at 20 lux for Migrate Technology geolocators (Krüger et al. 2017)

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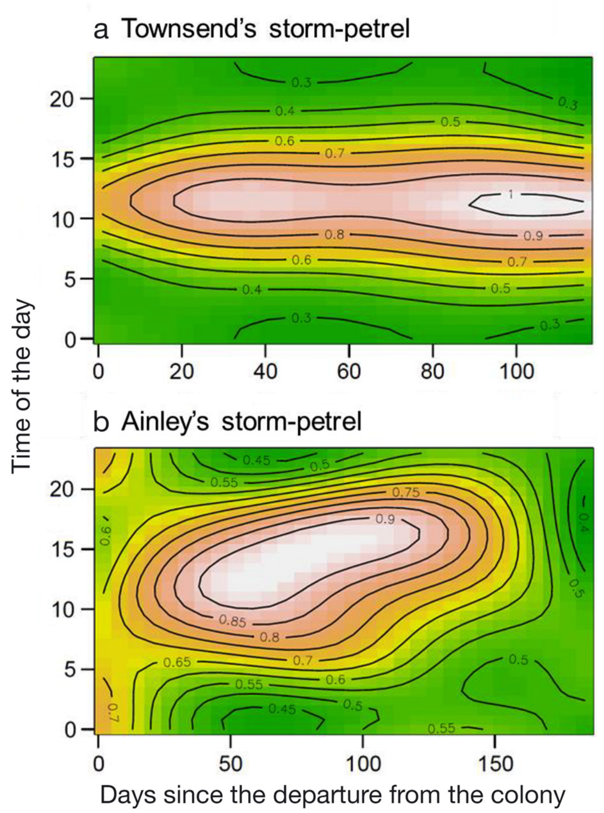

Fig. 4. Proportion of time on water by (a) Townsend's and (b) Ainley's storm-petrels during their respective non-breeding period in winter and summer, shown in relation to time of day and the days since departure from the colony, using wet-dry data from geolocators. Green areas: time spent flying; white areas: time resting on the sea surface; yellow and orange areas: intermediate proportions of time between resting and flying. Analyses carried out using generalized additive mixed modeling, with predictors including days since departure from the colony, time of day, and moon illumination

lapped their non-breeding areas and, in both cases, these areas lack any protection and are not identified as KBAs. Both species are primarily nocturnal throughout their non-breeding period, with Ainley's storm-petrel spending a slightly larger amount of time resting on the sea surface than Townsend's storm-petrel, but no differences in the NFI nor in the total amount of hours flying per day.

Specifically, Townsend's storm-petrels migrated towards the south of Guadalupe Island, with the main concentration of birds near Socorro, Revillagigedo, and Clipperton Islands, near 10° N. These areas mostly match the distribution suggested in the literature by at-sea surveys (Crossin 1968). However, 3 out of 7 birds traveled farther south to the high seas, reaching latitudes of 10° S, an area that was not stated in the literature. Conversely, Ainley's storm-petrel mainly migrated westwards, in the vicinity of the northern part of Hawaii. These results bring new insights into the distribution suggested in the literature by at-sea surveys, which proposed that Ainley's storm-petrel visited Clarion Island, Revillagigedo Island until the Galapagos (Crossin 1968, Kirwan et al. 2014, Sieburth et al. 2023). The discrepancy between the literature and our data may arise from different sources. The relatively small sample size of our study, with only 4 Ainley's storm-petrels tracked, possibly may not have captured the full spectrum of the migratory strategies of the population. Alternatively, the areas documented previously might have been frequented by only a minority of the birds, leading to an overemphasis on their significance due to potential spatial biases in Ainley's storm-petrel movement sightings.

Considering that both species are nocturnal, light pollution could be a major threat, generating 'fall-outs' in vessels, as reported for the closely related Leach's storm-petrel at sea (Gjerdrum et al. 2021, Burt 2022). Although we only found 6 events of relevant levels of artificial light detected by the geolocators, our approach is biased toward birds that survived the whole non-breeding season. Thus, geolocators of birds that approach light pollution sources would not have been recovered. In any case, light pollution could be regulated within these areas, mainly to prevent potential threats. Another relevant threat at sea for the 2 species could be plastic pollution. In particular, the area visited by Ainley's storm-petrel is next to one of the highest plastic concentrations in the world (Clark et al. 2023). Since plastics have been reported at high frequencies in the closely related Leach's storm-petrel (Bond & Lavers 2013, Pollet et al. 2023), it is also likely to occur for Ainley's storm-petrel. However, further research is needed to fully understand the impacts of light and plastic pollution on these species.

The identified areas for both species are not protected nor prioritized for protection, potentially exposing them to future threats. Further, the large extent of the non-breeding areas for both species, which cover several marine ecoregions and jurisdictions, might be a challenge for implementing protection areas that effectively safeguard their ecological needs and movements. Such patterns have been previously reported for other tropical and sub-tropical seabirds during their non-breeding season (Trevail et al. 2023), suggesting that this is a common issue for seabird conservation in these regions. However, large areas might also spread the risk of facing different threats, as the birds may encounter different levels of human impact and environmental variability across their range, and may have the ability to shift their distribution in response to changing conditions.

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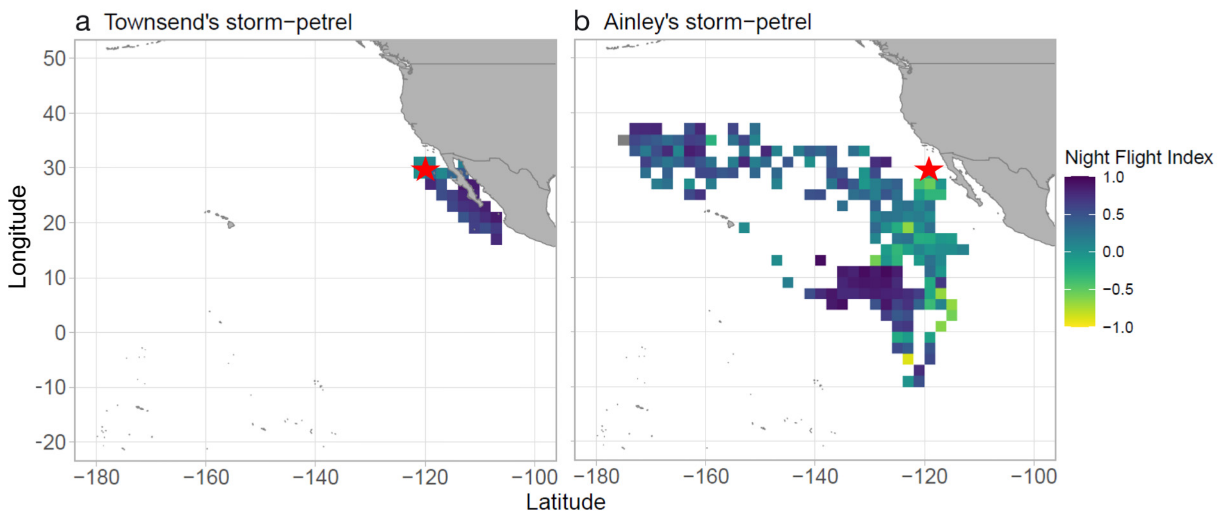

Fig. 5. Night flight index (NFI) during the non-breeding period for (a) Townsend's and (b) Ainley's storm-petrels in winter and summer, respectively. NFI calculated from daily wet-dry data and the positions modeled with SGAT, both obtained from geolocators. NFI calculated with the difference between the proportions of time in flight at night and daylight divided by the maximum of the 2 values (Dias et al. 2012) and is represented on a scale where higher values (in blue) indicate areas where birds predominantly fly at night, while lower values (in yellow) indicate areas where birds mainly fly during daylight. Red star: Guadalupe Island

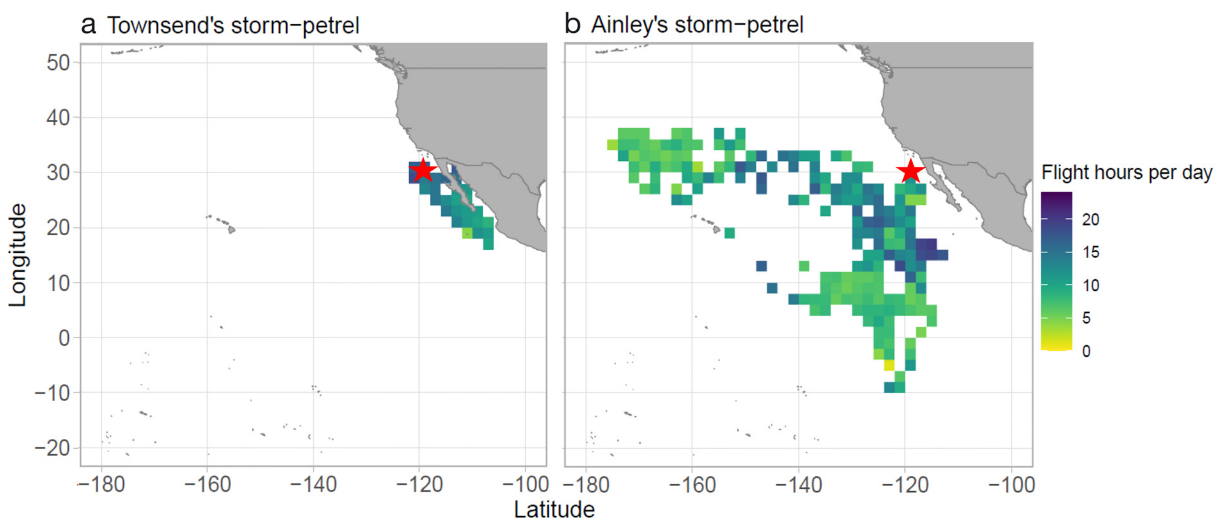

Fig. 6. Flight hours per day for (a) Townsend's and (b) Ainley's storm-petrels during the non-breeding period in winter and summer respectively, calculated by compiling daily wet-dry data using geolocators and combining it with the positions modeled with SGAT. Absolute time spent flying is depicted on a 0–24 hour scale, where higher values represent areas where birds spent more time flying, and lower values represent areas where birds spent fewer hours flying. Red star: Guadalupe Island

The fact that we had low return rates of Ainley's storm-petrel (4 out of 15 birds) might be of concern, since it might show a potential impact of tags. However, we only visited the islet at 4 different events to recover the geolocators, since the tide conditions made it impossible to land on the islet in winter. Further, we did not handle control birds to understand whether return rates were similar to tagged birds to avoid an unnecessary impact. However, considering that this is a threatened species, new information should be collected to understand whether handling these storm-petrels might affect their survival.

We observed differing activity patterns between the 2 species throughout the non-breeding season. Ainley's storm-petrels spent more time on the water than Townsend's storm-petrels. This difference might be related to Ainley's storm-petrel having its non-breeding season in the summer, which features shorter

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nights. In contrast, Townsend's storm-petrel has its non-breeding season in the winter, characterized by longer nights. This is supported by the fact that we did not find differences in the nocturnality between both species. Alternatively, waters used by Ainley's storm-petrels during the boreal summer may be more productive than those used by Townsend's storm-petrels in winter, meaning the former may meet their energetic requirements with less flying effort than the latter. Also, we found that the activity patterns of both species were influenced by the moon's illumination at night, with the birds spending more time on the water on darker nights. These patterns have also been documented for some other storm-petrel species, such as the white-faced storm-petrel *Pelagodroma marina* (Medrano et al. 2024), but not for other storm-petrel species, such as the European storm-petrel *Hydrobates pelagicus* or the Cape Verde storm-petrel *H. jabejabe* (Medrano et al. 2022, Militão et al. 2022).

Concerning the evolutionary implications of our findings, we found that these 2 subtropical species diverged in their ecological niche, especially in their spatial use. When allochronic populations winter in a shared non-breeding area, birds from one population may trail those from the other during the return migration, thus promoting ecological and genetic connectivity between the 2 populations. However, our findings indicate that Townsend's and Ainley's storm-petrels migrate and winter in distinct regions. This spatial divergence complicates dispersal events and limits connectivity between the 2 populations, reinforcing their reproductive isolation. Ecological divergence between allochronic populations that already speciated has been previously reported for some physiological traits, like proteins that are related with thermoregulation (Wang et al. 2022). Conversely, allochronic populations breeding in tropical systems did not show such a divergence in their space utilization during the non-breeding period (Medrano et al. 2022). This lack of spatial separation may facilitate connectivity and inhibit speciation from occurring. Hence, our findings support the hypothesis that divergence in the migration and wintering areas between allochronic populations could be a crucial factor in sympatric speciation, which is more likely to happen in seasonal environments like the Northern Pacific.

Our research shows that Townsend's and Ainley's storm-petrels spend their non-breeding period in several jurisdictions, including Mexico, the USA, and France, but most of their time on the high seas. Given that both species are primarily active at night, addressing light pollution from stationary platforms and vessels passing in these areas becomes a significant concern. Considering the threatened status of both species, there is reason for concern, particularly because the protection of the high seas is limited, and its management presents significant challenges.

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