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Photo: Kate Sutherland

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Satellite tracking supports hypotheses of breeding allochrony and allopatry in the Endangered *Pterodroma hasitata* (Black-capped Petrel, Diablotin)

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Cover Page: *Pterodroma hasitata* (Black-capped Petrel) photographed in the Gulf Stream off Dare, North Carolina, USA, on 9 May 2021, by Kate Sutherland (Macaulay Library ML336585691); top: light form; bottom: dark form.

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Abstract

Pterodroma hasitata, the Black-capped Petrel (locally known as Diablotin), is the only extant *Pterodroma* petrel nesting in the Caribbean. The species is listed as globally Endangered by the IUCN and was recently listed as endangered under the U.S. Endangered Species Act. *Pterodroma hasitata* show a phenotypic gradient, ranging from a darker, smaller form to a paler, heavier form, that is reflected in a strong genetic structure. This phylogenetic divergence suggests the existence of at least two distinct breeding populations. We report on pre-breeding movements of two male *Pterodroma hasitata*, one of each form, tracked by satellite from non-breeding areas in Gulf Stream waters of the western North Atlantic Ocean to breeding locations in Hispaniola in late 2019. Based on a combination of tracking locations, location error classes, battery voltage, and satellite communication schedules, we infer that the light-form petrel visited a nest in central Dominican Republic during 2 to 8 October and 9 to 15 October, and the dark form visited a nest in southeastern Haiti during 9 to 22 November and 29 November to 3 December. This information supports earlier suggestions that *Pterodroma hasitata* forms breed in allochrony and in allopatry, both of which may be a driver of speciation.

Keywords

biologging, Black-capped Petrel, breeding allochrony, breeding allopatry, endangered species, *Pterodroma hasitata*, seabird

Resumen

El rastreo satelital respalda las hipótesis de alocronía y alopatría reproductivas en *Pterodroma hasitata* (Petrel Antillano, Diablotín), especie En Peligro de extinción • *Pterodroma hasitata*, conocida comúnmente como Petrel Antillano (y localmente como Diablotín), es la única especie existente del género *Pterodroma* que actualmente anida en el Caribe. La especie está clasificada como En Peligro a nivel global por la UICN y ha sido recientemente incluida en la lista de especies en peligro de extinción bajo la Ley de Especies en Peligro de los Estados Unidos. *Pterodroma hasitata* muestra un gradiente fenotípico que va desde una forma más oscura y de menor tamaño hasta una forma más clara y de mayor peso, lo que se refleja en una marcada estructura genética. Esta divergencia filogenética sugiere la existencia de al menos dos poblaciones reproductoras diferenciadas. En este trabajo informamos sobre los movimientos pre-reproductivos de dos machos de *Pterodroma hasitata* —uno de cada forma—, rastreados por satélite desde sus áreas no reproductivas en las aguas de la Corriente del Golfo, en el Atlántico noroccidental, hasta sus zonas de cría en La Española a finales de 2019. A partir de una combinación de datos de geolocalización, grupos de error posicional, voltajes de batería y horarios de comunicación satelital, inferimos que el individuo de forma clara visitó un nido en el centro de la República Dominicana entre el 2 y el 8 de octubre y nuevamente del 9 al 15 de octubre; mientras que el individuo de forma oscura visitó un nido en el sureste de Haití del 9 al 22 de noviembre y del 29 de noviembre al 3 de diciembre. Estos resultados respaldan observaciones previas que sugieren que las distintas formas de *Pterodroma hasitata* se reproducen de manera alocrónica y alopátrica, factores que podrían actuar como motores de especiación.

Palabras clave

alocronía reproductiva, alopatría reproductiva, ave marina, bioregistro, especie en peligro, Petrel Antillano, *Pterodroma hasitata*

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Résumé

Le suivi par satellite soutient les hypothèses d'allochronie et d'allopatrie de reproduction chez *Pterodroma hasitata* (Pétrel diablotin), espèce clasée en danger d'extinction • *Pterodroma hasitata*, le Pétrel diablotin, est la seule espèce existante du genre *Pterodroma* à nicher dans la Caraïbe. L'espèce est classée par l'UICN comme en danger au niveau mondial et a récemment été classée comme en danger au titre de la loi américaine sur les espèces menacées (Endangered Species Act). *Pterodroma hasitata* présente un gradient phénotypique, allant d'une forme plus sombre et plus petite à une forme plus pâle et plus grande, reflété dans une forte structure génétique. Cette divergence phylogénétique suggère l'existence de deux populations reproductrices distinctes. Nous faisons état des déplacements prénuptiaux de deux mâles *Pterodroma hasitata* (un de chaque forme) suivis par satellite depuis les zones fréquentées en dehors de la période de reproduction dans les eaux du Gulf Stream de l'ouest de l'Atlantique Nord jusqu'aux sites de reproduction à Hispaniola fin 2019. En combinant les localisations par satellite, les classes d'erreurs de localisation, les tensions de batterie et les programmations de communication par satellite, nous pouvons déduire que le pétrel de forme claire a visité un nid dans le centre de la République dominicaine entre le 2 et le 8 octobre et entre le 9 et le 15 octobre, et que le pétrel de forme sombre a visité un nid dans le sud-est d'Haïti entre le 9 et le 22 novembre et entre le 29 novembre et le 3 décembre. Ces informations confortent les suggestions antérieures selon lesquelles les formes de Pétrels diablotins nichent en allochronie et en allopatrie, ce qui peut être un facteur de spéciation.

Mots clés

allochronie de reproduction, allopatrie de reproduction, bio-logging, espèce en danger, oiseau marin, Pétrel diablotin, *Pterodroma hasitata*

Wildlife populations of conservation concern face acute disturbances that place them at risk of extirpation. These can either include historic stressors, e.g., geologic or weather-related, or anthropic stressors, e.g., habitat destruction or introduction of invasive species. Conservation efforts are guided by principles of redundancy (a species' capacity to persist despite the loss of a population), representation (the existence of genetic and phenotypic diversity within the species), and resiliency (the species' ability to withstand stochastic disturbances; Shaffer and Stein 2000). However, the effective application of these principles often requires comprehensive information that may be incomplete or entirely lacking. For example, limited understanding of genetic partitioning within populations may prevent adapted conservation actions, potentially resulting in the loss of a significant proportion of genetic variation in these populations (Ennos *et al.* 2005, Danckwerts *et al.* 2021).

In seabirds, genetic differentiation can occur due to various isolating mechanisms. In particular, as many species of seabird demonstrate high levels of colony philopatry, reproductive isolation remains one of the principal mechanisms for genetic structure (Friesen *et al.* 2007a). Reproductive isolation may be further driven by social mechanisms, such as differences in the extent of philopatry between sexes in *Uria lomvia* (Thick-billed Murre; Ibarguchi *et al.* 2011), temporal mechanisms, such as breeding allochrony in the sympatric *Hydrobates jabejabe* (Cape Verde Storm-Petrel; Medrano *et al.* 2022), or geographic ranges, such as pantropical biogeographic isolation in *Sula sula* (Red-footed Booby; Le Corre 1999). In some cases, a combination of some or all of these mechanisms may contribute to reproductive isolation (Danckwerts *et al.* 2021).

Pterodroma hasitata, the Black-capped Petrel, known locally as Diablotin, is the only extant *Pterodroma* petrel nesting in the Caribbean. The species is listed as globally Endangered by the International Union for Conservation of Nature (BirdLife 2018) and was recently listed as endangered under the U.S. Endangered Species Act, in part because the breeding population is both low in abundance and negatively affected by habitat loss due to deforestation and forest fires and by predation by nonnative mammals (U.S. Fish and Wildlife Service 2023). Two morphotypes have been described (dark and light, with an intermediate gradient) that differ in size and by the amount of white plumage on the face, back of the neck, and under-wing feathers (Fig. 1; Howell and Patteson 2008, Satgé *et al.* 2023a). These phenotypic differences are explained by a fixed population structure, with a strong genetic divergence between the two forms (Manly *et al.* 2013), suggesting the existence of distinct populations that are isolated geographically, temporally, or both (Howell and Patteson 2008, Manly *et al.* 2013, Satgé *et al.* 2023b). The dark form begins the breeding period with visits to nesting grounds during mid-November; egg-laying occurs in mid-January, hatching in mid-March, and fledging approximately during mid-June (Satgé *et al.* 2023a). Analyses of molt patterns suggest that the light form may breed 1 to 1.5 months earlier (Howell and Patteson 2008, Manly *et al.* 2013). To date, about 140 *Pterodroma hasitata* nesting burrows have been located, all on Hispaniola. Breeding areas have been found in La Visite and Morne Vincent in Haiti, and Loma del Toro, Loma Quemada, and Valle Nuevo in the Dominican Republic. Breeding is probable in Dominica (based on radar and visual observations of adults in appropriate habitat) and suspected in Cuba, Jamaica, and Guadeloupe (Wheeler *et al.* 2021). To date, breeding activity of the dark form has been documented in Haiti and the western Dominican Republic (Loma del Toro and Loma Quemada), while breeding activity of the light form has only been documented in the central Dominican Republic (Valle Nuevo; Satgé *et al.* 2023a).

Using satellite tracking of *Pterodroma hasitata* captured at sea in their non-breeding range in the western North Atlantic, the objectives of this study were to (1) track individuals back to breeding areas in an attempt to locate previously undocumented areas, and (2) assess differences in breeding connectivity and timing of movements between the dark and light forms.

Methods

Fieldwork

During 8 to 14 May 2019, we captured *Pterodroma hasitata* in Gulf Stream waters, about 60 km southeast of Cape Hatteras, North Carolina, USA; an area where foraging *P. hasitata* are commonly found during the non-breeding season

Fig. 1. *Pterodroma hasitata* individuals, captured and tagged at sea off Cape Hatteras, North Carolina, USA. (a) to (c), Petrel 442 (dark form), on 14 May 2019. (d) to (e), Petrel 462 (light form), on 9 May 2019. Lateral views and upper and lower wings are shown. Photographs by Y.G. Satgé.

(Simons *et al.* 2013). After assessing captured petrels for general condition, we banded each with an individually numbered metal band (U.S. Geological Survey Bird Banding Laboratory, Maryland, USA). We photographed the bird's profiles, upper wings, and under wings, and classified each as either a dark-, intermediate-, or light-form bird. We deployed solar-powered Argos platform terminal transmitters (PTTs, also called satellite transmitters) of two types: eight GT-5GS [GeoTrak Inc., North Carolina, USA], weighing 8.5 g; and two 5g-Solar-PTT [Microwave Telemetry Inc., Maryland, USA], weighing 8.5 g. Using four subcutaneous sutures, the satellite transmitters were attached dorsally on petrels whose body mass was > 350 g. Satellite transmitters had a duty cycle of 6 h 'on' followed by 28 h 'off' (GeoTrak) or 5 h 'on' and 48 h 'off' (Microwave Telemetry), where 'on' means that location data are being recorded and battery power is being used, and 'off' means that location data are not being recorded and battery power is not being used. These configurations were a trade-off between maximizing data collection, maximizing solar-powered battery recharge during 'off' periods, and minimizing battery discharge in the eventuality that petrels were underground during 'on' periods. We collected a few drops of blood onto filter paper from one metatarsal vein for genetic sexing (Fridolfsson and Ellegren 1999). Before release, we placed equipped birds in a holding crate lined with a dry cloth towel until chest feathers were preened (about 20 min). We refer readers to Satgé *et al.* (2023b) for details of capture methods, transmitter deployment, and a discussion of breeding status. All animal handling was performed under Clemson University's Animal Care and Use protocol AUP2019-033. Banding and PTT deployment were

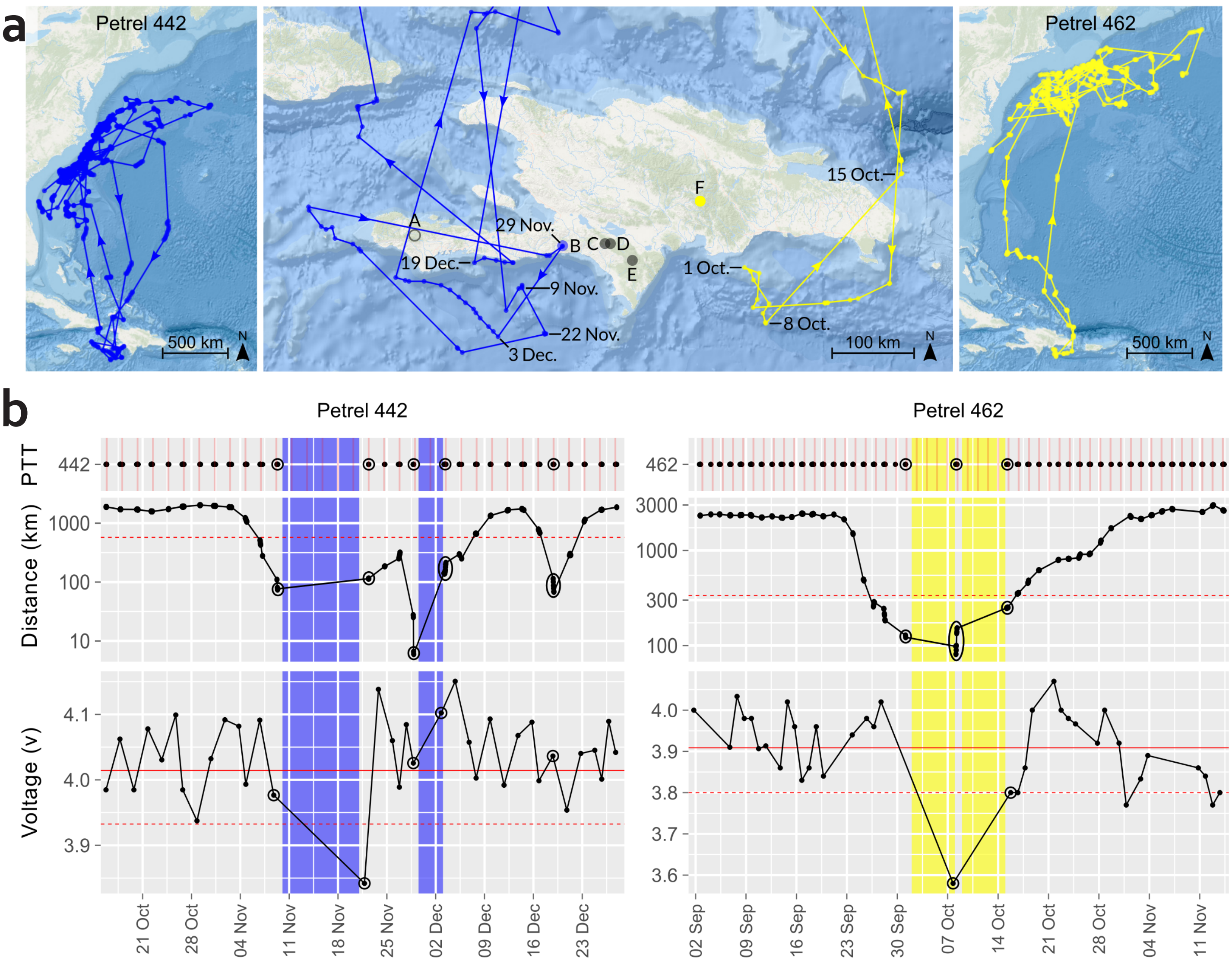

Fig. 2. Movements and accessory tracking information of two *Pterodroma hasitata* tracked to the vicinity of known breeding sites on Hispaniola, September–December 2019. (a) Left and right panels: map of movements of each petrel for the entire tracking period (petrel 442: 14 May 2019 to 24 January 2020; petrel 462: 9 May to 14 November 2019). Center panel: map of movements of both tracked petrels in close proximity of Hispaniola. Dates represent day when petrels were closest to a known breeding site. Circles represent known (filled) or suspected (outlined) breeding sites on Hispaniola: A: Pic Macaya, Haiti; B: La Visite, Haiti; C: Morne Vincent, Haiti; D: Loma del Toro, Dominican Republic; E: Loma Quemada, Dominican Republic; and F: Valle Nuevo, Dominican Republic. The blue circle (B) represents the most likely breeding site visited by petrel 442, and the yellow circle (F) the most likely breeding site visited by petrel 462. Esri Ocean Basemap. (b) For all panels, black ovals represent dates shown on the center map in (a); shaded areas show periods of suspected visits to breeding sites. Top panels: dates of communications between platform terminal transmitters (PTTs) and satellites; vertical red bars represent scheduled communications, and black dots represent actual communications. Middle panels: distance (logarithmic) to most likely breeding site; horizontal dashed lines represent a distance of 574 km (petrel 442) and 334 km (petrel 462), respectively, based on the distance flown by a petrel during half of each transmitter's 'off' period. Bottom panels: battery levels of PTTs; horizontal solid red lines represent mean battery level, and horizontal dashed red lines represent 10th percentile of all the voltages during the period shown.

authorized by the USGS Bird Banding Lab (permit #22408). The tracking data are publicly available (see Satgé *et al.* 2023c).

Assessment of visits to breeding areas

To improve the accuracy of Argos location estimates (whose estimated errors range from less than 100 m to more than 100 km; CLS 2016), we filtered PTT locations and estimated the most probable "true" location using a continuous-time random walk state-space model (package aniMotum in R; Jonsen *et al.* 2023). We kept only fitted locations where the standard error for longitude and latitude was less than 10.3 km (i.e., the 95th percentile of the error radius of Argos location classes 0–3). We assumed that locations near known breeding sites were likely to indicate some form of breeding activity (e.g., prospecting or nest initiation). We also assumed that breeding activity (e.g., occupancy of a burrow) would lead to gaps in communications between the satellite transmitter and satellite system and to low voltage levels of the satellite transmitter. Therefore, for locations during a period assessed within one month before and one month after a suspected visit to a breeding site, we used three criteria to posit breeding activity, requiring that at least two be confirmed for a location to be classified as a likely visit to a nest or breeding site. First, we calculated the distance from the transmitter location to the nearest documented breeding site with function distGeo in package geosphere in R (Hijmans 2019). Second, we used location and metadata from each transmitter to assess gaps in satellite communication. Third, we compared mean daily battery voltage with the overall mean voltage during the assessed period.

Unless locations were recorded within less than 10 km from a known breeding site, we posited breeding activity when at least two of the following criteria were met: (1) GeoTrak and Microwave Telemetry transmitters were within 334 km or 574 km of a documented breeding site, respectively (i.e., the distance flown by a petrel during half of the transmitter's 'off' period at a median average hourly speed of 23.9 km/hr, calculated from Jodice *et al.* 2015 and Satgé *et al.* 2019); (2) gaps in satellite communication exceeded 56 hr or 96 hr, respectively (i.e., 2 times the typical 'off' period) indicating the bird may be under thick cover and the transmitter is thus incapable of transmitting; or (3) the transmitter's voltage following a suspected visit was within the 10th percentile (i.e., lowest 10% range) of all voltage levels for that transmitter during the assessment period, representing a difference with regular voltage levels great enough that it could not be due to the normal battery charge/discharge process but instead was likely due to the bird being under thick cover where the solar panels could not recharge the transmitter. R scripts used to perform the analyses and create Fig. 2 are available at https://github.com/YvanSG/PterodromaHasitata_JCO_2025.

Results

We captured 10 *Pterodroma hasitata* between 8 and 14 May 2019: three females and seven males. We classified five petrels as dark forms, four as light forms, and one as intermediate. Deployed PTTs ranged between 1.85% and 2.30% of body mass (mean: 2.16%). Processing time ranged from 13 to 23 min (mean: 18 min) per individual. Petrels were tracked for 11 to 255 days (mean: 102.1 days ± 74.2 SD; median: 108.5 days). We refer readers to Satgé *et al.* (2023b) for further details on capture effort and success, petrel morphometrics, and movements within the western North Atlantic.

Of the 10 transmitters deployed, eight were no longer transmitting at the onset of the 2019 breeding season and two were still transmitting: petrel 442 (male dark form) and petrel 462 (male light form; Fig. 1). Both individuals subsequently made southerly trips to the Caribbean (Fig. 2). Here, we describe the movement patterns and data on transmitter performance for each, and how these data were used to infer or posit breeding activity.

Based on location and transmitter data, we suspect petrel 462 was at a breeding site during early to mid October 2019. He departed pelagic waters along Georges Bank off Cape Cod, Massachusetts, USA between 21 and 22 September 2019, reached the Puerto Rico Trench on 27 September, and transited the Mona Passage between 27 and 28 September (for locations of marine areas visited by petrels, we refer the reader to Figure 1 in Satgé *et al.* 2023b). On 29 September, a class-A Argos location (i.e., a location with unbounded accuracy estimation, calculated from three satellite messages only) was recorded about 8 km to the east of the known breeding area of Valle Nuevo National Park, Dominican Republic (Fig. 2a, circle F). This location had an error radius of 21.5 km (which includes coastal areas in the Dominican Republic) and was not retained by our continuous-time random walk state-space model. This was the only location recorded over land for this individual. On 1 October 2019, petrel 462 was at sea, about 122 km to the southeast of the known breeding area at Valle Nuevo. Between 1 and 15 October, scheduled satellite communications did not occur, except for a short burst on 8 October: on that day, petrel 462 was at sea, about 118 km (range: 81–152 km, *n* = 8 locations) to the southeast of Valle Nuevo, and the battery level was 3.58 V (Fig. 2b). On 15 October, petrel 462 was heading north of the Mona Passage 248 km from Valle Nuevo, and the battery level was 3.8 V. He made multiple stops in the southern reaches of the Sargasso Sea along the Antilles Current, and on 1 November, he had returned to pelagic waters off the Virginian ecoregion where he remained until locations were no longer being received from the transmitter on 14 November. For the remainder of the tracking duration (16 October to 14 November 2019), battery levels remained high (mean = 3.88 V ± 0.10 SD; range: 3.66–4.10 V), and satellite communications occurred as scheduled. Between 1 September and 14 November, the mean battery voltage was 3.91 V ± 0.10 SD.

Based on location and transmitter data, we suspect petrel 442 was at a breeding site during November and early December 2019. He made two trips from the Gulf Stream to the Caribbean during the time he was being tracked. Between 31 October and 2 November 2019, he departed the waters of the Gulf Stream northeast of Cape Hatteras and traveled southward through the Hatteras Abyssal Plain and the Sargasso Sea. On 7 November, he reached the Turks and Caicos shelf and subsequently passed through the Windward Passage. On 9 November, petrel 442 was located at sea about 83 km (range: 74–110 km, *n* = 4 locations) southwest of the nearest known breeding site at the La Visite escarpment of Haiti (Fig. 2a, circle B). Between 9 and 22 November, scheduled satellite communications did not occur (Fig. 2b). On 22 November, he was at sea about 114 km south of La Visite (range: 114–115 km, *n* = 4 locations), and the battery level was 3.84 V. Between 24 and 27 November, he occupied neritic and semi-pelagic waters south and west of the Haitian peninsula, and within about 250 km of La Visite. At the start of 29 November, petrel 442 was within range of the La Visite breeding site: 6 to 7 km (*n* = 2 locations). Satellite communications failed to occur between 29 November and 3 December. On 3 December, he was at sea about 160 km (range: 139–213 km) southwest of La Visite, traveling west, and the battery level was 4.1 V. On 5 December, he passed through the Windward Passage and traveled through the western extent of the Hatteras Abyssal Plain to Gulf Stream waters south of Cape Hatteras. He remained there until 14 December, when he initiated a second trip to the Caribbean. Limited details are available, but, on 17 December, he was located traveling south through the Antilles Current. On 19 December, the bird was located about 2.5 to 10 km offshore of the southcentral coast of the Haitian peninsula and 86 km (range: 68–114 km, *n* = 6 locations) away from La Visite; the battery level was 4.05 V. On 21 December, petrel 442 was traveling north through the Windward Passage, 291 km (range: 283–302 km, *n* = 8 locations) away from La Visite; the battery level was 3.95 V. On 25 December, he had returned to Gulf Stream waters of the Carolinian ecoregion. Except for a trip to the vicinity of the Caryn Seamount in the northern extent of the Hatteras Abyssal Plain, he remained there until the last transmission from the transmitter was received on 24 January 2020. For the remainder of the tracking duration (21 December 2019 to 24 January 2020), battery levels remained relatively high (mean = 3.98 V ± 0.06 SD; range: 3.85–4.12 V), and satellite communications occurred as scheduled. Between 15 October and 29 December, the mean battery voltage was 4.04 V ± 0.06 SD.

Discussion

Our study supports the hypotheses of allochrony and allopatry between the two color forms of *Pterodroma hasitata*. The two birds we tracked traveled from the same tagging location (i.e., non-breeding foraging area) in the western North Atlantic off of Cape Hatteras to two different breeding areas in Hispaniola (separated by about 180 km) during two different periods of time. In late September 2019, the light-form petrel traveled from Georges Bank to eastern Hispaniola, where it appeared to be active at a breeding site during early October, likely in Valle Nuevo National Park, in the Cordillera Central of the Dominican Republic. Valle Nuevo was confirmed as a nesting area in 2017 (Rupp 2017); between 2017 and 2024, about 30 nests were located (E. Rupp, Grupo Jaragua, pers. comm.). In October 2019, the dark-form petrel traveled from the continental shelf off Hatteras, North Carolina, USA to the La Visite breeding area of eastern Haiti, where it appeared to be active during mid-November, and then again during late November/early December. Although none of the birds we tracked led us to discover previously unknown breeding areas, our study supported and broadened our understanding of connectivity of *Pterodroma hasitata* between foraging areas in the western North Atlantic and breeding sites in Hispaniola. Connectivity between the breeding area of Loma del Toro in the southwestern Dominican Republic and Gulf Stream waters of the western North Atlantic was confirmed in dark-form petrels by Jodice *et al.* (2015), but this study is the first to explicitly link the marine and terrestrial areas of a light-form *Pterodroma hasitata* and to confirm the link between Gulf Stream waters and the breeding area of La Visite.

To infer breeding activity, we used a combination of tracking locations, satellite communication schedules, and battery voltage. Ordinarily, satellite transmitters can inform about visits to broad breeding areas. However, PTT duty cycles, which are designed to optimize tracking time over battery usage, may limit the temporal and spatial precision needed to confirm breeding activity based solely on location data, particularly for smaller-sized solar units (Northrup *et al.* 2018). Indeed, the quality of locations obtained by Doppler effect (as is the case with PTTs) is variable and depends on the number and location of Argos satellites within view and reach during the limited period when the transmitter is on, and on the number of messages received from those satellites (CLS 2016). In seabirds that spend time underground at the breeding site, the number and quality of location records in breeding areas is generally decreased. Additionally, when underground or exposed to low or limited light levels, PTTs cannot transmit data as scheduled nor fully sustain an adequate voltage (Ens *et al.* 2008, Spencer *et al.* 2014). Because *Pterodroma hasitata* are active at sea during daylight hours (Haney 1987, Simons *et al.* 2013), solar-powered transmitters can transmit and recharge adequately during flight and foraging activity. Therefore, it is possible to use a combination of scheduled satellite communications that were missed and low voltage levels to identify periods of limited satellite connectivity and low-light input in solar-powered transmitters, i.e., periods when petrels are suspected to be in densely forested areas or underground.

Our analysis used the distance between a transmitter location and a known breeding site as a criterion to posit breeding activity. Due to the limited size of the solar panels and charging capacity, the transmitters we used require extended 'off' periods during which the location and movements of *Pterodroma hasitata* could not be determined. Because of these long 'off' periods, the distance threshold we used to posit breeding activity (574 km) was particularly high for the Microwave Telemetry transmitter (48-hr off period) deployed on petrel 442. While we do not claim that every location within 574 km of a breeding site posits breeding activity, camera trapping of petrels tracked with PTTs or GPS loggers showed that petrels traveling large distances towards breeding area typically return to their burrow, even when tracking locations are missing near the breeding site (Jodice *et al.* 2015, Satgé *et al.* 2019). Therefore, we suggest that the distance threshold remains a valuable criterion when used in combination with communication schedules and voltage levels.

Our results support the suggestion that dark-form petrels nest predominantly in Haiti and the adjacent southwestern

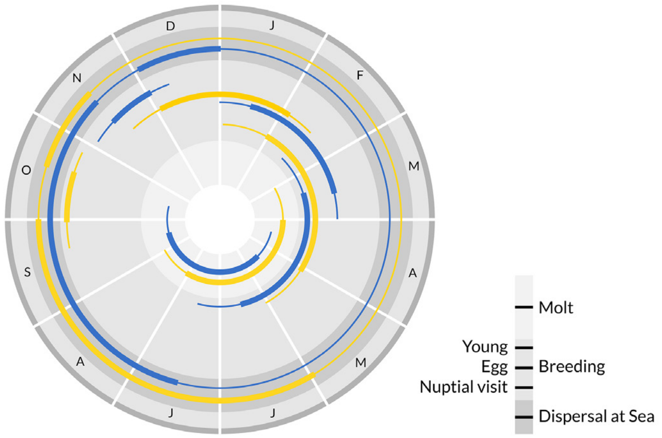

Fig. 3. Revised annual cycle of breeding, molt, and migration in *Pterodroma hasitata*, showing distinct phenologies between dark and light forms. Blue = dark form; yellow = light form. Thick lines show peak activity; thin lines, off-peak. Based on Simons *et al.* (2013), Howell and Patteson (2008), and this study.

Dominican Republic, and light-form petrels nest in Valle Nuevo National Park in the central Dominican Republic (Satgé *et al.* 2023a). Nevertheless, this apparent allopatry may not be complete given that at least one dark-form petrel has been observed nesting among light-form petrels in Valle Nuevo (E. Rupp, Grupo Jaragua, pers. comm.). Therefore, if dark and light forms have breeding distributions that are predominantly distinct, Valle Nuevo may be an area where these two populations overlap. Nonetheless, the breeding distribution of the light phenotype, its population size, and any form-specific threats remain poorly understood.

Although limited (and potentially influenced by individual variability and differences in age and breeding status between the two petrels), our data also support earlier indications based on molt and phenology in the Gulf Stream (Howell and Patteson 2008, Manly *et al.* 2013) and nest monitoring at breeding sites (Rupp and Satgé 2023) that light-form petrels breed 1 to 1.5 months earlier than the dark form. Our data support that the light form appears to breed from early October to late April, while the dark form appears to breed from mid-November to mid-June (Fig. 3).

Despite the small sample size of our study, we demonstrated the feasibility of capturing petrels at sea and subsequently tracking them from marine foraging areas to terrestrial breeding areas. Our results indicate that at-sea captures from other areas (e.g., offshore Dominica and Cuba) could lead to additional data on the location and timing of the use of breeding areas. Additionally, our results indicate that researchers wanting to use tracking data to confirm whether *Pterodroma hasitata* morphotypes are breeding in allochrony and allopatry may consider capturing petrels closer to the end of the non-breeding period, and use tracking devices with a higher spatial precision (e.g., GPS-quality) and temporal frequency. For example, the integration of GPS technology in new transmitter designs was instrumental in locating unknown nesting areas of *Pterodroma sandwichensis*, the 'ua'u or Hawaiian Petrel (Raine *et al.* 2022). At breeding sites, researchers may consider assessing a representative sample of nests in each nesting area and enhancing monitoring to more thoroughly document nest-attendance patterns (e.g., using remote cameras; Pagenaud *et al.* 2025).

In vagile species, genetic differentiation may be a consequence of distribution (Friesen 2015, Wiley *et al.* 2012), phenology (Friesen *et al.* 2007b), dispersal (Burridge and Waters 2020), or ecological niche (Ryan *et al.* 2014). The apparent allochrony and, possibly, allopatry in the two color forms of *Pterodroma hasitata* supported by data from this study may, therefore, be contributing to a speciation process as initial drivers of genetic structure in the population, or by contributing to divergence at any stage along the process (Taylor and Friesen 2017). Other mechanisms, such as non-breeding spatial segregation (Satgé *et al.* 2023b), may also be operating and could contribute to genetic differentiation in this species, although the causes and the importance of each mechanism remain untested and warrant additional investigation. Nevertheless, in light of threats affecting *Pterodroma hasitata* at breeding areas (Wheeler *et al.* 2021), conserving the species' representation and redundancy would also conserve evolutionary processes, allowing adaptive responses to environmental changes (Ennos *et al.* 2005).

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Author Contributions

All authors planned the study and participated in field data collection; YGS conducted data analyses and created figures; YGS, PGRJ, BSK, and CPG worked on manuscript drafts; YGS and PGRJ reviewed and edited the final manuscript; BK, PGRJ, and YGS secured funding and collaborations to support this study.

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