

Diverse foraging strategies of breeding Swinhoe's Storm-petrel in the productive marginal sea of the Northwest Pacific

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ABSTRACT

Understanding the foraging behavior is essential for investigating seabird ecology and conservation, as well as monitoring the well-being of the marine environment. Breeding seabirds adopt diverse foraging strategies to maximize energy gains and cope with the intensified challenges of parenting and self-maintenance. Such trade-off may ~~plamg~~ from the heterogeneity of food resources and the ~~foragrain~~ constraints of

Individuals are expected to optimize their energy intake and trade between self-maintaining and parental care in the demanding breeding period (Pyle, 1984; Riebel, 1984). Seabird individuals might adopt various foraging strategies to cope with these tasks (Baduini and Hyrenbach, 2018; Mamara and Houston, 2018). Both intrinsic i.e., physiological differences for individual specialization and extrinsic i.e., environmental factors can drive the variation of foraging strategies within geographical populations or even a breeding colony (Phillips et al., 2018; Clay et al., 2019; Jessopp et al., 2019). Empirical studies have suggested that the heterogeneity and state-dependent pre-

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and captured by hands when birds landed on the ground or entered the burrows at night. PS-HF loggers (Hunan Global Messenger Technology Co., Ltd., H B) with solar panels were used to determine the at-sea distribution and classify foraging trips. The dimension of the logger is $30\text{ mm} \times 30\text{ mm} \times 30\text{ mm}$ with a pliable external antenna 100 mm , and the average weight with attachment is $1.5 \pm 0.5\text{ g}$. PS devices were programmed to obtain location every 1 h and transmit the data every hour when birds return to the reception range 100 m of the HF receiver pole, installed at a building roof at the top of the island around 10 m elevation. Accuracy of PS positioning ranges from 10 to 20 m. If the device fails to obtain a connection with PS satellites, the accuracy of the point will be marked as “invalid”. The HF receiver is also solar-powered and uploads the data to the back-end database via the GSM cell phone network. Upon capture, we measured the morphology data, including body weight, wing length, bill length, tarsus length, and wing area and calculated wing loading. Then, we attached the devices using a wing-loop backpack harness (Lago et al., 2019). Once the handling was done, birds were released at the same capture location, and the whole process was within 1 h for each bird. To reduce the impacts and stress due to handling, we did not take the blood sample; thus, there was no information on sex for tracked birds.

The average body weight of captured birds was $110 \pm 10\text{ g}$. The devices and harness weighted $1.5 \pm 0.5\text{ g}$ of the tracked birds' body mass under the empirical threshold value (Green et al., 2019). The average bill length was $45 \pm 5\text{ mm}$, wing length $110 \pm 10\text{ cm}$, tarsus $25 \pm 5\text{ mm}$, wing area $150 \pm 20\text{ cm}^2$ and wing loading $0.01 \pm 0.02\text{ g cm}^{-2}$. Original morphological data are shown in Appendix Table S1. We excluded two individuals with malfunctioning devices that the birds might directly go back to long incubation shifts in burrows after release, which drained the battery. In the end, individual tracking duration ranges from 1 to 30 days, with an average of 15 ± 5 days.

Statistical analysis

Without further indication, we processed and analyzed the data in R (R Core Team, 2023). The average values are shown in mean $\pm$ standard deviation, and the significance level is 0.05. We measured the tag performance by first calculating the ratio of the total number of fixing attempts (including invalid points) to the expected record number of tracking duration, representing battery performance. Then, we calculated the ratio of successful points to the expected PS fixes according to the tracking duration, which represents the positioning success rate.

We first filtered the PS dataset to remove the locations which failed to fix and the locations within the breeding colony boundary. The coarse and irregular resolution of positions limits our ability to apply sophisticated algorithms, such as Hidden Markov Models, to identify foraging behavior at sea (Michelot et al., 2019). Storm-petrels typically use surface seizing techniques to forage (Brooke, 2004). We, therefore, defined PS positions with altitudes lower than 10 m above sea level as foraging. To assess the foraging habitat selection of Swinhoe's Storm-petrels at Yellow Sea, we used the Resource Selection Function to compare the features of used and available habitats within the home range, i.e., Johnson's third order selection, using “amt” package (Johnson, Signer et al., 2019). For each foraging point, we generated 1000 random points with the same timestamp within the Minimum Convex Polygon (MCP) home range to measure the habitat availability using the “ade4” package (Calenge, 2006).

Based on the previous literature of seabird at-sea distribution, we used a set of static and dynamic habitat variables, including sea surface temperature, bathymetry, distance to the shore, and marine primary productivity, which was measured by chlorophyll A mass concentration (Huillfeldt et al., 2019; De la Cruz et al., 2020). Sea surface temperature

Swinhoe's Storm-petrels are shown in Fig. . Environmental conditions of the two foraging strategies significantly differ in water depth $t = 1.04$, $p = 0.30$, distance to coast $t = 1.04$, $p = 0.30$ and sea surface temperature $t = -0.01$, $p = 0.99$. We did not find the impact of chlorophyll concentration $t = 0.01$, $p = 0.99$ and wind conditions wind support $t = 0.01$, $p = 0.99$, crosswind $t = -0.01$, $p = 0.99$ on foraging strategies. Individuals who were capable of conducting long southeastward trips had significantly longer wings $t = 0.01$, $p = 0.99$ and tendency of lower wing loading $t = -0.01$, $p = 0.99$, but were not different in body weight $t = -0.01$, $p = 0.99$, tarsus $t = 0.01$, $p = 0.99$, bill $t = 0.01$, $p = 0.99$ and wing area $t = 0.01$, $p = 0.99$ see Fig. .

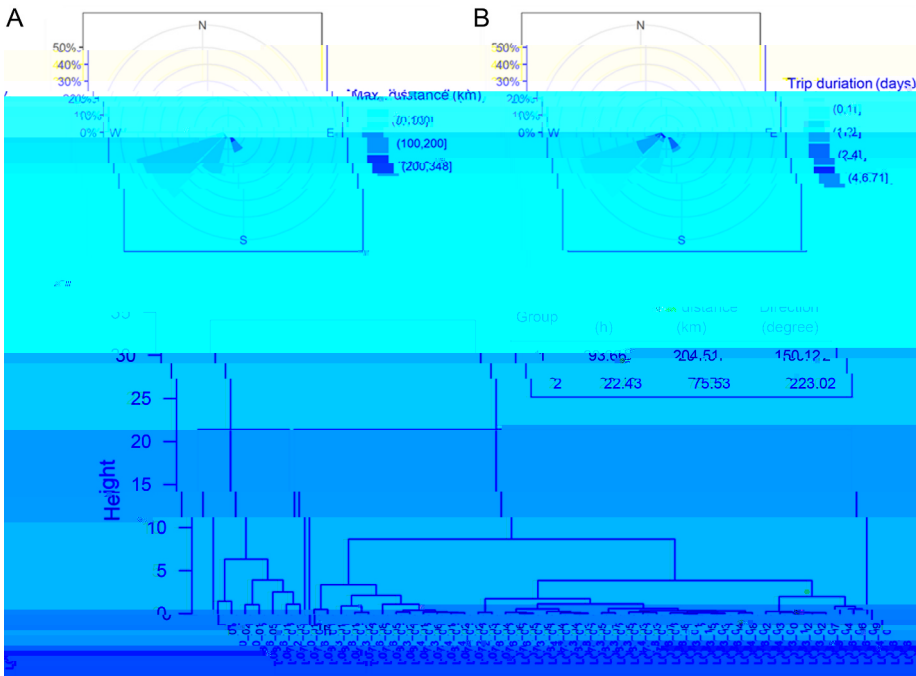
In this research, we studied the foraging behavior of a mysterious tubenose species, the Swinhoe's Storm-Petrels, using PS-HF telemetry devices in a highly productive continental shelf of the Northwest Pacific during the breeding season. Consistent with our predictions, Swinhoe's Storm-petrels preferred nearshore marine habitats with shallow water and adopted mostly short foraging trips during breeding. Although foraging trip metrics were not significantly different from unimodal distribution separately, diversified foraging strategies emerged when considering the combination of foraging direction, duration and maximum distance. The infrequent long southeastward foraging trips were distinguishable from short southwestward trips and were different in bathymetry, distance to the coast and sea surface temperature. Foraging strategies were also flexible between individuals, which could be explained by wing morphology.

High marine primary productivity 1.0 ± 0.5 mg m⁻² might facilitate Swinhoe's Storm-petrels of Dagong island foraging exclusively on the continental shelf of Yellow Sea China and travelling a short distance from the colony most of the time. In comparison, Leach's Storm-petrel closely relative species of Swinhoe's Storm-petrel foraged long distances $100 - 200$ m and mostly on shelf slope with low chlorophyll A concentration of less than 0.5 mg m⁻² Heddd et al., . The nearshore distribution of Swinhoe's Storm-petrels that we observed agrees with the relationship of Storm-petrels' plumage and distribution in the Eastern Pacific, in which dark plumage Storm-petrel species occurred more in the continental shelf and light-rumped Storm-petrels occupied the depth pelagic ocean Spear and Ainley, . The dark rump plumage of Storm-petrels, such as in Swinhoe's, might S

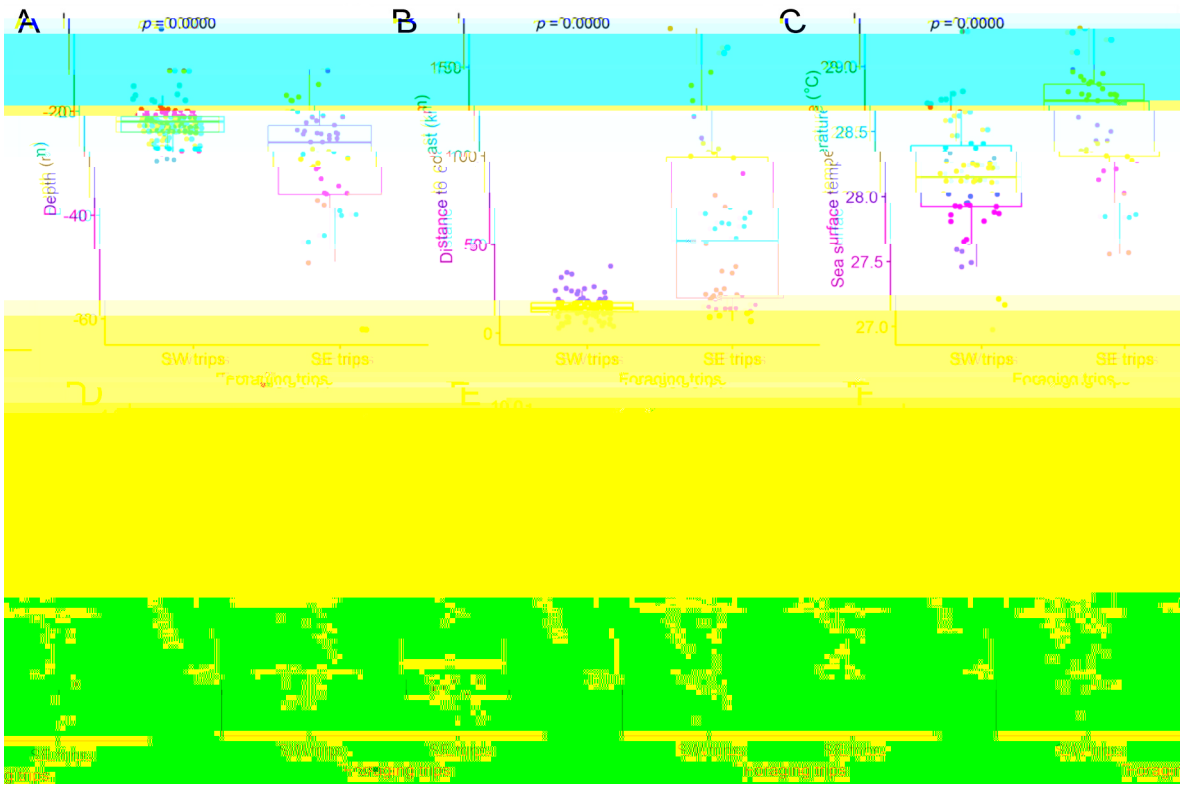
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$n = 10$ and short southwestward trips $n = 10$. Duration, maximum distance and direction significantly differed between groups Wilcoxon test, all value < 0.05 . Four Swinhoe's Storm-petrels exclusively performed the southwest short trips. One bird only went to the southeast, and three birds adopted both strategies and went in two directions Table .

The comparison of extrinsic factors on the foraging strategy of



Diversified foraging trips $n =$ of breeding Swinhoe's Storm-petrels at Dagong Island, the Yellow Sea, China. Upper panel windrose plots of direction, frequency, and maximum distance to the colony A and duration B. Lower panel cluster dendrogram of foraging trip metrics and mean value of grouped foraging trip metrics. The foraging trips of Storm-petrel clustered into two: a few long trips to the southeast direction group, $n =$, and the majority of short trips went to the southwest group, $n =$. Trip IDs are shown at the bottom of the dendrogram. For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.



Comparison of environmental features of two groups of foraging trips towards southeast and southwest direction relative to the breeding colony. Environment variables include A water depth, B distance to the coast, C sea surface temperature, D chlorophyll A concentration, E wind support and F crosswind. The values of the t -test or Wilcoxon test are shown in each boxplot.

species [Pollet et al.,](#) [Neves et al.,](#) . The longer trips might also be a sex-specific strategy for females to compensate for the energy expenditure of eggs [Maucler et al.,](#) . Unfortunately, due to the various logistic constraints to access the breeding colony, we had no information on the breeding stage and the sex of the tracked individuals, thus requiring further study to conclude the role of foraging

Foraging longer distances is costly both time- and energy-wise for seabirds, so we expect longer trips to target highly productive areas and potentially supported by favorable wind [Clay et al.,](#) and [Phillips et al.,](#) . Unexpectedly, we did not find chlorophyll A concentrations and wind conditions differ between southeast and southwest trips. One potential explanation might be the spatial-temporal foraging strategy. For tracking and remote sensing data [r  millet et al.,](#) . Another data explanation might be that the Swinhoe's Storm-petrels were attracted by specific unknown resources in the deep sea with warmer temperatures and far from the coast. Seabirds are strongly associated with oceanographic features such as water masses [Ballance et al.,](#) . In the bottom of the Yellow Sea, the Yellow Sea Cold Water Mass provides a refuge for North Pacific temperate fauna, resulting in high biodiversity and concentration of zooplankton deep down the Ocean [Liu,](#) . Therefore, it is reasonable to speculate that the cold-water fauna in the Yellow Sea Cold Water Mass might attract Swinhoe's Storm-petrels to travel long distances for food.

We found that foraging strategies were flexible between individuals of Swinhoe's Storm-petrels, suggesting a certain degree of individual specialization [Bolnic et al.,](#) . It might be that morphology might explain the inter-individual variation as longer wing and lower wing loading would facilitate a faster flying speed for longer foraging distances in seabirds [Clay et al.,](#) and [a](#) . We also found that foraging strategies were flexible within individuals. Capturing birds and deploying biologging devices might cause additional energy costs, triggering long-distance foraging for self-maintenance. However, we think it is not likely the case and the foraging strategies were neither related to the body weight

nor handling time. Therefore, the causes of intra-individual variation require further investigation.

Tracking small-sized seabirds is still challenging, as living in the underground burrow and long incubation shifts hinder the charging of solar batteries and GPS signal reception. Although we had a small number of tracked individuals, we obtained a comparable number of foraging trips owing to a longer tracking period [Clay et al.,](#) and [Bolton,](#) .

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provides novel insights into the small-sized seabird foraging ecology in the marginal sea of the Northwest Pacific. Swinhoe's Storm-petrels that forage on the continental shelf exhibit diverse foraging strategies despite high marine productivity. This result highlights the significance of both external environmental factors and internal individual characteristics in shaping their foraging choices. Even though Swinhoe's Storm-petrels mostly roamed nearshore compared to their sibling species, the foraging trips were far beyond the boundary of Dagong Island Nature Reserve, urging the need to expand or establish new marine protected areas. Therefore, our work is especially relevant to achieve the "× goal of unming-Montreal Global Biodiversity Framework", as only . of China's maritime area is protected by far Zhou et al., . We encourage future research on Procellariiformes in the Northwest Pacific, including conducting a systematic population survey across the breeding region, studying diets and migration, evaluating local threats, establishing a long-term monitoring regime, etc.

The authors, who included licensed bird ringers, strictly followed the Chinese Wild Animal Protection Law requirements and were approved by the Dagong Island Ecosystem Provincial Nature Reserve. All the activities of captured and banded birds were supervised, collaborated and under the license of Jingdao Bird Ringing Station.

The authors declare that they have no competing interests.

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PS Tracing data are available at the Movebank Repository Cheng et al., . Communication log data of devices with HF receivers for data interpolation are provided in Appendix Table S .

Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. Investigation. Supervision, Project administration, Investigation. Investigation, Data curation. Investigation, Data curation. Investigation. Supervision, Project administration. Investigation. Writing – review & editing, Supervision, Resources, Project administration, Funding acquisition, Conceptualization.

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- Arcilla, N., Choi, C.Y., Oza, I., Lepczyk, C.A., . Invasive species and Pacific island bird conservation: a selective review of recent research featuring case studies of Swinhoe's Storm-petrel and the Oinawa and Guam rail. *J. Ornithol.*, S –S .
- Baduini, C.L., Hyrenbach, D., . Biogeography of procellariiform foraging strategies does ocean productivity influence provisioning? *Mar. Ornithol.*, – .
- Ballance, L.T., Pitman, R.L., Fiedler, P.C., . Oceanographic influences on seabirds and cetaceans of the eastern tropical Pacific: a review. *Prog. Oceanogr.*, – .
- Beal, M., Oppel, S., Handley, J., Pearmain, E.J., Morera-Puol, ., Carneiro, A.P.B., et al., . Tracking Balaenarctica: a package for identifying important sites for biodiversity from tracking data. *Methods Ecol. Evol.*, – .
- BirdLife International, . *Yrobate onorhi*. IUCN red list threat. SPECIES <https://doi.org/10.2305/IUCN.UK.2019.2.RLTS.T1.A1.en>. Accessed October .
- Boersma, P.D., room, M.J., . Conservation of storm-petrels in the North Pacific. In *The Status, Ecology and Conservation of Marine Birds in North Pacific*. Canadian Wildlife Service Special Publication, Ottawa, Ontario, Canada.
- Bolnic, D.L., Svanbäck, R., Fordyce, J.A., Yang, L.H., Davis, J.M., Hulseley, C.D., et al., . Individual specialization. *Am. Nat.*, – .
- Bolton, M., . PS tracking reveals highly consistent use of restricted foraging areas by European Storm-Petrels *Yrobate elagicu* breeding at the largest U colony: implications for conservation management. *Bird. Conserv. Int.*, – .
- Bond, A.L., McClelland, T., Jones, I.L., Lavers, J.L., yser, T., . Stable isotopes confirm community patterns in foraging among Hawaiian Procellariiformes. *aterbirds*, – .
- Bretagnolle, ., . Adaptive significance of seabird coloration: the case of Procellariiformes. *Am. Nat.*, – .
- Broome, M., . *Albatrosses and Petrels across the world*. Oxford University Press, Oxford.
- Calenge, C., . The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. *Ecol. Model.*, – .
- Carboneras, C., Jutglar, F., de Juana, E., irwan, M., . Swinhoe's storm-petrel *Yrobate onorhi*. In del Hoyo, J., Elliott, A., Sargatal, J., Christie, D.A., de Juana, E. Eds., *Birds of the world*. Cornell Lab of Ornithology, Ithaca, NY, USA.
- Choi, C.Y., Nam, H.Y., Par, J., Lee, ., . Swinhoe's Storm Petrels *ceano ro a onorhi* show no apparent sexual dimorphism in size and color. *Ornithol. Sci.*, – .
- Claustre, H., Maritorena, S., . The many shades of Ocean Blue. *Science*, – .
- Clay, T.A., Joo, R., eimers irch, H., Phillips, R.A., den Ouden, O., Basille, M., et al., . a. Sex-specific effects of wind on the flight decisions of a sexually dimorphic soaring bird. *J. Anim. Ecol.*, – .
- Clay, T.A., Oppel, S., Lavers, J.L., Phillips, R.A., Broome, M. de L., b. Divergent foraging strategies during incubation of an unusually wide-ranging seabird, the Murphy's petrel. *Mar. Biol.*, – .
- Collins, S.M., Hedd, A., Fife, D.A., ilson, D.R., Montevecchi, .A., . Foraging paths of breeding Leach's Storm-Petrels in relation to offshore oil platforms, Breeding Stage, and Year. *Front. Mar. Sci.*, .
- Cui, Z., . Study on reproduction and migration of ancient murrelet. *Chin. J. Zool.*, – . In Chinese .
- Cui, Z., . Study on breeding and migration of Swinhoe's Storm-Petrel. *Chin. J. Zool.*, – . In Chinese .
- Dalgaard, P., H . *Introduction* M.,

- Huang, X., Zhao, Y., Liu, Y., . . . Using light-level geolocations to monitor incubation behavior of a cavity-nesting bird *Uria lomvia*. *Avian Res*, 13, 1–10.
- Jessopp, M., Arneill, P.E., Nylinen, M., Bennison, A., Rogan, E., . . . Central place foraging drives niche partitioning in seabirds. *Oikos*, 121, 100–110.
- Johnson, D., . . . The comparison of usage and availability measurements for evaluating resource preference. *Ecology*, 75, 1416–1421.
- Kays, R., Davidson, S.C., Berger, M., Bohrer, G., Fiedler, S., Flacour, A., et al., . . . The Movebank system for studying global animal movement and demography. *Methods Ecol. Evol.*, 10, 1–10.
- Lago, P., Austad, M., Metzger, B.J., . . . Partial migration in the mediterranean storm-petrel *Hydrobia pelagicula*. *Mar. Ornithol.*, 48, 1–10.
- Lascelles, B., Taylor, P.R., Miller, M., R., Dias, M.P., Oppel, S., Torres, L., et al., . . . Applying global criteria to tracking data to define important areas for marine conservation. *Divers. Distrib.*, 25, 1–10.
- Liu, D., ang, X., . . . A preliminary study on ring study of Streaked Shearwater and Swinhoe's Storm-Petrel in coastal islands of Hainan. *Sichuan J. Zool.*, 58, 1–10. In Chinese.
- Liu, J.Y., . . . Status of marine biodiversity of the China seas. *PLoS One*, 15, e0230000.
- Liu, J., ang, C., . . . obari, T., Liu, H., Rabouille, C., Fennel, G., . . . Biogeochemistry and ecosystems of continental margins in the western North Pacific Ocean and their interactions and responses to external forcing – an overview and synthesis. *Biogeosciences*, 18, 1–10.
- Liu, Y., Jiang, G., . . . Marine bird resources and their conservation status in the Yellow Sea in China. *Bull. Biol.*, 10, 1–10. In Chinese.
- Ma, S., Liu, D., Tian, Y., Fu, C., Li, J., Ju, P., et al., . . . Critical transitions and ecological resilience of large marine ecosystems in the Northwestern Pacific in response to global warming. *Global Change Biol.*, 28, 1–10.
- Maechler, M., . . . Package 'diptest'. *R Pac. Ag. Extension*, 1–10. R J. Lang. Environ. Stat. Comput. Austria R Found. Stat. Comput., Vienna.
- Matsumoto, S., Yamamoto, T., Sawabe, R., Ohshimo, S., Yoda, K., . . . The Changjiang River discharge affects the distribution of foraging seabirds. *Mar. Ecol. Prog. Ser.*, 450, 1–10.
- Matsumoto, S., Yamamoto, T., Yamamoto, M., Zavalaga, C.B., Yoda, K., . . . Sex-related differences in the foraging movement of streaked shearwaters *Alonecetes leucorhoa* breeding on Awashima Island in the sea of Japan. *Ornithol. Sci.*, 19, 1–10.
- Mauc, R.A., Pratte, I., Hedde, A., Pollet, I.L., Jones, P.L., Montevecchi, C.A., et al., . . . Female and male Leach's Storm-Petrels *Hydrobia leucorhoa* pursue