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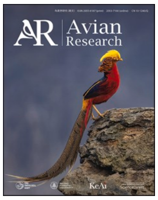

Diverse foraging strategies of breeding Swinhoe's Storm-petrel in the productive marginal sea of the Northwest Pacific

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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 stem from the heterogeneity of food resources and the constraints of central place foraging. Nevertheless, abundant marine productivity could alleviate the energy limitation for seabirds, resulting in a consistent foraging approach. Here, we investigated the foraging strategy during the breeding season of a cryptic small-sized seabird, Swinhoe's Storm-petrel (*Hydrobates monorhis*), in the Yellow Sea, a productive marginal sea of the Northwest Pacific. Using GPS tracking, we evaluated habitat preference, quantified the foraging strategy, and tested if environmental conditions and individual traits influence foraging trips. We found that Swinhoe's Storm-petrels preferred nearshore areas with shallow water and engaged in primarily short foraging trips. Distinctive south-eastward and southwestward strategies emerged when combining trip metrics, including foraging direction, duration, and maximum distance. The bathymetry, proximity to the coastline, and sea surface temperature differed in two foraging strategies. Foraging strategies exhibited flexibility between individuals, potentially explained by wing morphology, in which longer-winged birds are more likely to embark on longer-distance foraging trips. These findings highlight the impact of environmental factors and individual traits on seabirds' foraging decisions in productive marginal sea ecosystems. Our study also provides valuable insights into the foraging ecology of this Asian endemic storm-petrel.

1. Introduction

During the breeding season, birds have a strong obligation to return frequently to their nests in order to incubate or feed their chicks. As a result, their foraging ranges are very limited in space and time (Orians and Pearson, 1979; Phillips et al., 2017). In the marine environment, the heterogeneity and patchiness of food resources intensify birds' energy and time constraints (Phillips et al., 2017; Weimerskirch, 2007). Consequently, the trade-off between terrestrial breeding and oceanic feeding shapes the evolution of seabirds' unique life history strategies (Ricklefs, 1990; Schreiber and Burger, 2001; Young and Ballance, 2023). Seabirds are characterized by distinctive life history traits such as long life expectancy, low fecundity, prolonged and energetically expensive parental care; therefore, they are highly vulnerable to threats (Ricklefs, 1990; Schreiber and Burger, 2001; Brooke, 2004). Seabirds are also experts in flying long distances to obtain food and meet their energy demands, and a well-known example is the large body-sized Wandering Albatross (*Diomedea exulans*) (Brooke, 2004). Even for the small-sized Leach's Storm-petrel (*Hydrobates leucorhous*), the foraging range could also extend over 2000 km (Pollet et al., 2014).

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Individuals are expected to optimize their energy intake and trade between self-maintaining and parental care in the demanding breeding period (Pyke, 1984; Ricklefs, 1990). Seabird individuals might adopt various foraging strategies to cope with these tasks (Baduini and Hyrenbach, 2003; Mcnamara and Houston, 2008). Both intrinsic (i.e., physiological differences or individual specialization) and extrinsic (i.e., environment conditions) factors can drive the variation of foraging strategies within geographical populations or even a breeding colony (Phillips et al., 2017; Clay et al., 2019a; Jessopp et al., 2020). Empirical studies have suggested that the heterogeneity and scale-depended predictability of food resources are the critical determinants of seabirds' movement and foraging during the breeding season (Baduini and Hyrenbach, 2003; Riotte-Lambert and Matthiopoulos, 2020).

Two commonly observed foraging strategies in seabirds are sex-specific and dual foraging, also known as bimodal foraging. Sex-specific foraging behaviors primarily arise from the difference in sex roles. For instance, females tend to forage over longer distances and duration during pre-laying exodus or incubation stages to compensate for the energy consumption of egg formation (Gatt et al., 2019; Mauck et al., 2023), or males foraging further away in the highly productive area to prepare for the male-biased incubation shifts in early incubation period (Pinet et al., 2012). Seabirds also commonly employ the dual foraging strategy, i.e., long trips for self-maintenance, alternating with short but frequent trips for chick provision (Baduini and Hyrenbach, 2003; Phillips et al., 2023). The diet difference between parents and chicks could also reflect the dual foraging strategy (Baduini and Hyrenbach, 2003; Bond et al., 2010). The likelihood of adopting a dual foraging strategy was found to grow as the disparities in habitat quality became more pronounced, and longer trips were more likely to target the highly productive area measured by higher chlorophyll A concentrations (Baduini and Hyrenbach, 2003; Phillips et al., 2023). Besides sex-specific and dual foraging strategies, diversified behavior may be directly associated with individual characteristics such as body mass and favorable wind conditions during foraging (Clay et al., 2019a).

Despite small seabirds, i.e., Storm-petrels in families of Hydrobatidae and Oceanitidae, are essential components of marine ecosystems worldwide; however, their ecology is poorly known compared to their larger counterparts in Procellariiformes due to their cryptic nature and the limitations of study technologies (Boersma and Groom, 1993; Phillips et al., 2023). Our knowledge of Storm-petrels' foraging behavior is hindered by the limits of tracking devices, such as the low spatial resolution of the geolocator (Mauck et al., 2023). Therefore, it is challenging to delineate general patterns of Storm-petrels' foraging strategies (Phillips et al., 2023). For instance, the foraging strategies of Leach's Storm-petrel, the most studied species of the family, were inconsistent across the breeding period and colony (Hedd et al., 2018; Mauck et al., 2023; Tyson et al., 2022).

Swinhoe's Storm-petrel (*Hydrobates monorhis*) belongs to the uniformly dark brown clade of Hydrobatidae, and limited knowledge of its biology and ecology is known (Carboneras et al., 2021). It breeds at the islets of the marginal seas in Far East Russia, Japan, Korea and China (Carboneras et al., 2021). The breeding range of Swinhoe's Storm-petrel is located at the widest continental shelf in the Eastern Hemisphere and is characterized by high marine productivity owing to ocean currents, coastal upwelling, and land-derived nutrients (Claustre and Maritorena, 2003; Liu, 2013; Liu et al., 2014). The Northwest Pacific contains seven Large Marine Ecosystems (LMEs) that contribute to nearly a quarter of the world's marine fisheries catch and provide tremendous socioeconomic and ecosystem services (Ma et al., 2021). At the same time, with few exceptions, such as Streaked Shearwater (*Calonectris leucomelas*), very little research attention has been paid to the seabird foraging ecology in this region (Matsumoto et al., 2016; Yamamoto et al., 2011). Swinhoe's Storm-petrel's foraging behavior and at-sea distribution during breeding season remain mysterious.

In this study, we studied the breeding Swinhoe's Storm-petrel at Dagong Island, Yellow Sea, China. We delineated the foraging habitat features, identified foraging strategies and the explaining factors of the foraging strategies of Swinhoe's Storm-petrel. We first determine the features of the foraging habitat by using the Resource Selection Function (Signer et al., 2019). Because of the high marine productivity of the region, we expected the Swinhoe's Storm-petrel to forage close to the shore and on the continental shelf. Secondly, to test whether the highly productive foraging habitats could result in a homogeneous foraging strategy, we measure the trip metrics and check if a unimodal pattern emerges from the results as we expect. Lastly, we look at the relationships between foraging behaviors with extrinsic (environmental features) and intrinsic (morphology traits) factors to explain the foraging decision of Swinhoe's Storm-petrel.

2. Materials and methods

2.1. Study site

Fieldwork was conducted at Dagong Island (35.96° N, 120.49° E), a small oval-shaped islet in the Yellow Sea south of Qingdao City, Shandong Province, China. Dagong Island is located 14.8 km from the land, with an area of 0.142 km^2, a coastline that stretches 0.61 km and a maximum altitude of 120 m. The main habitats include woodlands, shrubs, bare rocks and intertidal zones (Sai, 1993). Dagong Island is the most important breeding colony of Swinhoe's Storm-petrel, Streaked Shearwater and Ancient Murrelet (*Synthliboramphus antiquus*) in China (Cui, 1993, 1998; Sai, 1993). Since 2001, Dagong Island Ecosystem Provincial Nature Reserve has been established to protect the island ecosystem and seabirds, including the adjacent sea covering an area of 15.86 km^2 (Liu and Jiang, 2013). The distance between the nature reserve boundary and the breeding colony is less than 5 km.

2.2. Study species

Swinhoe's Storm-petrel is categorized as Near Threatened in the IUCN Red list, and the current global population estimation ranges from 65,000 to 260,000 mature individuals (BirdLife International, 2018). The main threats to Swinhoe's Storm-petrel include invasive plants, mammalian predators, and human activities (Arcilla et al., 2015; Sato et al., 2010). Currently, the main threats of Swinhoe's Storm-petrel at Dagong island include predation from local breeding Peregrine Falcon (*Falco peregrinus*) and other migratory raptors, vegetation degradation due to feral goats and rabbits, and fatal entanglement with deserted fishing nets (Xue, unpublished data).

Swinhoe's Storm-petrel arrives on Dagong Island in late May, with egg laying in early July, egg hatching in mid-August, and departure in late October (Liu and Wang, 1993; Cui, 1998). The nesting habitats of Swinhoe's Storm-petrel widely spread across the island, mainly in bare rocks, mixture of rock and vegetation, and brushes (Cui, 1998). Breeding birds build nests in burrows under rocks or excavate out of the earth under the vegetation (~20–50 cm depth), lay a single clutch of one egg, and form loose colonies (Cui, 1998; Carboneras et al., 2021). Swinhoe's Storm-petrel also uses the burrows of Ancient Murrelets, who have finished breeding and left (Cui, 1998). Female Swinhoe's Storm-petrel has slightly but not significantly larger wing lengths and tails than males at Chibaldo Islet, Republic of Korea, showing no other apparent sexual dimorphism (Choi et al., 2011). Little is known about the diets and foraging habitats of this species. In July 1991, the stomach contents of one dissected individual included small fish at Dagong Island (Cui, 1998). In Maldives, scavenging in company with whales were observed (Carboneras et al., 2021).

2.3. GPS-VHF devices deployment

We captured and deployed tracking devices on 10 Swinhoe's Storm-petrels on August 9, 2021, in the late incubation and early chick-rearing period (Cui, 1998). Birds were chosen haphazardly among the colony and captured by hands when birds landed on the ground or entered the burrows at night. GPS-VHF loggers (Hunan Global Messenger Technology Co., Ltd., HQBV0702) with solar panels were used to determine the at-sea distribution and classify foraging trips. The dimension of the logger is 18 mm × 12 mm × 7 mm with a pliable external antenna (85 mm), and the average weight with attachment is 2.10 ± 0.04 g. GPS devices were programmed to obtain location every 4 h and transmit the data every hour when birds return to the reception range (1–1.5 km) of the VHF receiver pole, installed at a building roof at the top of the island (around 130 m elevation). Accuracy of GPS positioning ranges from 5 to 100 m. If the device fails to obtain a connection with GPS satellites, the accuracy of the point will be marked as "invalid". The VHF 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 48.61 ± 4.27 g. The devices and harness weighted 4.34 ± 0.31% of the tracked birds' body mass under the empirical threshold value (Geen et al., 2019). The average bill length was 15.09 ± 0.83 mm, wing length 16.16 ± 0.45 cm, tarsus 21.63 ± 1.46 mm, wing area 268.36 ± 24.88 cm^2 and wing loading 0.18 ± 0.02 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 11 to 22 days, with an average of 14.75 ± 3.73 days.

2.4. Data processing and statistical analyses

Without further indication, we processed and analyzed the data in R 4.0.4 (R Core Team, 2023). The average values are shown in mean ± 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 GPS fixes according to the tracking duration, which represents the positioning success rate.

We first filtered the GPS 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., 2016). Storm-petrels typically use surface seizing techniques to forage (Brooke, 2004). We, therefore, defined GPS positions with altitudes lower than 50 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, 1980; Signer et al., 2019). For each foraging point, we generated 100 random points with the same timestamp within the Minimum Convex Polygon (MCP) home range to measure the habitat availability using the "adehabitatHR" 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 (Quillfeldt et al., 2020; De la Cruz et al., 2023). Sea surface temperature (SST) and chlorophyll A mass concentration were obtained from MODIS Ocean Aqua OceanColor (4 km, 8 days) dataset through the Environmental Data Automated Track Annotation System (Env-DATA) on Movebank (Dodge et al., 2013; Kays et al., 2021). Water depth was extracted from ETOPO 2022 bathymetric data by using "marmap" package (Pante and Simon-Bouhet, 2013). Distance to the land was obtained from GMT intermediate distance from the coast (Stumpf and Kuring, 2009).

When the birds were incubating in the burrows, the GPS device often failed to locate the position, creating gappy data. To mitigate the incompleteness of data, we used the communication log data of devices with VHF receivers that contain the timestamps and the logger IDs to interpolate the GPS data. Tracking devices only transmit the data within the reception range of the VHF receiver, so we used the receiver's location to substitute the missing data in the trajectory. Next, we segmented the individual trajectory into foraging trips using "track2KBA" package and calculated trip metrics, including trip duration, maximum distance to the colony, and trip direction (Lascelles et al., 2016; Beal et al., 2021). Incomplete trips were removed in the subsequent analysis. To test the unimodality of the Swinhoe's Storm-petrels foraging trips, we performed Hartigans' Dip Test using the package "diptest" for each trip metric (Maechler, 2013). We further used Ward's Hierarchical Cluster Analysis to detect discontinuous groups in foraging trips to identify foraging strategies based on trip metrics and graphically determined the number of clusters using a scree plot (Tinker et al., 2007; Schwarz et al., 2021).

In addition to the environmental variables in habitat selection analysis, we also included wind conditions as they have been shown to relate to movement decisions in many seabird species (Matsumoto et al., 2017; Mauck et al., 2023). U and V wind components (10 m above group) were derived from ERA5 data using the Env-DATA system and converted into wind support and crosswind for each point (Safi et al., 2013). The positive wind support value is the tailwind condition, and the negative is the headwind. The larger the crosswind, the more likely birds will drift away from their destination by the wind. We compared the environmental variables between different foraging strategies and morphology differences between individuals who took different strategies. We used comparison tests (e.g., *t*-test, Wilcoxon test, ANOVA) depending on the number of trip clusters and data distribution (Dalgaard, 2008).

3. Results

In August 2021, Swinhoe's Storm-petrels roamed in a large area (MCP estimated 43382.89 km^2) between latitude 33° N to 36° N, south of the breeding colony. Individual tracking trajectories are shown in Fig. 1. Birds foraged in habitat patches on the continental shelf (water depth 24.45 ± 7.57 m, range 4–62 m), with features of varied chlorophyll concentration (1.61 ± 0.79 mg/m^3, range 0.46–3.95 mg/m^3) and warm water (sea surface temperature 28.32 ± 0.48 °C, range 26.97–29.30 °C). All the foraging locations were within the Exclusive Economic Zone of China (distance 29.41 ± 34.86 km, range 2–172 km). The Resource Selection Function suggests Swinhoe's Storm-petrels preferred shallow water and nearshore regions; meanwhile, chlorophyll concentration and sea surface temperature did not influence the foraging decision (Table 1). Boxplots of environmental features of used and available locations are shown in Appendix Fig. S1.

We obtained 48 complete foraging trips from 8 individuals; each bird had at least two trips (range 2–11; see details in Table 2). Swinhoe's Storm-petrels left the colony in a sector with an angle range from 135.74° to 238.13°. Duration and distance of foraging trips were diversified, range from 0.17 to 6.71 days (mean 1.37 ± 1.42 days), and 25.95–347.76 km (mean 94.34 ± 59.06 km), respectively. Hartigans' Dip Test suggests the *p* values of trip metrics (i.e., trip duration, trip maximum distance and trip direction) were all larger than 0.05, indicating no significant difference from unimodality. Nevertheless, Ward's hierarchical cluster analysis and scree plot detected two foraging strategies (Fig. 2), which were characterized by long southeastward trips (*n*

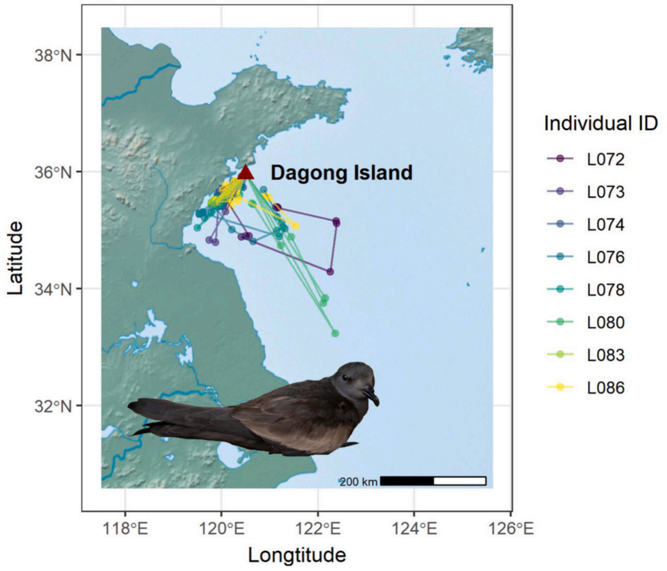


Fig. 1. Tracking trajectory of breeding Swinhoe's Storm-petrels (individuals $n = 8$) in August 2021 at Dagong island (filled triangle). Individuals' tracks are represented by lines and dots in colors. Two individuals with insufficient data are not shown on the map. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Table 1

Resource selection function results of Swinhoe's Storm-petrels at Dagong Island, Yellow Sea, China. Significant p value is shown in bold.

Predictors	Habitat selection within the home range			
	Estimates	Std. error	Z value	p
(Intercept)	52.862	77.377	0.683	0.494
Water depth	0.013	0.005	2.779	**0.005**
Distance to coast	−0.044	0.005	−8.476	**<0.000**
Chlorophyll A concentration	−0.161	0.110	−1.464	0.143
Sea surface temperature	−0.196	0.257	−0.763	0.446

Table 2

Deployment summary of GPS-VHF tagged Swinhoe's Storm-petrels ($n = 8$) at Dagong island, Yellow Sea China. All the birds were tagged on August 9, 2021. Two individuals whose data are insufficient for the analysis are not shown in the table.

ID	Tracked days	Completed trips[a]	Number of GPS fixes[b]	Tag performance	
				Battery performance	Positioning success rate
L072	6.06	2 (1)	67 (18)	93.06%	25.00%
L073	20.07	5 (0)	95 (13)	62.50%	8.55%
L074	15.46	8 (0)	100 (26)	94.34%	24.53%
L076	11.60	5 (2)	69 (36)	98.57%	51.43%
L078	12.37	5 (0)	84 (15)	94.38%	16.85%
L080	9.89	3 (3)	80 (8)	86.02%	8.60%
L083	11.45	11 (0)	66 (30)	92.96%	42.25%
L086	16.53	9 (1)	94 (36)	92.16%	35.29%

[a] Number of southeast trips are shown in the brackets.

[b] Number of successful GPS fixes are shown in the brackets.

= 7) and short southwestward trips ($n = 41$). Duration, maximum distance and direction significantly differed between groups (Wilcoxon test, all p value < 0.001). 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 2).

The comparison of extrinsic factors on the foraging strategy of Swinhoe's Storm-petrels are shown in Fig. 3. Environmental conditions of the two foraging strategies significantly differ in water depth ($w = 3530$, $p = 0.00$), distance to coast ($w = 790$, $p = 0.00$) and sea surface temperature ($t = -4.91$, $p = 0.00$). We did not find the impact of chlorophyll concentration ($w = 717$, $p = 0.21$) and wind conditions (wind support $w = 2114$, $p = 0.76$, crosswind $t = -1.21$, $p = 0.23$) on foraging strategies. Individuals who were capable of conducting long southeastward trips had significantly longer wings ($t = 3.76$, $p = 0.011$) and tendency of lower wing loading ($t = -2.52$, $p = 0.06$), but were not different in body weight ($t = -1.37$, $p = 0.24$), tarsus ($w = 6$, $p = 0.69$), bill ($t = 0.21$, $p = 0.84$) and wing area ($t = 0.78$, $p = 0.47$) (see Fig. 4).

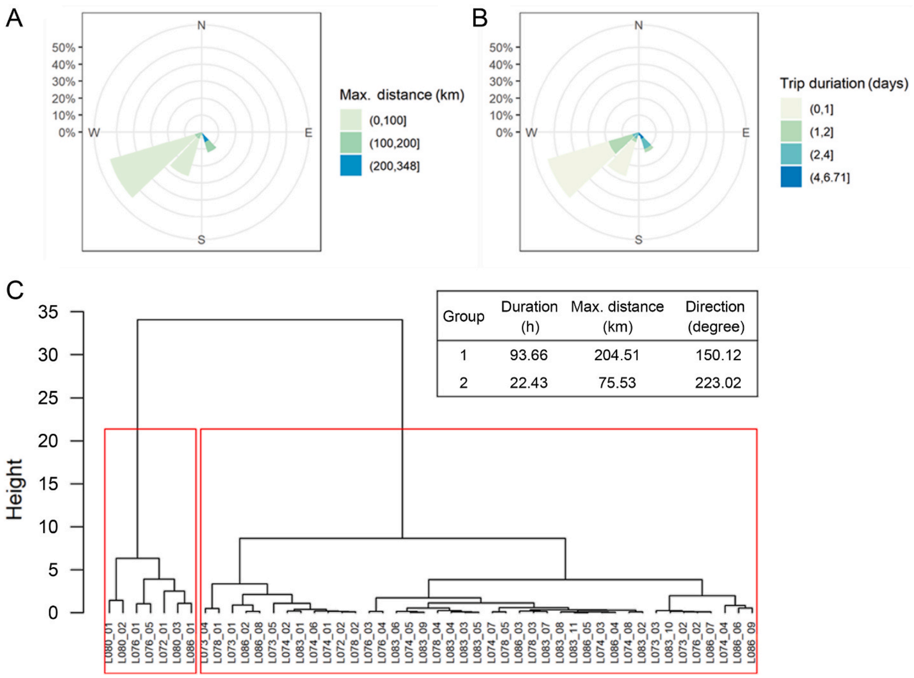
4. Discussion

In this research, we studied the foraging behavior of a mysterious tubenose species, the Swinhoe's Storm -Petrels, using GPS-VHF 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 (1.6 ± 0.79 mg/m^3) 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 (∼400–800 km) and mostly on shelf slop with low chlorophyll A concentration of less than 0.6 mg/m^3 (Hedd et al., 2018). 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, 2007). The dark rump plumage of Storm-petrels, such as in Swinhoe's, might have evolved as an anti-predator adaptation to deal with the harassment from nearshore predators such as gulls (Bretagnolle, 1993).

Several seabirds, such as Leach's Storm Petrels and Tristram's Storm-petrel (*Hydrobates tristrami*), exhibit a bimodal distribution of long and short foraging trips during the breeding season or display age-depended differences in diet (Bond et al., 2010; Collins et al., 2022; Phillips et al., 2023). The dual foraging strategy is predicated on the assumption of limited resources. Consequently, species could switch from bimodal distributed foraging to unimodal foraging under favorite conditions. This phenomenon has been observed in Cory's Shearwater (*Calonectris diomedea*) and Westland Petrel (*Procellaria westlandica*) (Granadeiro et al., 1998; Poupart et al., 2020). In our study, the distributions of duration, distance, and direction of foraging trips could not be distinguished statistically from unimodal, as expected in productive marginal sea ecosystems. However, previous studies usually used single trip metric, i.e., trip distance (sometimes together with trip duration, which is highly correlated with distance), to test dual foraging strategy (Collins et al., 2022; Phillips et al., 2023). When considering all the trip metrics, two divergent strategies emerged from the foraging trips of Swinhoe's Storm-petrels, though frequency varied between strategies (Fig. 2).

Southeastward foraging trips of Swinhoe's Storm-petrels were infrequent and associated with longer distances and duration. Meanwhile, southwestward trips were short and more frequent. We speculate that the incubation individuals took longer trips, and chick provision parents went for short trips based on the results of other Storm-petrel



Group	Duration (h)	Max. distance (km)	Direction (degree)
1	93.66	204.51	150.12
2	22.43	75.53	223.02

Fig. 2. Diversified foraging trips ($n = 48$) 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 Ward's hierarchical clustering 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 1, $n = 7$), and the majority of short trips went to the southwest (group 2, $n = 41$). 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.)

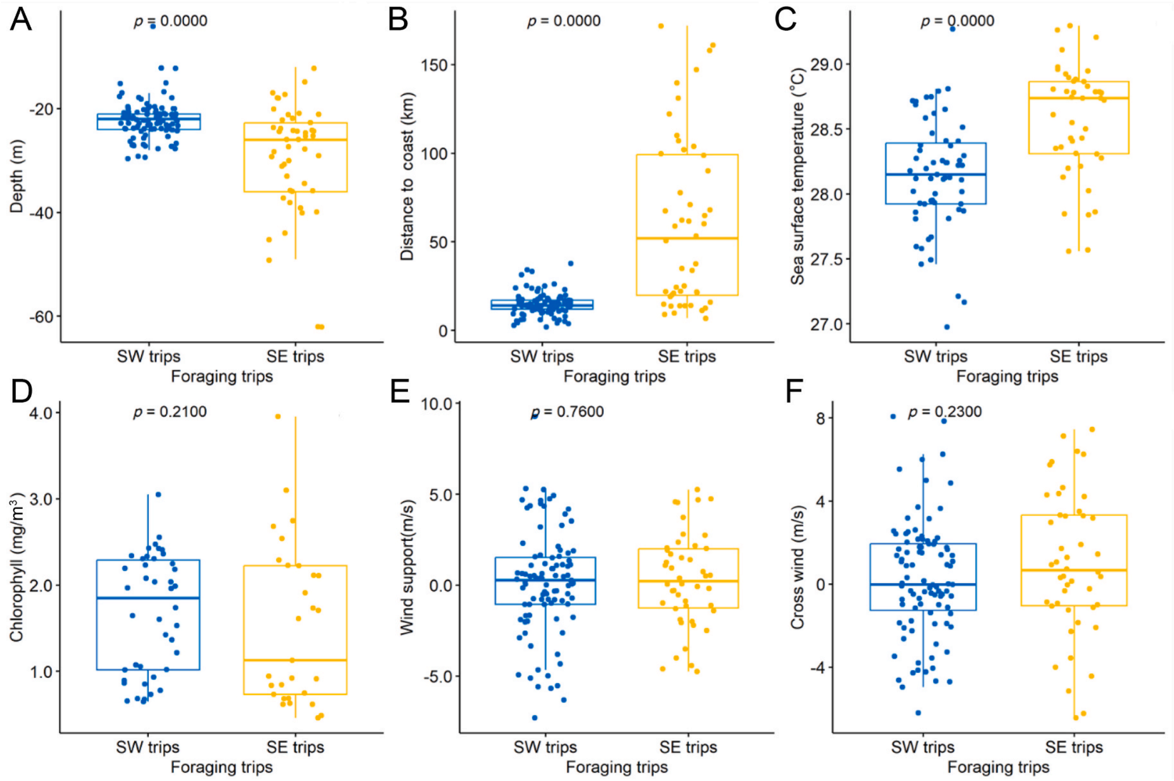


Fig. 3. Comparison of environmental features of two groups of foraging trips towards southeast and southwest direction relative to the breeding colony. Environment variables include (A) water depth, (B) distance to the coast, (C) sea surface temperature, (D) chlorophyll A concentration, (E) wind support and (F) crosswind. The p values of the t-test or Wilcoxon test are shown in each boxplot.

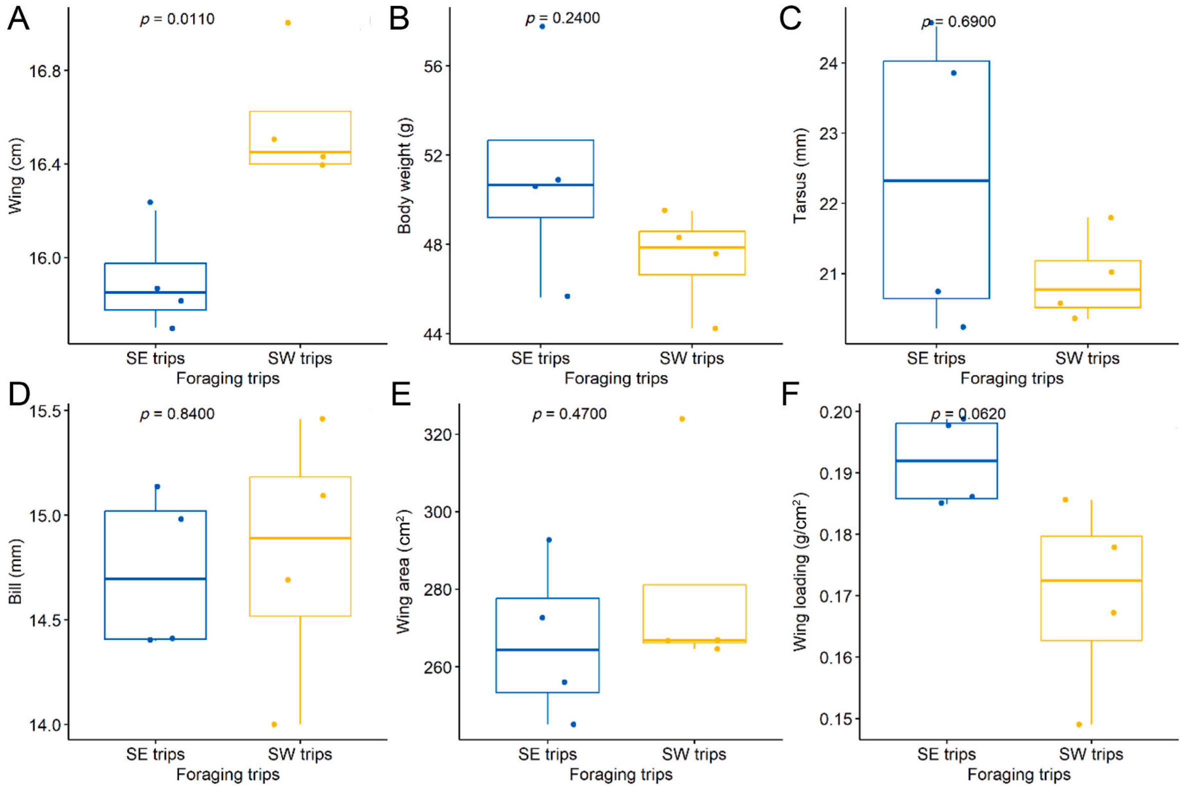


Fig. 4. Difference in the morphology of Swinhoe's Storm-petrels that performed southeast and southwest foraging trips respectively: (A) wing length, (B) body mass, (C) tarsus length, (D) bill length, (E) wing area and (F) wing loading. The *p* values of the *t*-test or Wilcoxon test are shown in each boxplot. Individuals who took two directions were grouped with the southeast strategy.

species (Pollet et al., 2014; Neves et al., 2023). The longer trips might also be a sex-specific strategy for females to compensate for the energy expenditure of eggs (Mauck et al., 2023). 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.

Foraging longer distances is costly both time- and energy-wise for seabirds, so we expect longer trips to target highly productive areas and potently supported by favorable wind (Clay et al., 2019a; Phillips et al., 2023). Unexpectedly, we did not find chlorophyll A concentrations and wind conditions differ between southeast and southwest trips. One potential explanation is the spatial-temporal mismatch between the GPS tracking and remote sensing data (Grémillet et al., 2008). Another explanation might be that the Swinhoe's Storm-petrels were attracted by specific unknown resources in the deep sea with warmer surface temperatures and far from the coast. Seabirds are strongly associated with oceanographic features such as water mass (Ballance et al., 2006). In the bottom of the Yellow Sea, the Yellow Sea Cold Water Mass provides a refuge for North Pacific temperate fauna, resulting in a high biodiversity and concentration of zooplankton deep down the Ocean (Liu, 2013). 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 (Bolnick et al., 2003). Wing 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., 2019a). 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-maintaining. However, we think it is not likely the case as 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., 2019b; Bolton, 2020). Repeated measurements of the same individual's foraging trips also provide a glimpse of individual specialization and flexibility (Bolnick et al., 2003). Coarse temporal resolution and irregularity of GPS data limited our ability to delineate Swinhoe's Storm-petrels' foraging behavior on a finer scale. We mitigate the issue using the VHF communication log data to interpolate the missing data. The low positioning success rate rather than battery performance (Table 2) suggests the missing data mainly were due to GPS positioning failure caused by malfunction of the external antenna or indicated incubation and chick brooding behavior (Ozsanlav-Harris et al., 2022). In our case, a geolocator might be more suitable for capturing behavior details, such as the incubation rhythm of cave-breeding birds (Huang et al., 2021). However, it is insufficient to define the short-distance movement because the geolocation accuracy is approximately 200 km, which exceeds the average foraging distance of Swinhoe's Storm-petrels (Hedd et al., 2018).

Seabirds are crucial food web components and well-used ecological indicators for marine ecosystems (Natsukawa and Sergio, 2022; Pereira et al., 2022). Understanding foraging behavior is essential for studying seabird ecology and monitoring the health of the marine environment (Young and Ballance, 2023). Meanwhile, understanding the foraging behavior and distribution range of animals are important for identifying key sites for biodiversity and designing adequate marine protection areas (Hays et al., 2019; Davies et al., 2021; Pereira et al., 2022). We acknowledge that our results are constrained by the small number of tracked individuals and the short study period. Nonetheless, this study 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 "30 × 30" goal of Kunming-Montreal Global Biodiversity Framework, as only 4.1% of China's maritime area is protected by far (Zhou et al., 2020). 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.

Ethics statement

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 handed birds were supervised, collaborated and under the license of Qingdao Bird Ringing Station.

Declaration of competing interest

The authors declare that they have no competing interests.

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Data accessibility

GPS Tracking data are available at the Movebank Repository (Cheng et al., 2024). Communication log data of devices with VHF receivers for data interpolation are provided in Appendix Table S2.

CRediT authorship contribution statement

Yachang Cheng: Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Lei Zhu:** Investigation. **Lin Xue:** Supervision, Project administration, Investigation. **Shisheng Ma:** Investigation, Data curation. **Nan Jia:** Investigation, Data curation. **Shaoping Zang:** Investigation. **Zhihai Cao:** Supervision, Project administration. **Jing Yuan:** Investigation. **Yang Liu:** Writing – review & editing, Supervision, Resources, Project administration, Funding acquisition, Conceptualization.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.avrs.2023.100157.

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