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Comparing spatial differences in behavioral pattern transition of Black-tailed gull during post breeding season in the Korean peninsula

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Parents adjust their foraging effort according to the chick and their own body condition and dual foraging strategy is one of the foraging tactics parents replenish their own reserves while feeding their chicks. During the post-breeding season, seabirds disperse to recover their own body condition and prepare for the next breeding season. Recently, we discovered Black-tailed gulls (*Larus crassirostris*) breeding around the Korean Peninsula occasionally foraging long trips during the late fledging, however, our understanding of the behavioral patterns of Black-tailed gulls during the late fledging and post-breeding, as well as its inter-colonial differences, remains considerably limited. Here, we employed 92 GPS trackers to adult Black-tailed gulls (*Larus crassirostris*) from six breeding colonies around the Korean peninsula (Yellow Sea—three colonies, South Sea—one colony, and East Sea—two colonies). To determine the foraging investment during the fledging, we suggested the flight efficiency in each trip as the ratio of maximum foraging distance (i.e., straight line distance) to total foraging distance (i.e., sum of all consecutive distance for each trip). Overall, the mean flight efficiency of the long foraging trips were lower than 57% (40.76 ± 13.07%) whereas that of the short foraging trips were over 74% (80.87 ± 4.03%). This may suggest that Black-tailed gulls may visited more than one foraging site during the long foraging trip while they flew directly between the foraging site and breeding colony during the short foraging trip to invest more in their juvenile. Moreover, longer maximum foraging distance with higher flight efficiency observed in the East Sea may indicate a balance between the costs (such as energy expended during foraging or food competition near breeding sites) and the benefits (quantity and quality of food obtained). Our findings revealed the flight behavior of Black-tailed gulls during the late fledging and post breeding, across six breeding colonies, which have different competition pressures and proximity to foraging site.

During the breeding season, parents adjust their foraging effort according to the chick and their own body condition[1–4]. Dual foraging strategy is one of the foraging tactics in which parents alternate between short and long foraging trips to replenish their own reserves while feeding their chicks. Although dividing foraging trips into short or long is determined by foraging duration, it is known that parents travel to shorter distances during short foraging trips to maximize the provisioning rate and switch to more distant and productive areas when they need to fulfill their own energy requirements. During long foraging trips, parents may also stay on the water for digestion, condensing swallowed prey for deliver efficiency[5], simply drift with the waves for rest[6]. Dual foraging has been recorded in many taxa such as shearwaters[7,8], prions[4] and albatrosses[9]. However, even the same species in the same breeding colony flexibly change foraging strategy based on the resource availability[8]. Recently, we discovered Black-tailed gulls (*Larus crassirostris*) breeding around the Korean Peninsula occasionally foraging long trips based on the data we collected (see Method and Result). Although little is known about the foraging strategies of Black-tailed gulls, we assumed that Black-tailed gulls also utilize a dual foraging strategy.

After chicks fledge, seabirds disperse to wintering sites to recover their own body condition and prepare for the next breeding season. Many papers investigate whether previous breeding conditions influence the timing

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of migration and wintering behavior (i.e., carry-over effect;[10,11]). In the experimental study, deliberately egg-removed Cory's Shearwaters (*Calonectris diomedea*) (i.e., failed breeding parents) left the breeding colony earlier but arrived at the wintering site similar to the controlled group[12]. Also, Manx Shearwater (*Puffinus puffinus*) with longer breeding efforts (i.e., switching original chicks to younger ones) migrated later and search more food during at the wintering site[10]. Since seabirds exhibit fidelity to wintering sites[13] and migration requires extensive energy usage, seabirds minimize the cost of migration, which is either represented by migration duration or total energy usage[14]. It has been reported that gulls minimize energy usage during the migration, traveling longer and taking indirect routes to the wintering site[13,15, 16]. However, there is still a knowledge gap that needs to be illustrate the relationship between migration timing and migration behavior.

Density dependent competition within and between breeding colonies influences both the breeding and non-breeding seasons. An increase in breeding density intensifies competition for food, forcing parents to forage further[17]. Thus, breeding colonies with larger breeding densities forage further than low density breeding colonies[18]. The Population of neighboring colonies also affects foraging distance. Although proximity to neighboring colonies should be in considered, the population of breeding colonies within foraging range causes foraging site segregation[19,20], and many reports indicate that high density breeding colonies utilize wider foraging ranges[21,22]. Population density also plays a role in determining migration distance, as high density populations tend to disperse over greater distances than those with lower densities[23,24].

The ocean surrounding the Korean Peninsula can be divided into three Seas (the Yellow Sea, the South Sea, and the East Sea) based on depth, coastal land use, and breeding population distribution. It is known that there are 48 breeding colonies in the Yellow Sea, one in the South Sea, and three in the East Sea[25]. The breeding season of Black-tailed gulls spans from April to July[26], and they widely disperse at the end of the breeding season from Northern Japan to East China ([27,28]; also see Study area of Material and Method, and Fig. 1 for more details). However, little is known about the difference in foraging behavior and dispersal patterns among these breeding colonies. We deployed 160 GPS trackers on adult Black-tailed gulls from May 22, 2021, to June 10, 2021, in eight breeding colonies. Among them, 56 Black-tailed gulls are removed due to the malfunctioning devices, long disconnection durations, and not engaging in breeding. Additionally, 12 Black tailed gulls from two breeding colonies were removed from the analysis due to insufficient sample size (see S1 in Supplementary information for more details).

This study aims to investigate flight characteristics of late fledging and post-breeding among six breeding colonies of Black-tailed gulls. Specifically, our first objective is to explore the dual foraging strategy of Black-tailed gulls during the late fledging stage and compare differences between breeding colonies. Black-tailed gulls are generalists consuming fish, invertebrates (such as squid or shrimp), and anthropogenic food sources (fishery by-product or grain). We hypothesize that breeding colonies with high competition pressure will foraging longer distance during short foraging trips. However, this pattern may not show during long foraging trips, as gulls may visit preferable foraging sites to reserve their energy needs compared to short foraging trips where they

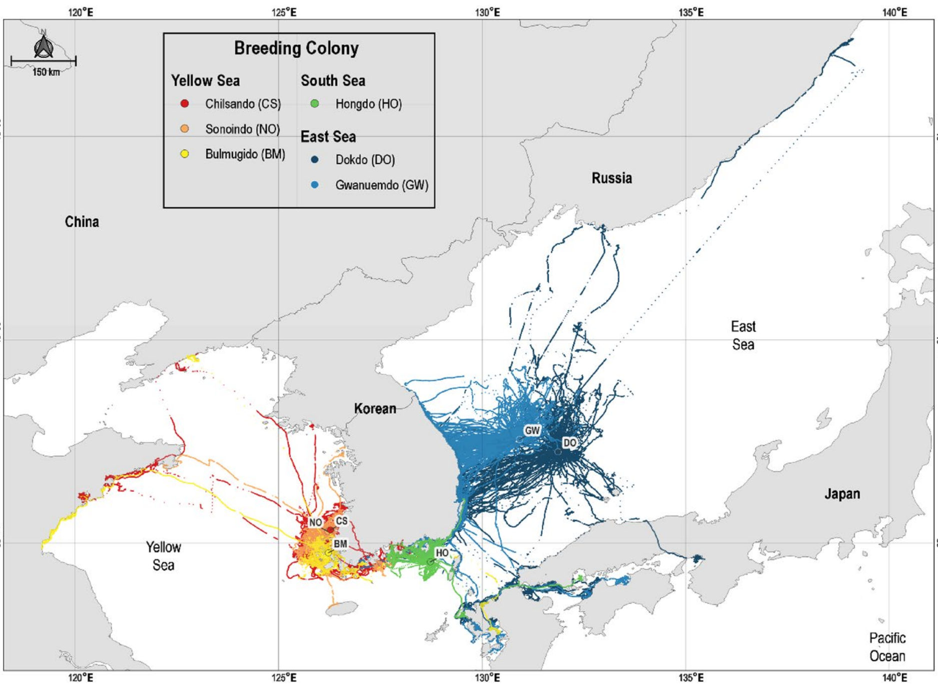

Figure 1. Location of breeding colonies and dispersal range of each breeding colony during June to July in 2021. GPS locations of 92 individuals breeding and in six breeding colonies during June to July in 2021. Each color corresponds to different colonies: red dot – Chilsando (CS), orange dot – Sonoindo (NO), yellow dot – Bulmugido (BM), green dot – Hongo (HO), blue dot – Gwaneumdo (GW), and dark blue dot – Dokdo (DO).

primarily serve parental duties. Secondly, we examine the migration pattern of Black-tailed gulls and compare differences between breeding colonies. We hypothesize that early migrants will have a low average distance per day and low first day flight efficiency.

For the dual foraging strategy, we utilize the maximum foraging distance from the breeding colony to determine the foraging range, and the foraging efficiency to evaluate whether trips serve a purpose beyond chick provision. Notably, foraging efficiency, which is the ratio of maximum foraging distance to the total distance traveled during each trip, closer to 100 indicates that gulls flew straight to their destination and back to the breeding colony (see S2 in Supplementary information for more details)[29,30]. Since Black-tailed gulls are generalist and fishery yield during the June to July in 2021 was the same as previous year, parents likely acquired prey as usual. With this information, we assume that parents would not waste energy leaving breeding colonies without gaining energy, either for their chick or themselves. By this assumption, low foraging efficiency suggests that parents visited multiple patches to gather more prey and increase energy flow for both themselves and their chicks. As our data were not fully collected until the end of the non-breeding season, we confined our data to the end of July. Therefore, we calculated average distance per day and first day flight efficiency to normalize distance or flight efficiency variable.

Results

Foraging behavior

With GPS data collected from 92 Black-tailed gulls breeding near Korean Peninsula, a total of 6,302 foraging recordings in six breeding colonies were collected from June 1 to July 31, 2021 (Table 1). The number of long foraging trips (e.g., flight duration more than 48 h, see Method for details) was 188, which accounted for 2.98% of the total. The average of short foraging trips for all breeding colonies was more that 75%, whereas that of long foraging trips was less than 60%, indicating that Black-tailed gulls engaged in both short (leaving breeding colony less than 48 h; See S2 in Supplementary information for more detail) and long foraging trip during the breeding season.

The flight frequency of each breeding colony exhibited distinct patterns between short and long foraging trip. The foraging frequency of short foraging trips did not significantly differ between all three Seas (ANOVA, $F_{2,89} = 1.726$, $p = 0.184$) or breeding colonies ($F_{5,86} = 1.589$, $p = 0.172$; Fig. 2 (A)). In contrast, the foraging frequency of long foraging trips in the Yellow Sea (2.21 ± 1.43, count of long foraging trips) was significantly lower than that in the East Sea (3.43 ± 1.71 count of long foraging trips; $F_{2,145} = 50.1$, $p < 0.001$). However, there was no significant difference between the South Sea and both the Yellow Sea and the East Sea. Specifically, the foraging frequency of long foraging trips was significantly lower in Sonoindo than in Dokdo ($F_{5,64} = 3.064$, $p = 0.015$; Turkey HSD post-hoc test, p = 0.016; Fig. 2 (B)).

Comparing among three Seas, the maximum foraging distance of short foraging trips was the lowest in the East Sea (11.95 ± 32.15 km; ANOVA, $F_{2,6111} = 122.1$, $p < 0.001$) whereas the foraging efficiency was the lowest in the Yellow Sea (79.08 ± 16.63%; $F_{2,6111} = 48.76$, $p < 0.001$). When additionally compare breeding colonies within each Seas the maximum foraging distance between Dokdo and Gwaneumdo in East Sea was not significantly different ($F_{1,2279} = 1.777$, $p = 0.183$), however foraging efficiency of Gwaneumdo was significantly lower than that of Dokdo ($F_{2,2647} = 11.44$, $p < 0.001$). In Yellow Sea, the maximum foraging distance was the shortest on Bulmugido ($F_{2,3461} = 23.79$, $p < 0.001$), whereas the foraging efficiency was the highest on Bulmugido, followed by Chilsando and Sonoindo ($F_{2,3461} = 54.24$, $p < 0.001$; Table 1, Fig. 3 (A) and (C)).

Sea	Breeding colony (N)		Total no. of trip	No. of foraging trip per individual	Maximum foraging distance per trip (m)	Foraging efficiency per trip	Maximum dispersal distance (m)
Yellow Sea	BM (10)	< 48	682	66.5 ± 50.3	17.12 ± 13.28	74.20 ± 18.04	184.13 ± 183.23
		≥ 48		2.83 ± 1.33	32.29 ± 13.82	26.68 ± 6.95	
	CS (23)	< 48	1276	53.6 ± 23.8	23.87 ± 20.55	78.16 ± 17.78	368.54 ± 133.78
		≥ 48		2.39 ± 1.61	68.30 ± 36.68	27.16 ± 13.1	
	NO (18)	< 48	1581	87 ± 45.5	22.25 ± 23.05	81.87 ± 14.37	422.31 ± 70.57
		≥ 48		1.5 ± 0.85	54.16 ± 27.09	35.34 ± 15.12	
South Sea	HO (10)	< 48	386	36.9 ± 28.1	26.79 ± 23.37	84.25 ± 13.96	134.15 ± 93.20
		≥ 48		2.12 ± 1.25	77.53 ± 19.41	44.78 ± 16.42	
East Sea	DO (13)	< 48	878	64.4 ± 47	13.13 ± 32.05	84.88 ± 14.84	106.55 ± 104.22
		≥ 48		3.73 ± 1.74	269.76 ± 181.94	54.18 ± 12.96	
	GW (18)	< 48	1499	80.2 ± 94.3	11.27 ± 32.20	81.85 ± 15.96	274.7 ± 271.54
		≥ 48		3.24 ± 1.71	179.22 ± 34.15	56.42 ± 10.61	

Table 1. Statistical result of behavior pattern variables by each breeding colony in Korean peninsula: CS-Chilsando, NO-Sonoindo, BM-Bulmugido, HO-Hongdo, DO-Dokdo, GW-Gwaneumdo (mean ± sd). Statistical result of foraging less than 48 h (< 48) and foraging more than 48 h (≥ 48) were separately calculated for No. of foraging trip per individual, Maximum foraging distance fer trip, Foraging efficiency per trip. The sample size (N) for each breeding colonies is written next to the breeding colony. Movement data tracked by GPS was collected during June to July 2021.

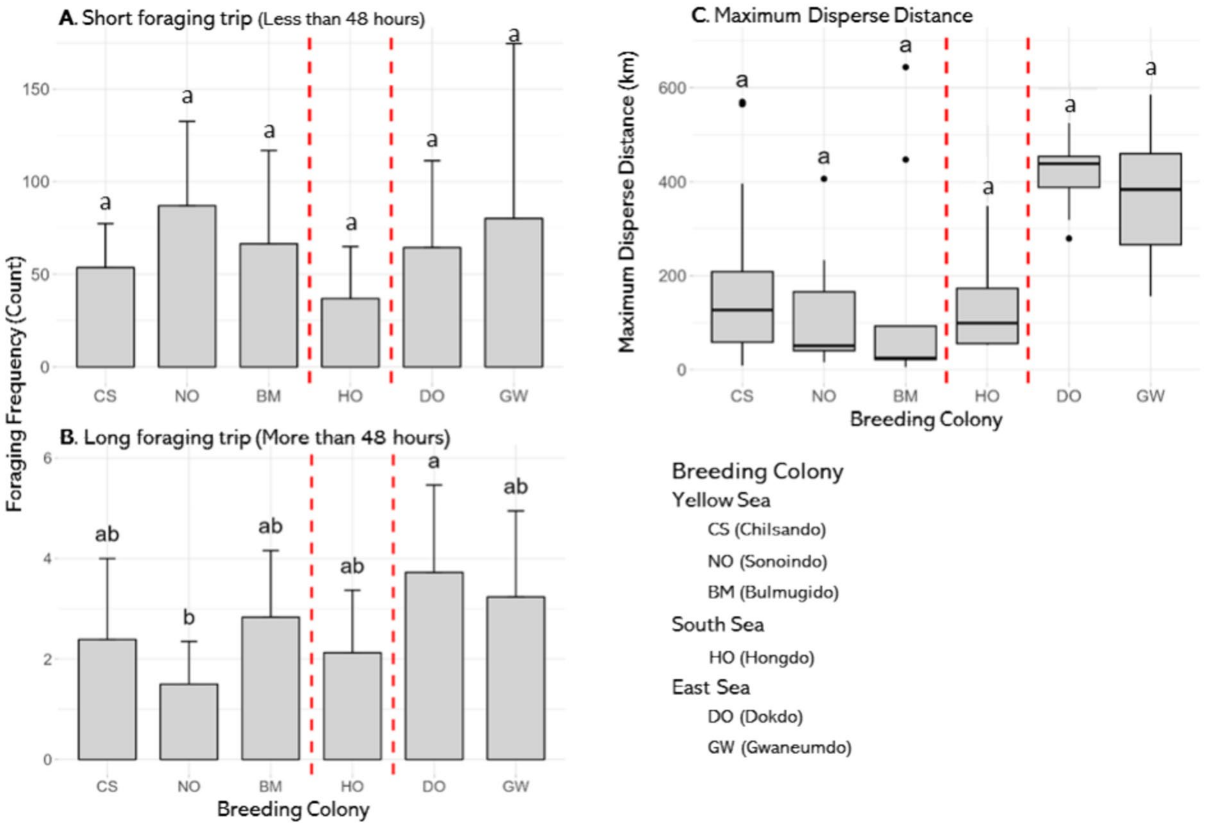

Figure 2. Comparison of mean foraging frequency (± sd) and maximum disperse distance(km) of Black-tailed gulls breeding in six breeding colonies. (**A**) Foraging frequency of short foraging trips (foraging duration less than 48 h). (**B**) Foraging frequency of long foraging trips (foraging duration more than 48 h). (**C**) Maximum disperse distance of each breeding colonies of Black-tailed gulls near Korean peninsula. Maximum dispersal distance refers to the maximum linear distance from the breeding colony that each gull travels when completely leaving their breeding colony. Note that red dash-line separates the three Sea (East: DO (Dokdo, n = 13) and GW (Gwaneumdo, n = 18), South: HO (Hongdo, n = 10), Yellow: CS (Chilsando, n = 23), NO (Sonoindo, n = 18), BM (Bulmugido, n = 10)). The different characters on the bars indicate significant differences. GPS data was collected during June to July 2021. Tables 1, 2, 3, and Fig. 1 for more details.

Sea	Breeding colony	Location	Area (m^2)	Population size	Distance to the Korean Peninsula (km)	Reference
Yellow Sea	Bulmugido	N 34° 45′ 32.4	32,590	1,300	12	[48]
		E 126° 13′ 26.4				
	Sonoindo	N 35° 17′ 6	18,446	5,900	9	[49]
		E 126° 12′ 32.4				
	Chilsando	N 35° 19′ 19.2	41,355	26,457	7	[49]
		E 126° 16′ 30,41				
South Sea	Hongdo	N 34° 32′ 13.2	98,380	113,458	20	[25]
		E 128° 43′ 58.8				
East Sea	Gwaneumdo	N 37° 32′ 34.8	71,405	1,000	161	[50]
		E 130° 55′ 15.6				
	Dokdo	N 37° 3′ 18.6372	73,297	15,000	235	[51]
		E 132° 59′ 2.4324				

Table 2. Environmental conditions of each breeding colonies. Note that the area and population size of Dokdo comprise all east and west island.

Regarding long foraging trips, we observed an opposite trend in maximum foraging distance and foraging efficiency between three Seas and breeding colonies. The East Sea had longest maximum foraging differences (217.89 ± 128.95 km; $F_{2,183} = 64.27$, $p < 0.001$) and highest foraging efficiency (55.46 ± 11.66%; $F_{5,182} = 40.09$, $p < 0.001$), meanwhile, the Yellow Sea had the shortest maximum foraging distances (57.31 ± 34.06 km) and lowest foraging efficiency (28.69 ± 12.74%). The pattern of long foraging trips between breeding colonies also showed a different pattern than that of short foraging trips. In the East Sea, the maximum foraging distance of Dokdo was significantly higher than that of Gwaneumdo ($F_{1,94} = 13.05$, $p < 0.001$); however, no difference was observed in their foraging efficiency ($F_{1,94} = 0.864$, $p = 0.355$). For the Yellow Sea, the shortest maximum foraging distance and lowest foraging efficiency were observed on Bulmugido, whereas the highest foraging efficiency was observed on Sonoindo; with no significant difference among the colonies ($F_{2,72} = 2.686$, $p = 0.075$; Table 1, Fig. 3 (B) and (D)).

Dispersal behavior

Among 92 gulls, 85 individuals entirely dispersed from their breeding colonies. Black-tailed gulls breeding in the Yellow Sea either stayed near their breeding colony or flew overseas to China. Most individuals in the East Sea initially flew to the coasts of the Korean Peninsula, following the coastal line to the southern part of peninsula, and then flew to Japan. Only a few flew directly to Japan. Individuals in the South Sea initially flew to the nearest coast of the Korean Peninsula, but all eventually flew southward to Japan. There was little overlap in post-breeding sites between the three Seas (Fig. 1). The Yellow Sea populations left the breeding colonies nine days earlier than the South Sea populations ($F_{2,89} = 29.38$, $p < 0.001$; Yellow-South, $p = 0.046$). However, there was no time difference in leaving the breeding colonies among six breeding colonies ($F_{4,77} = 1.465$, $p = 0.221$). The maximum dispersal distance of the East Sea was 391.09 km (± 113.41), approximately 2.5 times more than that of the other two Seas ($F_{2,89} = 29.38$, $p < 0.001$). However, no difference was observed in the maximum dispersal distance among the six breeding colonies (Yellow and South: $F_{3,57} = 0.849$, $p = 0.473$, East Sea: $F_{1,29} = 1.739$, $p = 0.198$, Fig. 2 (C)). Overall, our results suggest that leaving the breeding colony earlier was associated with shorter daily dispersal distance (Fig. 4 (A)) and higher dispersal efficiency (Fig. 4 (B)); however, no significant differences were observed among breeding colonies (See Supplementary Table S2, S3).

Discussion

We aimed to explore the dual foraging strategy and migration patterns of Black-tailed gulls across six colonies using GPS tracking data. Our data revealed that short foraging trips in all breeding colonies had higher foraging efficiency that that of long foraging trips, and long foraging trips usually occurred during late June to early July which was close to time when individuals completely left their breeding colony. Seabirds strategize their flight patterns during the breeding season to simultaneously maximize offspring growth and self-maintenance after breeding[31]. As the breeding progress, parent's body condition deteriorates[32,33] and parents regulate their parental effort not to exceed the optimal amount of parental investment[31,34,35]. Thus, the long foraging trips in our data may indicate that Black-tailed gulls breeding around the Korean Peninsula engage in a dual foraging strategy.

The foraging distance of short foraging trips was significantly different between Seas, but there was no difference among Seas except Bulmugido. However, the foraging efficiency differed in most of the breeding colonies. Population density is positively correlated with the foraging range due to prey depletion near the breeding colony or to minimize intraspecific competition[17,18,21,22,36]. Hongdo, which has highest breeding density of all colonies, showed longest foraging distance followed by Chilsando, aligning with the outcome of previous studies[21]. Interestingly, Sonoindo and Bulmugido had longer foraging distances than Dokdo, despite their population density being not even close to half of Dokdo's. Additionally, the foraging distance between Chilsando and Sonoindo had no significant difference. Almost 90% of the total breeding colonies around the Korean Peninsula are in the Yellow Sea and Sonoindo and Bulmugido is closely located to Chilsando, as well as other unknown breeding colonies. Thus, the long foraging distance may result in inter-colonial competition. This may be also supported by the low foraging efficiency of the breeding colonies located in the Yellow Sea compared to those in the South Sea or East Sea. Although Chilsando and Sonoindo had similar foraging distances, their foraging efficiency was significantly different, which may indicate that foraging segregation occurred; however, this needs further research.

Breeding colonies located in the Yellow Sea exhibit significantly smaller foraging ranges during long foraging trips compared to those in the East Sea. Interestingly, the order of foraging range during these long foraging trips aligns with the distance from the Korean Peninsula. Species within the *Larus* genus are well-known opportunists, often trailing fishboats or foraging at ports for fishery discards[37–39]. Consequently, parents may favor easily accessible anthropogenic food sources located in distant places over unpredictable natural ones within short distance, balancing the costs (such as energy expended during foraging or food competition near breeding sites) against the benefits (quantity and quality of food obtained)[17,36]. This preference could explain the notably lower foraging efficiency observed in the Yellow Sea colonies compared to those in the South Sea or the East Sea. Individuals from the East Sea, having to travel longer distances to reach the Korean Peninsula, exhibited higher flight efficiency. The diminishing foraging efficiency in the Yellow Sea colonies may also be due to the following fishery boat; not only commercial vessels but also recreational ones frequently traverse the Yellow Sea. However, confirmation of this assumption requires further investigation, particularly regarding the overlap between fishing boat routes and foraging trips.

Because the purpose of wintering for seabirds is to recover their body condition and prepare for the next pre-breeding season, strategize migration patterns is crucial for maximizing fitness[10]. Most of Black-tailed gulls we observed remained along the coast of the peninsula where they usually foraged during the breeding season, following the costal line similar to other gulls in previous research[15,16] Fewer gulls flew directly to neighboring countries (e.g., China, Japan, etc.). Across all breeding colonies, Black-tailed gulls departing earlier tended to cover shorter distances compared to those leaving later. Additionally, except for Hongdo and Gwandeumdo, gulls departing breeding colonies earlier exhibited lower flight efficiency than those leaving later. Studies on migrating seabirds have shown similar energetic costs between strategies[40,41] and gulls tend to minimize energy expenditure during migration[13,15, 16]. Thus, we suggest that gulls leaving early slowly reach their wintering site with lower flight efficiency, whereas those leaving later fly more directly to the wintering site. However, further research on complete migration patterns is necessary.

Overall, this study discusses how both foraging behavior in the late stage of breeding and migration patterns in the post-breeding may be affected by the proximity to the foraging site or conspecific competition pressure of the breeding colony. This study presents novel findings regarding the diverse foraging and dispersal patterns of Black-tailed gulls across different breeding colonies during the late fledge and post-breeding period with fine-scale GPS tracking. However, due to the limitation of relying solely on GPS location data, further studies such as observing foraging behavior throughout entire breeding season is necessary to confirm our discussion.

Materials and method

Study species

The Black-tailed gull, a medium-sized gulls, primarily exhibited in East Asia, including South Korea, China, and Japan. Its breeding season typically spans from April to July. Black-tailed gulls predominantly fed on fish, such as anchovy, and invertebrates like squid or shellfish[42]. However, being generalists, they also frequent city ports, fish farms, or rice fields for anthropogenic food sources and even trail fishing boats to scavenge for bycatch. Therefore, their well-known foraging sites are located on the Korean Peninsula. While there remains a knowledge gap regarding the dispersal patterns of Black-tailed gulls during the non-breeding period, Kown[28] reported that gulls breeding in Hongdo disperse about 43 km to the nearest coast on the Korean Peninsula, which they typically visit during the breeding season. In contrast, Hong et al.[27] discovered that gulls breeding in Dokdo migrate approximately 350 km to Oki Island in Japan for wintering, based on GPS tracking data. Black-tailed gulls breeding in China and dispersing to the Yellow Sea exhibit high variation in dispersal distance and timing[43]. This flexibility in diet and dispersal pattern makes Black-tailed gulls a suitable species for studying foraging and dispersal behavior across different breeding colonies.

Study area

This study was conducted on six main breeding colonies of Black-tailed gull: Bulmugido, Chilsando, and Sonoindo in the Yellow Sea; Hongdo in the South Sea; and Dokdo and Gwaneumdo in the East Sea (Fig. 1). Breeding colonies in the Yellow Sea are densely clustered according to latitude, and Black-tailed gulls, along with diverse seabird species, breed here due to the relatively shorter distances from tidal flats, estuaries, and coasts. In addition, the abundance of paddy fields behind tidal flats and presence of numerous fishing boats engaged in freshwater fishery provide additional food sources. In contrast, breeding colonies in the East Sea are located farthest from the Korean Peninsula, and foraging sites are limited to either the open ocean closely located to the colonies or three ports near Gwaneumdo, or far-located city ports on the Korean Peninsula. Specifically, for Dokdo, the abundant plankton and diverse fish species within 4 km of the open ocean around breeding colony[44] suggest that food sources could be secured from relatively shorter distances compared to the Yellow Sea. Hongdo, situated in the South Sea, is geographically positioned in the middle of the Korean Peninsula and the northwestern Japan. Although this breeding colony is the only one that forages to the southern coast area of the Korean Peninsula, it has the highest breeding density of Black-tailed gulls[25] indicating that Black-tailed gulls are subject to high competition pressure[45]. Climatic conditions such as temperature or wind speed were found not to be significantly different between breeding colonies, as tested prior to this study. Additionally, all breeding colonies are composed of grasslands and rock cliffs. Therefore, the foraging or dispersal pattern between breeding colonies could be highly related to competition pressure (which could be represented by colony size and population) and the distance to the predictable foraging site (Fig. 2).

GPS tracking of Black-tailed gulls

A total of 160 adult Black-tailed gulls were captured with bow net from their breeding colonies and deployed with GPS trackers from May 22, 2021, to June 10, 2021. Among them, 92 birds (43 females [46.7%] and 49 males [53.2%]; Table 3; See also Table S1 in Supplementary information for details) that had devices steadily obtaining GPS location until early August were studied further. The devices (LEGO, OMNI, Druid Technology) were attached in the form of a harness using Teflon tape. Although it was suggested that transmitters should weight no more than 3% of the body mass[46], it is permissible to attach devices up to 5% of the body weight[47]. The trackers weighed 18.7 g (LEGO, $68\times21\times16$ mm^3) and 10.4 g (OMNI, $50.8\times24.2\times12.8$ mm^3), which was 3.36% (LEGO, ca. 557.10 g) and 2.00% (OMNI ca. 520.03 g) of the weight of Black-tailed gulls, respectively. The location coordinate collection interval for each device was set to 30 min. When three or more coordinates exceeding the standard speed (e.g., 5 m/s) appeared consecutively, additional coordinates were collected every 20 s to minimize errors due to loss of location information during flight.

Behavior patterns

June to July is the late stage of breeding season for the Black-tailed gulls, a period mixed with various events such as juvenile fledging and adult migration to wintering or stopover sites. In this study, the location coordinates were divided into cases located inside the breeding colony (In) and those located outside (Out) to accurately analyze the behavioral characteristics of the individuals. When an individual departed from a breeding colony and returned (i.e., coordinates were recorded repeatedly as In and Out), we defined it as foraging (see also Supplementary information S4 for details). Out of 92 Black-tailed gulls tracked in this study, 85 completely left

Coast	Breeding colony	Female	Male	Total
Yellow Sea	Bulmugido	1	9	10
	Chilsando	11	12	23
	Sonoindo	8	10	18
South Sea	Hongdo	3	7	10
East Sea	Dokdo	8	5	13
	Gwaneumdo	12	6	18
Total		43	49	92

Table 3. Number of Black-tailed gulls from which collected GPS data for this study. The initial GPS deployment was conducted on 160 adult Black-tailed gulls. However, due to the device malfunction or morality of individuals, data from 92 gulls were utilized for this study. See also Table S1 in Supplementary information for details.

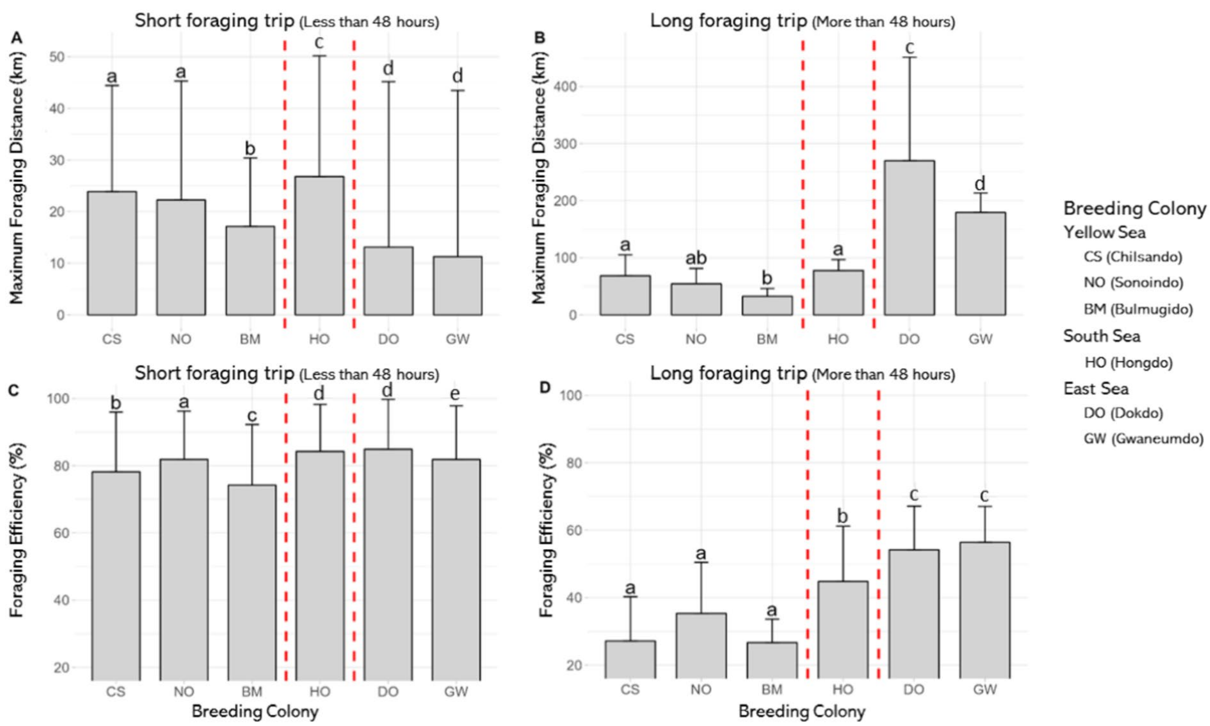

Figure 3. Comparison of mean maximum foraging distance and foraging efficiency of Black-tail gulls breeding in six breeding colonies (± sd) in Black-tailed gulls. (**A**) Maximum foraging distance with less than 48 h, (**B**) Maximum foraging distance with over 48 h, (**C**) Foraging efficiency with less than 48 h, and (**D**) Foraging efficiency with over 48 h among breeding colonies of black-tailed gulls in Korean peninsula. Note that red dash-line presented to separate three Coast (East: DO (Dokdo, n = 13) and GW (Gwaneumdo, n = 18), South: HO (Hongdo, n = 10), Yellow (west): CS (Chilsando, n = 23), NO (Sonoindo, n = 18), BM (Bulmugido, n = 10)). The different characters on the bars indicate significant differences. Movement data tracked by GPS was collected during June to July 2021. Table 1, Table 3, and Fig. 1 for more details.

before July 31; leaving the breeding colony and moving away since departure (Out) until July 31 was defined as migration. Some individuals left the breeding colony to settle in nearby shores or other areas (i.e., wintering sites, etc.).

The foraging behavior of Black-tailed gulls was categorized into short and long foraging trips based on the duration of the foraging. Short foraging trips typically involve feeding juveniles [32, 52], while long foraging trips serve purposes such as self-feeding or resting[10], and provisioning food to chicks. Therefore, foraging trips lasting less than 48 h were classified as short foraging trips, whereas those lasting longer than 48 h were classified as long foraging trips (see Figure S3 in Supplementary information for more details). Foraging characteristics during the fledge were described using maximum foraging distance and foraging efficiency, calculated for each return flight after the birds left the breeding colony. The maximum foraging distance was defined as the greatest linear distance traveled from the breeding colony while foraging efficiency was defined as the percentage of maximum foraging distance to the sum of the total distance traveled during each flight. Foraging efficiency ranges from 0 to 100%, with 100% indicating that Black-tailed gulls flew only between the destination and the breeding colony, while a foraging efficiency of less than 100% indicates that additional flights were taken.

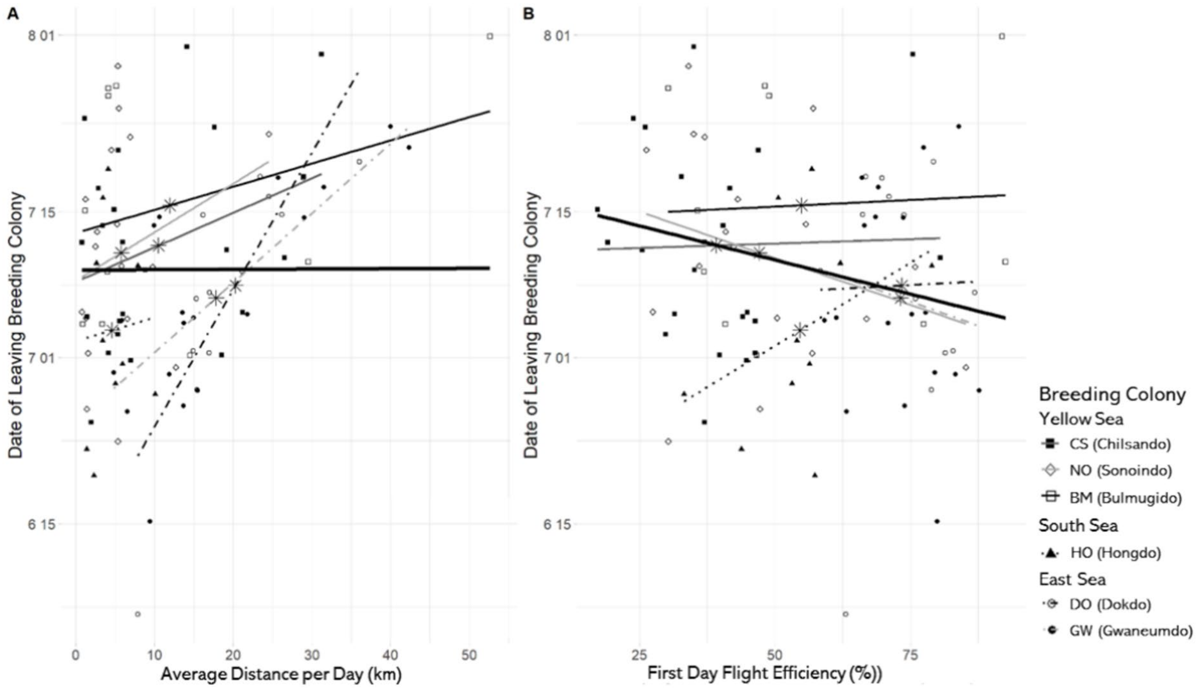

Figure 4. Date of leaving breeding colony in related to (**A**) average distance per day and (**B**) first day flying efficiency among breeding colonies of Black-tailed gulls in Korean peninsula. CS (Chilsando): full square dots and dark grey solid line, NO (Sonoindo): diamond dots and grey solid line, BM (Bulmugido): empty square dots and black solid line, HO (Hongdo): triangle dots and black dotted line, DO (Dokdo): empty dots and dashed-dot line, GW (Gwaneumdo): full dots and dashed-dot line. Note that black thick solid line presented linear regression for all 92 individuals analyzed in this paper. See Table1, Table 3, and Fig. 1 for more detail.

Migration behaviors were described using maximum disperse distance, average distance per day and first day flight efficiency. Maximum disperse distance was defined as the maximum linear distance traveled from the breeding colonies until July 31. A higher maximum disperse distance indicates that the Black-tailed gulls ventured farther from their breeding colony after the breeding is over. Due to variations in migration duration and total distance traveled per day among individuals until end of July, and our aim to investigate the behavior difference among breeding colonies from end of the breeding to the start of the migration, we focused on average flight distance and flight efficiency immediately after individuals left their breeding colony. Average distance per day was calculated by dividing maximum disperse distance by the number of days from leaving the breeding site until the end of July. A higher the average distance per day indicates that Black-tailed gulls moved faster from the breeding colony, while a lower average distance per day suggests that they stayed closer. First day flight efficiency was determined by dividing the maximum linear distance traveled on the first day of migration by the sum of the total distance traveled. A high first day flight efficiency implies that Black-tailed gulls traveled directly to their destination, whereas a low first day flight efficiency indicates that gulls may have wandered to various sites before reaching their wintering or stopover site.

Statistical analysis

The differences in the flight characteristics among Black-tailed gulls across different Seas in the Korean Peninsula (the Yellow Sea, the South Sea, and the East Sea) and their breeding colonies were analyzed using ANOVA (Analysis of Variance), The analysis assessed each variable related to foraging (maximum foraging distance, foraging efficiency) and migration (maximum dispersal distance, average distance per day, and first day flight efficiency) separately with Seas and breeding colonies. After ANOVA, Tukey HSD post-hoc test was conducted for the post-hoc analysis both among the three Seas and among the six breeding colonies. To identify colonial and individual differences in migration efficiency and dispersal pattern, linear regression of breeding colonies was applied for average distance per day, and first day flight efficiency, respectively. Data are represented as mean ± SD. The GPS data was analyzed using QGIS (3.10.2) and the R software (4.2.2).

Ethical note

The capturing of birds and entry into the breeding colonies was approved by Institutional Animal Care and Use committee (IACUC) of National Institute of Ecology. All methods and procedures were conducted following guidelines of the IACUC. To minimize potential stress, handling time was kept to a minimum, and after deploying the device, we ensured that gulls flew away freely.

Data availability statement

The data that support the findings of this study are available on request from the corresponding author.

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Conceptualization: S.Y.L. and W.S.L.; methodology: S.Y.L. and W.S.L.; formal analysis and investigation: S.Y.L and W.S.L.; writing: S.Y.L. and W.S.L. All authors read and approved the final manuscript.

Competing interests

The authors declare no competing interests.

Additional information

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