

Spatio-temporal responses of black-tailed gulls to natural and anthropogenic food resources

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ABSTRACT: Urbanization affects animal movements. However, how urban omnivores respond to natural and human-related food sources with different spatio-temporal structures remains poorly understood. Here, we used animal-borne GPS, video data loggers and high-resolution mapping to examine the foraging behaviour of black-tailed gulls *Larus crassirostris* during their incubation and hatching period. As expected, the gulls fed not only on natural food at sea (e.g. anchovy and cuttlefish), but also on human-related food sources in 3 kinds of feeding grounds on land, i.e. fishery- or meat-processing plants or markets, private houses and paddy fields. Furthermore, the gulls responded to the different temporal and spatial dynamics of the feeding grounds. The gulls were distributed among these feeding grounds in response to the availability and ephemerality of each food source. Natural-food foraging trips (i.e. ocean) and anthropogenic-food trips (i.e. inland) have different spatial properties, showing a Lévy search of $\mu = 2$ with larger foraging range and patterns closer to ballistic movement with smaller foraging range, respectively. Thus, the gulls responded flexibly to the contrasting food resources of natural and human-related food sources with different temporal and spatial heterogeneities.

KEY WORDS: *Larus crassirostris* · Habitat use · Seabirds · GPS · Video · Data logger · Movement

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INTRODUCTION

Urbanization affects diet, reproduction, survival and population in various animal taxa (Ditchkoff et al. 2006), leading to human–wildlife conflicts in urban and surrounding environments (Conover 2002). This may often be triggered by modified feeding opportunities in the urban environment (Bolger 2001, Marzluff 2001, Chamberlain et al. 2009), followed by changes in the foraging behaviour of animals (Fleischer et al. 2003). However, little is known about the ways in which omnivorous animals move in environments where anthropogenic and natural food sources with different spatio-temporal structures are available. Such information is important not only for a basic understanding of behavioural plasticity within the context of movement ecology (Nathan et

al. 2008), but also for a comprehensive understanding of a species' adaptation to urban and surrounding regions, such as rural and marine habitats, and to provide tools for the improved management of urban animals (Caro 2007).

Anthropogenic and natural resources exhibit different temporal characteristics. The urban landscape structure has extremely high spatial habitat fragmentation produced by many different land uses (McKinney 2008), associated with temporal heterogeneity on an hourly basis, as human activities tend to be greatest during specific times of day (Ditchkoff et al. 2006). Similarly, natural prey items also change their activity or distribution in relation to time (e.g. diurnal vertical migrations of lanternfish *Myctophidae*; Paxton 1967). Therefore, animals will respond to the temporal heterogeneity of each feeding ground

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and distribute themselves accordingly to optimise their food intake, such as by nocturnality in urban areas (Santos et al. 2010) as well as in natural settings (Sjöberg 1989, Zavalaga et al. 2011). In addition, on a finer scale, natural and human-related prey habitats exhibit different ephemerality (i.e. temporal stability), which may affect individual behaviours such as residence time in each foraging ground.

In addition to temporal properties, the spatial structures of food resources can affect the movement patterns of animals (Skórka et al. 2009). For example, home range sizes reflect food availability (i.e. prey abundance modified by its accessibility) and often differ between animals living in natural and urban environments (Belant et al. 1998, Marzluff et al. 2001). Moreover, urban food resources have more predictable spatial structures, and, thus, animals with relatively high spatial memory capacities do not need to search over wide ranges for these resources, but travel directly with ballistic movements (James et al. 2011). Conversely, foragers may adopt efficient movement strategies to locate natural food that is patchily distributed in low concentrations on spatial scales beyond a searcher's sensory range, such as in the marine environment (Viswanathan et al. 1999, Sims 2010, de Jager et al. 2011). Thus, omnivorous animals are likely to switch flexibly between these different types of movement patterns in relation to natural and human-related prey availability (Bartumeus et al. 2010).

Gulls of the genera *Larus* and *Chroicocephalus* are a group of seabirds that frequently occur in urban areas. They are omnivorous, with a diverse diet based on natural (i.e. fish) and anthropogenic food sources such as refuse dumps and agricultural habitats (Pierotti & Annett 1991, Rock 2005, Duhem et al. 2008, Schwemmer et al. 2008, Ramos et al. 2009). These food sources of human origin can contribute to the reproductive performance of gulls either in a positive (Pons 1992, Weiser & Powell 2010) or a negative way (Belant et al. 1998, Pierotti & Annett 2001) and can, thus, affect population size (Duhem et al. 2008).

In this study, we deployed animal-borne data loggers on black-tailed gulls *Larus crassirostris* to evaluate their spatio-temporal responses to natural and anthropogenic food sources during their incubation and hatching period. We recorded their movements using GPS data loggers with fast sampling rates (Kohno & Yoda 2011); the data were mapped in high resolution. In addition, we used video camera data loggers (Moll et al. 2007, Rutz et al. 2007, Yoda et al. 2011) and collected stomach samples to obtain direct evidence of the use of human-related food resources.

MATERIALS AND METHODS

Study sites, studied species and field experiments

We conducted our study from May to June 2010 on Kabushima Island (40° 32' N, 141° 33' E), Hachinohe City, Japan. Annually, 30 000 to 35 000 black-tailed gulls breed at Kabushima. We captured 45 adult individuals using a dip net or by hand during the incubation and hatching period (Fig. 1). We deployed GPS

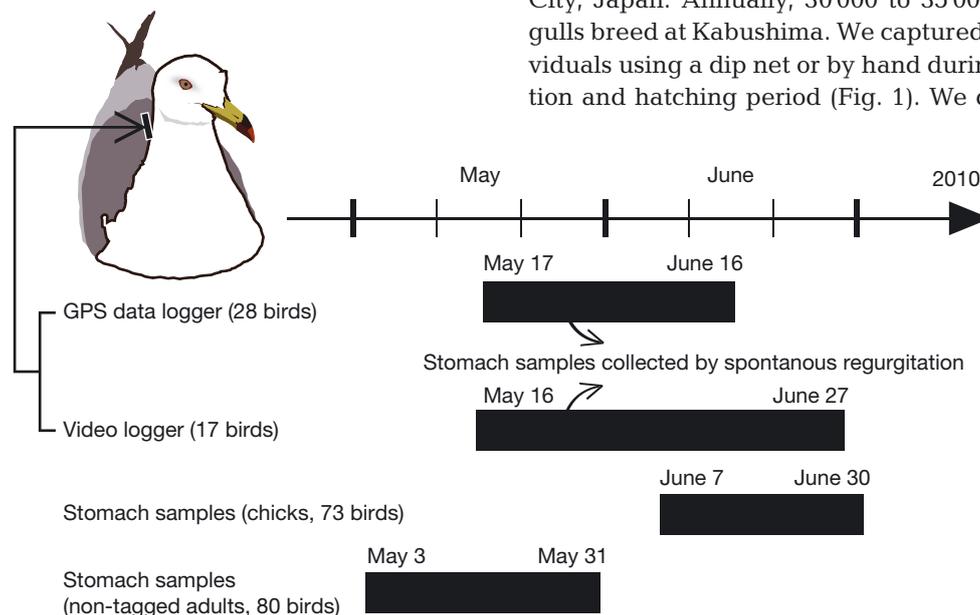


Fig. 1. *Larus crassirostris*. Experimental schedules for the deployment of data loggers and collection of stomach contents. We did not deploy GPS and video loggers simultaneously on a bird

loggers on 28 and video camera data logger on 17 adult gulls. Data loggers were attached to their backs using waterproof tape (Tesa).

A GPS data logger consisted of a GPS receiver with an antenna (GiPSy, Technosmart) operated by a lithium-ion polymer battery. Loggers were set to take a positional fix every 1 s. The overall weight was 39 g, corresponding to 6.9% of bird mass. The GPS data logger could record 25 h of data. We used a video camera data logger (LY30, 19 × 68 mm, Benco) after improving its waterproof sealing. The video lens faced forward or backward on the bird. This camera had a 280 mAh Li-polymer battery and 4 GB memory and could record for 2 h. The resolution was 478 × 359 or 736 × 480 pixels, with a frame rate of 30 frames per second. The overall weight was 27 g, corresponding to 4.8% of bird mass. We did not deploy GPS and video loggers simultaneously. The gulls did not appear to be negatively affected by the loggers or by the handling by researchers. However, because the data logger we used is relatively large (Phillips et al. 2003), we carefully examined its effect on breeding. For this, we compared the egg hatching success (i.e. brood size divided by clutch size) between tagged gulls and control gulls using a generalized linear model with binomial errors and Akaike's information criterion corrected for small sample size (AICc), and ranked the models with and without logger effects by Akaike weights (Burnham & Anderson 1998). If both models were not strongly selected (AICc difference < 2), we used model averaging to calculate the predicted values (Burnham & Anderson 1998). We recaptured the tagged individuals after 1 to several days to reduce any long-term effects on them and then downloaded the data to computers.

We collected stomach contents by spontaneous regurgitations to determine the diets of tagged gulls during the deployment or recovery. In addition, we collected the stomach contents of non-tagged adults and chicks in May and June, respectively, to investigate diets at the population level. Their stomach contents were identified visually to species or categories (e.g. Japanese anchovy *Engraulis japonicus*, chickens, bread).

To detect feeding grounds, direct observation was conducted frequently at several possible feeding grounds recorded by GPS, such as Hachinohe Port (HP), some rice *Oryza sativa* L. paddy fields, fishery- or meat-processing plants or markets and rivers. In

addition, we conducted a questionnaire asking what time gulls appeared and what they ate or what people fed them at several private properties where we could not directly observe the feeding gulls.

Data analysis

We defined a trip as a period when a bird was away from the nest for > 1 h.

GPS records indicated that the distribution of instantaneous ground speeds was bimodal (Fig. 2). This was similar to the distribution of the GPS positions when they were re-sampled every 10 s (Fig. 2) to check the effects of fine-scale resolution problems (Ryan et al. 2004). We used a value of 15 km h⁻¹ as the threshold value of 2 behavioural modes (Bartumeus 2009): flight and non-flight.

We examined visually the habitat types where the gulls were resting or feeding using high-resolution satellite images through Google maps API (www.google.com/apis/maps) on Matlab version 7.1 (MathWorks). We categorized 11 habitat types, 4 of which were considered to be feeding grounds from diet samples, video data and questionnaires (see details in Results): sea water (hereafter, sea), paddy fields, fishery- or meat-processing plants or markets and a house named House R1. Others were river, beach or rocks along the coast, sea at HP, artificial structures at HP such as the sea dike, parking lot or wharf around the port, artificial structures outside HP such as the coastal dike and other houses. We first extracted flight phases and then calculated the time between the end of one flight and the beginning of the next as the residence time in each habitat. We chose this approach because flight phase data incur fewer problems from high sampling noise than do staying data (Ryan et al.

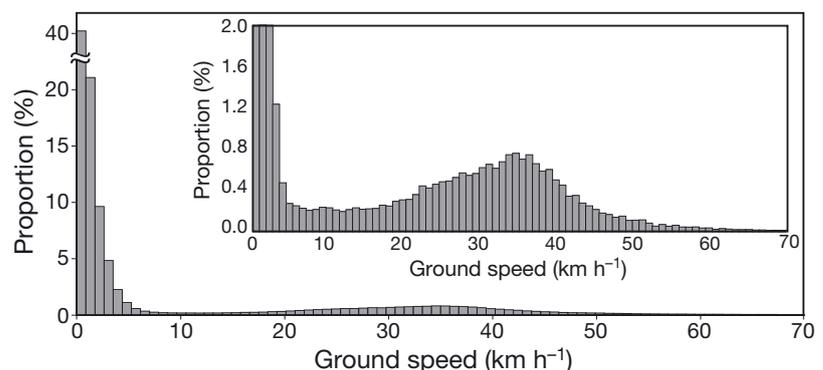


Fig. 2. *Larus crassirostris*. Frequency distributions of ground speeds recorded by GPS between 2 locations during trips. Inset = enlarged frequency distribution of GPS positions re-sampled every 10 s to check the effect of the fine-scale resolution problem

2004). The number of feeding grounds was calculated in relation to the time of day when the bird first reached a feeding ground. For this analysis, the data were pooled across all birds and trips.

We allocated complete trips into 4 types on a coarse scale (i.e. on the order of 1 to 10 km; Wakefield et al. 2009) based on fine-scale habitat use. If the proportion of total time spent at sea at HP and artificial structures at HP was ~100% of the time spent in all habitats, we designated the trips Port trips. If the proportion of total time spent at paddy fields, river and private houses was >30% of the time spent in all habitats, then we defined the trips as Inland trips. If the time spent at sea was >5%, we defined the trips as Ocean trips. The other trips were designated as 'mixed' trips. In this study, this definition was mutually exclusive.

We calculated trip duration, trip range (defined as the maximum distance travelled) and total distance travelled for the 4 trip types. The total distance travelled could be overestimated due to increased noise caused by the fine-scale sampling (Ryan et al. 2004). Therefore, we re-sampled GPS positions every 10 s to reduce this problem (Ryan et al. 2004). We compared these 3 parameters between trip types using general linear models, AIC and the *t*-value for the model terms.

Lévy analysis

To analyse the spatial search strategy, we compared the frequency distribution of flight distances between habitats (i.e. the start and end points of a flight). The tail of the distribution can be described by a general power (Pareto) distribution (Viswanathan et al. 1996):

$$P(x) \approx x^{-\mu} \quad (1)$$

where x is a statistical event corresponding to a movement length, $P(x)$ is the probability of this event happening and μ is the characteristic constant of the movement. The Lévy flight hypothesis is only concerned with the tail; the distribution of short movements is not relevant. We define the start of the tail by x_{\min} . The definition of movement length has varied among studies (see Edwards 2011). Here, we defined the movement length as the net displacement between 2 habitats, which is close to Viswanathan et al.'s (1996) definition (i.e. the distance between feeding events). We compared the directness of flights (i.e. straightness index, net displacement divided by total distance travelled during each flight)

using linear mixed models, treating the trip number nested in individual birds as a random effect. Linear mixed models were run using the LME4 package (Bates & Maechler 2010). The significance of the fixed effects was obtained from 100 000 Markov chain Monte Carlo (MCMC) simulations, performed using the pvals function in the LANGUAGER package (Baayen 2007). The values of μ indicate different random walk families and could signal ecologically important shifts in behaviour (Sims 2010): close to $\mu \geq 3$ is the domain of Brownian movement, $1 < \mu < 3$ corresponds to the domain of Lévy flights and $\mu = 1$ would correspond to completely directed flight. Within the Lévy flight regime, the optimal μ , which in turn generates an optimal search strategy in terms of prey encounter, depends on certain landscape features, with $\mu \approx 2$ being a typical empirical value (Viswanathan et al. 1999, Sims 2010, Raposo et al. 2011).

We calculated μ for complete trips among Inland and Ocean trips with trip ranges of >5 km to examine search patterns beyond frequently used areas (i.e. the trip range of Port trips). We did not use Port trips because Port trips were not related to feeding. The μ was estimated by maximum-likelihood estimation (MLE; Edwards 2008, Clauset et al. 2009) rather than by the widely used linear regression method because there are several problems with the latter (Edwards 2008). The MLE μ is computed by inserting flight distances x in the equation:

$$\mu = 1 + n \left[\sum_{i=1}^n \ln \frac{x_i}{x_{\min}} \right]^{-1} \quad (2)$$

where x_i , $i = 1 \dots n$ are the flight distances such that $x_i \geq x_{\min}$; see Edwards (2008) or Classet et al. (2009). We estimated the lower bounds x_{\min} and the p values of the goodness-of-fit based on the Kolmogorov-Smirnov (KS) statistic, following Clauset et al. (2009). For each possible choice of x_{\min} , μ was estimated and the corresponding KS statistic was calculated. Then x_{\min} was selected to yield the minimum KS statistic (Clauset et al. 2009). In our calculations, we used a level of statistical significance of $p > 0.1$, following Clauset et al. (2009). In practice, we used the `plfit`, `plplot` and `plpva` functions (<http://tuvalu.santafe.edu/~aaronc/powerlaws/>) constructed by Clauset et al. (2009). To confirm whether our Lévy-flight fits were better than exponential distribution, we examined the sign of the log-likelihood ratio, where positive values indicate that the power-law model is favoured (Clauset et al. 2009). We compared exponential distribution with the power-law model with or without the lower bounds x_{\min} , because the lower bounds may affect the fit.

Data were analysed using Matlab version 7.1 (MathWorks) and R version 2.7.2 (R Development Core Team 2008).

RESULTS

Logger effects

Akaike weights showed no difference in the hatching rate between control birds ($n = 91$) and tagged birds ($n = 25$); the null model (AICc = 230.58, Akaike weight = 0.73) was preferred over the logger-effect model (AICc = 232.55, Akaike weight = 0.27). As the difference in AICc was 2, we showed the parameter estimates obtained by model averaging; we did not find significant adverse effects of data loggers on hatching rates (Table 1). However, because the coefficient for the logger effect was very small but still negative (Table 1), we should be cautious about the logger effect on the gulls.

GPS analysis

The GPS loggers recorded 58 trips, consisting of 42 complete trips and 16 trips with truncated data due to exhausted batteries. Gulls showed diverse movement patterns during this period (Fig. 3).

Table 1. Model-averaged coefficients ($\beta \pm$ SD) and p-values from 2 models, relating hatching rates to data logger carried, with and without the logger

Variable	$\beta \pm$ SD	p
Intercept	-0.54 ± 0.11	<0.0001
Logger	-0.02 ± 0.14	0.44

Trip durations were not different between trip types (AIC with the effect of trip types: 236.0, AIC without the effect of trip types: 235.2). The trip range and total distance travelled were different between trip types (AICs of trip range model were 316.4 and 334.9 and those of total distance model were 412.8 and 431.8 with and without the effect of trip types, respectively), with greater foraging range ($t = 3.0$, $p < 0.01$) and total distance travelled ($t = 2.7$, $p < 0.05$) for Ocean trips than for the other types of trips. Tracks re-sampled every 10 s showed a decrease of 11.9% in the total distance travelled (Table 2), but the results did not change.

The gulls visited different feeding grounds at different times of the day (Fig. 4). The cumulative frequency of the residence time in feeding grounds indicated that gulls stayed for less time at each feeding ground at sea compared to at fishery- or meat-

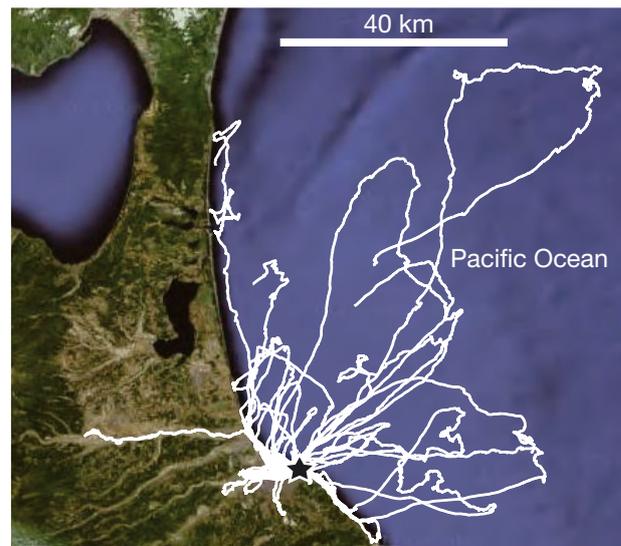


Fig. 3. *Larus crassirostris*. GPS recordings of gull trips ($n = 58$ trips; 42 complete trips and 16 with truncated data). ★: Kabushima Island

Table 2. *Larus crassirostris*. Foraging trips made by black-tailed gulls. All means \pm SD; minimum and maximum values in (). *: distance of re-sampled GPS positions every 10 s

Trip type	n	Trip duration (h)	Trip range (km)	Distance travelled (km)	Distance travelled (km)*
Port	16	4.26 ± 2.50 (1.02, 9.10)	4.36 ± 0.25 (3.80, 4.71)	16.66 ± 3.16 (10.18, 22.21)	14.30 ± 2.31 (9.52, 19.69)
Inland	8	6.45 ± 4.41 (1.26, 12.83)	11.07 ± 10.04 (4.48, 35.11)	43.50 ± 29.15 (16.94, 109.0)	38.31 ± 27.66 (15.25, 102.0)
Ocean	12	7.13 ± 5.04 (1.02, 13.68)	24.31 ± 16.08 (3.16, 59.31)	80.70 ± 51.30 (13.78, 173.0)	74.35 ± 48.10 (12.84, 163.0)
Mixed	6	4.43 ± 2.22 (2.23, 6.89)	7.69 ± 3.84 (4.36, 13.25)	29.45 ± 13.35 (16.30, 45.34)	26.10 ± 12.49 (14.09, 42.27)
All trips	42	5.52 ± 3.84 (1.02, 13.68)	11.81 ± 12.59 (3.16, 59.31)	41.90 ± 39.86 (10.18, 173.0)	37.72 ± 37.41 (9.52, 163.0)

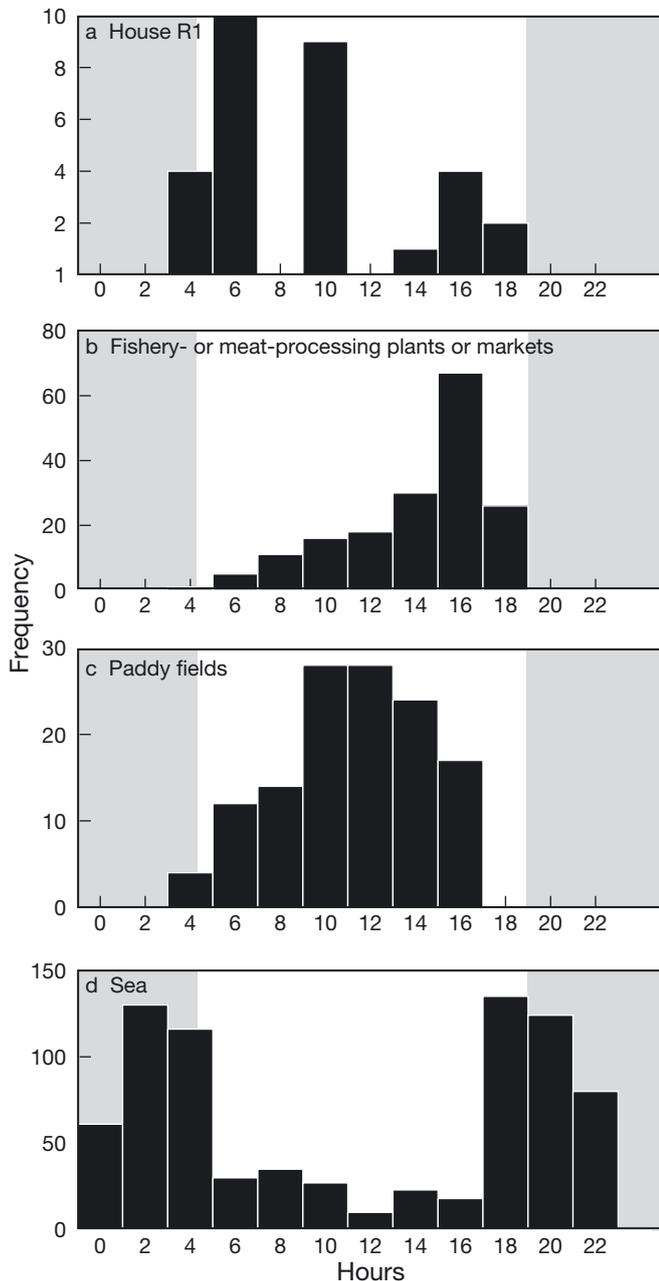


Fig. 4. *Larus crassirostris*. Total number of gulls at feeding grounds: (a) House R1, (b) fishery- or meat-processing plants or markets, (c) paddy fields and (d) sea in relation to time of day. Shading indicates night time

processing plants or markets, paddy fields and House R1 (Fig. 5).

The straightness index did not differ between trip types ($p > 0.5$) with straightness indices [mean \pm SD (n)] of 0.72 ± 0.25 (245), 0.73 ± 0.24 (266), 0.75 ± 0.24 (581) and 0.69 ± 0.26 (128) for Port, Inland, Ocean and mixed trips, respectively. Thus, the directness of each distance was the same between trip types. The

sign of the log likelihood showed that all the power-law models with the lower bounds were favoured over the exponential models ($n = 16$). However, the signs were reversed for 5 trips (31%) if no lower bounds were set. The Lévy index (Fig. 6) was significantly different between Inland trips ($\mu = 1.49 \pm 0.18$, $n = 6$, $p = 0.17 \pm 0.24$) and Ocean trips ($\mu = 2.04 \pm 0.48$, $n = 10$, $p = 0.52 \pm 0.31$, Wilcoxon rank sum test, $W = 5$, $p < 0.01$).

Diet samples, video data loggers and questionnaires

Stomach samples of tagged gulls (23 ind.) included fish, mainly Japanese anchovy (44% by occurrence, $n = 11$), bread (12%, $n = 3$), other fish (12%, $n = 3$), shellfish (8%, $n = 2$), chicken (8%, $n = 2$), confectioneries (4%, $n = 1$), cuttlefish (*Sepia* spp., 4%, $n = 1$), insects (4%, $n = 1$) and other ($n = 1$). Diet samples from non-tagged adults in May (80 ind.) were composed of Japanese anchovy (34.0%, $n = 33$), cuttlefish (22.7%, $n = 22$), other fish (11.3%, $n = 11$), shellfish (10.3%, $n = 10$), insects (4.1%, $n = 4$) and other ($n = 17$), whereas samples from chicks in June (73 ind.) were composed of Japanese anchovy (56.6%, $n = 47$), insects (13.3%, $n = 11$) and other ($n = 25$).

Video loggers showed various activities of tagged gulls, such as flying over the sea with a congener (Fig. 7a), flying over the town (Fig. 7b), and resting on the water surface (Fig. 7c), although the short recording time (2 h) prevented us from recording the full range of trips and some behaviours such as feeding at sea or in paddy fields. Video data showed strong evidence of tagged gulls feeding at House R1 (4 km from the colony), where a person provided bread and many gulls (20 birds or more, including doves) congregated at ~07:00 h (Fig. 7d). Fighting over bread was recorded between tagged gulls and other gulls (Fig. 7e). No feeding was recorded around HP from any bird with a video logger ($n = 8$) that remained there.

The completed questionnaire from House R1 revealed that a person there fed bread or fish to black-tailed gulls, doves and crows on a fixed time schedule in the morning and early evening. Some meat-processing plants stated that gulls fed on meat at their garbage dumps.

On the basis of the GPS paths, diet samples, video data and questionnaires, in addition to the fact that gulls obtain insects in paddy fields (Komatsu 1935), we concluded that sea, paddy fields, fishery- or meat-processing plants or markets and House R1 were the main feeding grounds for the gulls.

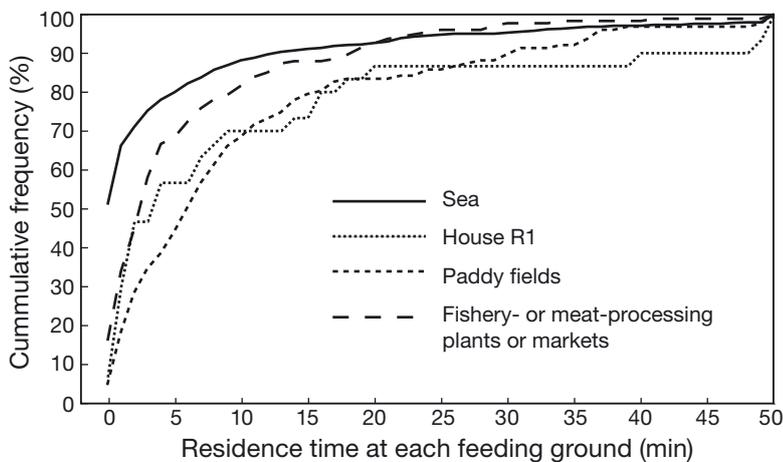


Fig. 5. *Larus crassirostris*. Cumulative frequency distribution of residence time at each feeding ground (see key). Black-tailed gulls spent shorter periods at sea than at other feeding grounds

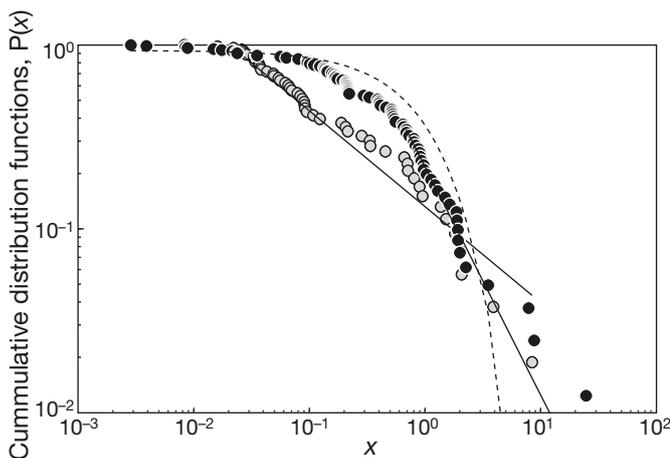


Fig. 6. *Larus crassirostris*. Examples of the cumulative distribution functions and their maximum likelihood power-law fits of flight distances, x , for the Ocean trip (\bullet ; $\mu = 2.2$, $n = 81$, $x_{\min} = 0.69$, $p = 0.89$) and the Inland trip (\circ ; $\mu = 1.5$, $n = 53$, $x_{\min} = 0.02$, $p = 0.20$). We used a level of statistical significance of $p > 0.1$, following Clauset et al. (2009). Dotted line: exponential distribution with the rate of 0.94 fitted for the Ocean trip (see text)

DISCUSSION

Our study showed that the gulls were not only likely to prey on fish and cuttlefish at sea, but also likely to utilise anthropogenic food sources in 3 feeding grounds on land, i.e. fishery- or meat-processing plants or markets, a private house and paddy fields. Although such feeding habits have been known for many years, we showed for the first time that the gulls responded flexibly to contrasting natural and human-related food resources with different temporal and spatial heterogeneities.

Temporal responses to natural and anthropogenic food resources

The black-tailed gulls visited 4 feeding grounds at different times of day (Fig. 4), indicating differences in the time when the food resources were available (Fig. 4). Human activity or the outcome of the activity tends to be highest within a specific time window (Ditchkoff et al. 2006), causing some feeding grounds to be available during limited periods of time. In fact, the times spent at House R1 and at the fishery- or meat-processing plants or markets were not distributed normally or uniformly; the distributions were discrete-like at House R1 and skewed toward afternoons at the fishery- or meat-

processing plants or markets. These temporal patterns are expected to reflect the human activities of feeding and discarding food sources, respectively, as supported by findings from the video loggers (Fig. 7d) and questionnaires. Conversely, gulls used the paddy fields exclusively during daylight hours and the time of day during which this habitat was used exhibits a bell-shaped distribution with the highest peak around noon. Black-tailed gulls feed on aquatic insects at paddy fields (Komatsu 1935). The water in paddy fields has diurnal temperature cycles (Kuwagata et al. 2008), which may control the activities of aquatic insects, and accordingly, affect their availability and ease of capture for gulls.

Interestingly, gulls are highly nocturnal at sea, indicating that black-tailed gulls likely benefit from nocturnal foraging. Most bird species, including gulls, are diurnal, but at least 18 gull species, including *Larus* gulls, have been reported to show nocturnal behaviour (Burger & Staine 1993, McNeil et al. 1993) and 2 *Larus* gulls (ring-billed gulls *L. delawarensis* and gray gulls *L. modestus*) have a physiological retinal adaptation that allows for diurnal and nocturnal behaviour (Emond et al. 2006). Cuttlefish, a main prey item of black-tailed gulls, are nocturnal (Okutani 1987) and migrate upward in shallow water and die after spawning (Le Goff & Daguzan 1991), thus making post-spawning die-offs potentially available to seabirds (Croxall & Prince 1994). Conversely, there is no clear evidence that Japanese anchovy show vertical migrations (Ohshimo & Hamatsu 1996, Ohshimo 2004). Alternatively, gulls may associate with lighted fishing vessels at night (Arcos & Oro 2002), as Japanese anchovy respond to and aggregate at artificial lights (Hasegawa 1995).



Fig. 7. *Larus crassirostris*. Images obtained from video cameras attached to the gulls' back to record either (a, b, d, e) forward or (c) backward views. (a) A gull following a congener over the sea (i.e. Ocean trip), (b) a gull flying in the urban environment, (c) a gull resting around the estuary at Hachinohe Port with other black-tailed gulls, (d) a person feeding bread crusts to black-tailed gulls at House R1 at ~07:00 h and (e1–5) sequential images of fighting over bread between the tagged gull and a gull at House R1. The tagged gull lost the fight over the bread

The residence time in each feeding habitat can show the mobility and temporal stability of prey species. The residence time at sea was the shortest among the feeding grounds (Fig. 5), indicating that natural prey may be a more ephemeral resource, available for only short periods (i.e. up to 10 min), than are anthropogenic foods on land. In fact, Japanese anchovy occur in ephemeral and small (<25 m length and <20 m thick) groups (Aoyama & Mimoto 1970).

Spatial responses to natural and anthropogenic food resources

In this study, the trip range and total distance travelled for Inland trips, consisting of anthropogenic feeding grounds, were half those of Ocean trips (Table 2). Thus, natural food resources are further

from home than are urban ones and the travel cost would be higher for Ocean trips than for the other trips. However, the gulls might experience much higher competition for resources in the urban environment (Shochat et al. 2004). In fact, attraction to anthropogenic foods is highly likely to lead to strong intra- and inter-specific competition such as at House R1 (Fig. 7e), which would incur additional costs in terms of energy expenditure or injury to individuals caused by fights. The increased density of conspecifics can cause depletions in seabird food around colonies (Ashmole 1963), as found for double-crested cormorants *Phalacrocorax auritus*, which deplete sedentary flatfish in predictable locations (Birt et al. 1987). It is important to note that the gulls might face increased competition at sea (Schwemmer & Garthe 2005). Although we could not record the intra-specific competition at sea, such as foraging behind fish-

ing vessels, due to the limitation of video recording time, the possible competition at sea may also generate additional trade-offs between distance, availability and foraging success.

The distribution of flight distances showed Lévy flights properties, although exponential distribution was the better fit for 30% of the trips without the lower bounds. Ocean and Inland trips showed contrasting movement properties with Lévy exponents of $\mu = 2$ for Ocean trips and patterns closer to directed movement for Inland trips. The Lévy search strategy, with power-law exponents of $\mu = 2$, was theorized to be the most efficient movement pattern for locating sparse and patchy prey at spatial scales beyond a searcher's sensory range, such as is typical for the ocean (Viswanathan et al. 1999, Humphries et al. 2010, Sims 2010, Raposo et al. 2011). Although the gulls may follow fishing boats during the night, these boats may also show Lévy flight patterns of $\mu = 2$ (Bertrand et al. 2007; but see criticism by Edwards 2011) and the gull movements may be associated with the movement of fishing vessels. In contrast to non-informed optimal search patterns at sea, the more ballistic movements of Inland trips may indicate that urban food resources are more predictable compared to natural ones and that gulls have some knowledge of food resources in space and time. This result suggesting that the gulls changed their movements in relation to the landscapes sheds light on the problems of interpreting a Lévy search pattern without accurate knowledge of the landscape properties and memory capabilities of the animals involved (Raposo et al. 2011).

CONCLUSIONS

As the human population increases, human-wildlife relationships change (Conover 2002). At the present site, the use of paddy fields by gulls was reported more than 75 yr ago and conflicts between people and black-tailed gulls were described (Komatsu 1935). As the city's population has increased fourfold with the development of fisheries and industry, the black-tailed gulls observed in our study preyed on a wider variety of anthropogenic food resources and showed flexible responses to the temporal and spatial variability of contrasting types of habitat. Further investigations such as individual specialization and variability in foraging strategy would be interesting and are needed to better understand human-gull relationships as gull behavioural plasticity may affect breeding success or population dynamics.

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