Individual differences in foraging site fidelity are not related to time-activity budgets in Herring Gulls

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Many populations consist of individuals that differ consistently in their foraging behaviour through resource or foraging site selection. Foraging site fidelity has been reported in several seabird species as a common phenomenon. It is considered especially beneficial in spatially and/or temporally predictable environments in which fidelity is thought to increase energy intake, thereby affecting time-energy budgets. However, the consequences for activity and energy budget have not been adequately tested. In this paper, we studied the consequences of fine-scale foraging site fidelity in adult Herring Gulls *Larus argentatus* in a highly predictable foraging environment with distinct foraging patches. We measured their time-activity budgets using GPS tracking and tri-axial acceleration measurements, which also made it possible to estimate energy expenditure. Individual variation in foraging site fidelity was high, some individuals spending most of their time on a single foraging patch and others spending the same amount of time in up to 21 patches. While time and activity budgets differed between individuals, we found no clear relationship with foraging site fidelity. We did find a relationship between the size of the birds and the level of site fidelity; faithful birds tend to have a larger body size. Although differences in foraging time and habitat use between individuals could play a role in the results of the current study, short-term consequences of variation in foraging site fidelity within a population remain elusive, even when focusing on individuals with a similar foraging specialization (Blue Mussels *Mytilus edulis*). Studying individuals over multiple years and under varying environmental conditions may provide better insight into the consequences and plasticity of foraging site fidelity.

Keywords: accelerometer, behavioural consistency, bio-logging, central-place forager, energy expenditure, fine-scale foraging behaviour, GPS tracking, seabird.

Many populations consist of individuals that differ consistently in their food choice and foraging strategy. A common form of such variation is foraging site fidelity, where some individuals exploit a more limited set of foraging sites than others (Switzer 1993, Bradshaw *et al.* 2004, Piper 2011, Wakefield *et al.* 2015, McIntyre *et al.* 2017, Patrick & Weimerskirch 2017). Despite the important role of site fidelity in space use, proximate causes and

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associated fitness consequences have only been reported in a few cases (Piper 2011). Site fidelity may increase energy intake and thereby affect time-activity budgets. For example, site-faithful individuals could reach higher energy intake rates through improved local knowledge about the quality and availability of prey (Irons 1998, Hamer *et al.* 2001). In addition, foragers will become acquainted with their immediate competitors when the majority of them are also site-faithful, and eventually spend less time on aggression and interference competition (Eason & Hannon 1994,

Leiser & Itzkowitz 1999, Wolf & Trillmich 2007), while leaving more time for self-maintenance or investing in offspring.

The occurrence of foraging site fidelity has been related to characteristics of the environment and resources within it. For fidelity to be an advantageous strategy, prey should be spatially and/or temporally predictable and not likely to be depleted (Andersson 1980, Irons 1998, Arthur *et al.* 2015). However, even when environments seem to be predictable and have abundant resources, some animals within the same population show a low degree of site fidelity (Piper 2011, Patrick & Weimerskirch 2014, Wakefield *et al.* 2015, McIntyre *et al.* 2017). This raises the question of whether there are negative consequences of having lower site fidelity for time-energy budgets. Foraging site fidelity has been widely reported in seabirds at coarse to mesoscale scales (tens to hundreds of kilometres) (Irons 1998, Weimerskirch 2007, Wakefield *et al.* 2015) and at a finer scale (< 10 km) (Kotzerka *et al.* 2011). However, the relationship between site fidelity and time-energy budgets has barely been studied in these systems.

Understanding the extent to which individual differences in site fidelity influence time-energy budgets can be extremely challenging in free-ranging birds. For example, foraging site fidelity could be a consequence of specialization in diet or habitat (Woo *et al.* 2008, Wakefield *et al.* 2015) or demands on time, energy and food quality may change during the annual cycle and subsequently affect foraging site fidelity (Annett & Pierotti 1989, Votier *et al.* 2017). Some of these factors can be accounted for when working with systems that have been extensively studied. One well-studied species of seabird is the Herring Gull *Larus argentatus*. Herring Gulls, like many other *Larus* species, are dietary generalists on the species level, but individuals have different foraging strategies (Morris & Black 1980, Gorke & Brandl 1986, McCleery & Sibly 1986, Pierotti & Annett 1990, Irons 1998). Herring Gulls breeding on the island of Texel, the Netherlands, forage during incubation mainly on a predictable and abundant resource, Blue Mussels *Mytilus edulis* (Camphuysen 2013, Van Donk *et al.* 2017). These mussels grow on breakwaters which are human-made coastal defence structures. Breakwaters form discrete foraging patches which are linearly arranged and equidistant from each other, with similar resource quality and quantity between patches. This provides an opportunity to study individual differences in foraging behaviour and consequences of site fidelity while foraging on the same predictable resource.

We studied foraging site fidelity and time-activity budgets of adult breeding gulls during the incubation period, in which both sexes are involved equally, for three reasons. First, we focus on incubation to control for possible changes in demands during different breeding phases. Second, we can control for differences in diet by selecting individuals with a similar dietary specialization, as gulls in this system feed primarily on Blue Mussels during incubation (Camphuysen 2013, Van Donk *et al.* 2017). Finally, incubation is an important period for increasing energy reserves, as Herring Gulls recover from the physical impacts of egg-laying (females) and extra food provisioning in the pre-laying phase (males to females) (Hario *et al.* 1991). Therefore, the time and energy spent on foraging is of great importance during incubation.

The aim of the study was to investigate whether fine-scale foraging site fidelity is related to time-activity budgets by focusing our analysis on individuals that primarily use the same resource organized in discrete patches. We quantified time-activity budgets of individual Herring Gulls and estimated energy expenditure using GPS tracking and tri-axial acceleration measurements. We expected that site-faithful individuals spend more time in the breeding territory as they need less time for foraging (supplementary-fed Herring Gulls stay longer in the colony; Niebuhr 1983), spend a larger proportion of time on inactive behaviour during foraging (self-maintenance) or use less energy during foraging as they spend less time on searching, social interactions and commuting between patches. Herring Gulls are sexually dimorphic, and both sex and body size can influence their hierarchy (Monaghan 1980, Sibly & McCleery 1983). This may result in competitive interference within feeding patches, with females or smaller individuals being displaced more frequently than males and hence being less site-faithful. We therefore also tested whether body size or sex influenced the level of site fidelity or time-activity budgets.

METHODS

Study system

The study was based on a breeding colony on the island of Texel, the Netherlands (53°00′N,

04°43′E) between the western Wadden Sea and the southern North Sea (Fig. 1a). Approximately 4000 pairs of Herring Gulls breed sympatrically with around 11 000 pairs of Lesser Black-backed Gulls *Larus fuscus* (Camphuysen & Gronert, 2010). We have permission to work in the colony and catch, ring and tag Herring Gulls under the permit Art 75 of the Dutch 'Flora & Faunawet' FF/75A/2014003, an annually renewed ringing permit issued by Vogeltrekstation Wageningen for ringer-licensed E29 Camphuysen, an annually renewed research permit issued by Saatsbosbeheer Divisie grond en gebouwen, and a permit for animal experiments (tracking Herring Gulls) issued by the 'Nederlandse Voedsel- en Warenautoriteit', Ministry of Economics, TRC/VWA/20132090. The foraging and breeding ecology of Herring Gulls breeding on the island have been studied for over 10 years. Based on analysed prey remains found on breeding territories over the study period, the main foraging habitat includes arable land, urban areas, sea (North Sea and Wadden Sea) and coastal areas including beach and breakwaters. Breakwaters are human-made coastal defence structures colonized by Blue Mussels which are expected to provide the main diet during the incubation period (up to 70% of pellets contained mussels) (Camphuysen *et al.* 2008, Camphuysen 2013, Van Donk *et al.* 2017). These foraging patches are found within 35 km of the colony, along the North Sea coast between Texel and Schoorl (Fig. 1a) and are organized in discrete patches, comparable in structure and size, and linearly arranged with similar distance (~ 200 m along the coast of Noord-Holland and ~ 400 m along the coast of Texel) in-between neighbouring breakwaters (Fig. 1b). The quality of Blue Mussels is generally similar between different breakwaters and there is no indication of depletion of resources through the year (Dekker *et al.* 2014). Although there is no evidence of resource depletion, the number of birds can cause interference competition (Vahl *et al.* 2005). Furthermore, gulls are uniformly distributed over the breakwaters, with more or less similar numbers of gulls per breakwater.

Data collection

To obtain time-activity budgets of Herring Gulls at a fine spatial and temporal scale, GPS trackers of the UvA Bird Tracking System were used (Bouten *et al.* 2013). These trackers measure the geographical location (with a mean position error of 3 m for measurement intervals of 60 s and 30 m for intervals of 600 s), time (UTC), altitude above mean sea level (m), ground speed (km/h) and acceleration in three directions (surge (x), sway (y) and heave (z)). Tracking devices were calibrated to convert x, y and z acceleration data to gravitational force (1 g_n = 9.81 m/s^2). A total of 31 adult Herring Gulls (17 males and 14 females) were equipped with GPS trackers between 2013 and 2015. Birds were trapped during incubation using a walk-in trap. The birds were colour-ringed and a solar-powered GPS tracker (ranging from 17.1 to 19.7 g) was mounted with a 3-g non-flexible Teflon harness on the back of the bird. We sexed each bird on the basis of biometrics (head plus bill length) with only 5% expected misidentification (Coulson *et al.* 1983) and made size measurements including bill depth (at base, 0.1 mm), tarsus length (mm), wing length (mm) and body mass (g). We calculated a body size index to analyse the effect of size in later analyses using the first principal component (PC) of tarsus length, wing length and head plus bill length (Benson *et al.* 2003). To associate a high body size index score with a large body size, we multiplied the PC by –1 (Table S1). The mean body mass (± standard deviation) of tagged females was 887 ± 49 g and that of males 1016 ± 59 g. Birds were released immediately after being instrumented, which was usually within 20 min of capture. As recommended for seabirds (Phillips *et al.* 2003), the GPS tracker and harness weighed < 3% of the body mass of the birds (average mass of tracker and harness combined 2.4% of female body mass, 2.1% of male body mass). Although the mass of the trackers is not excessive, we cannot exclude the possibility that the devices affected the birds in another way. Thaxter *et al.* (2016) showed that GPS trackers, which were attached in the same way as the trackers in our study, did not affect (short-term) breeding productivity and winter return rates in the closely related Lesser Black-backed Gull. In our study, there was some indication that birds with GPS trackers had lower return rates than expected; 70% of individuals with a GPS tracker were seen again the next year, which is lower than a rough estimate of 90% survival of adult Herring Gulls of this colony. Also, birds with a GPS tracker appeared to have a lower likelihood of breeding again in the next season; 62% of the birds bred again in the next season, which is lower than expected. Roughly, birds of this colony
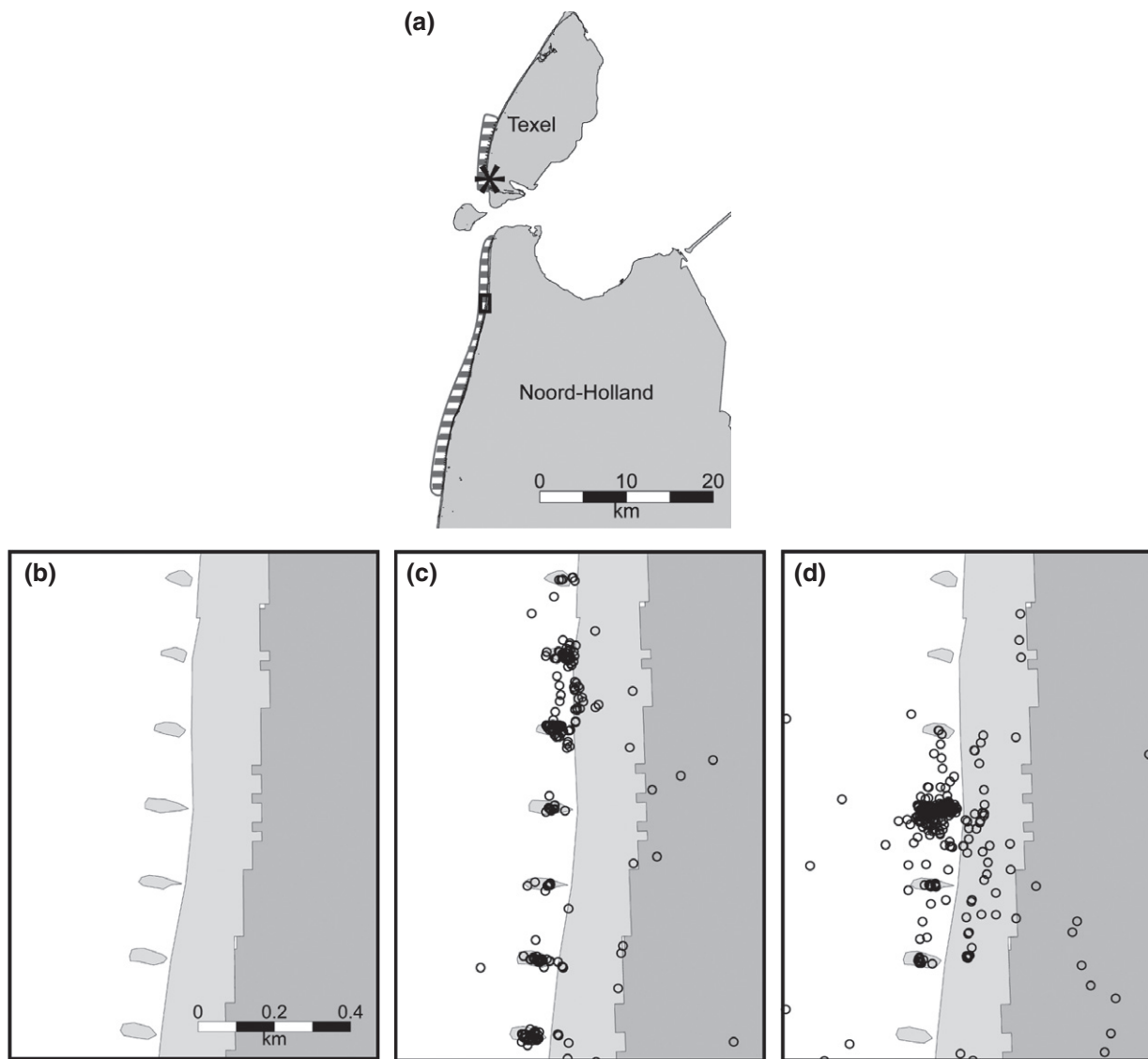
Figure 1. Map of the study system at different spatial scales. (a) Overview of the study area. The breeding colony is indicated with an asterisk. Breakwaters are situated along the North Sea coast (both on the island of Texel and on the mainland). The dashed area indicates where breakwaters are situated. The square on (a) indicates the area shown on a larger scale (b, c, d). (b) Map of seven breakwaters along the coast of Noord-Holland. (c, d) Examples of area use of respectively an individual with low foraging site fidelity (bird-year 1600_2013, SFI 2.36) and a very site-faithful individual (bird-year 6016_2013, SFI 0.52) on a selection of breakwaters (shown in b) during 14 days of incubation. Every point corresponds to one GPS fix.

breed once every 1.5 years, which is 75% of breeding individuals. Here, we saw a difference between the sexes, as only 30% of females bred again the following season, compared with 82% of males. However, birds with a tracker did not have a lower hatching success than the average hatching success of the breeding colony in the same period (65.5% for the colony compared with 65.6% for birds with GPS trackers). Besides, we attached some GPS trackers to birds which had already been colour-ringed (*n* = 7) in earlier breeding seasons. This gave us the opportunity to compare foraging sites and sometimes even winter areas before and after attachment of the tracker. These birds still visited the same foraging and wintering areas, suggesting that foraging behaviour had not changed.

A GPS location was taken every 10 min inside the breeding territory and every 5 min outside the breeding territory. We occasionally took higher resolution measurements on trackers with an empty memory and full battery for other analyses. As differences in resolution might influence comparison between individuals, we resampled the data once every 5 min before analysing the data. Tri-axial acceleration was periodically measured at 20 Hz for 1 s immediately after a GPS fix.

Habitat use and selection of birds

We made use of bird-year combinations in our analysis, as two birds were tracked over 2–3 years (bird ID 1600 and 6016). We will therefore use the term 'bird-year' for the rest of the Methods and Results section. To focus on the potential impact of site fidelity without confounding effects of time and energy constraints that may differ across the breeding season, we compared breeding birds during incubation only. We assumed that individuals that breed and have a nest with eggs are in comparable physical condition. During this period, both males and females return regularly to the colony to defend the territory and incubate the eggs. This is also the period during which Blue Mussels are the most predominant part of the Herring Gull diet (Van Donk *et al.* 2017). We only used GPS and accelerometer data of breeding birds that had a nest with eggs for at least 5 days after tagging, or the full breeding period of birds that had a nest with eggs which received a tracker in earlier breeding seasons (range 5–31 days). Herring Gulls are considered a generalist species; they have a broad prey spectrum and habitat use (Morris & Black 1980, Gorke & Brandl 1986, McCleery & Sibly 1986, Pierotti & Annett 1990, Irons 1998). To remove the potential confounding effect of diet, we compared site fidelity among birds in a given year of which the breakwaters are the most visited foraging habitat compared with other potential foraging habitats.

Habitat use was calculated by assigning every GPS fix to either the breeding territory (< 100 m around the nest) or potential foraging habitats around the colony. We took every GPS position into account, apart from when an animal was commuting (i.e. when an individual was flying in a straight line from one place to the other). To select these GPS positions, we made use of an expectation maximization binary clustering for behavioural annotation, which used turning angle and velocity obtained from successive locations to cluster GPS positions in four behavioural categories (Garriga *et al.* 2016a). The categories are: high velocity/low turn (HL), high velocity/high turn (HH), low velocity/low turn (LL) and low velocity/high turn (LH). We assumed that an animal was commuting when velocity was high and turning angle low (HL category). We applied the clustering algorithm per individual in a given year using the R package *EmbC* and applied a presmoothing procedure which is provided by the package to account for temporal associations (Garriga *et al.* 2016b). Subsequently, we assigned every non-commuting GPS position to a habitat. We defined the following habitats: sea (North Sea and Wadden Sea), breakwaters, beach, arable land (including ponds, forest and nature areas) and urban areas. Sea and arable land were defined using GDAM January 2012 European boundaries polygon shapefiles (Hijmans 2012). The beach habitat was based on LGN5 (Landelijke Grondgebruikskartering 5) (Hazeu 2005), which provides information about land use in the Netherlands. Urban areas were based on the QGIS openlayer plugin of OpenStreetMap Humanitarian Data Model in which cities, towns and dump sites around the breeding colony were selected. The breakwaters were delineated based on the QGIS openlayer plugin GOOGLE EARTH which uses GOOGLE EARTH images. Every breakwater along the coast of Texel and Noord-Holland was given a unique number (QGIS Development Team 2009, version 2.18). A total of 165 breakwaters were available for the birds until 2014; after 2014 there were 119 breakwaters left due to coastal protection activities. Often, the area around the breakwater is also available for foraging gulls during low tide (pers. obs.) and therefore we also assigned GPS points closer than 50 m to the breakwater to the habitat breakwater. Each GPS location was also assigned a duration (s) which was calculated by averaging the backward and forward intervals between relocations, providing a 'centred duration'. Gaps in the data occurred and the 'centred duration' of GPS measurements before and after gaps was sometimes disproportionally long. We therefore removed the GPS measurements which had a 'centred duration' deviating more than 10 min from the measurement scheme. Using the centred duration and habitat class assigned to each location, we calculated the percentage of time

spent outside the breeding territory while not commuting in every foraging habitat by dividing total time spent in a habitat by the total time spent outside the breeding colony per bird-year. The percentage of time spent in each habitat was then ranked from high to low and birds that preferred the breakwaters (most time spent) over other foraging habitats were selected for further analysis (Fig. 2, $n = 17$, eight females and nine males). The selected animals spent 39–70% of their time outside the colony while non-commuting on breakwaters (Table 1). The distribution of GPS locations around the breeding territory of all incubating animals and the selected individuals are shown in Figure 3(a) and 3(b), respectively. We defined foraging trips as the first location outside the breeding territory until the next location within the breeding territory. The maximum (great circle) distance (km) travelled from the breeding colony was calculated per trip.

Site fidelity index (SFI)

Site fidelity of birds was determined per bird-year by analysing the time an individual spent near every breakwater. For each bird-year, we first calculated the time spent in the proximity (i.e. closer than 50 m) of every breakwater when not commuting, using the rgeos package in R (Bivand & Rundel 2016). We calculated the percentage of time spent on each breakwater as the time spent near each breakwater divided by the total time spent on all breakwaters. To only include breakwaters which were of significance in the total time, we excluded from the calculation breakwaters on which individuals spent < 2% of their total time spent on breakwaters. Site fidelity was calculated per bird-year as the Shannon index, which is given as SFI $= - \sum_i p_i \ln p_i$ where p_i is the percentage time spent on each breakwater (Shannon & Weaver 1949). A high SFI value corresponds to an animal with low site fidelity ('diverse' patch use), whereas a low SFI corresponds to an animal with high site fidelity ('non-diverse' patch use) (Fig. S1). Breakwaters are used as foraging habitat; however, animals also rest and digest their food on breakwaters. To check whether the breakwaters were not used solely for resting by some individuals, we also calculated the site fidelity index based on foraging behaviour ('terrestrial movement') solely. The two measurements were highly correlated and thus we decided that it was valid to use all behaviours for the calculation of site fidelity (Fig. S2).

Relationship between SFI and time-activity budgets

We expected that highly site-faithful individuals with breakwaters as their principal feeding area can spend more time in the breeding colony to defend their territory or can spend less energy outside the breeding territory by spending more time resting. To test whether site fidelity is related to the time and energy budget of individual Herring Gulls, we calculated: (1) time spent in the breeding territory, (2) proportion of time spent on inactive behaviour outside the breeding territory and (3) daily energy expenditure outside the breeding territory; these are explained further below. For analyses (2) and (3) we excluded one bird-year because of missing acceleration measurements (see Table 1). For the calculation of SFI we only used GPS locations close to and on the breakwaters, but we used all GPS locations to calculate the time-activity budget. As we selected individuals with breakwaters as their principal feeding area, we assumed that most of the time dedicated to foraging was done on breakwaters. As breakwaters are an intertidal foraging habitat, they are only available at low tide, which should be taken into consideration. Habitat around the breakwaters is also often used (Fig. 3b), for instance for waiting, preening and digesting.

(1)   Time spent in the breeding territory

We calculated the average hours per day spent in the breeding territory for every bird-year combination calculated as every GPS position that was closer than 100 m to their nest-site. To analyse whether SFI was correlated to the time individuals per bird-year spent in their breeding territory, a linear mixed-effect model was fitted. The full model contained SFI and sex as fixed effects, average hours per day in breeding territory as the dependent variable, and random intercepts for bird ID and year to account for differences between individuals and yearly fluctuations in foraging effort.

(2)   Proportion of time spent on inactive behaviour outside the breeding territory

To calculate the activity budget of birds within a given year we trained a random forest machine-learning algorithm for the classification
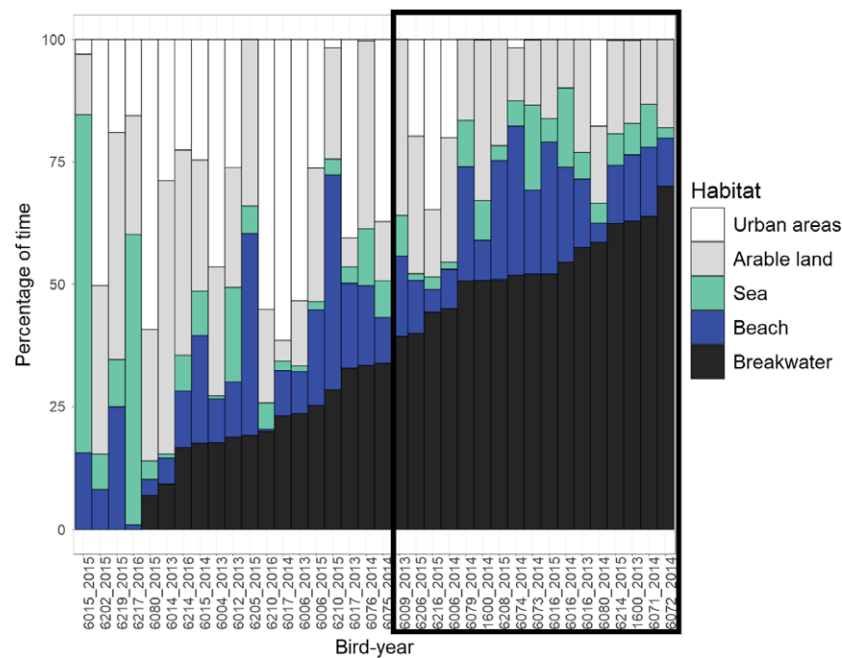
Figure 2. Overview of habitat use outside the breeding territory while not commuting per bird-year combination. Habitat use is shown in percentage of time spent in different possible foraging habitats near the colony, which are urban areas, arable land, sea, beach and breakwaters. Data are organized in ascending percentage of time spent on breakwaters, where Blue Mussels are the primary resource. Individuals that spend most of their time on breakwaters compared with other habitats within a given year and that are used in further analysis are shown within the black square. [Colour figure can be viewed at wileyonlinelibrary.com]

of accelerometer data (Shamoun-Baranes *et al.* 2016) using two datasets. The first dataset is based on annotated accelerometer data of Lesser Black-backed Gulls (Shamoun-Baranes *et al.* 2016). The second dataset contained annotated accelerometer data of six Herring Gulls (three males and three females) with synchronized video recordings while foraging on breakwaters. The two species are comparable in size and morphology, and most behaviour and accelerometer patterns were clearly similar. We first distinguished 11 different behaviours (Table S2), which we aggregated into four behavioural classes: (1) inactive behaviour (sitting or standing and floating on the water), (2) terrestrial movement (walking, looking for food, standing while looking for food, handling prey, other movements), (3) flapping flight (regular and extreme flapping flight) and (4) soaring flight (regular soaring and manoeuvring). In total, 8472 segments of acceleration measurements lasting 0.5 s were used for annotation. We calculated 37 data features from the tracking data that could be used to classify behaviour and reduced the number of features to 17

(Table S2) (Shamoun-Baranes *et al.* 2016). The random forest classifier used 50 trees and was trained on a random subset of 70% of the annotated data. Accuracy was tested with the remaining 30% of the data. The final model, with an overall accuracy of predicting the 11 behaviours of 94%, was used to classify all unclassified accelerometer data.

Proportions of the different behavioural classes were calculated by the accumulated time spent on one of the activities divided by the total duration of measurements per bird-year. As proportions always sum up to one, they impose some constraints on the variance and covariance of the data. To allow the use of standard statistical techniques we transformed the data by taking the log transformation of the proportion of inactive behaviour over the proportion of active behaviour (terrestrial movement, flapping flight and soaring flight) (Aitchison 1986, Warton & Hui 2011).

A linear mixed-effect model was fitted that contained SFI, sex and body size index as fixed effects, the (transformed) proportion of inactive behaviour as the dependent variable, and

Table 1. Overview of bird-year combinations used in the study with their site fidelity index (SFI) and their time-activity budget.

Bird-year combination	SFI	Colony (h/day)	Prop. Inactive	Prop. Terr.	Prop. Soar	Prop. Flap	Energy (kJ/day)	Prop. return	B. time (%)
1600_2014	2.65	12.56	0.55	0.27	0.07	0.11	623	0.20	51
1600_2013	2.36	13.39	0.37	0.34	0.12	0.17	701	0.21	63
6074_2014	2.33	13.37	0.59	0.20	0.12	0.09	554	0.29	52
6208_2015	2.31	12.06	0.62	0.23	0.09	0.06	602	0.16	51
6079_2014	2.28	12.24	0.57	0.26	0.09	0.08	637	0.37	51
6006_2014	2.04	13.85	0.58	0.21	0.08	0.13	653	0.29	45
6216_2015	2.01	14.63	0.53	0.31	0.07	0.09	520	0.47	44
6206_2015	1.76	15.21	0.54	0.20	0.16	0.10	471	0.75	40
6009_2013	1.70	11.75	0.44	0.40	0.13	0.02	534	0.33	39
6214_2015	1.62	16.30	0.46	0.32	0.11	0.11	478	0.58	62
6016_2015	1.51	15.31	0.59	0.27	0.09	0.07	515	0.49	52
6072_2014	1.43	16.94	0.50	0.38	0.07	0.05	305	0.42	70
6073_2014	1.29	14.83	0.60	0.20	0.08	0.11	505	0.49	52
6071_2014	1.10	13.91	0.45	0.29	0.12	0.14	709	0.70	64
6016_2014	0.63	15.82	0.62	0.23	0.06	0.09	500	0.43	55
6016_2013	0.51	14.24	0.55	0.31	0.07	0.07	561	0.48	58
6080_2014[a]	0.19	9.72	–	–	–	–	–	0.70	59

Average hours per day spent in the breeding territory (Colony), the proportion of time spent during foraging trips on inactive behaviour (Prop. Inactive), terrestrial movement (Prop. Terr), soaring flight (Prop. Soar) or flapping flight (Prop. Flap), daily energy spent while on foraging trips (kJ/day), the proportion of foraging trips where birds return to the favourite breakwater (Prop. return) and the percentage of time outside the breeding territory spent on breakwaters (B. time). The table is organized in descending order according to SFI score. A high SFI value corresponds to an animal with low site fidelity ('diverse' patch use), and a low SFI corresponds to an animal with high site fidelity ('non-diverse' patch use). The two examples of bird-year combinations shown in Fig. 1(c,d) are highlighted in grey, representing two individuals with similar daily energy expenditure during foraging trips but contrasting SFI. [a]Bird-year that was excluded from some analysis because of too few acceleration measurements.
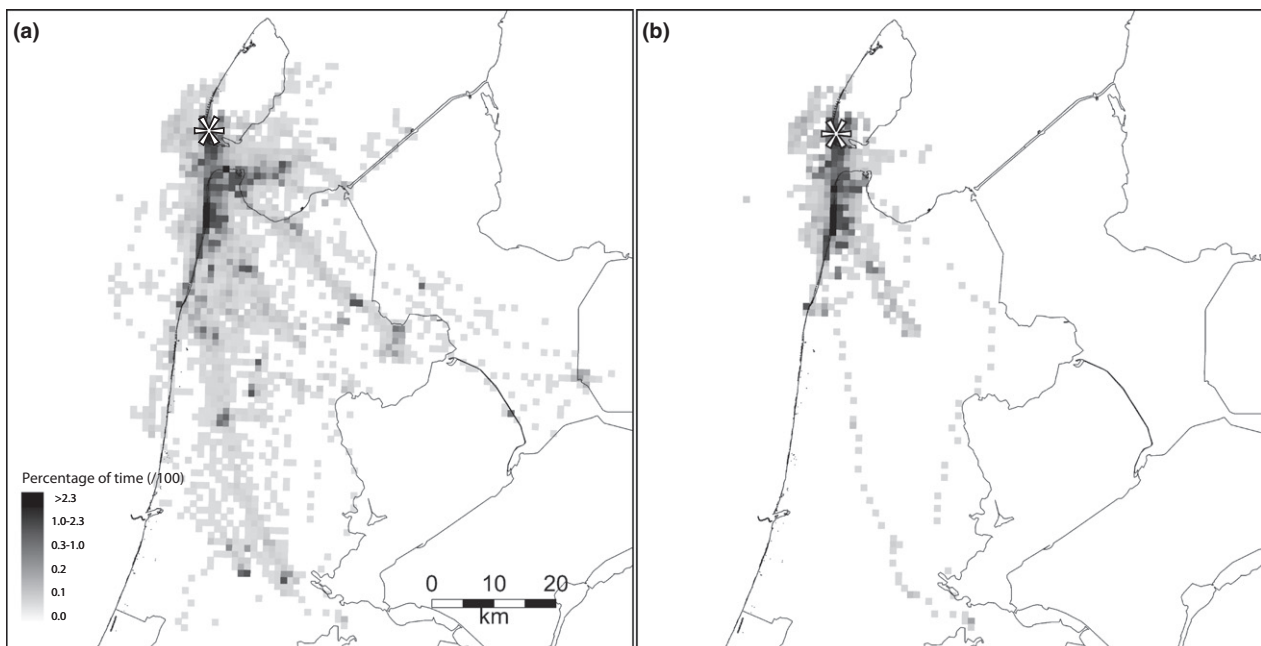
Figure 3. Distribution of all GPS locations of incubating Herring Gulls carrying a tracker and a nest with eggs for at least 5 days (a) and distribution of the animals that favoured breakwaters over other foraging habitat (b). The breeding colony is indicated with an asterisk.

random intercepts for bird ID and year to account for differences between individuals and yearly fluctuations in foraging effort. In this model, we also added average maximum distance from the colony as a fixed effect, calculated as the average of the maximum distance travelled away from the colony per foraging trip (Table S1), as this might affect the time spent on flying and thus the total time spent on active behaviour.

(3) Daily energy expenditure outside the breeding territory

To estimate energy expenditure outside the breeding territories, we made estimations of metabolic rates (kJ) for the four classified behaviours (Collins *et al.* 2016). Inactive behaviour has low energetic cost, whereas flapping flight is estimated to be the most costly form of locomotion. Variation in time spent on flapping flight might therefore drive variation in energy expenditure (Norberg 1990, Collins *et al.* 2016). We calculated the basal metabolic rate (BMR) in kJ/day as $2.3 \times$ body mass $(g)^{0.774}$ at capture (Bryant & Furness 1995). As the BMR does not account for thermoregulation when temperature is lower or higher than the thermo-neutral zone, digestion or small body movements, we calculated the costs for the behaviour 'inactive' as the resting metabolic rate (RMR); $1.7 \times$ BMR (Baudinette & Schmidt-Nielsen 1974, Furness 1978). We estimated the cost of terrestrial movement as $2 \times$ BMR (based on the formula for cost of walking in Bautista *et al.* 1998) using 0.4 m/s, the average speed measured by the GPS of all bird-year combinations during terrestrial movement. For the cost of flight, we calculated energetic expenditure as $2 \times$ RMR for soaring flight (Baudinette & Schmidt-Nielsen 1974) and $7 \times$ RMR for flapping flight (Tucker 1972). We calculated the average number of hours birds in a given year spent on the four classified behaviours (using values from Table 1) and multiplied these values by the energetic estimations we made to calculate the average energy expenditure outside the breeding colony (kJ/day).

To analyse whether energetic expenditure was correlated to SFI, we fitted a linear mixed-effect model. The full model contained SFI and sex as fixed effects, daily energy expenditure outside the breeding territory as the dependent variable,

and random intercepts for bird ID and year to account for differences between individuals and yearly fluctuations in foraging effort. We also added average maximum distance from the colony as a fixed effect, calculated as the average of the maximum distance travelled away from the colony per foraging trip, as this might affect the time spent on flying and thus energy expenditure.

Relationship between SFI, body size and sex

To analyse whether SFI is determined by sex or size, a linear mixed-effect model was fitted. The full model contained sex and body size index as fixed effects and SFI as the dependent variable and random intercept for bird ID.

Statistical analysis

All models were fitted using the lmer function from the lme4 package in R version 3.3.2 (Bates *et al.* 2015). Full models were compared with models containing all possible combinations of fixed effects using the aictab function from the AICCMODAVG package (Mazerolle 2017). To assess whether the final model was valid in explaining the data, a comparison between the final model and a null model which only contained the random factor was made using ANOVA and *P*-values were obtained by likelihood-ratio tests. We reported the model estimates with standard errors and marginal *R*-squared values for mixed models (as in Nakagawa & Schielzeth 2013) of the best models (lowest Akaike information criterion (AIC)) as well as the models in which the AIC difference with the best model is < 2 in the text. Full models and AIC values are reported in Tables S3–S6.

RESULTS

Habitat use and selection of birds

The percentage of time spent in the main habitat zones outside the breeding territory per bird-year combination varied greatly between individuals (Fig. 2, *n* = 36). For further analysis, we selected bird-year combinations for which the preferred foraging habitat (most time spent compared with other foraging habitats) are breakwaters (*n* = 17 bird-years, 14 individual birds, seven females and

seven males). The selected birds spent 39–70% of their time outside the breeding territory while not commuting on breakwaters (Fig. 2, Table 1). Figure 3 shows the distribution of GPS locations during the incubation period of all Herring Gulls with a GPS tracker (Fig. 3a) and the GPS locations of the selected birds (Fig. 3b). Although the selected birds still spent considerable time in other habitats (Fig. 2), most locations in other foraging habitat were concentrated around the breakwaters at sea and on the mainland (Fig. 3b).

Site fidelity index

The SFI differed between bird-year combinations that have breakwaters as their preferred foraging habitat (Table 1), ranging from an SFI of 0.19 to 2.65. The most site-faithful bird spent 92% of its time on breakwaters on a single breakwater. All birds returned regularly to their most visited breakwater (16–75% of their foraging trips, Table 1). Two extreme examples are shown in Figure 1(c,d), in which the space use of two individual Herring Gulls in 2013 is plotted on the same selection of breakwaters. These two birds spent the same percentage of time on breakwaters (Table 1, highlighted) but have very different SFI scores. The bird shown in Figure 1(c) (1600_2013) divided its foraging time over several breakwaters and had thus a high SFI score (SFI = 2.36). The bird shown in Figure 1(d) (6016_2013) was highly site-faithful, spending 79% of its breakwater time on one breakwater (SFI = 0.51).

Relationship between SFI and time-activity budgets

(1) SFI and time spent in the breeding territory

The average time spent per day in the breeding territory varied among bird-year combinations (13.76 ± 1.85 h). The two most extreme birds differed by 7 h/day in the time they spent in the colony (minimum = 9.7 h/day, maximum = 16.9 h/day; Table 1). However, we did not find a significant linear relationship with SFI or an effect of sex (Table 2).

(2) SFI and proportion of time spent on inactive behaviour outside the breeding territory

Time spent inactive outside the breeding territory differed among bird-years, ranging from 37% to 62% (54 ± 7%, Table 1). The most active bird (1600_2013) was moving around 63% of the time during foraging trips, whereas other birds were active less than half of the time outside the colony (Fig. 4, Table 1). However, the time that birds spent inactive was not related to SFI or the other fixed factors in the model (Table 2).

(3) SFI and daily energy expenditure outside the breeding territory

The estimated daily energy expenditure outside the breeding territory ranged from 305 to 709 kJ/day (554 ± 101, Table 1). We did not find a significant linear relationship between daily energy expenditure outside the breeding territory and SFI or other fixed factors in the model (Table 2).

Relationship between SFI, body size and sex

We investigated whether foraging site fidelity might be driven in part by body size or sex, given differences in competitive strength (interference competition). Highly site-faithful birds had a larger body size (Fig. 5). The best model included body size index as a fixed factor and significantly differed from the null model (Table 3).

DISCUSSION

We investigated the consequences of fine-scale foraging site fidelity in adult Herring Gulls with similar dietary specialization during incubation. The study system was especially suitable for investigating this question in free-ranging animals because of the predictable and homogeneous foraging environment organized in distinct foraging patches and the technical ability to measure fine-scale behaviour 24 h/day and across an entire breeding season. By making a detailed description of time-activity budgets of the birds using GPS trackers with tri-axial acceleration, we showed remarkable differences between individuals in habitat use (Fig. 2), fine-scale foraging site fidelity on breakwaters (Fig. 1c,d, Table 1), and time and energy use (Fig. 4, Table 1). Highly site-faithful birds tend to have a larger body size (Fig. 5). In this study we focused on the incubation phase, during which individuals face similar time and energy constraints. We found no clear (short-term)

Table 2. Model results of the relationship between SFI and proxies for time-activity budgets: (1) time spent in the breeding territory in hours (Colony time), (2) transformed proportion of time spent on inactive behaviour outside the breeding territory (Inactive behav.) and (3) daily energy expenditure outside the breeding territory in kJ (Energy exp.) tested using a mixed model with random intercept for bird ID and year.

Dependent variable	Fixed effect	AIC	Intercept $\pm$ se	Fixed effect estimate $\pm$ se	df	χ^2	P	$m.R^2$
(1) Colony time	Sex (M)	81.05	13.98 ± 0.70	-0.56 ± 0.99	1	0.32	0.57	0.02
(1) Colony time	SFI	81.36	13.72 ± 1.13	-0.01 ± 0.61	1	0.00	0.98	0.00
(2) Inactive behav.	Sex (M)	19.27	0.03 ± 0.12	0.13 ± 0.13	1	0.70	0.40	0.05
(2) Inactive behav.	Distance	19.56	0.18 ± 0.21	-0.01 ± 0.02	1	0.41	0.52	0.02
(2) Inactive behav.	SFI	19.93	0.03 ± 0.24	0.02 ± 0.12	1	0.03	0.86	0.00
(2) Inactive behav.	Size	19.95	0.07 ± 0.13	0.00 ± 0.00	1	0.02	0.89	0.00
(3) Energy exp.	Distance	201.78	459.96 ± 69.59	10.62 ± 6.47	1	1.88	0.17	0.13
(3) Energy exp.	Sex (M)	201.83	527.90 ± 41.38	76.17 ± 54.23	1	1.84	0.18	0.13
(3) Energy exp.	Size	202.99	566.87 ± 34.34	1.52 ± 1.83	1	0.67	0.41	0.06

Model estimates and model results, among which marginal R-squared ($m.R^2$) of best models are shown (lowest AIC) and the models in which the AIC difference with the best model is < 2. Models with an ΔAIC > 2 are shown in Tables S3–S5. For the fixed effect Sex, category female was used as the reference level (Intercept) and the fixed effect estimate is thus the value for males (M).
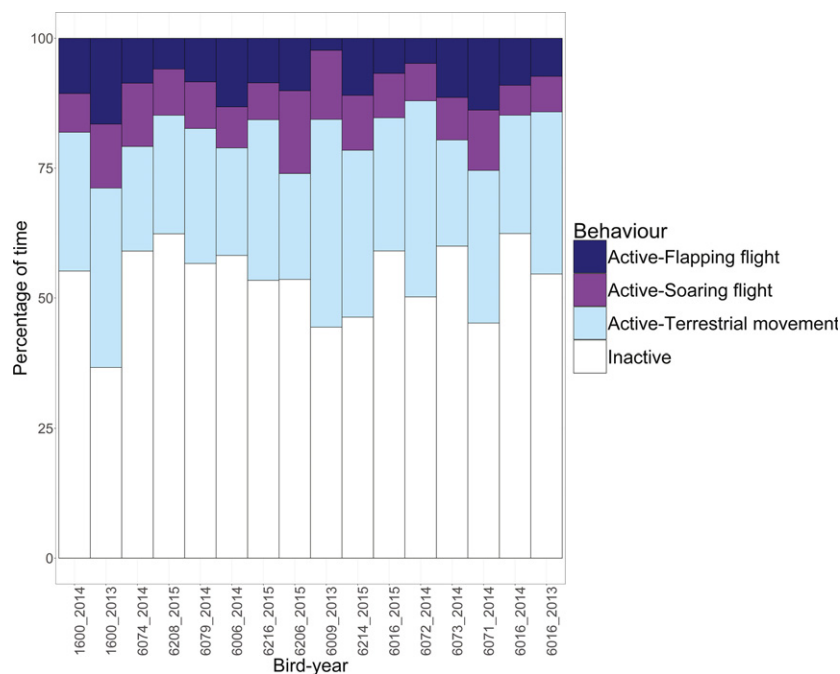

Figure 4. Behaviour outside the breeding territory per bird-year combination of selected birds. Behavioural classes are shown as the percentage of time spent on inactive behaviour (sitting, standing, floating) or active behaviour (flapping and soaring flight and terrestrial movement). Bird-year combinations are ordered from left to right on descending SFI (for values see Table 1). Bird-year 6080_2014 was excluded from this graph due to too few acceleration measurements. [Colour figure can be viewed at wileyonlinelibrary.com]

consequences of fine-scale foraging site fidelity; highly site-faithful individuals did not spent more time in the breeding territory or more time inactive, and did not have a lower daily energy expenditure outside the breeding territory. Although this result was contradictory to our expectations, there are several possibilities as to how variation in site fidelity could exist in
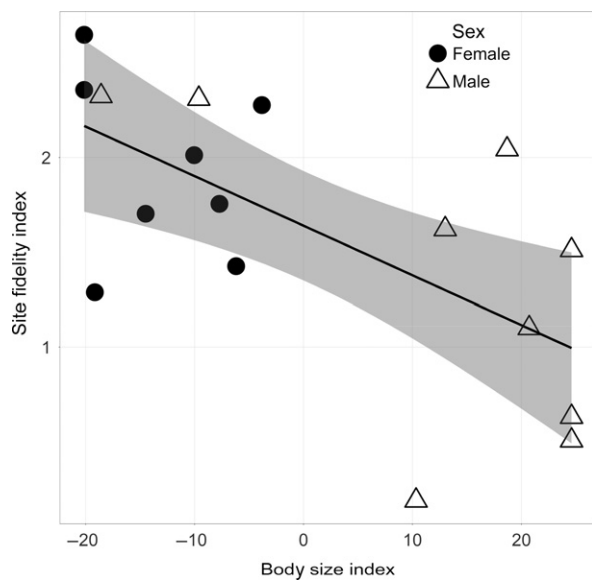
Figure 5. The relationship between body size and SFI. A low body size index indicates a bird with a small body size. A low SFI indicates a bird in a given year with high foraging site fidelity. Every point represents one bird-year combination (*n* = 17). Linear regression is shown (line) with standard error (shaded area). The shape of the point indicates the sex of the bird.

populations without clear short-term benefits, as discussed below.

The importance of other foraging habitats

Herring Gulls are generalist species and have many ways of foraging–flying, walking, pulling or fighting, as well as standing still and observing the environment, waiting for a feeding opportunity. We therefore chose to use all GPS locations outside the breeding territory, independent of behavioural class and habitat, to calculate time-activity budgets. For the animals with breakwaters as their principal feeding habitat, we assumed that most of the time dedicated to foraging is spent on breakwaters. Animals that eat bivalves such as Blue Mussels have to spend time digesting these prey to break the shells in their stomach. They do this on

breakwaters during low tide, but they may also move to other places such as agricultural fields or nearby rooftops to rest and digest, especially at high tide, when breakwaters are not available. In addition, these animals often spent time on the beach, waiting for the breakwaters to appear at low tide, or at sea, when disturbed by people or dogs (CJC, SvD & JSB pers. obs.; Fig. 1c,d). Figure 3(b) seems to confirm this idea, as most of the GPS locations which are not situated on breakwaters are concentrated around the coastline. As we did not include waiting and digesting time around breakwaters in the total time spent on breakwaters, the relative time spent outside the colony on foraging-related behaviour on breakwaters is probably higher than we reported (Table 1) compared with other foraging habitat that does not disappear at high tide, such as sea, urban areas and arable land. Nevertheless, the time spent in other foraging habitats could influence time-activity budgets, especially when animals forage in an 'urban area' which contains prey types of high caloric value that are important for reproductive output and condition (Pons 1992, Van Donk *et al.* 2017). However, we did not find evidence for this in our data, as there was no relationship between the time our selected animals spent on breakwaters and either the level of site fidelity (Table 1) or the time-activity budget (Fig. S3, Table 1).

How can variation in site fidelity be maintained in populations?

We did not find clear consequences of fine-scale foraging site fidelity in our study. However, we did see differences in the level of fine-scale foraging site fidelity between individuals. We discuss three other hypotheses, besides the variation spent on breakwaters, as to why this variation may exist in the population with no apparent proximate advantages or disadvantages.

Fitzpatrick *et al.* (2007) suggested that variation in certain traits remains in populations due to negative frequency-dependent selection. This mechanism

Table 3. Model results of the relationship between SFI and body size tested using a mixed model with random intercept for bird ID.

Dependent variable	Fixed effect	AIC	Intercept ± se	Fixed effect estimate ± se	df	χ^2	*P*	*m.R²*
SFI	Size	31.20	1.71 ± 0.11	−0.02 ± 0.01	1	6.21	0.01	0.47

Model estimates and model results of the best model are shown (lowest AIC). Models with a ∆AIC > 2 are shown in Table S6.

selects against common phenotypes, thereby creating fitness advantages for the rarer phenotypes (Maynard Smith & Price 1973, Wilson & Yoshimura 1994, Pruitt & Riechert 2009, Patrick & Weimerskirch 2017). For birds, negative frequency-dependent selection is often suggested to be an important mechanism in regulating consistent variation in behavioural traits, but evidence for this is largely absent (Kurvers *et al.* 2012). The few studies that have investigated this mechanism (in Oystercatchers *Haematopus ostralegus ostralegus* and Barnacle Geese *Branta leucopsis*) could not find evidence for this hypothesis (Van de Pol *et al.* 2010, Kurvers *et al.* 2012). Currently, we do not have any evidence to support this hypothesis.

A second hypothesis is that there are pros and cons associated with foraging site fidelity. Site-faithful individuals might have higher food intake on their specific foraging spot but have less flexibility to respond to environmental change because they have less knowledge about their wider environment and therefore cannot easily switch between foraging patches or resources (Wilson & Yoshimura 1994, Bolnick *et al.* 2003, Wakefield *et al.* 2015). For instance, in our study system, highly site-faithful individuals might profit less from unexpected food bonanzas such as mass mortality of Razor Clams *Ensis directus* that sometimes wash ashore (Armonies & Reise 1999). Besides missing food bonanzas, site-faithful individuals may be more vulnerable to environmental change (Kotzerka *et al.* 2011). Changes in the environment are also taking place in our system. Due to coastal protection activities, the creation of new dunes and sand supplementation has already covered important foraging patches (breakwaters) (van Koningsveld & Mulder 2004, Freriks 2015, Wenneker *et al.* 2016). These changes create a natural experiment in which we can test whether individuals with high site fidelity can adapt less well when their foraging habitat is disappearing.

A third hypothesis to explain our findings is that individuals benefit from being site-faithful in the long term or even over an individual's lifetime, as foraging behaviour is often consistent over years in marine animals (Bradshaw *et al.* 2004, Wakefield *et al.* 2015). The importance of foraging site fidelity might only become apparent in very demanding times of an animal's life cycle, for instance when animals have to feed their young. In a study on Black-Browed Albatrosses *Thalassarche melanophris*, site fidelity within a certain year was

positively associated with reproductive success (Patrick & Weimerskirch 2017). Measuring foraging site fidelity and analysing potential consequences during longer periods might help to elucidate the mechanisms and consequences of site fidelity. In the current study, the sample size was too low to measure the consequences of site fidelity over years. However, the two individual birds that were measured over more than 1 year (bird ID 1600 and 6016, Table 1) were quite consistent in their level of site fidelity; bird ID 1600 had the lowest site fidelity measured over 2 years of all individual birds in this study, whereas, by comparison, bird ID 6016 was very site-faithful over 3 years (Table 1).

The role of size in the level of foraging site fidelity

Individual differences in foraging strategies are often related to morphology or sex (González-Solís *et al.* 2000, Lewis *et al.* 2002, Camphuysen *et al.* 2015). In our study, variation in foraging site fidelity was also not randomly distributed over the population. We found a significant relationship between foraging site fidelity and size, larger individuals tending to be more site-faithful. Herring Gulls are sexually dimorphic and therefore sex and size are difficult to disentangle. Also, body size is clearly not the only variable that influences the variation in foraging site fidelity, as some large individuals in our study are not highly site-faithful (Fig. 5). Although the results are not conclusive, they do suggest that larger individuals are better able to deal with competition and defend their specific foraging patch, whereas smaller individuals are displaced more frequently from feeding patches. However, it is also possible that larger individuals have to balance other trade-offs compared with smaller individuals. For instance, flying is more expensive for larger/heavier individuals and therefore it might be more rewarding to be site-faithful compared with smaller individuals with lower costs of moving between foraging patches. In the current study, we used rough estimations for energy expenditure of different behaviours based on literature values. Investigating energetic costs among individuals with different morphology and time-activity budgets would benefit from a method in which energy expenditure can be investigated on the level of an individual. Several studies have investigated the relationship

between overall dynamic body acceleration (ODBA), measured with GPS devices, and energy expenditure, and ODBA has been used as a proxy for energy expenditure (Wilson *et al.* 2006, Gleiss *et al.* 2011, Hicks *et al.* 2017). However, ODBA is not comparable between terrestrial movement and flight, probably due to the different muscle groups involved in each kind of behaviour (Laich *et al.* 2011). Improving estimates of energy expenditure based on body acceleration which can be measured throughout an annual cycle may help to gain more insight into individual differences in energy expenditure (Hicks *et al.* 2017).

CONCLUSION AND FUTURE DIRECTIONS

We studied Herring Gulls foraging in a food landscape that is heavily shaped by humans. This created a unique situation to study individual differences in fine-scale habitat use. In this way, we were able to add empirical data to increase knowledge on the consequences of fine-scale foraging site fidelity, an important phenomenon in space use (Wolf & Trillmich 2007, Brischoux *et al.* 2009, Lowther *et al.* 2012). Although individuals varied in their foraging site fidelity, we did not find evidence that this behaviour comes with an advantage in terms of their time-activity budgets in the system we studied. As discussed, many environmental and individual processes can be involved in shaping variation in foraging site fidelity. Bio-logging, especially with GPS, has created new opportunities for studying the consequences of foraging site fidelity at a level of detail that was not possible in the past. Where feasible, future studies should focus on the consequences of site fidelity within individuals over longer time-spans, to explore different constraints within the annual cycle. In addition, we recommend studies on the consequences of different strategies under changing food conditions, and comparing consequences not only within but also between species.

AUTHOR CONTRIBUTIONS

SvD carried out the statistical analysis and drafted the manuscript with support from JSB, JvdM and CJC; CJC leads a long-term study on Herring Gulls; CJC and SvD conducted fieldwork, JSB assisted with GPS tracking; WB supported the collection and analysis of acceleration data; SvD, JSB, JvdM and CJC discussed the analytical approach. All authors discussed results and contributed to the final manuscript.

DATA ACCESSIBILITY

Raw data files used in the analysis are available on 4TU. Centre for Research Data; https://doi.org/10.4121/uuid:67054ff9-a724-4130-ad97-2c88b1de7a79

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. Example of two individuals with contrasting foraging site fidelity.

Figure S2. Standardized major axis analysis between the Shannon index based on all data points on and near (< 50 m) the breakwaters and the Shannon index based on all terrestrial activity on and near (< 50 m) the breakwaters.

Figure S3. Relationship between the percentage of time on breakwaters and time-activity budgets of individuals with breakwaters as principal foraging habitat.

Table S1. Overview of bird-year combinations used in this study.

Table S2. Definition of 11 activity classes of Herring Gulls used to annotate tri-axial acceleration data.

Table S3. Full models and their AIC values testing the relationship between SFI and the dependent variable average time spent in the breeding territory per bird in a given year.

Table S4. Full models and their AIC values testing the relationship between SFI and the dependent variable-transformed proportion of time spent inactive during foraging trips.

Table S5. Full models and their AIC values testing the relationship between SFI and the dependent variable daily energy expenditure during foraging trips.

Table S6. Full models and their AIC values testing the relationship between SFI, body size and sex.