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Weather- and human-related shifts in feeding conditions promote the use of built-up areas by an avian opportunist

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HIGHLIGHTS

- Gulls relied mainly on fishery discards (males) and agricultural fields (females).
- Strong wind raises the energetic cost of feeding at sea, and gulls go there less.
- Dry weather decreases trip frequency and makes agricultural fields unattractive.
- Built-up habitats buffer for the unavailability of marine or fields foraging.
- Increasing food demand for reproduction is met by feeding more in built-up sites.

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ABSTRACT

Human activities benefit a range of animal species, the resulting presence of which in cities can have negative societal consequences. One example are food subsidies, which buffer natural variation in food availability and allow these species to maintain larger populations. These buffers will likely gain importance under future environmental change whereby natural food sources become increasingly unavailable. To inform on the current importance of different habitats for a bird reliant on human-made food subsidies (Lesser Black-backed Gull \textit{Larus fuscus}), and its possible population response toward changes in climate and the availability of these subsidies, we characterized population-level short-term responses to variation in drivers of local food availability, both natural (weather related) and anthropogenic (fisheries activity). We expected foraging effort to vary in relation to local wind speed and soil moisture, as well as to the alternation of fisheries activity between weekdays and weekends. Individuals were predicted to adjust their foraging habitat use in response to these environmentally driven variations in effort. To this end, we analyzed GPS tracking data of 45 breeding individuals, between 2013 and 2018, nesting in the Port of Zeebrugge, Belgium. Effort was approximated as the energy expenditure rate per trip, the daily time spent away from the colony and the trip frequency, which were analyzed by means of linear mixed effects models. Habitat use per trip was compared between marine, agricultural fields and built-up areas (cities, industry and cattle farms), in a multinomial logistic model. Marine areas and agricultural fields were most frequently exploited, but all considered stressors (wind, dry conditions and inactivity of fisheries) resulted in a higher use of built-up areas. Stronger winds increased the energetic cost of foraging at sea, and thus diminished the use of marine areas, as also did the inactivity of fisheries in weekends. Dry conditions diminished the use of fields and decreased trip frequency. Built-up areas thus constitute a buffer for the variation in food availability at sea and in agricultural fields. The expected increase in frequency and severity of extreme weather events (storms...
1. Introduction

The growing global human population continues to transform ecosystems for their use (Ellis 2015; Crutzen 2002), resulting in an increased number of human-wildlife conflicts, with negative impacts on both biodiversity and societies (Peterson et al. 2010; Nyhus 2016). While a majority of species currently suffers from population decreases, shrinking distributions and extinctions (Stork 2010; McKinney 2008; Shochat et al. 2006), some have benefited from human action (McKinney 2002; Elmhagen et al. 2017; Sih, Ferrari, and Harris 2011; Lowry, Lill, and Wong 2013). For the latter, human activities provide enhanced means of shelter (Raven and Coulson 1997; G. Shannon et al. 2014), dispersion (Mack et al. 2000; Ricciardi 2007) or feeding (Oro et al. 2013; Plaza and Lambertucci 2017), while to humans, urban-adapted fauna may entail costs in the form of nuisance (Lyytimäki et al. 2008; Hadidian 2015), damage to assets (Conover, Butikofer, and Decker 2018; Khor Plaza and Lambertucci 2017), and to humans, urban-adapted fauna may entail costs in the form of nuisance (Lyytimäki et al. 2008; Hadidian 2015), damage to assets (Conover, Butikofer, and Decker 2018; Khor).

In Europe, the Lesser Black-backed Gull (Larus fuscus), Herring Gull (Larus argentatus) and Yellow-legged Gull (Larus michahellis) often rely on anthropogenic food subsidies (Campbell-Hunt et al. 2015; van Donk et al. 2019; Moreno et al. 2010). Defined here as all food that is made available by human action. This includes mainly fishery discards, organisms in agricultural fields and pastures, made available through plowing and other activities (Garthe et al. 2016), as well as garbage and processed food obtained at urban sites (e.g. Alonso et al. 2015; Navarro et al. 2017; Zorrozua et al. 2020; Garthe et al. 2016; Ramírez et al. 2020). Flexibility in the exploitation of various human-mediated sources of food (van Toor et al. 2017) has enabled an increased presence of these species in cities, where their abundance and conspicuousness entail their perception as a nuisance with social costs (Rock 2005; Belant 1997; Huig, Buijs, and Kleyheeg 2016).

In the near future, legislation operating at a European level is expected to impact food availability for gull populations. First, the closure of open-air garbage dumps (in accordance with the European Union Landfill Directive 1999/31/EC) curtails the use of refuse by gulls (Steigerwald et al. 2015) – although not completely (Weiser and Powell 2011; Spelt et al. 2021) – and second, the European landing obligation (i.e. a ban on discarding), implemented from 2019 onwards (Bicknell et al. 2013), should eventually make fishery discards no longer available to scavengers. Furthermore, and according to current projections, the local climate will tend to present more frequent periods of drought as well as storm events, particularly in summer, coinciding with the gull breeding season (Grillakis 2019; Ruosteenoja et al. 2018; Ruosteenoja, Vihma, and Venäläinen 2019; Matte et al., 2019; Leduc et al. 2019). These changes in weather variability and severity may in turn further reduce the availability of food. On the one hand, stronger winds could decrease the net benefit of foraging by increasing its energetic cost. Flapping flight may be favored over gliding or soaring under strong winds, rising the energetic cost of movement, as suggested by Gabrielsen, Mehlin, and Nagy (1987) for Black-Legged Kittiwakes (Rissa tridactyla), although Martineau et al. (2015) found no such effect for the more terrestrial Ring-billed Gulls (Larus delawarensis). On the other hand, due to more frequent and prolonged droughts, food may become less accessible to gulls in agricultural fields and pastures. Indeed, decreased soil moisture is associated with a lower abundance of organisms such as fly (O. Diptera) larvae (Briones, Ineson, & Picarce, 1997) and earthworms (Ivask et al. 2008; Lavelle and Spain 2002), counted among the most frequently obtained items by large gulls when foraging inland (see Sotillo et al. 2019b supplementary material and Garthe et al. 2016; Sibly and McCleery 1983).

Our goal was to identify, among a set of factors postulated to affect food availability for breeding Lesser Black-backed Gulls, those that effectively induce a response in terms of foraging effort (time investment, energy investment and frequency of foraging) and affect the selection of foraging habitat types (marine habitat, built-up sites or fields and pastures).

Regarding foraging effort, we hypothesize that: (i) Wind speed affects the required energetic investment during foraging. If energetic costs of foraging increase under higher wind speed, we predict that the frequency of foraging trips and/or distances covered during feeding trips will decrease under such conditions; (ii) Soil moisture affects the required time investment. If search times in fields and pastures under dry soil conditions increase, we predict that the time individuals spend away from their nest during foraging trips will increase under such conditions, while the frequency of foraging trips will decrease; (iii) Growing brood demand for food affects foraging effort. As growing chicks demand a higher food intake rate, we predict parents to increase their foraging effort proportional to the growth of their chicks.

Regarding habitat use, while the inactivity of fisheries during weekends is expected to reduce marine foraging, the responses to weather are hypothesized to reflect the corresponding weather effects on foraging effort. We therefore predict that (i) increasing wind speeds decrease the use of habitats where they rise the required energy investment, (ii) low soil moisture decreases the use of fields and pastures, and (iii) growing food demand from the brood is met by a greater reliance on the habitat type that requires the lowest foraging investments.

2. Methods

To meet our goal, we first tested to what extent weather variables (wind speed and soil moisture), expected human behavior (assumed weekly trends in fisheries activity) and increasing brood demand for food (approximated as the aggregated chick size) affect foraging effort expressed as: (i) distance travelled per trip (ii) estimated trip energy expenditure, (iii) daily time spent away from the colony and (iv) daily trip frequency. Second, we tested whether variation in these same factors drives the relative use of three foraging habitat types: (i) marine habitat: mainly fisheries discards, although also occasional foraging on swimming crabs, (ii) agricultural fields and pastures devoted to cattle: mainly soil invertebrates, but also small mammals made available by ploughing and mowing, and (iii) built-up habitat: sources of garbage and processed food in built-up areas such as cities, industrial sites and cattle farms. We therefore analyzed high-resolution GPS tracking data of adult individuals nesting in a densely populated coastal landscape during the chick rearing period, when individuals face an increasing parental foraging effort due to the growing food demands of their brood (Sotillo et al. 2019a). We assumed that, during this highly demanding period,
individuals exploit their preferred food source whenever available.

### 2.1. GPS tracking

We analyzed movement data of 45 adult Lesser Black-backed Gulls (i.e., at least 4 years of age) nesting in the port of Zeebrugge (51°20'56.2"N 3°10'25.0"E) during the period 2013–2018. The number of breeding pairs in this location decreased from 3331 in 2013 to 1181 in 2014, due to predation by foxes and nesting habitat loss, and fluctuated between those values in subsequent years (Stienen et al. 2019). The studied birds were equipped with UVa-BiTS GPS tracking devices (Bouten et al. 2013; Stienen et al. 2016) during egg incubation. Gulls were captured in their nest using a walk-in trap, and the GPS devices were attached with a wing harness of Teflon ribbon threaded with a nylon string, using only knots, with a reef knot in the tracheal pit as in Thaxter et al. (2014). The devices weighed 13.5 g + 5 g harness (2 to 3 % of individuals’ body mass) and measured 61x25x10 mm, and the Teflon ribbon was 6.5 mm wide.

Brood size was standardized at 2 chicks per nest, which were cross-fostered with first- or second-laid eggs from haphazardly selected nests of non-tracked birds in the vicinity; each nest belonging to a tracked bird therefore received 2 eggs sourced from nests of non-tracked birds, and its original eggs were distributed among these non-tracking nests. With this, we standardized offspring food demand and promoted hatching synchrony (within ca. 24 h) in broods. In most years, only the nests of tracked birds were monitored, but in a pilot study run in 2016 by monitoring 19 non-modified nests, 14 of these (74 %) had 3 nests. With this, we do not expect this population to be food-stressed.

Only data pertaining to the chick rearing stage were used in the present analyses, including all data from the hatching date of the first chick until the youngest chick reached 30 days of age. We did not include the incubation stage in our analysis given the limited and irregular sample size: GPS trackers are installed during incubation, and cross-fostering takes place early enough so that the tracked individual’s original eggs do not hatch before. As the eggs sourced for cross-fostering are pipping, this also reduced the number of days with tracking data corresponding to the incubation stage. Position data was recorded at a minimum resolution of one GPS fix every 3 or 5 min when outside of a 2.4 km² area delimiting the nesting colony, and one fix every 20 min when inside this area, with at least 60 m accuracy.

### 2.2. Foraging trips

A trip was defined as all positions recorded from the first GPS fix beyond a 5 km radius from the center of the colony until the next fix recorded inside this perimeter. Trips were assigned to the day when they were initiated. Next, GPS positions were classified as either commuting flights, resting or foraging behavior. To this end, we trained and validated a random forest classifier using an expert-annotated dataset containing 128 tracking days, based on path geometry (distance and turning angle between consecutive points), body movement derived from the accelerometer profile, as in Shamoun-Baranes, Bouten, van Loon, Metier & Camphuysen (2016), and habitat derived from the Corine Land Cover dataset (see below), with a 3-point moving input-window. Precision/recall for flight, rest and forage was, respectively, 90/97%, 82/87% and 74/87%. See supporting information for a description of the classifier.

Of a total 4633 recorded trips, 3887 (84 %) contained at least one position that had been classified as foraging by the random forest algorithm. Only these trips were considered to be foraging trips, hence excluding 746 cases without evidence of foraging (supplementary material figs. S1 and S3 to S6). Consequently, the number of analyzed trips per individual and year ranged from 19 to 129 (supplementary material fig. S9).

Habitat data were obtained from the Corine Land Cover dataset (European Environment Agency 2016) with a spatial resolution of 100 m, and building outlines were obtained from the Large-scale Reference File of the Flemish Government (Grootschalig Referentiebestand – GRB. Available online at overheid.vlaanderen.be/informatie-vlaanderen/producten-diensten/basiskaart-vlaanderen-grb). Spatial data had WGS 84 as geodetic datum, and were graphically represented using the Web Mercator projection. Each recorded position was assigned the Corine habitat category corresponding to its coordinates. Then, assuming that most potential misclassifications based on Corine Land Cover Data would happen between the fields and built-up categories, due to their patchy distribution as opposed to the homogeneous distribution of the marine habitat, all positions recorded within 50 m of the center of a building were classified as built-up (supplementary material tables S1 and S2). Urban green areas (parks, gardens and sports fields) were included in the built-up category (supplementary material table S2; Corine Tier 3 category “Nonagricultural vegetated areas”). Of a total 234,967 foraging fixes, 1422 (<1 %) did not fall into any of the above categories, and were excluded from analyses.

Based on the habitats where foraging positions were recorded, each trip was classified into a main habitat type: (1) marine, (2) fields and pastures or (3) built-up (Fig. 1). Only one habitat type was assigned per trip, selecting the type where most foraging positions were recorded. While virtually all marine trips only had foraging positions at sea, trips to fields and pastures often contained a number of foraging positions inside built-up areas, and vice versa (see supplementary material fig. S6 for a summary of the distribution of foraging positions per trip). An overlap between both terrestrial habitat types within a single trip may occur if an individual indeed forages at several distinct habitats of each type, or if positions near a boundary between habitats are misclassified, and instances of both cases were found in our data. We considered that classifying each trip into its main foraging habitat type suited best our hypotheses because the effects analyzed in this study are expected to vary among successive trips and not within a single trip, and because most (69 %) terrestrial trips had more than 80 % of foraging positions within a single habitat type. In 37 (1 %) terrestrial trips, exactly half of foraging positions were registered within each habitat type (built-up and fields), and in 2 trips half of positions were recorded in fields and half at sea. These trips were classified in the fields category.

The distances covered per trip were estimated by summing the haversine distances between consecutive points, and the maximum distance away from the colony recorded per trip was identified from the set of haversine distances between each registered position and the

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**Fig. 1.** Examples of foraging identified from track patterns. (A) In fields and pastures (see also Fig. S3). (B) Given the dynamic distribution of foraging opportunities at sea, combined with the apparent lack of features, trips with complex movement patterns, including drifting on sea surface, gliding flight and more disordered short-step displacements are likely to correspond to marine foraging. At built-up sites, these being point food sources surrounded by fields (C see also Fig. S4) and urban sites such as garbage processing facilities (D see also Fig. S5).
center of the colony. Given the strong dependence of the total distance travelled on the maximum distance to the colony ($R^2 = 0.9; p < 0.001$; see also supplementary material fig. S13), only the latter parameter was analyzed as an aspect of foraging effort.

Relative energy expenditure due to body acceleration was approximated by calculating the mean Overall Dynamic Body Acceleration (ODBA; Wilson et al. 2006, 2020) per trip, in all recorded trips for which accelerometer data were available (all years except 2014). In this subset, each GPS fix had an associated accelerometer sample taken at 20 Hz for 10 s. Tri-axial acceleration measurements were converted into units of $g$ ($1 \text{ g} = 9.81 \text{ m s}^{-2}$), and the sum of ODBA in the $x$ (surge), $y$ (sway) and $z$ (heave) directions was defined as:

$$\text{ODBA} = |\text{DA}_x| + |\text{DA}_y| + |\text{DA}_z|$$

Where DA is the mean dynamic acceleration component on the $x$, $y$ and $z$ axis, obtained by subtracting the estimate for static acceleration (i.e. that due to the Earth’s gravitational field) from the corresponding accelerometer measurement. Static acceleration was approximated as the running mean over the full 10 s sample of all measurements along each axis.

### 2.3. Drivers of foraging behavior

Weather was assessed as wind speed (m/s) and soil moisture (%). Wind speed was calculated from the East ($u$ component) and North ($v$ component) wind components at the surface level obtained from the NCEP NCAR Reanalysis dataset (Kalnay et al. 1996) with the RNCPE package (Kemp et al. 2012) in R (R Development Core Team 2020). Values for these vectors are available at a spatial resolution of $2.5 \times 2.5^\circ$ and temporal resolution of 6 h (supplementary material fig. S10). These values were then interpolated spatially and temporally at each recorded position following the linear interpolation method as in Kemp et al. (2012), and an average was derived per trip and per day. Soil moisture was approximated as the percentage soil water saturation, based on 15-minute resolution data obtained from the web portal of the Flemish water managers and knowledge institutes (www.waterinfo.be). We used the average of 3 measuring stations evenly distributed within the area containing all feeding positions classified as within fields (supplementary material fig. S11).

Local fisheries are primarily composed of shrimp- and beam-trawlers, landing in Belgium and The Netherlands, and are ostensibly less active during weekends due to the inactivity of Dutch vessels (Syst et al. 2016). Trips were therefore classified as taking place during a working day (Monday through Friday) or in the weekend (Saturday and Sunday). Finally, aggregated chick size per nest was approximated by the average of 3 measuring stations evenly distributed within the area containing all feeding positions classified as within fields (supplementary material fig. S11).

Food intake rates of chicks increase along their growth trajectory (van der Meer et al. 2016). Trips were therefore classified as taking place during a working day (Monday through Friday) or in the weekend (Saturday and Sunday). Finally, aggregated chick size per nest was approximated by the average of 3 measuring stations evenly distributed within the area containing all feeding positions classified as within fields (supplementary material fig. S11).

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### 2.4. Data analysis

Regarding the analysis of foraging effort, the maximum distance away from the colony recorded per trip, the mean energy expenditure per trip (ODBA; g) and the total time (hours) spent outside of the colony per individual and day were analyzed using Gaussian mixed effects models, while the number of foraging trips performed per individual and day (trip frequency) was analyzed by means of Poisson mixed effects models. We included as fixed effects the soil moisture, the average surface wind speed during the trip, chick size, a factor indicating weekdays or weekends, and the individual’s sex. The calendar year and bird identity were included as random intercepts.

Given that energy expenditure (based on ODBA) was assessed on a trip basis, and that each trip was assigned to one main foraging habitat type, the analysis of mean trip ODBA also included a habitat type factor. To test if the effect of weather variables (wind speed and soil moisture) is dependent on the habitat type (marine, fields or built-up), the interactions between these weather variables and the habitat type factor were as well included. Habitat use was not included in the models of time spent outside the colony and trip frequency because these were assessed on a daily basis. In these models, the interaction between weather variables was included, to test whether the combination of wind speeds and low soil moisture) has a synergistic effect on the analyzed variables, in which case a negative coefficient would be expected for the interaction.

Models were fitted using package lme4 (Bates et al. 2019) in R. No model selection procedure by stepwise addition or deletion of explanatory variables was performed, to avoid biases in parameter estimates (Whittingham et al. 2006). The significance of main effects, interaction terms, and random intercepts was tested by performing a likelihood ratio test between the full model and a model without the term in question (see supplementary material tables S3 to S6). For the case of main effects of variables involved in interactions, their significance was assessed only when the interaction was not found to be significant, by running a likelihood ratio test between a model without the interaction and a model without the interaction and the term in question. Marginal means and coefficients were estimated for the full models using package emmeans (Lenth 2019). All plots were produced with packages ggplot2 (Wickham 2016), ggeffects (Lüdecke 2018) and gridExtra (Augue 2017). Collinearity between the explanatory variables included in all analyses was assessed graphically by plotting each possible pair of variables, as well as calculating their correlation (supplementary material fig. S12).

To explore the distribution of foraging habitat specialization among individuals, the relative use of the three considered habitat types was reduced to a single diversity metric – Shannon’s equitability index ($E_q$), calculated as Shannon’s diversity index ($H$; C. E. Shannon 1948) divided by the logarithm of the number of classes:

$$E_q = -\frac{\sum [p_i \ln p_i]}{\ln k}$$

where $p_i$ is the proportion of total trips directed to each of the three considered habitat types by tracked individual $i$, and $k$ is the number of classes (here, three habitat types). If $p_i = 0$, then the $p_i X \ln p_i$ term is set to 0. $E_q$ ranges from 0 (individuals specialized in a single habitat type) to 1 (maximum diversity in habitat use).

The habitat classification per trip was modeled using a multinomial logistic regression, with foraging habitat type as response, the built-up habitats being the baseline category. The explanatory variables were sex, chick size, the weekend factor, and the trip-averaged wind speed and soil moisture. The continuous explanatory variables (chick size, wind speed and soil moisture) were standardized to have mean 0 and standard deviation 1. Successive trips performed by a same individual may be expected to not be independent given the temporal autocorrelation of the drivers of habitat use, and the possibility of a tendency to visit a habitat where the individual was recently successful. To account for this possibility, we also included the habitat where foraging took place in the previous trip as explanatory variable in all models. To assess whether the choice of baseline category of the response variable affected the model predictions, predicted values for the fitted dataset were compared between models fitted using each of the three habitat types as
baseline category. In 99% of cases, the predictions were less than 5 percentage points apart (supplementary material fig. S15).

The habitat use model was fitted using a numerical, Bayesian approach. In the absence of any starting assumption on the real values of the model parameters, we used a moderately informative default prior with Normal distribution, mean 0 and variance 1 for the $\beta$ parameters (i.e., model intercepts and slopes) estimates (see e.g. Gelman, Lee, and Guo 2015), and the package default priors (Student t-distribution $\nu = 3$, mean 0, variance 10) for the residual variance (see supplementary material fig. S14 for an account of model prior and posterior distributions). Bird identity was included as a grouping factor. The model was fitted with the Markov Chain Monte Carlo algorithm using 3 chains with 50,000 epochs of burn-in time, and a thinning rate of 10. Initial parameter values were randomly generated, and chain convergence was determined using the Gelman-Rubin statistic (convergence assumed to be reached if $R < 1.1$; Gelman and Rubin 1992). Models were fitted in the Stan computational framework (http://mc-stan.org/), accessed with the brms package (Bürkner, 2017) in R. Highest posterior density credible intervals were obtained using package emmeans.

2.5. Animal welfare

In accordance to Belgian legislation, all actions exerted on GPS-tracked individuals and their foster chicks, as well as the cross-fostering procedure, have been approved by the University of Antwerp Ethical Committee (project Ethics Committee number 2013–73). Broods were cross-fostered before hatching, and none of the resulting brood sizes exceeded the natural range of 3 eggs. Non-tracked foster parents were not caught, handled or sampled.

3. Results

3.1. Foraging effort

The tracked individuals showed distinct movement patterns between the three considered foraging habitat types, and in relation to wind speed, soil moisture and chick growth. While trips to built-up habitats demanded the furthest displacements away from the colony, those at sea the shortest, and trips to fields were intermediate, marine trips involved the highest energy expenditure rates (approximated as mean trip ODBA), and these rates did not differ between the two terrestrial habitat types (Table 1).

The effects of wind speed and soil moisture on foraging effort were habitat-dependent (Fig. 2). Wind speed had no apparent effect on the distances travelled, and while energy expenditure of marine trips increased with wind speed, energy expenditure of trips to either built-up habitats or fields remained stable along the wind speed gradient. Increasing soil moisture resulted in shorter distances travelled to forage in built-up habitats, not only slightly with wind speed, nor an interaction between the weather variables are statistically significant for mean trip ODBA, were rather negligible in size (Table 1).

The daily time spent outside the colony varied largely, between 0 (full day spent inside) and 24 h (full day spent outside). It increased only slightly with wind speed – an average 4.8 min per m/s increase in wind speed amounts to a maximum increase of about one hour in the range of observed wind speeds in our study – while it was unaffected by soil moisture, and did not vary significantly between sexes (Table 2). Individuals spent more time outside the colony during weekends and with increasing chick size (Fig. 2 middle-top). Per day, individuals initiated between 0 (in 361 instances) and 5 trips (in 6 instances), with a median of 1 and mean of 1.5 daily trips. In general, trip frequency was higher during weekends, and increased with the size of the chicks and with increasing soil moisture (Fig. 2 bottom). No significant effect of sex or wind speed, nor an interaction between the weather variables are observed in the model (Table 2).

3.2. Foraging habitat use

Habitat types were rather evenly distributed in their use over the population: a majority of foraging trips were directed toward fields (38 %) and the sea (37 %), while the remaining 25 % involved built-up sites. Of all trips to built-up sites, 60 % were in urban habitats, and 40 % in cattle farms. This reflects the fact that most individuals followed a generalist habitat use pattern (Equitability index $E_q$ median 0.81 and standard deviation 0.23; see also fig. S8). On the more specialized end of...
Fig. 2. Variation in foraging effort against weather variables and chick growth. TOP: maximum distance away from the colony registered per trip. MIDDLE-TOP: energy expenditure approximated as mean trip ODBA value, per habitat type. MIDDLE-BOTTOM: time expenditure as total time spent outside the colony per individual and day. BOTTOM: total number of trips initiated per individual and day (trip frequency). Points are averages calculated for segments of, respectively, 0.5 m/s (wind speed), 1 % (soil moisture) or 1 cm (chick size), separately for weekdays (black) and weekend (orange), size of points is proportional to the number of observations. Lines represent significant relationships with the corresponding continuous explanatory variable, separately by level of categorical variables with a significant effect. Rug plots represent the distribution of observations along the gradient of the corresponding continuous variable, per year. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
In this model, the weekend effect appears to be sex-specific, given that increased by 11% in weekends. Although no interactions were included females were more frequently observed foraging at fields than males and these were all marine foragers and males.

The foraging radius of marine trips was the smallest of all three habitat types considered, and we do not expect the availability of discards to be particularly low at greater distances offshore (see e.g. Fig. 1 in Sys et al. 2016, where no wind effects were found), while this effect was negligible for foraging on terrestrial food sources. Our hypothesis that soil moisture affects time investments was also confirmed by the fact that trip frequencies were higher during more humid conditions, without a parallel increase in the daily time spent outside the colony. As predicted, individuals increased their foraging effort in response to growing brood demands, in terms of daily number of trips performed and the total time spent outside the colony. The average energetic expenditure per trip, however, remained relatively constant. The relative use of the three considered habitat types was hypothesized to respond to the variables that affected the required foraging time and energy investments in them. The relative use of marine foraging did indeed decrease at higher wind speeds, when trips at sea became more energetically costly, while the use of fields and pasture followed the predicted positive trend with respect to soil moisture.

Wind speed, soil moisture and chick size also influenced habitat use (Table 3). Increasing wind speeds reduced the prevalence of marine foraging, which is replaced by foraging in fields and built-up areas (Fig. 4). Similarly, higher soil moisture resulted in an increase in foraging in fields and a lower prevalence of foraging at sea and built-up sites – most notably for females and during weekends. Finally, the increasing food demand by the developing brood translated into an increase in the relative use of terrestrial areas and a decrease in the use of fields, while marine foraging remained rather stable.

### Table 2

Summary statistics and estimated model coefficients of the linear mixed model for the daily time spent outside the perimeter of the colony, and of the linear mixed model for the daily number of foraging trips initiated by breeding Lesser Black-backed Gulls.

<table>
<thead>
<tr>
<th>Dependent variable</th>
<th>Explanatory variable</th>
<th>Estimated marginal mean or coefficient ± s.e.</th>
<th>P</th>
</tr>
</thead>
<tbody>
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<td>Daily time outside of colony (hours) Random effects</td>
<td>Year</td>
<td>12.98 ± 0.79</td>
<td>&lt;0.001</td>
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<td>Individual</td>
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<td>480.94 ± 0.01</td>
<td>&lt;0.001</td>
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<td>Weekend</td>
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<td>24.16 ± 0.01</td>
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<td>0.0002 ± 0.99</td>
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<tr>
<td>Male</td>
<td></td>
<td>0.10 ± 0.00</td>
<td>0.97 ± 0.00</td>
</tr>
<tr>
<td>Wind speed (m/s)</td>
<td></td>
<td>0.08 ± 0.04</td>
<td>5.7 ± 0.02</td>
</tr>
<tr>
<td>Soil moisture (%)</td>
<td></td>
<td>-0.01 ± 0.02</td>
<td>0.23 ± 0.63</td>
</tr>
<tr>
<td>Chick size (cm)</td>
<td></td>
<td>0.31 ± 0.03</td>
<td>119.63 ± 0.00</td>
</tr>
<tr>
<td>Wind speed × Soil moisture</td>
<td></td>
<td>0.004 ± 0.003</td>
<td>1.2 ± 0.27</td>
</tr>
<tr>
<td>Daily number of trips initiated Random effects</td>
<td>Year</td>
<td>3.19 ± 0.07</td>
<td>0.07</td>
</tr>
<tr>
<td>Individual</td>
<td></td>
<td>205.23 ± 0.00</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Weekend</td>
<td></td>
<td>12.77 ± 0.12</td>
<td>12 ± 0.00</td>
</tr>
<tr>
<td>Weekday</td>
<td></td>
<td>14.6 ± 0.12</td>
<td>14.6 ± 0.12</td>
</tr>
<tr>
<td>Female</td>
<td></td>
<td>1.38 ± 0.14</td>
<td>0.02 ± 0.89</td>
</tr>
<tr>
<td>Male</td>
<td></td>
<td>1.35 ± 0.14</td>
<td>0.25 ± 0.03</td>
</tr>
<tr>
<td>Wind speed (m/s)</td>
<td></td>
<td>-0.02 ± 0.00</td>
<td>1.11 ± 0.29</td>
</tr>
<tr>
<td>Soil moisture (%)</td>
<td></td>
<td>0.17 ± 0.05</td>
<td>8.61 ± 0.00</td>
</tr>
<tr>
<td>Chick size (cm)</td>
<td></td>
<td>0.18 ± 0.04</td>
<td>20.08 ± 0.00</td>
</tr>
<tr>
<td>Wind speed × Soil moisture</td>
<td></td>
<td>0.02 ± 0.79</td>
<td>0.37 ± 0.00</td>
</tr>
</tbody>
</table>

The distribution, 3 individuals had an equitability index lower than 0.3, and these were all marine foragers and males. At the population level, the probability of selecting a marine, agricultural or built-up habitat varied between sexes, as well as between weekdays and weekends (Table 3). As expected, the prevalence of marine foraging plummeted from 44% of trips in weekdays to 18% in weekends (Fig. 3B), and would thus be more affected by the inactivity of fisheries.

Foraging behavior to the variation in weather, in terms of foraging effort and habitat use. The hypothesis that wind speed affects energy expenditure of foraging trips was confirmed only for trips at sea, where, as predicted, increased wind speeds raised the energy expenditure (as opposed to Isaksson et al. 2016, where no wind effects were found), while this effect was negligible for foraging on terrestrial food sources. Our hypothesis that soil moisture affects time investments was also confirmed by the fact that trip frequencies were higher during more humid conditions, without a parallel increase in the daily time spent outside the colony. As predicted, individuals increased their foraging effort in response to growing brood demands, in terms of daily number of trips performed and the total time spent outside the colony. The average energetic expenditure per trip, however, remained relatively constant. The relative use of the three considered habitat types was hypothesized to respond to the variables that affected the required foraging time and energy investments in them. The relative use of marine foraging did indeed decrease at higher wind speeds, when trips at sea became more energetically costly, while the use of fields and pastures followed the predicted positive trend with respect to soil moisture.

Trips to built-up habitats, as well as those to fields, showed lower energetic demands than those at sea. However, despite the fact that trips to fields involved shorter distances away from the nest, their use decreased with growing chick size, while the use of built-up habitat increased. Based on this combined outcome, we cannot confirm our last prediction that breeding individuals opt for the habitat type involving the smallest investments in terms of both time and energy when pressed to provide increasing amounts of food to their growing brood.

Energy expenditure was consistently higher at sea than on land, which may explain the spatially constrained pattern of marine foraging: the foraging radius of marine trips was the smallest of all three habitat types considered, and we do not expect the availability of discards to be particularly low at greater distances offshore (see e.g. Fig. 1 in Sys et al. 2016). Central place foragers have elsewhere been found to incur larger energetic costs to obtain prey with a higher energy density (Patenaude-
However, the mentioned studies include built-up habitats among those where higher energy expenditures are observed. This may to a certain extent be related to differing spatial niche characteristics: for instance in the case of sympatric Herring and Lesser Black-backed Gulls, the former have a characteristically shorter foraging radius than the latter (Camphuysen 1995; Sotillo et al. 2014).

The observed decrease in the population’s relative use of marine...
foraging with increasing wind speeds suggests that this habitat loses attractiveness as its use becomes costlier. On the other hand, rather than the increasing energetic cost of foraging at sea, it may be argued that it is the inactivity of fisheries during the roughest sea conditions that drives a decrease in marine foraging with increasing wind speeds. The wind speed ranges included in our analyses are far below values corresponding to storm conditions (conventionally, wind speeds above 24.5 m/s), but a certain degree of underestimation can be expected due to the rather low spatial and temporal resolution of NCEP data. Another factor potentially mediating the availability of food at sea could be the sea state (wave height, swell, turbulence), which is also directly related to wind. Although we cannot rule out these other mechanisms, they all still imply that strong wind negatively impacts the availability of fishery discards as a food source.

Soil moisture was unrelated to the time spent away from the colony, but its increase was associated with a higher trip frequency, which is likely to translate into a higher brood provisioning rate. This increase in trip frequency was likely driven by an enhanced use of fields and pastures, given that the prevalence of trips to this foraging habitat type related strongly to soil moisture. It is striking that increasing soil moisture reduced the distances travelled to forage in built-up sites, but not in fields and pastures. Because this trend occurs in parallel to an enhanced use of fields, it suggests that long-distance trips to built-up areas are no longer necessary to obtain sufficient food in wet conditions, but individuals still sometimes feed on built-up sites that are close to the colony. Some of these foraging trips directed to built-up sites under wet conditions could correspond to gulls making use of urban green areas, as documented by Spelt et al. (2019). In any case, the efficiency of breeding gulls in provisioning their brood can be expected to be enhanced by wet weather conditions. At the lowest soil moisture values, trips to fields and pastures do not completely disappear, as gulls may still forage on prey types whose availability is independent of this environmental variable, such as small mammals stunned by hay rakes, above-soil arthropods, or behind manure spreader trucks. Under dry conditions, a lower prevalence of foraging trips to fields and a lower trip frequency may therefore occur if individuals shift to alternative habitats (marine or built-up) where they are less efficient, or visit fields but take longer to find foraging opportunities. Under both of these options, the periodicity of chick provisioning, the total amount of food provided and the time parents can be at the nest to protect chicks against predation may be compromised.

As opposed to low soil moisture, adverse foraging conditions at sea (high wind speed) did not decrease the frequency of foraging trips, and individuals spent a similar time outside the colony but shifted to foraging in fields or built-up areas. Similar resource shifts have been observed for this species in the Wadden Sea, where female Lesser Black-backed Gulls replace marine foraging by agricultural fields in weekends, without decreasing the amount of time spent away from the nest (Tyson et al. 2015). In sexually dimorphic birds, differences in foraging habitat use between females and males can be interpreted in terms of dominance of the larger sex (Lewis et al. 2005; Greig, Coulson, and Monaghan 1985). This behavioral trend might provide a mechanism reducing competition within the breeding pair, a bet-hedging strategy where the probability of both parents failing to find food is reduced by avoiding to forage in the same habitat, or a means for nutritional complementation of the brood diet. A proposed sexual trend in dominance does however not necessarily imply differences in foraging efficiency, at least regarding effort: although males went more often to sea, the energy expenditure, time spent away from the colony and trips per day were similar in both sexes.

Overall, the sea and fields were the most relied-upon foraging habitats. Marine foraging was more often performed by males and during weekdays, as previously reported by Sotillo et al. (2019a) and Camphuysen et al. (2015), but again contrary to findings in Inaksson et al. (2016), where no such trend was found. Built-up areas, although the least frequently visited foraging habitat type in total, saw their use enhanced by all considered stressors: adverse weather conditions (stronger winds and low soil moisture), increasing chick size, and the inactivity of fisheries in weekends all resulted in a greater reliance on this habitat type. Distant, but reliable and rich foraging built-up sites, such as food- or garbage-processing plants, may thus represent a backup option to ensure chick- and self-provisioning under adverse conditions, albeit with a lower efficiency. Breeding Lesser Black-backed Gulls indeed show a strong fidelity to such sites, even after switching to a more distant nesting location (Kavelaars et al. 2020). In any case, the here described weekly behavioral trends for gulls should not be interpreted as proof that these birds have any conscience of the human division of time into weekdays and weekends.

It is important to highlight that in our habitat use model, by using a categorical response variable (the habitat type), the outcome depends on the number and definition of its categories. Here, we opted for a classification into 3 categories to minimize analytical complexity, while still capturing variation in habitat use implying different diets (marine fish and invertebrates at sea, terrestrial unprocessed food in fields and processed food in built-up habitat), as well as modes of feeding (see supplementary material Sections 1 and 2). While the existence of a binary option between a marine trip and a trip inland seems clear, some terrestrial trips had indications of mixed foraging in both fields and built-up habitat (see supplementary material fig. S6). This arises from the patchy and imbricated distribution of both habitats in the study landscape, which implies a certain degree of ambiguity in the classification of trips. By classifying trips into the dominant category within them, some nuance was lost in the quantification of habitat use. It can for instance be argued that, while a decision whether to forage at sea or on land is taken upon leaving the colony, the decision whether to feed in a field or at a built-up site may be taken after exploring the available opportunities on land, and therefore result in some time spent in both types of terrestrial habitat.

Despite the above-mentioned caveat, our results show that built-up areas (cities, industry and cattle/poultry farms) allowed breeding individuals to buffer for fluctuations in the availability of largely exploited food sources at sea and in agricultural fields and pastures. They also suggest that foraging at sea or in fields and pastures is favored to a certain extent, when available, over built-up areas in this population (cf. Coulson and Coulson 2008; Garthe et al. 2016). Marine foraging has on occasions been assumed to be the preferred or main strategy for large gulls during breeding in studies documenting their use of fishery discards (Camphuysen 1995; Kubetzki and Garthe 2003; Schwemmer and Garthe 2005). Van Donk et al. (2017) questioned the interpretation of foraging choices in gulls on the base of nutritional optimization, describing a situation where a low-cost foraging option on low energy density prey (intertidal invertebrates) is preferred to foraging at sea or in built-up areas, while resulting in poorer reproductive performance. Conversely, Pierotti and Annett (1991) reported that specialization on intertidal invertebrates better fits the nutritional requirements of reproduction. This apparent discrepancy may be due to differences in nutritional requirements between the stages of reproduction studied: chick rearing in van Donk et al. (2017) and egg-formation in Pierotti and Annett (1991). In our study case, the sea or fields and pastures could provide either more appropriate food composition than built-up areas, lower foraging costs in terms of time and energy investments (van Donk et al. 2019), or a lower perceived predation risk (Sorace 2002), but we did not find evidence for widespread individual specialization in any particular habitat type. The observed use of built-up sites with advancing chick growth may then be due to changes in the dietary requirements of reproduction, where particular components, such as calcium (suggested by Pierotti and Annett 1991, 1990; Schwemmer and Garthe 2005) are no longer the priority, but rather a high energy input (Orent, Klaassen, and Zwaan 1987; van der Meer et al. 2020).

Temporal fluctuations in food availability at built-up sites were not considered in this study, but could play a role in the attractiveness of this
habitat. For instance, weekend trips to urban environments may be encouraged by a higher food availability due to the greater influx of tourists in coastal cities. This factor could in turn interact with weather variables, as tourist attendance can be expected to be higher in dry weather (Falk 2014). However, the diversity of food sources at built-up sites (see e.g. Méndez et al. 2020; Huig, Buijs, and Kleyheeg 2016) hinders a straightforward interpretation of food availability at these habitats, and it is unknown which cues gulls may use to detect higher food availability in urban environments. This diversity of food sources and types additionally hinders the assessment of the dietary quality of food sourced at built-up sites: while the composition of food obtained at sea (fish and invertebrates) and fields and pastures (earthworms, small mammals and insects) varies within a limited range, that of processed foods (e.g. butcheries, bread, fried potato) varies widely both in nutrient composition and energy density (for details, see Sotillo et al. 2019b supplementary material).

The predominantly mixed foraging strategies observed in our study population may become less frequent if future climate conditions tend toward a higher frequency of strong winds and dry weather periods. Although built-up areas can function as backup feeding sites and be adequate for self-maintenance, it is yet unclear whether they may compensate for a permanent reduction in the availability of other food sources during reproduction. The widespread use of fishery discards by Lesser Black-backed Gulls in the North Sea (Schwemmer and Garthe 2005; Corman et al. 2016; Camphuysen et al., 1996) and their increased use of marine habitats during chick-rearing (Garthe et al. 1999; Sotillo et al. 2014; Isaaksson et al. 2016; Markones, Dierschke, and Garthe 2009), are suggestive of a preference for fish in chick provisioning. This notion is reinforced by the negative relationship between the amount of terrestrial food and breeding performance in gulls (Sotillo et al. 2019b; O’Hanlon, McGill, and Nager 2017), although a fish-based diet also implies hidden costs, such as a high concentration of anthropogenic pollutants (Santos et al. 2020). O’Hanlon et al. (2020) suggest that rather than the terrestrial diet itself being detrimental to reproduction, it is the combined use of different resources, instead of individual specialization in either resource, that relates to a poorer performance, as specialized individuals might be more efficient foragers than generalists (following Bolnick et al. 2003). Along these lines, Lesser black-backed Gull colonies have elsewhere been found to be viable by relying on terrestrial resources (Gyimesi et al. 2016; Spelt et al. 2019). Finally, the disappearance of discards may not put an end to marine foraging if enough food can be found independent of this human activity. While discards are the main proportion of the marine diet in Lesser Black-backed Gulls nesting along the shores of the Southern North Sea, these have as well been documented to feed on swimming crabs and other non-anthropogenic marine prey (Schwemmer and Garthe 2005; Camphuysen et al. 2015). Such naturally occurring prey may well represent a viable main food source for these populations (Luczak et al. 2012), and as such buffer for the decrease in the availability of discards (as suggested by Corman et al. 2016).

In our study landscape -the Belgian coastal region- the Lesser Black-backed Gull is a recent breeder. Expansion of breeding populations along the Belgian Coast proceeded from the Netherlands: its first few nests were observed in 1985 at the Dutch border (Stienen, Van Waeyenberge, and Vercruysse 2002; Seys et al. 1998). Populations in the southernmost region of the Netherlands also first appeared in the 1980s and strongly increased during the 1990s (Strucker, Hoekstein, and Weidt 2016). The expansion of this species in Northwestern Europe has been attributed to the bans on hunting and egging, combined with their efficient use of anthropogenic food subsidies (see Ross-Smith et al. 2014 and references therein), two factors that were up to now difficult to disentangle. In the Zeefrugge colony, which hosts the largest number of nests in Belgium, numbers peaked in 2011 with 4760 breeding pairs (Adriaens et al. 2012). These numbers have since decreased, with 3333 pairs in 2013, and fluctuating between 1000 and 1500 pairs in the period 2014 to 2018. This decrease was however mainly due to predation by foxes, followed by the destruction of what used to be the main nesting areas (Stienen et al. 2019), and thus cannot be linked to fluctuations in the local foraging landscape. An ongoing trend for more prevalent roof nesting (François 2002) further complicates the assessment of this species’ demography in relation to the ongoing environmental changes.

To predict whether locally breeding Lesser Black-backed Gulls can maintain their current population while becoming increasingly dependent on built-up areas for foraging under the expected environmental change, or whether they need to exploit marine resources and agricultural fields alongside urbanized areas, the fitness consequences of different foraging strategies, best expressed as the differential recruitment into the breeding population, need to be further studied. This is a challenging task, particularly in a long-lived species where adults typically dispose of multiple reproductive attempts. Additional complexity arises from bi-parental care, making reproductive output the result of the integrated efforts of both parents, as well as from inconsistency in pair formation, extra-pair couplings, and changes in nesting sites between consecutive years. Bi-parental GPS tracking and mark-resighting of juveniles could provide the necessary information, but these studies are still largely lacking in the current literature (e.g. Kavelaars et al. 2018).

5. Conclusions

Given the contribution of anthropogenic food subsidies to their increase in abundance during the second half of the twentieth century (Garthe, Camphuysen, and Furness 1996; Sherley et al., 2020; Spaans 1998; Harris 1970), gulls came to be counted among the winners of human action. Presently, they are expected to find themselves subject to the effect of multiple stressors arising from this very same human action (Ross-Smith et al. 2014). The combination of more frequent and severe droughts and storms in summer, together with a discards ban, could eventually result in prolonged periods within the breeding season where cities, industries and cattle farms will be the only places where these gulls may find sufficient food to raise their chicks. Foraging shifts toward urban specialization could allow current populations to cope with these changes. An increased presence of gulls in cities and other built-up sites should therefore be contemplated by policy-makers. Considering the negative public image of large gulls (Rock 2005), more effort may be necessary in mitigating current and potential gull-human conflicts, without losing sight of the benefits that the presence of this wildlife species can bring to urbanized landscapes (Soulbury and White 2015; Campbell 2019). In this respect, live monitoring of tracking data from gulls can help identify sources of food associated to illicit or undesirable human activities in urban, rural and marine areas (Navarro et al. 2016).

CRediT authorship contribution statement

Alejandro Sotillo: Conceptualization, Methodology, Formal analysis, Writing – original draft. Jan M. Baert: Conceptualization, Methodology, Formal analysis, Data curation, Writing – review & editing. Wendt Müller: Conceptualization, Resources, Writing – review & editing, Project administration. Eric W.M. Stienen: Conceptualization, Investigation, Writing – review & editing. Judy Shamoun-Baranes: Methodology, Resources, Writing – review & editing. Amadeu M.V.M. Soares: Funding acquisition, Supervision. Luc Lens: Conceptualization, Resources, Writing – review & editing, Supervision, Project administration.

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