Chapter

City Gulls and Their Rural Neighbours: Changes in Escape and Agonistic Behaviour along a Rural-To-Urban Gradient

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Abstract

Since industrial revolution, human population size has increased sevenfold and became increasingly urban with currently 54% of the world's population living in cities. Although urbanisation has generally a negative impact on wildlife, some species such as sea gulls (*Larus* spp.), have successfully adapted to human-dominated habitats. Gull populations breeding in coastal cities have increased since WWII, while at the same time declining in their natural breeding habitats. This is mainly attributed to gulls being generalist scavengers that benefit from increased food availability in urbanised areas (e.g., landfills, human discard), but also to increased ambient temperatures and the absence of predators. The rising

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presence of gulls in coastal cities leads to increasing numbers of human-gull conflict, mainly due to their bold or even aggressive behaviour towards humans. In our study, we explored behavioural changes in escape and agonistic behaviour of Herring (*L. argentatus*) and Lesser black-backed gulls (*L. fuscus*) along a rural-to-urban gradient in Liverpool City and the Sefton Coast. A total of 48 approach experiments were conducted to measure flight initiation distance (FID), flight distance and escape speed, which were used as dependent variables in three Generalized Linear Models (GLMs), including 'species' as the fixed factor and 'degree of urbanisation' as a covariate. A total of 230 video-recordings obtained during feeding sessions were used to establish the rate of agonistic interactions at 22 sampling locations with differing degrees of urbanisation. In total, 585 agonistic interactions of Herring gulls and 103 of Lesser black-backed gulls were recorded. Number of agonistic interactions (incl. long calls, mew calls, oblique posture, jabbing, pecking) was used as the dependent variable in a Generalized Poisson Log Linear Regression Model, using 'species' as the fixed factor, 'degree of urbanisation' and 'group size' as covariates. In both species, shorter FID, shorter flight distance, a reduced escape speed and increased numbers of agonistic interactions were significantly related to increased urbanisation, suggesting greater boldness and aggression in city gulls. Moreover, Herring gulls performed significantly higher rates of agonistic interactions than Lesser black-backed gulls. Moreover, boldness was significantly correlated to aggression when both species were lumped.

Keywords: urbanisation, *Larus argentatus*, *L. fuscus*, aggression, boldness, group size

INTRODUCTION

The human population has not only increased sevenfold since the dawn of industrialisation, but also became increasingly urban. In 2014, 54% of the world's population lived in cities, a value that is predicted to reach 66% in 2050 (UN, 2014). Europe is one of the most urbanised regions worldwide, with 73% of humans residing in urban areas (UN, 2014). In the United States, urbanisation–along with agriculture and the introduction of invasive species–is one of the major causes for the increasing loss of biodiversity in recent decades (Czech and Krausman, 1997; IPBES, 2019). For example, Adams (2005) reported a consistent decline in species richness and population size of the native avifauna with increasing urbanisation. Two main aspects, i.e., increasing human population density and land use intensification characterize this process (Marzluff, 2001). Both factors lead to human disturbance, habitat replacement and fragmentation, and a prevalence of anthropogenic food sources (Sol et al., 2013). Human disturbance is considered hereby the most crucial factor affecting wildlife (Lethlean et al., 2017). Human disturbance is defined as the response of an animal to the presence of a negative stimulus, such as a human or another potential predator (Weston et al., 2012). Increased disturbance negatively affects the utilisation of resources and therefore compromises reproduction and population growth. Reduced foraging times, due to increased vigilance, will lead to more intra-specific competition and thus to more aggression (Atwell et al., 2012). Certain bird species adapt very well to human activities, resulting in reduced flight responses but also in higher rates of aggression, not only towards conspecifics but also towards humans (Burger, 1981; Burger and Gochfeld, 1991).

Although urbanisation has generally a negative impact on wildlife, some species, such as gulls (*Larus* spp.) have successfully adapted to human-dominated habitats by synchronising their foraging and reproductive behaviour to urban conditions and human activities (Belant, 1997; Washburn et al., 2013). Gulls are scavengers that can use a wide variety of habitats, food sources and foraging strategies (Burger, 1981). Their generalist diet and the ability to apply any seabird foraging strategy (except underwater pursuit) allows them to exploit a wider range of food types than other aquatic birds such as terns or waders (Pierotti and Annett, 1995). Coastal towns provide diverse food types of terrestrial, aquatic and anthropogenic origin, seducing gulls to scavenge on a wealth of human waste products (Washburn et al., 2013) and stealing food from pets, farm and zoo animals (Solman et al., 1983).

In Europe, mainly two species of gulls (i.e., Lesser black-backed gull, *Larus fuscus* and Herring gull, *Larus argentatus*) increased their population density in urban areas, while at the same time declining in their natural breeding and foraging habitats (Belant, 1997; Lloyd et al., 2010). Counts of urban gulls in European cities showed a significant increase in numbers throughout the second half of the 20th century (Shamoun-Baranes and Camphuysen, 2013). In Britain alone, 1,310 nesting pairs were counted on town buildings in the 1960s (Cramp, 1971), while in 2004 the total urban population of Herring and Lesser black-backed gulls had increased to 100,000 nesting pairs (Rock, 2005). Despite this considerable population increase in cities, the overall population size of both species in Britain is declining. Both species are thus protected since 1981 by the 'Wildlife and Countryside Act', prohibiting to kill, injure or capture living birds, or to damage or destroy their nests (Eaton et al., 2015). However, the proliferation of gulls into cities led to increasing numbers of human-gull conflict (Huig et al., 2016). Gulls cause noise (especially during breeding season), litter the environment (faecal droppings and by scavenging), and damage property (physical damage and fouling on roof constructions; Rock, 2005). Moreover, they pose serious hazards to aircrafts (Blokpoel, 1976), transmit diseases (Mudge and Ferns, 1982; Butterfield et al., 1983), contaminate water reservoirs (Butterfield et al., 1983; Clark et al., 2015), and show aggressive behaviour towards humans, especially during the chick-rearing period (Møller, 2009). Consequently, the activities and behaviour of urban gulls became an increasing nuisance to city dwellers, also because of the financial implications their activities pose to property owners and city councils.

Increased food availability is considered to be the main reason for gulls to breed more and more in cities (Washburn et al., 2013). Urban environments provide anthropogenic food sources that are otherwise inaccessible to sea birds including landfill sites, refuse bins and human food casually discarded (Washburn et al., 2013). The colonisation of cities started in Britain after World War II (Rock, 2012), provisioned by increased food availability in newly established disposal areas for municipal waste and, more important, because of the 1956 'Clean Air Act' that banned burning of domestic garbage on site (Parslow, 1967). After the 'Clean Air Act' took effect, landfills became the main food source for gulls when foraging away from their natural feeding habitats (tidal flats, offshore fishing areas, beaches, etc. Clark et al., 2015). Moreover, due to uncontrolled garbage disposal and deliberate feeding of wild and feral birds in our modern cities, scavenging on human food remains became another reliable food resource for urban gulls (Rock, 2005). Rock (2005, 2012) suggested, that the primary reason for the increase in urban gull populations is not only augmented food availability but also improved safety. Urban structures, especially flat roofs of multi-storey office buildings provide ideal nesting conditions, preventing any mammalian predator from raiding a nest. Moreover, Pierotti and Annett (2001) reported that Western gulls (*Larus occidentalis*) prefer to build their nests at locations that provide shelter from strong winds and icy temperatures. Average city temperatures are generally 4 to 6°C higher than in surrounding rural areas, allowing gulls to start breeding earlier in the year and thus having the opportunity to raise two or even three broods per year (Møller and Ibáñez-Álamo, 2012).

With our current study, we attempted to explore behavioural changes in urban gulls; focusing on the effects that urbanisation has on their escape and agonistic behaviour. Along a rural-to-urban gradient, we compared boldness and aggressiveness of two gull species (i.e., Herring gull and Lesser black-backed gull). It was expected that gulls, foraging in the city, show bolder escape behaviour than individuals foraging in rural, natural feeding habitats (Fernández-Juricic et al., 2002; Møller, 2008; Díaz et al., 2013). We thus predicted that the flight initiation distance (FID), the flight distance and the escape speed decrease with increasing urbanisation. Assuming that increased rates of aggression are beneficial when competing for limiting resources (Milinski and Parker 1991; Keddy, 2001), urban gulls were expected to be more aggressive towards other gulls and thus show higher rates of agonistic interactions than their rural counterparts. This would require that food resources are more limited in urban than in rural areas, which is evidently not the case since urban gulls generally encounter higher food availability than their rural counterparts. On the other hand, gull densities were two- (Lesser black-backed gull) to six-fold (Herring gull) higher in the city (Griffin, 2019), resulting therefore in increased competition. We thus predicted the frequency of agonistic interactions between and within gull species to increase with increasing urbanisation. Since Herring gulls are resident in the study area, occupying breeding territories around the year (Wronski, unpubl. data), we predicted them to be more aggressive (higher rates of agonistic interactions) than migrating

Lesser black-backed gulls (Rock, 2002; Olsen and Larsson, 2005), arriving in the study area when Herring gulls have already occupied well-established territories and foraging perches. Based on studies of other social bird species (poultry; Hughes et al., 1997; Bilcík and Keeling, 2000; Estevez et al., 2002), we expected rates of agonistic interaction to be higher in larger groups than in small groups. Finally, we tested the relationship between boldness (FID) and aggression (agonistic interactions), whereby short FIDs should correspond to high frequencies of agonistic interactions and vice versa (Adams et al., 1998; Ariyomo and Watt, 2012).

MATERIAL AND METHODS

Study Area and Species

In total, 22 sampling locations were established along the Sefton Coast of north-west England (Merseyside). Twelve locations were located within the administrative boundaries of Liverpool, one in Crosby and nine in Southport (Table 1, Figure 1). To avoid resampling of the same individuals, sampling locations were set 0.5 to 20 km apart. Sampling locations were chosen to reflect the diversity of urban (docks, urban parks, pedestrian zones) and rural habitats (fields, beaches and saltmarshes) present at Merseyside. Two species of gulls were included in our study, the Lesser black-backed gull (*Larus fuscus*), a migrant wintering in southern Spain, Portugal and northern Africa and the Herring gull (*Larus argentatus*), a resident species, staying all year in the study area (Rock, 2002; Olsen and Larsson, 2005). Identification of species was facilitated by figures and descriptions in Olsen and Larsson (2005).

Table 1. Coordinates and degree of urbanisation of 22 sampling locations, set in three study areas (Liverpool, Crosby, Southport) along the Sefton Coast in Great Britain (see Figure 1)

Location	Coordinates	Urbanisation degree (%)

	N	W	urban + suburban/2	adjusted for water
Liverpool - Albert Docks*	53.398444	- 2.993028	50.93*	99.99
Liverpool - Botanic Gardens	53.406385	- 2.941806	64.87	
Liverpool - Canning Dock*	53.401779	- 2.995227	51.50*	99.99
Liverpool - London Road	53.409245	- 2.974608	89.39	
Liverpool - Metquater	53.406331	- 2.985220	99.14	
Liverpool – Liverpool Museum*	53.403129	- 2.996256	50.43*	99.99
Liverpool - Pier Head Village*	53.404615	- 2.996778	54.15*	99.99
Liverpool - Rosebery Street	53.394365	- 2.962112	72.46	
Liverpool - Saint John's Gardens	53.408806	- 2.981031	93.77	
Liverpool - Sefton Park	53.378017	- 2.937829	35.58	
Liverpool - Water Fountain	53.402615	- 2.989047	94.42	
Liverpool - Wheel*	53.398787	- 2.989827	75.61*	98.24
Crosby - Boating Lake	53.473984	- 3.034279	28.43	
Southport - Beach South	53.650418	- 3.021175	26.89	
Southport - Beach North	53.655122	- 3.015524	19.13	
Southport - Car Park	53.653386	- 3.005279	60.36	
Southport - King's Gardens	53.647449	- 3.011752	66.71	
Southport - Lakeside Inn	53.654391	- 3.004354	52.29	
Southport - Marine Drive	53.651023	- 3.018577	30.90	
Southport - Marine Lake	53.650366	- 3.009501	63.53	
Southport - Ocean Plaza	53.652699	- 3.014894	27.07	
Southport - Pier	53.653061	- 3.016813	23.73	

* indicates locations at which the degree of urbanisation was adjusted for areas covered by water (see text for explanation).

Escape Behaviour (Boldness)

Data were collected during the breeding season of both gull species, i.e., from 2nd June to 29th July 2018, predominantly in the afternoon between 12:00 and 18:00 GMT. Observations were carried out under similar weather conditions (sunny or partly cloudy, no rain, wind less than 10 m/s). During summer 2018, several ‘heat waves’ stroke England and sampling was suspended on days exceeding 23°C ambient temperature. To obtain data related to escape behaviour, a total of 48 approach experiments (27 for Herring gulls and 21 for Lesser black-backed gulls) were conducted by a single observer at 12 sampling locations established in Liverpool and along the Sefton Coast. The experimental design was derived from procedures described in Holmern et al. (2016), and only solitary birds perching on the ground with no signs of vigilance or aggression were included in experimental approaches. Before experiments started, the starting distance (Figure 2), i.e., the distance between observer and the focal gull was established using a hand-held rangefinder (Bushnell Pro XE). Subsequently, the observer walked at slow, steady pace (1-2 m/s) directly towards the focal individual. Once the focal animal initiated its flight (or walked away), time recording was started using a stopwatch. Subsequently, the distance between the observer and the point of departure was measured (flight initiation distance; FID; Figure 2). After the gull landed (or stopped walking), the escape time was recorded and the flight distance measured (Figure 2). The escape speed was then calculated as the flight distance divided by the flight time.

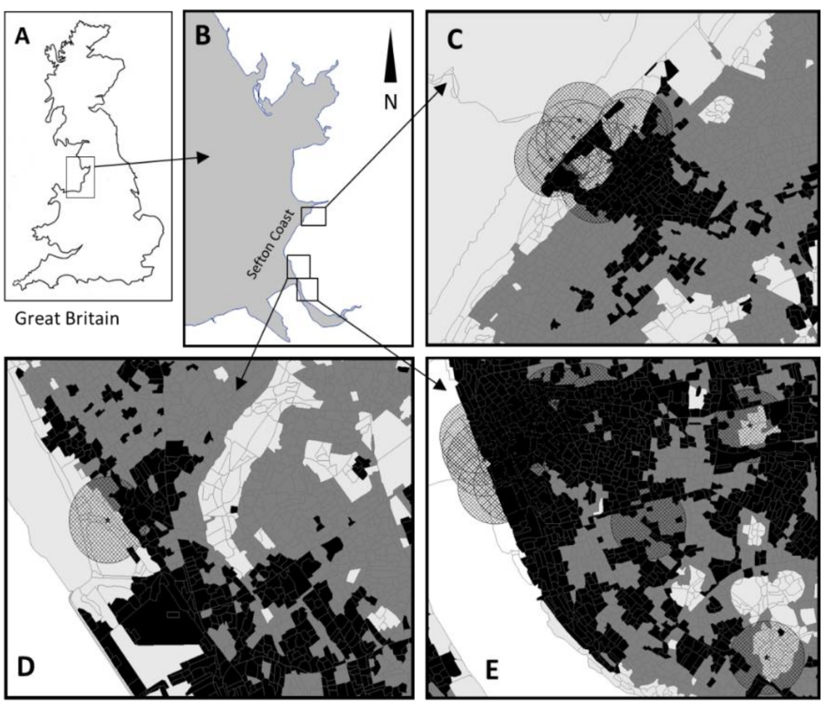

Figure 1. A) Location of Sefton Coast in Great Britain, B) position of three study areas along the Sefton Coast. Land Cover Map 2015 (Rowland et al., 2017) of C) Southport, D) Crosby and E) Liverpool. Black: urban land cover class, dark grey: sub-urban land

cover class, light grey: all other land cover classes, white: River Mersey. Stars indicate sampling sites, hatched circles defined by a radius of 500 m (0.78 km^2) depict area for which urbanisation degree was calculated (for sampling sites along Liverpool waterfront, portions covered by the river (water) were excluded from our calculations; see text for explanation).

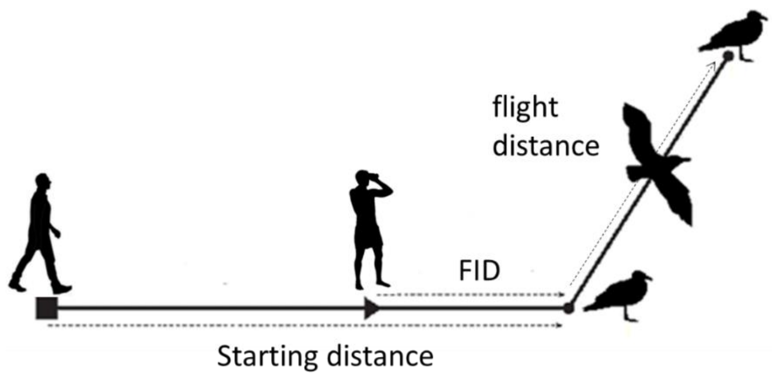

Figure 2. Schematised view of gull approach experiments carried out at 12 sampling locations along a rural-to-urban gradient. Starting distance and flight initiation distance (FID) are shown by coarse dotted lines, whereas the flight distance is indicated by the fine dotted line. Black square: starting point of the approach, black triangle: direction of approach and point where the approacher stops when the focal individual initiates the flight, black circles: locations of focal animal before and after flight.

Agonistic Behaviour (Aggression)

To obtain data on five agonistic behaviours, a total of 65 video sequences were recorded (Apple© iPhone 8 Plus) and analysed in the laboratory using a personal computer. Agonistic behaviours as defined by Tinbergen (1960; Figure 3) included: A) long calls in forward posture, B) mew calls (a long-drawn, often plaintive call, performed with the bill widely open), C) oblique posture with long call (a hoarse call, followed by one or two muffled, high-pitched calls and a series of loud calls), D) jabbing (fast thrusts, usually with open bill in the direction of the opponent, and E) pecking (fast thrusts, eventually pecking the opponent). Video recordings were carried out during randomly encountered feeding sessions, triggered by carelessly discarded food items or by passer-by's feeding gulls at one of the 19 sampling locations established in Liverpool and along the Sefton Coast. Videos sequences of different length (2 to 21 minutes) were divided into 30-second intervals and the number of each behaviour type (inter- and intra-specific agonistic interactions), as well as the group size were determined for each interval. In total, 230 intervals (140 for Herring gulls and 90 for Lesser black-backed gulls) were analysed.

Degree of Urbanisation

The Great Britain Land Cover Map (Rowland et al., 2017) was used to quantitatively estimate the degree of urbanisation within a circular area defined by a radius of 500 m (0.78 km^2) around each sampling location (see below), using ArcGIS version 10.2.2 (ESRI, 2014). Two land cover classes were defined to determine the degree of urbanisation: A) the urban land cover class including densely urbanised areas, such as city centres, with little or no vegetation, but also dock sides, car parks and industrial estates, and B) the suburban land cover class including residential areas where the spectral signature is a mix of buildings and vegetation (Rowland et al., 2017). The degree of urbanisation at each sampling location was calculated as the percentage proportion of the urban land cover class, plus the proportion of the suburban land cover class, divided by two (Table 1). For five locations along the Liverpool waterfront, percentage urbanisation was calculated by excluding those parts of the circular area that were covered by water (Table 1, Figure 1). The degree of urbanisation in highly urbanised areas was 100%, while in the least urbanised area only 19% (Table 1).

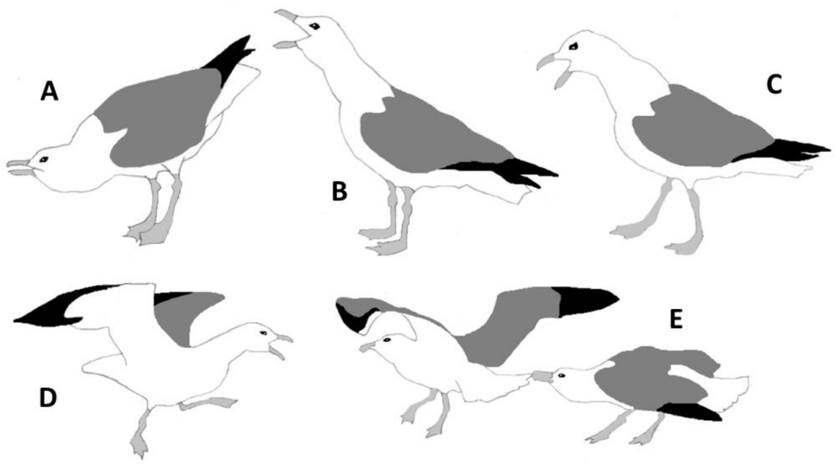

Figure 3. Types of agonistic behaviours recorded at 19 sampling locations along the Sefton Coast in Great Britain: A) long calls in forward posture, B) mew calls, C) oblique posture with long call, D) jabbing, and E) pecking (after Tinbergen, 1960).

Statistical Analysis

Prior to statistical analyses, three variables denoting escape behaviour (i.e., FID, flight distance and escape speed) were square root-transformed to achieve normal distribution. In our first analysis, we subjected three dependent variables denoting escape behaviour to three General Linear Models (GLMs), including 'species' as the fixed factor and 'degree of urbanisation' as the covariate. The interaction term 'Species × degree of urbanisation' was included in the initial model but removed from the final model using a stepwise backwards elimination procedure if $p > 0.05$. Since FID might be affected by the starting distance (i.e., initial distance at which the focal gull was first seen; Blumenstein, 2006), we included 'starting distance' as a second covariate in the FID model. In a second analysis, we subjected the number of agonistic interactions per interval at each sampling location (dependent variable) to a Generalized Poisson Log Linear Regression Model, including 'species' as the fixed factor, 'group size' and 'degree of urbanisation' as covariates. Initially, all two-way interaction terms were included into our model but removed if $p > 0.05$. All models were conducted using the *glm* function in the R-package '*stats*'. Finally, we examined the relationship between boldness (average FID for each species) and aggression (mean number agonistic interaction per interval and species divided by group size) at each location, using Spearman's rank correlation. Data for both, FID and agonistic interactions, were obtained from only seven locations (Liverpool-Pier Head Village, Crosby-Boating Lake, Liverpool-Water Fountain, Southport-Lakeside Inn, Southport-Marine Drive, Southport-Ocean Plaza). All statistical analyses were performed in R 3.5.1 software (R Core Team, 2018).

RESULTS

Escape Behaviour (Boldness)

Mean (±SE) FID of Herring gulls was 5.63 ± 0.63 m, while that of Lesser black-backed gulls was 7.29 ± 0.96 m. Mean (±SE) flight distance of Herring gulls was 4.63 ± 0.59 m, that of Lesser black-backed gulls was 3.29 ± 0.53 m. Mean (±SE) escape speed was 1.01 ± 0.12 m/s for Herring gulls and 0.84 ± 0.13 m/s for Lesser black-backed gulls. The degree of urbanisation had significant negative effects on all three escape behaviours (Table 2, Figure 4a, b, c), indicating a decrease of FID, flight distance and escape speed—or an increase of boldness—with increasing degree of urbanisation. Starting distance had a positive significant effect on FID. Compared to Herring gulls, Lesser black-backed gulls had a significantly shorter flight distance.

Agonistic Behaviour (Aggression)

A total of 585 agonistic interactions (129 forward posture, 49 mew call, 80 oblique posture, 226 jabbing and 101 pecking) was observed in Herring gulls, while a total of 103 agonistic interactions was recorded for Lesser black-backed gulls (23 forward posture, 14 mew call, 26 oblique posture, 35 jabbing and 5 pecking). The degree of urbanisation showed a significant positive effect on the agonistic behaviour of gulls, indicating higher rates of agonistic interaction (aggression) in urban areas (Table 3, Figure 4d). Hereby, Herring gulls showed higher rates of agonistic interaction than Lesser black-backed gulls (Table 3, Figure 4d). Moreover, group size had a significant positive effect on agonistic interactions (Table 3).

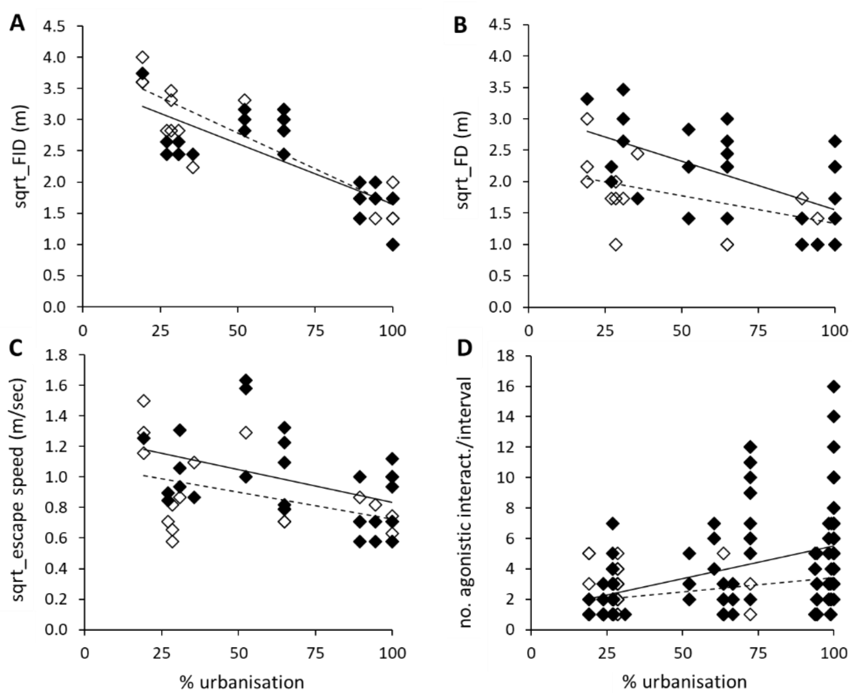

Figure 4. A) Flight initiation distance (FID), B) flight distance and C) escape speed (all sqrt-transformed) in relation to the degree of urbanisation (percentage proportion); D) Total number of agonistic interactions per individual in relation to the degree of urbanisation (percentage proportion). Black squares: Herring gull, blank squares: Lesser black-backed gull. For visualisation linear regressions were depicted: solid line: Herring gull, dashed line: Lesser black-backed gull.

Table 2. Three General Linear Models using escape behaviour (FID, flight distance and escape speed) as dependent variables, 'species' as a

fixed factor and 'degree of urbanisation' as a covariate. 'Starting distance' was included as an additional covariate in the FID model

Model	Explanatory variables	Estimates	SE	*t*	*p*
FID	Degree of urbanisation	- 0.013	0.002	- 6.750	< **0.001**
	Starting Distance	0.075	0.011	6.536	< **0.001**
	Species (Lbb gull *vs* Herring gull)	0.100	0.097	1.024	0.311
Flight distance	Degree of urbanisation	- 0.012	0.003	- 4.401	< **0.001**
	Species (Lbb gull *vs* Herring gull)	- 0.453	0.169	- 2.684	**0.010**
Escape speed	Degree of urbanisation	- 0.004	0.001	- 3.302	**0.002**
	Species (Lbb gull *vs* Herring gull)	- 0.139	0.073	- 1.909	0.063

Significant results ($p < 0.05$) are shown in bold; SE: standard error, t: t-test statistic, Lbb gull: Lesser black-backed gull.

Table 3. Results of a Generalized Poisson Log Linear Regression Model using agonistic interactions as the dependent variable, 'species' as the fixed factor and 'group size' and 'degree of urbanisation' as covariates

Model	Explanatory variables	Estimates	SE	*z*	*p*
Agonistic interactions	Degree of urbanisation	0.014	0.002	7.011	< **0.001**
	Species (Lbb gull *vs* Herring gull)	- 0.296	0.099	- 2.979	**0.003**
	Group size	0.014	0.006	2.364	**0.018**

Significant results ($p < 0.05$) are shown in bold; SE: standard error, z: z-score, Lbb gull: Lesser black-backed gull.

Correlation of Boldness and Aggression

Spearman's rank correlation revealed a significant positive relationship between boldness (FID) and aggression (number of agonistic interactions per individual; $r = -0.710$, $p < 0.001$, Figure 5), suggesting that shy individuals (long FID) were less aggressive than bold individuals (short FID).

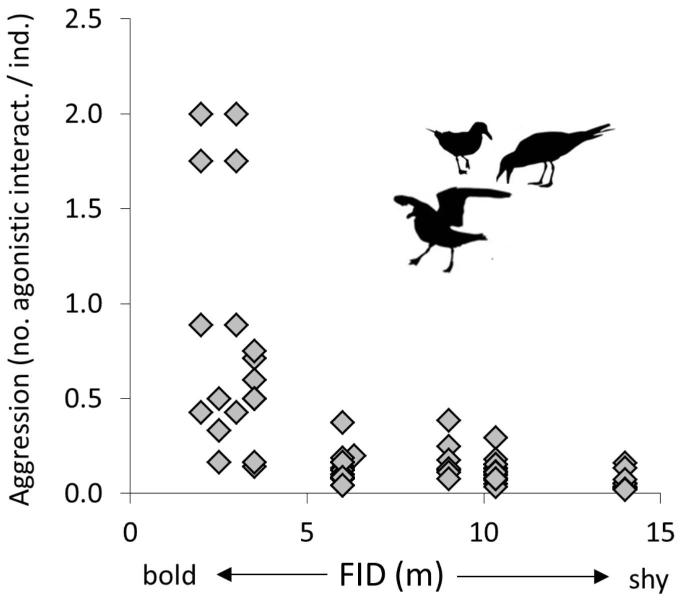

Figure 5. Spearman rank correlation between boldness (FID) and aggression (number of agonistic interactions per individual).

DISCUSSION

Gull densities (mainly Herring and Lesser black-backed gulls) in European coastal cities were constantly increasing since the 1960s, and their incursion into towns is commonly viewed as a nuisance (Packham and Connolly, 1992; Belant, 1997). Property owners and city dwellers tend to have negative perceptions of these birds, mainly because of the damage they cause (Carr and Reyes-Galindo, 2017), their scavenging habits and the noise they produce (Blokpoel and Tessier, 1986). For decades, various techniques to reduce the number of human-gull conflicts in towns were developed and applied (Warburton and Norton, 2009), but pest controlling measures (Belant and Ickes., 1996, 1997; Rock, 2012) showed little to no success (Rock, 2005). A study on the demonisation of urban gulls (i.e., their ‘antisocial behaviour’), reviewed articles published by the British press in 2015, disclosing the helplessness of all stakeholders and incidentally screaming for a more scientific approach (Carr and Reyes-Galindo, 2017). Despite the huge number of such anecdotal reports, the considerable effort of pest-controllers and a substantial public attention, there is a lack of proof on whether city-dwelling gulls perform ‘antisocial behaviour’, or in other words, whether they are bolder and more aggressive than their rural neighbours (Huig et al., 2016).

Escape Behaviour (Boldness)

Our study indeed confirmed a significant increase of boldness (i.e., shorter FIDs, flight distance and escape speed) with increasing degree of urbanisation (Table 2, Figure 4a-c). This finding was not unexpected and strongly corresponded to short FIDs reported from urban rabbit (*Oryctolagus cuniculus*; Ziege et al., 2013) and fox squirrel (*Scirius niger*) populations (McCleery, 2009), but also from numerous non-migrating birds across Europe (Fernández-Juricic et al., 2002; Møller, 2008; Díaz et al., 2013). FID is widely used as a measure of boldness (Evans et al., 2010), representing an unambiguous and easily quantifiable measure of behavioural adoptions (Beale, 2007). The distance at which an individual starts to escape from an approaching predator reflects the risk this individual is willing to take (Blumstein, 2006). To reduce the cost of escape, an individual can delay the flight until the costs of predator vigilance exceed the costs of escape (Blumstein, 2003). Furthermore, Nordell’s et al. (2017) study suggested a high individual flexibility, altering the escape response from case to case, based on the type of disturbance, the individuals’ experience and various environmental factors such as landscape, vegetation or climate. The most prominent environmental factor gulls encounter in our modern cities, are humans and their activities. Individual experiences of gulls strongly affect their escape behaviour as a result of a constant learning process and a prolonged habituation to human activities (Petrinovich and Patterson, 1982; Blumstein, 2003). Weston et al. (2012) therefore argued that short FIDs are equivalent to a low sensitivity to human disturbance and changing FIDs are the consequence of the urbanisation process in general (Møller, 2008). For example, due to constant feeding of birds in parks and city centres, it becomes beneficial for birds to behave bolder and tolerate shorter distances to a potential predator (Cooke, 1980). With increasing experience the former predator will change into another environmental factor that represents a source of food, rather than posing a threat to the bird.

Agonistic Behaviour (Aggression)

Moreover, our study also confirmed a significant increase of agonistic interactions with increasing degree of urbanisation (Table 3, Figure 4d) and is therefore in line with our prediction that urban gulls are more aggressive than their rural neighbours. Increased rates of aggression in urban environments were reported by a number of studies on different species (for review see Ryan and Partan, 2014). In accordance with those studies, we predicted that higher population densities at urban sampling locations (Griffin, 2019) lead to higher competition, which in turn causes a higher degree of intra-generic aggression, i.e., increased rates of agonistic interactions towards other gulls. Along the rural-to-urban gradient, Herring gulls showed significantly higher rates of agonistic interaction than Lesser black-backed gulls (Table 3). This was more pronounced in urban areas than in rural areas (Table 3, Figure 4d) and might be attributed to the different sample sizes obtained for each species (140 Herring gulls *vs* 90 Lesser black-backed gulls). Skewed sample sizes were due to higher Herring gull population densities at our urban sampling sites than at rural sites (Griffin, 2019). However, it is more likely that Herring gulls—a resident species spending all year in the study area—are more familiar and intimate with the local environment than Lesser black-backed gulls, a migrant species spending the winter in south-western Europe and northern Africa (Olsen and Larsson, 2005). Herring gulls establish breeding territories, which they also occupy during winter months when Lesser black-backed gulls are mostly absent (Wronski unpubl. data). Once the latter return, they compete with resident Herring gulls for breeding sites and for access to food, prompting Herring gulls to defend their well-established territories against the 'intruders'. Interestingly, our findings are in stark contrast to observations reported by Garthe et al. (1999) who found Lesser black-backed gulls to win significantly more interspecific, agonistic interactions than Herring gulls—at least during the chick-rearing period. Garthe et al. (1999) argued that Lesser black-backed gulls consumed food of apparently higher quality, i.e., natural food of marine origin, while Herring gulls foraged on by-catch, fish offal and human discard. They further concluded that Lesser black-backed gulls have occupied an empty niche in the natural habitat of the German wadden sea, rather than having outcompeted Herring gulls. We do not yet exactly know what Lesser black-backed gulls breeding in Liverpool consume, but since they are less often seen foraging in town or on tidal flats, it appears they go off-shore to exploit marine food resources rather than competing with Herring gulls for anthropogenic food in the city (Griffin, 2019).

Our study also revealed the number of agonistic interactions to increase with increasing group size (Table 3). Studies on laying hens found increased aggression with increasing group size if total group size did not exceed 120 (Bilcík and Keeling, 2000) or 260 (Nicol et al., 1999) individuals. In larger groups (300 to 700 individuals), however, reduced levels of aggression became prevalent (Hughes et al., 1997). Group sizes in our study did not exceed 47 individuals and are therefore in line with Bilcík and Keeling's (2000) results. However, there is reason for caution: as the number of individuals in a group increases, the costs of being aggressive whilst competing for food should also increase, simply because there are more potential competitors to be attacked (Syarifuddin and Kramer, 1996). Likewise, the benefits of being aggressive should decline, since it is more likely that, when attacking a competitor, food items will be lost to competing individuals, other than the one being attacked (Hixon, 1980; Grant, 1993; Syarifuddin and Kramer, 1996). This led to the assumption that the number of agonistic interactions should actually decrease with increasing group size (Marzluff and Heinrich 1991). This assumption contradicts our findings, which might be attributed to the fact that in more than 50% of recorded feeding sessions, group size was smaller than 15 individuals and thus beneficial to displace competing gulls from the feeding site.

In a final step, we related boldness (FID) to aggressiveness (number of agonistic interactions per individual) and found a strong positive correlation between escape and agonistic behaviour, indicating that shy individuals (long FID) were less aggressive than bold individuals (short FID, Figure 5). This result was not unexpected since boldness and aggressiveness are often closely linked (Adams et al., 1998; Ariyomo and Watt, 2012). Since data of both species were lumped in our analysis (i.e., to increase sample size), a separation between Herring and Lesser black-backed gulls was not possible. However, given that both species largely corresponded in our previous analysis, we assume that this result applies to both species.

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BIOGRAPHICAL SKETCH

Name: Torsten Wronski

Affiliation: Liverpool John Morres University, Liverpool, UK

Education: Corresponding author Torsten Wronski began his academic education in Hamburg, Germany, where he obtained his Bachelor of Science degree in 1997, followed by a Master of Science in 1999. His MSc study was carried out in cooperation with the German Technical Cooperation (GTZ) and the Integrated Pastoralist Development Program (IPDP) in Lake Mburo NP, Uganda, to develop a scheme for the sustainable utilization of impala antelopes in the adjacent Ankole Ranching Scheme. Here, Wronski focused on fire-induced changes in the foraging behavior of impala (*Aepyceros melampus*), comparing the relatively undisturbed National Park and the heavily used ranchlands surrounding the park.

In 2004, he obtained a PhD in Behavioral Ecology from the University of Hamburg. The study was carried out in Queen Elisabeth National Park, in Uganda, and was supported by the German Academic Exchange Service (DAAD). The study aimed at explaining why the bushbuck, the most common ungulate species in Africa, does not suffer from human impact while other antelope species are driven to the brink of extinction. The bushbuck is a generalist species, surviving in a number of human-modified habitats and is believed to be so successful because of its crepuscular and secretive lifestyle. Hence, Wronski studied the social and spatial organization of this overlooked antelope species.

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Research and Professional Experience: Following his time as a PhD student, he became a postdoctoral fellow at the Zoological Museum in Hamburg. He implemented a long-term research project on the phylo-geography and ecology of terrestrial gastropods in the tropical montane rain forests along the Albertine Rift Valley in East Africa (Uganda, Rwanda and DRC). The project is still ongoing and was funded by a research grant from the German Research Foundation (DFG) and several smaller grants from the Zoological Museum in Hamburg.

Professional Appointments: After his time as a postdoctoral fellow, Wronski moved to Saudi Arabia, where he headed the Field Conservation Department at King Khalid Wildlife Research Centre (KKWRC). Working with the Zoological Society of London (ZSL), he was involved in the management of several protected areas in Saudi Arabia and advised the Saudi Wildlife Authority (SWA) on wildlife reintroduction and conservation management. His work included scientific breeding of endangered ungulates, project planning and reporting, budgeting, and capacity building of Saudi rangers and protected area managers.

In early 2013, Wronski started teaching Ecology and Wildlife Management at the University of Rwanda. As a Senior Lecturer in the Department of Wildlife and Aquatic Resources Management, he educated future Rwandan wildlife managers and decision makers.

Later he was invited to join Northwest A&F University in Yangling, Shaanxi, P. R. China to teach Zoology and Wildlife Management. During this time, he engaged in the study of stress reduction in captive musk deer, an ungulate species that is kept in China for the production of musk, an extremely precious substance used as a carrier of odor and is thus important for the cosmetic industry, but also for traditional Chinese medicine.

Currently, he is working at Liverpool John Moores University as a Senior Lecturer in Wildlife Ecology. Wildlife in urban settings is particularly interesting with regard to adaptions of wildlife to an anthropogenically modified and disturbed environment. This phenomenon is particularly eminent in coastal towns like Liverpool where sea gulls become an increasing nuisance to property owners and city dwellers.

Honors: none

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