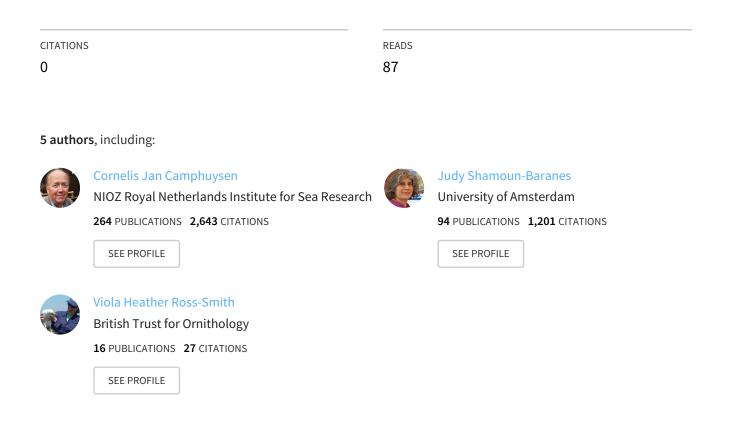
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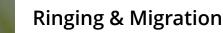


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ISSN: 0307-8698 (Print) 2159-8355 (Online) Journal homepage: http://www.tandfonline.com/loi/tram20

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To cite this article: Peter Rock, C.J. Camphuysen, Judy Shamoun-Baranes, Viola H. Ross-Smith & Ian P. Vaughan (2016) Results from the first GPS tracking of roof-nesting Herring Gulls Larus argentatus in the UK, Ringing & Migration, 31:1, 47-62, DOI: 10.1080/03078698.2016.1197698

To link to this article: http://dx.doi.org/10.1080/03078698.2016.1197698

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Results from the first GPS tracking of roof-nesting Herring Gulls *Larus argentatus* in the UK

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ABSTRACT

Recent developments in GPS tracking technology allow the movements of bird species to be followed in ever-greater detail. Seabird research is benefiting greatly, due to the challenges of tracking species that often roam widely out at sea. Amongst the gulls, one of the pressing issues is to understand the ecology of the relatively recent urban colonists and how they differ from their counterparts in traditional rural colonies. Here, we present what we believe are the first GPS results from roof-nesting gulls. Four adult Herring Gulls (two males, two females) were fitted with GPS tags in May 2014 in the seaside town of St Ives, Cornwall (breeding colony c 250 pairs), and tracked for c 100 days during the 2014 breeding season. We estimated the home ranges of the four individuals and how their movement behaviour varied through the 24-h period and across the breeding season. The results highlight how variable movement behaviour was among individuals: whilst one bird roamed widely (90% range estimate = 560 km²), heading >50 km offshore and often active at night or roosting at sea, two birds had small ranges (<10 km²), always attended the colony at night and rarely headed more than a few hundred metres offshore, with the fourth displaying intermediate behaviour. All of the birds regularly utilised a few key sites within the agricultural landscape south of St Ives. Whilst this study was too small to allow general conclusions to be drawn about urban Herring Gulls, it reinforces how variable individual behaviour can be amongst the large gulls and will be particularly interesting when applied to a larger sample of birds, especially in big urban gull colonies further inland.

The growth of urban, roof-nesting gull populations has been strong in many parts of the world in the last four decades, but has been particularly marked in the UK (Rock 2005). Between Operation Seafarer in 1969-70 (Cramp 1971) and Seabird 2000 (1998-2002; Mitchell et al 2004), the urban gull population increased by more than an order of magnitude and, since Seabird 2000, the number of colonised cities and towns in Britain & Ireland has more than doubled (PR, unpublished data). The upshot has been widespread public interest due, mainly, to perceived nuisance (eg noise, mess, damage and aggression towards people; Rock 2005), primarily from Herring Gulls Larus argentatus and Lesser Black-backed Gulls L. fuscus, resulting in a wide variety of control measures, including egg replacement, nest destruction and the netting of roofs. By contrast, the rural gull population has declined (JNCC 2015), leading to the Herring Gull being added to the UK Birds of Conservation Concern Red List in 2009, where it remained in the most recent revision (Eaton et al 2015). These changes in Herring

Gull population status led to its removal from general licences which, under the Wildlife & Countryside Act 1981, allowed birds to be legally killed. The 2010 amendment of the Act rendered lethal control of Herring Gulls illegal, although in urban areas provision is made for nest and egg destruction. Similar population trajectories and management difficulties for the large gulls are found also in other countries, eg the Netherlands (Camphuysen 2013) and France (Cadiou & Guyot 2012). These population changes and dissimilar fortunes suggest that there are important differences in the ecology and demography of rural and urban gulls, yet, partly because the population and range expansion of urban gulls is relatively recent and partly because of the logistical difficulties of working in urban areas (eg inaccessible nest sites and complex roofscapes), these birds remain relatively poorly studied compared to their rural counterparts (Rock 2005).

Ringing data, in particular colour-ringing studies since 1980, have provided insights into the movements

ARTICLE HISTORY Received 3 April 2016 Accepted 26 April 2016

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of the large gulls (eg Rock 1999, 2002, Hallgrimsson et al 2012, Ross-Smith et al 2015) and are beginning to illuminate the ecology of urban gulls (eg Rock 2005, Rock & Vaughan 2013). However, such studies are limited by the distribution of observers. This is a particular challenge for species with extensive home ranges which may include large water bodies and areas far offshore. The development of small and lightweight GPS tags from the late 1990s onwards opened up opportunities for a much closer understanding of the large gulls (eg Kube et al 2000). Although still limited by the cost of individual units, GPS tags can provide highfrequency, precise location data throughout the 24-h cycle over long periods, irrespective of distances covered (eg Kays et al 2015) or of movements at sea (eg Bouten et al 2013). Studies published so far have provided new insights into the migratory, breeding and foraging behaviours of large gulls (eg Klaassen et al 2011, Camphuysen et al 2015, Becares et al 2015, Thaxter et al 2015), including previously unknown behaviour, such as hours spent 'riding the tide' on the sea surface (Shamoun-Baranes et al 2011). All GPS studies on Herring and Lesser Black-backed Gulls published so far have concentrated on birds breeding in rural colonies, but there is obvious potential to apply the methods to roof-nesting, urban gulls. This could reveal not only key aspects of their behaviour and ecology, such as the relative importance of foraging locations in and out of town, but also the extent to which their behaviour differs from that of rural gulls.

Here we present the results from the first four urban Herring Gulls to be fitted with GPS trackers in the UK. The birds were nesting on rooftops in St Ives, Cornwall, and this study followed them through the 2014 breeding season (*c* 100 days). Given a sample size of four birds, we provide a simple analysis and comparison against previous studies of rural gulls before discussing how, in further GPS studies of urban gulls, these results can be used to direct and refine future research questions.

Methods

Study site and data collection

St Ives is a seaside resort in western Cornwall (50° 13'N 5° 29'W; Figure 1) with a human population of 11 400 (Cornwall Council 2015). It is popular with tourists and renowned for its food-snatching gulls. In 2014, St Ives supported a roof-nesting gull population of 248 pairs of large gulls: 239 pairs of Herring Gulls, five of Great Black-backed Gulls *L. marinus* and four pairs of Lesser Black-backed Gulls.

On 8 May 2014, four adult Herring Gulls (two males and two females) were nest-trapped (having become fully committed to incubation, thereby minimising the risk of nest desertion) on rooftops in St Ives and fitted with UvA-BiTS GPS tags (Bouten et al 2013; www.uvabits.nl), secured using Teflon wing harnesses (Thaxter et al 2014). The birds were also colour-ringed so that they could be identified individually in the field. For simplicity, the four individuals will be referred to by the serial numbers of their tags: G4036 and G4039 (males), and G4037 and G4038 (females). G4036 was recaptured during the 2015 breeding season and the harness removed. Building work required the removal of the receiver on G4038's roof on 3 August 2014, preventing further data collection and this bird continued to carry the GPS tag at least until 7 May 2015 (colour-ring sighting). The harness for G4037 was recovered next to its nest (last GPS fix obtained on 31 July 2014), but this bird was subsequently resighted at the Hayle Estuary roost nearby. Observations from Texel, the Netherlands, suggest that Herring Gulls (cf Lesser Black-backed Gulls) are capable of biting through harnesses (CJC, unpublished data). G4039 was not seen at the colony in 2015 and no colour-ring observations of this individual were reported, so it may have lost the harness or perished (last GPS fix 13 July 2014).

With every study that uses GPS tags or other devices, there is a risk of detrimental effects on the study animals, highlighting the need for studies to check that impacts are negligible (Kays *et al* 2015). The total weight of the GPS units was 18.5 g (GPS loggers 13.5 g, harness 5 g) equating to 2.2% of body mass for the smaller female (G4038) and 1.6% for the larger male (G4036) (range 890–1125 g). Studies using the same tags with Lesser Black-backed Gulls suggest no detectable effects on survival or breeding success, although the sample sizes were modest (Thaxter *et al* 2014, 2016, Camphuysen *et al* 2015).

Each solar-powered GPS tag had 32 Mb of data storage, downloadable when birds were in direct line of sight of the base station or relays; at the same time, the units were programmable remotely, allowing adjustments to be made to GPS-fix frequency (Bouten *et al* 2013). Over the study period, fix frequency was varied between five seconds and 30 minutes (mean 22 seconds), based on a trade-off between the rate of solar battery charging, the size of the data buffer and the frequency with which the birds were likely to pass the base station for data to be downloaded (Bouten *et al* 2013). Although some fascinating data for movement over the 2014/15 winter were obtained for G4036 (Figure A1), we restrict our main analysis to the breeding season (range 88–113 days), over which all four birds could be compared.

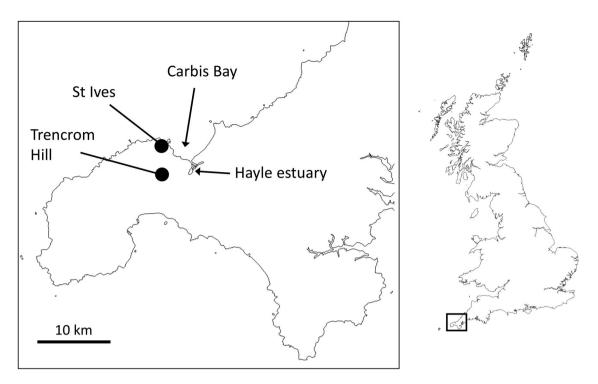


Figure 1. Location of St Ives along with locations referred to in the text. Coastline contains OS data © Crown copyright and database right (2016).

Data preparation and analysis

Previous tests have shown that the GPS tags used in this study have a mean positional error of <2 m (Bouten et al 2013). However, as with all GPS devices, the occasional error (outlier) occurs (ie where speed and distance were clearly mismatched). As an example, the large gulls are capable of achieving speeds of around 100 kph (Schmaljohann et al 2008; PR, unpublished data): on three occasions speeds were reported to be well in excess of this. Having excluded these few outliers, the data were processed in two ways for subsequent analysis. The first resampled the data to create a data set with fixes at regular ten-minute intervals for analysing the home ranges and activity patterns through the day and breeding season (see below). This captured the major movements of the birds, whilst minimising missing data. The second approach made use of the complete data set for each bird to provide maximum spatial and temporal resolution for identifying trips away from the nest and identifying detailed aspects of behaviour and habitat use.

Overall ranging patterns were analysed using a movement-based kernel density method to estimate the utilisation distribution (home range). This was based on the biased random bridges (BRB) method of estimating movement-based density (Benhamou & Cornélis 2010, Benhamou 2011), fitted in R v3.0 (R Core Development Team 2014) using the adehabitatHR

library (Calenge 2006). In contrast to traditional kernel density methods, this uses the times of GPS fixes as well as their locations, allowing the movements along tracks of sequential points to be followed and periods of inactivity to be identified (Benhamou & Cornélis 2010). For the current analysis it has the notable advantage over traditional kernel smoothing that the overall utilisation distribution can be broken down into its two constituent parts: first, how long an animal spends in a location, referred to as the intensity distribution (Benhamou & Riotte-Lambert 2012) and, second, how frequently it visits the same locations, which they named the recursion distribution. This can provide greater insight into how an animal utilises its home range, for example distinguishing areas visited rarely but for a long period from those visited regularly, but only briefly, which may produce the same overall level of utilisation.

We set the minimum smoothing parameter to be 100 m, and the maximum time threshold to be one hour, meaning that for calculating intensity and recursion a circle of radius 300 m was used, and separate visits to the same area were recorded only if the bird returned >1 h later (Benhamou & Riotte-Lambert 2012). The home range estimates were calculated from the 90th percentile of the utilisation distribution, as recommended by Börger *et al* (2006) who argue that the 95th is too sensitive to outliers. For intensity and recursion, we used the 30th percentile to highlight the areas used for the

longest periods or visited most frequently, following Benhamou & Riotte-Lambert (2012).

To look in greater detail at trips away from the nest the complete data sets were used, to maximise spatial and temporal resolution. Trip lengths were defined as the maximum Euclidean distance from the nesting colony. For ease of interpretation, we defined a buffer around the breeding colony to decide when a trip away from the nest had been initiated and some simple criteria to separate 'short', 'medium' and 'long' trips (Shamoun-Baranes et al 2011, Camphuysen et al 2015). A small, freshwater outflow behind the West Pier lies within 250 m of each nest in St Ives and was frequently used by all four birds at low tide (online supplementary Figure S4). Of 229 movements less than 300 m, only four lasted longer than 30 minutes and none lasted longer than 40 minutes. We regarded these visits as being concomitant with nest attendance, so set the threshold for a trip at 300 m. Where Camphuysen et al (2015) regarded a short (localised) foraging trip to be between 200 m and 3 km, we set our upper threshold for a 'short' trip at 6 km to encompass the Hayle estuary and much of the farmland south of St Ives (Figure A2). 'Medium' trips were 6-20 km and 'long' trips were defined as those > 20 km.

Finally, we looked at overall movement activity through the 24-h period and across the breeding season as a whole, using mean speed - including the periods when the bird was stationary - as a simple proxy for overall activity. Using the resampled data (ten-minute intervals), we calculated, first, the mean speed for each hour in the day across the breeding season and, second, the mean daily speed, based on the times and distances between consecutive fixes. To see whether birds were moving at night, we obtained sunrise and sunset times for St Ives from the US Naval Observatory (http://aa.usno.navy.mil/data/docs/RS_ OneYear.php) and filtered the time series to include only GPS fixes that were between two hours after sunset and two hours before sunrise, providing a relatively conservative definition of night.

Results

The four Herring Gulls completed almost 2300 trips during the breeding season and, between them, travelled more than 32 000 km but hidden within these figures were marked differences in individual behaviour. G4036 (male) and G4037 (female), which bred on the same roof, were the most and least active, respectively, with home ranges that varied by nearly two orders of magnitude (559.7 and 7.5 km²; Tables 1 & 2, Figure 2). G4036 and G4038 (female) were both seafarers (though G4036 rather more than G4038) often travelling further than 30 km offshore (maximum distances 86 km and 67 km respectively) whereas G4037 and G4039 (male) rarely went > 1 km offshore, usually when crossing parts of Carbis Bay to reach the Hayle Estuary (Figure 1). The home range of G4036 was primarily (92%) maritime, whereas the ranges of the other three birds were > 70% over land (Table 1). The ranges of G4037 and G4039 were small (< 10 km²) and almost entirely terrestrial (> 90%), whilst G4038 ranged primarily over land (72%) or within 3 km of the shore, in addition to occasional long trips out to sea (Figure 2).

On average, the four birds made two to four short trips and one or two medium-length trips from St Ives per day (Table 2). G4037 made a longer trip (>20 km) on average once every two days, whereas the other three birds made such a trip approximately once per day. In reality, these longer trips were not spread evenly across the period. Three of the birds showed increasing trip lengths and frequencies through the first half of the study, leading to a peak of overall activity (mean speed) before declining later in the season (Figures 3, A3). The exception was G4037, whose activity was around its maximum in the first half of the study, before gradually declining (Figure 3).

An analysis of activity across the 24-h period again highlighted clear differences across the four birds (Figures 3, A4). The activity of G4037 and G4039 was concentrated in the daytime, in contrast to G4038, which showed some nocturnal activity, and G4036, which was often active at night (Figure 3). G4037-39 all showed a maximum level of activity around dawn, consistent with early morning flights away from the colony, and again in early to mid afternoon. G4036 did not show the morning peak, but peaked around sunset, as it returned to the colony. At night, virtually all recorded movements were at sea. With one exception when G4039 roosted for part of a night on a rocky inshore islet (c 5 km west of St Ives), neither G4037 nor G4039 moved away from the colony at night, consistent with the minimal activity during this time (Figure 3). G4038 spent 12 nights away from the colony, primarily roosting on the sea several kilometres from shore, based upon the near-straight lines of GPS fixes at $\leq 0.5 \text{ ms}^{-1}$ ('riding the tide'; Shamoun-Baranes et al 2011; Figure A2). G4036 was away from the colony for at least part of 29 nights, often > 20 km from shore. Its nocturnal movements started only around halfway through the study period. On nine occasions it appeared to roost on the sea for the whole night, whereas the remainder were a mixture of returning to the colony in the first half of the night or relatively active nights spent at sea

Tracked individual	Sex	Tracking end date	Days tracked	Max distance from nest (km)	Home range (90% ud/km ²)	Onshore range (90% ud/km ²)	Offshore range (90% ud/km ²)
G4036	М	26 Aug	111	86	559.7	42.8	516.9
G4037	F	28 Aug	113	17	7.5	6.8	0.7
G4038	F	3 Aug	88	67	138.7	107.8	30.9
G4039	М	13 Aug	98	10	9.1	8.6	0.5

Table 1. Overview of Herring Gull tracking data beginning 8 May 2014, with home range estimates (based on 90% utilisation distribution/km²) for onshore and offshore usage.

involving a combination of flights as well as periods resting on the sea (generally for < 1.5 h).

Focusing on the utilisation distributions in the hinterland around St Ives, further patterns emerged (Figure 4). G4038 utilised a larger area than the other birds, regularly moving around the region south of the colony, with less frequent but prolonged visits to individual fields or groups of fields up to 12 km south and east (Figure 4; intensity). G4036 made repeated visits closer to St Ives, in particular showing less evidence of visits to fields more than 6 km from the colony (Figure 4). G4037 (female) and G4039 (male) had strikingly similar utilisation distributions covering a north-south strip from St Ives to an area approximately 5 km south of the breeding colony. This related to a farm and surrounding fields near Trencrom Hill (Figure 1, 50° 10'N 5° 28'W), which all four birds visited regularly (Figure 4; recursion). G4036 spent long periods on the roofs of the farm buildings, whereas G4037-8 spent more time in the nearby fields, and G4039 visited regularly but only briefly (Figure 4; intensity).

Examination of the complete data set for agricultural fields in the hinterland (highlighted by the intensity distributions) revealed individual birds frequently working backwards and forwards, systematically covering ground that historically was ploughed (Figure A5), possibly following farm machinery, *eg* harvesting, silage foraging, or hay-making.

The Hayle Estuary (Figure 1) was also visited regularly and, often, for long periods by G4036–38 and, to a lesser extent, by G4039 (Figure 4). Field visits revealed that this was a low-tide roost often holding 200–300 loafing gulls. In getting there, the birds usually appeared to use the rising currents of air generated by the scarp between St Ives and Hayle (online supplementary Figure S3).

Discussion

Consistent with studies on other *Larus* species and seabirds more generally, our results demonstrate the power of GPS tags to provide high-quality data on the movements of St Ives Herring Gulls. The four GPS tags provided a large number of fixes on each bird's location throughout day and night, and the many hours of sunshine during the study meant that the frequency of measurements was higher than in other studies of gulls carried out using this make of solarpowered tag. Previous tracking work has focused on rural colonies and, primarily, on Lesser Black-backed Gulls (*eg* Klaassen *et al* 2011, Shamoun-Baranes *et al* 2011, Bouten *et al* 2013, Camphuysen *et al* 2015, Thaxter *et al* 2015), making this the first detailed insight into the movement patterns of urban gulls in the UK and amongst the first to consider Herring Gull movements (Driesen 2014, Stienen *et al* 2016). We first consider some of the limitations of the work, before comparing our results to previous studies on large gulls and finally considering the potential applications to the study of urban gulls elsewhere in the UK.

The conclusions we can draw are tempered by two main limitations. The first is the small number of birds, precluding detailed statistical analysis. Additional birds would be needed, at more sites, to increase confidence that these four were representative of roofnesting Herring Gulls more generally, whilst further breeding seasons would be needed to capture betweenyear variation (Thaxter et al 2015). Nevertheless, this study illustrates the opportunities that are available to study birds breeding in urban environments. The second limitation was that little ground-truthing was undertaken, due to time constraints and finite resources, so that the reasons for birds using different locations could only be inferred from the BRB analysis, and was not investigated by collecting direct evidence. The GPS tags included tri-axial accelerometers which, when combined with field observations to calibrate activity patterns against behaviours (eg Shamoun-Baranes et al 2012), would help to bridge the gap between remote GPS data and detailed field observations. As in most studies using GPS tags to date, an analysis of the accelerometer data was beyond the scope of this paper, but the data are archived in a centralised, international spatial database (UvA-BiTS) and the necessary calibration work is planned for the next three years, at which point more detailed analysis of behaviour will be possible. A possible third limitation is that the GPS tags and harnesses may have altered the behaviour of the Herring Gulls. There were no reasons from our results to suspect problems of this

Table 2. Summary of foraging and other trips of four St lves Herring Gulls. Threshold for a trip is 300 m from the nest in any direction. Short trips are 0.3–6 km, medium trips are 6–20 km and long trips are above 20 km. Trips are defined as Euclidean distances. Journeys are defined as round trips.

Numbers of trips							
Individual	Short	Medium	Long	Total # trips	Max journey distance (km)	# journeys > 100 km	Total distance (km)
G4036	378 (53.6%)	191 (27.1%)	136 (19.3%)	705	348	53	14 947
G4037	242 (61.0%)	105 (26.4%)	50 (12.6%)	397	80	0	3147
G4038	435 (67.3%)	102 (15.8%)	109 (16.9%)	646	257	22	8357
G4039	209 (38.5%)	239 (44.0%)	95 (17.5%)	539	81	0	6209

type, but currently little work has been done with Herring Gulls to validate this assumption. However, work on the closely related Lesser Black-backed Gull suggests that breeding behaviour is unaffected by this make of GPS tag (Thaxter *et al* 2014, 2016).

An interesting result from this study was how variable the four birds were in terms of their range size, activity patterns and nocturnal behaviour. The range varied by two orders of magnitude across the four birds, with two being almost entirely terrestrial and one primarily marine. Terrestrial habitats comprised 7.6–94.5% of the home ranges, but the mean (67.6%) was similar to the combined value for 10 GPS-tracked Herring Gulls in the Netherlands (Driesen 2014). Two individuals were strictly diurnal, virtually always staying in the colony at night, whilst the other two often roosted at sea or were active at night later in the study period. Previous work tracking Lesser Black-backed Gulls has also shown differences between individuals (Thaxter *et al* 2015), but lesser in magnitude than the range seen here. Our results suggest that these Herring Gulls adopted very different, but seemingly successful foraging strategies

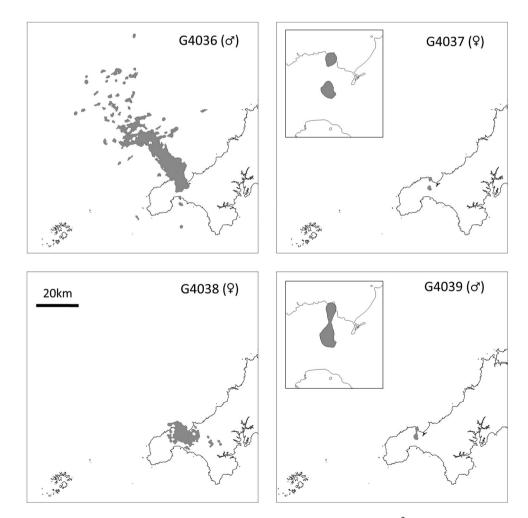


Figure 2. The 90th percentiles of the utilisation distributions for the four gulls. Patches <1 km² are removed for clarity. For G4037 and G4039, both of which had small home ranges, the inset shows an enlargement of the region around St lves. Coastline contains OS data © Crown copyright and database right (2016).

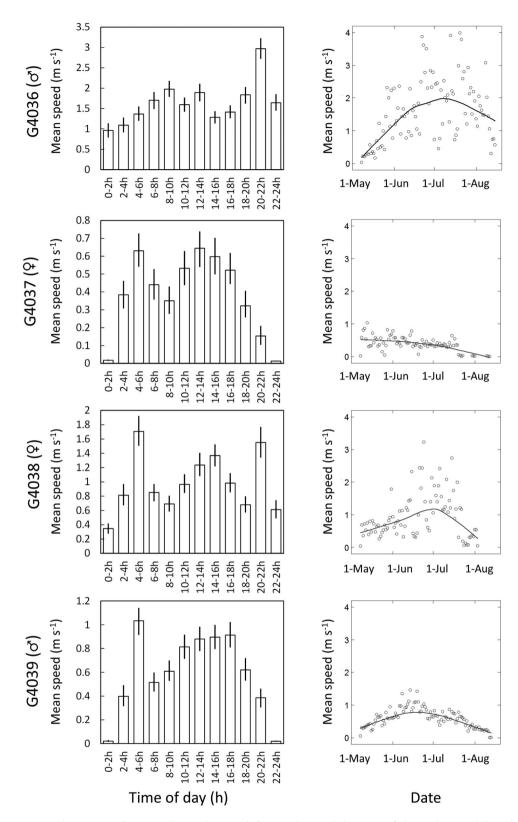


Figure 3. Mean activity (mean speed) across the study period, for two-hour subdivisions of the 24-h period (bar charts; error bars: bootstrapped 95% confidence intervals) and daily activity (scatter plots; solid line: LOESS smoother, points represent daily mean speeds).

through the 2014 breeding season. However, the small sample size prevented us from testing possible hypotheses for these differences. Previous work has suggested that there may be sex differences in foraging, with males travelling greater distances on foraging trips than females and spending longer away from the

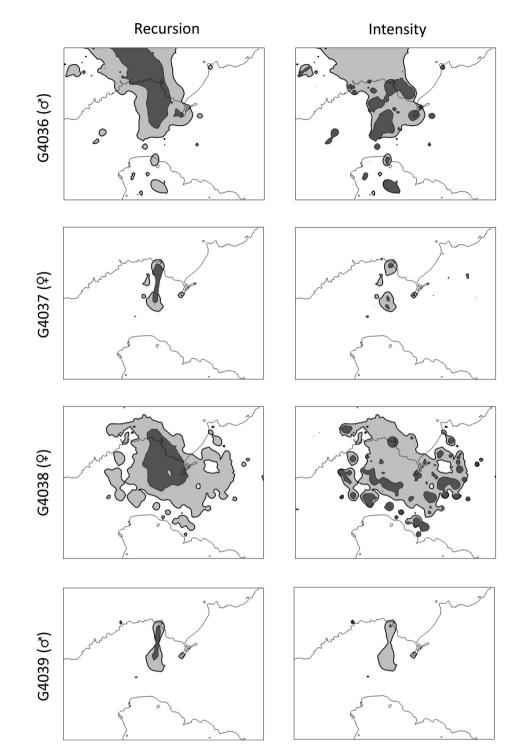


Figure 4. The 30th percentiles for the recursion and intensity distributions in the area immediately around St lves, representing frequency with which different parts of the range were used and the relative duration of visits respectively. Recursion and intensity are drawn with dark grey shading, superimposed on the overall 90% utilisation distribution (light grey shading). Coastline contains OS data © Crown copyright and database right (2016).

colony on their trips, but with females exploring a wider range of foraging opportunities (Camphuysen & Gronert 2012, Camphuysen *et al* 2015, Thaxter *et al* 2015). There was no clear sex difference in this study, with one male and one female displaying the short-ranging behaviour with little nocturnal activity, but scrutiny of individual GPS fixes provided some suggestion of wider ranging over land by females (Figure A2).

A second notable result was that, contrary to a general assumption regarding roof-nesting urban gulls, the St Ives birds appeared to make extensive use of marine and agricultural habitats for foraging, rather than

focusing upon anthropogenic foraging opportunities within the town. This is consistent with previous work on urban Lesser Black-backed Gulls, which used faecal analysis to infer that agricultural areas were important for foraging (Coulson & Coulson 2008). Our data revealed occasional GPS fixes for all four birds in the streets of St Ives close to their nests, which may refer to them picking up scraps of food (online supplementary Figure S1), but the amount of food available on the streets would have been unlikely to support a population in excess of 500 gulls. All birds appeared to rely heavily on terrestrial habitats for foraging, with two notable features. The first was a farm near Trencrom where ground-truthing revealed a large heap of animal feed that was uncovered daily, regularly attracting flocks of Herring Gulls. It was visited repeatedly by all four of the study birds, but most frequently by the two males, G4036 and G4039. The second was the use of individual fields, where birds probably benefited from the availability of invertebrates and other potential prey such as small mammals, nestlings and amphibians (Cramp & Simmons 1983) disturbed by farm machinery during activities such as hay cutting (Schwemmer et al 2008). The GPS tracks showed systematic coverage of areas of fields, consistent with birds walking along ploughed furrows, possibly indicative of planting (maize), harvesting (eg early potatoes), or silage collection, whereas a similarly ploughed field showed random coverage which may suggest silage cutting and drying (Figure A5). In this respect, individual fields were often used for a prolonged time, but visited only on a small number of days as, it is assumed, farming necessity demanded. Those individuals that roamed widely appeared to capitalise on the appearance of food sources in the agricultural landscape, but groundtruthing would be needed to investigate this precisely.

With the exception of G4039, all birds showed a progressively greater level of movement activity - more frequent and longer trips away from the colony through the breeding season, consistent with the results found by Camphuysen et al (2015) and Thaxter et al (2015) for Lesser Black-backed Gulls, and Patenaude-Monette et al (2014) for Ring-billed Gulls Larus delawarensis. Previous studies have shown how the diet of gulls varies through the breeding season (eg Steenweg et al 2011, Washburn et al 2013), and this may be linked to the changes we observed in ranging behaviour. In addition, the nocturnal activity and roosting on the sea demonstrated by G4036 and G4038 were largely restricted to the second half of the season. This may not always be the case: as part of a study of birds nesting around Leba harbour, Poland, in 2012

and 2013 (W. Meissner, pers comm), at least one GPStagged female Herring Gull spent several nights out at sea early in the breeding season (late May). Weekly activity maps for G4036, G4038 and G4039 reveal that they moved very little in the first two or three weeks after tagging (Figure A3). Whilst the hatch dates at these nests are not known, it is presumed that these three birds were fully engaged in incubation and that subsequent increases in movements corresponded to a more active foraging requirement during chick rearing. G4037, on the other hand, explored widely to begin with, before maintaining a stable pattern of movements until day 77 when no movements were recorded – possibly indicating when its harness was shed.

Potential to study urban gulls

Considering the widespread public interest in urban gulls, and vociferous complaints about them (Rock 2003), much remains unknown about why urban colonies are so successful, especially in contrast to their rural counterparts (Rock 2003, 2005). Gaps in our understanding could be addressed through wider use of GPS tags, particularly in combination with other research tools such as colour ringing, dietary analysis and monitoring breeding success. Key questions revolve around how urban gulls use the land- and seascapes surrounding their colonies and whether this differs from gulls breeding in nearby rural colonies. GPS tags not only allow the home ranges to be delineated, but also reveal in detail how different parts of the range are used and how this changes through time (from individual 24-h periods, through complete breeding seasons to multiple years; Thaxter et al 2015). In the current study we separated the overall utilisation distribution into areas used frequently (eg regular feeding/roosting locations) and those used rarely but intensively (eg sporadic feeding opportunities in agricultural fields). Combining accelerometer data with our existing GPS data will reveal the types of behaviour at different locations, whilst the addition of dietary analysis to GPS data could show how gulls use the wider landscape for foraging (eg Caron-Beaudoin et al 2013, Patenaude-Monette et al 2014). Ultimately, this might reveal the relative importance of different locations to supply different food sources at different times of year, such as easily digestible, energy-rich prey during the chick-rearing period (Steenweg et al 2011). GPS tags could also shed light on the relative importance of urban and rural habitats and the extent to which gulls breeding in both will utilise chance feeding opportunities, as appeared to be the case here with individual fields. In urban colonies it appears that,

where chick provisioning is optimal, fledging success is high (PR, unpublished data); contrasting this with nearby rural colonies may help to explain their population declines.

A corollary of the large number of urban colonies (> 500; PR, unpublished data) across Britain & Ireland is their diversity in terms of size, species composition, distance from the coast and land use in the surrounding area. St Ives is a relatively small urban colony in an area with a series of other small urban colonies (PR, unpublished data) and a similar number of rural birds thought to nest in small aggregations along the coast (M.J. Grantham, pers comm). With a coastal location, the ecology of the St Ives gulls might be more similar to that in rural colonies (cf those further upcountry and inland): in that context, it is interesting to note how important terrestrial habitats appeared to be to all four birds (three in particular). At the other extreme is the Severn Estuary, where at least 100 towns and cities support urban gulls (PR, unpublished data), many of which are > 20 km from the coast and some support > 2000 breeding pairs (eg 2011, Cardiff, Bristol and Gloucester; Rock unpublished data). This small study of roof-nesting Herring Gulls cannot answer fundamental questions about their ecology by itself but, when combined with other upcoming studies into urban gulls (eg those planned for 2016 in Bristol), should cast considerable light on their behaviour, ecology and demography, which could be usefully compared to results from birds at rural colonies. This is vital if we are to understand the success of urban gulls, the conservation needs of rural gulls and, potentially, to find sustainable strategies for managing what has become an apparently intractable issue in recent years.

Supplementary Material

Figures S1–S6 show GPS data overlaid onto images from ArcMap and Google Earth showing the activity of four adult Herring Gulls tagged in St Ives, Cornwall, in May 2014 and tracked through the 2014 breeding season.

Acknowledgements

We would like to thank Finestripe, the film makers who facilitated the whole project and Matt Ainsworth, in particular, who was instrumental in organising many of the practicalities. Many thanks to the owners of the buildings (The Cinema, the Co-op and the Porthminster Kitchen), to those who hosted relays (Alan & Sally Gillam and Gordon Mackie), but particularly to Sandra & Brian Trevenna for hosting the all-important base station. Mark Grantham supplied colour-rings and helped in many ways. Włodzimierz Meissner and Małgorzata Knitter supplied useful data from Poland and Shane Windsor provided insights and impetus for this paper. Thanks to all. We also thank the editor and reviewers for helpful suggestions.

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Appendix

Figures A1–A5 show GPS data overlaid onto images from ArcMap or simple maps from Ordnance Survey (OS) data to illustrate the activity of the four adult Herring Gulls tagged in St Ives, Cornwall in May 2014 and tracked through the 2014 breeding season. In addition, one bird (G4036) was tracked through the 2014/15 winter. Birds were assigned colours for GPS fixes which are consistent throughout: G4036, male, yellow; G4037, female, white; G4038, female, blue; G4039, male, red.

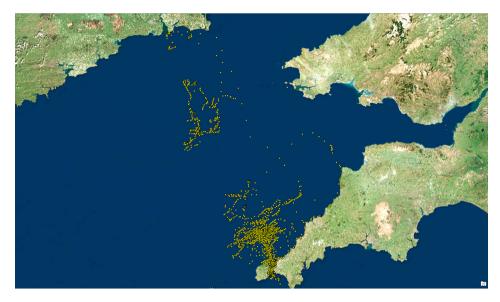


Figure A1. GPS fixes for G4036 between August 2014 and April 2015: visiting Lundy Island, Great Saltee, Little Saltee, Hook Head and the hinterland near Tramore. Herring Gulls breed on the Saltees and on rooftops in Dunmore East (PR pers obs). Basemap created using ArcGIS[®] software by Esri. ArcGIS[®] and ArcMapTM are the intellectual property of Esri and are used herein under licence. Copyright © Esri. All rights reserved.

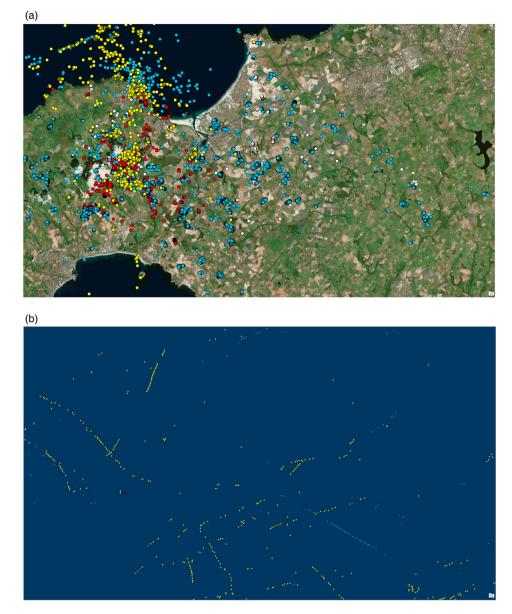


Figure A2. (a) Hinterland activity by all four birds: distribution of GPS fixes for males (yellow, red) and females (white, blue). Note how few male fixes are east of the Hayle Estuary (top left of centre). (b) Riding the tide: lines of fixes for G4036 and G4038 at a point approximately 45 km offshore at a bearing of 314° from St Ives. Basemap created using ArcGIS[®] software by Esri. ArcGIS[®] and ArcMapTM are the intellectual property of Esri and are used herein under licence. Copyright © Esri. All rights reserved.

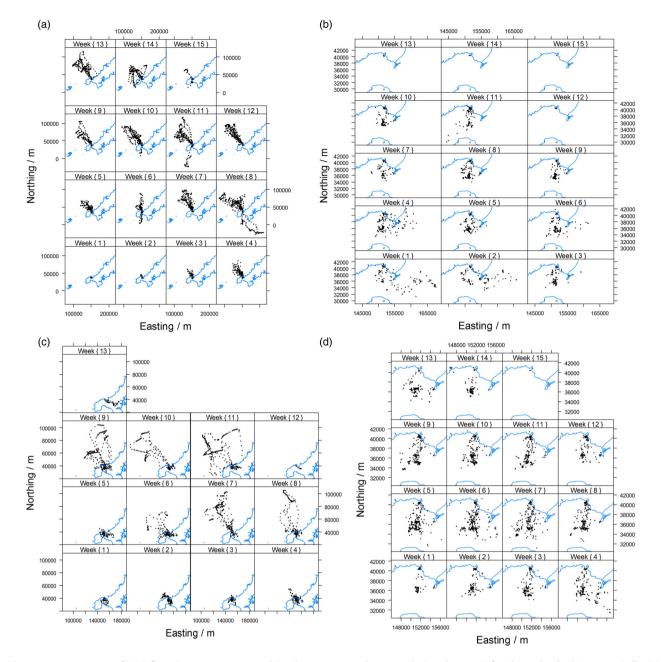


Figure A3. Locations of GPS fixes (ten-minute intervals) split into seven-day periods (weeks 1–15) for the individual Herring Gulls: (a) G4036, (b) G4037, (c) G4038, (d) G4039. Coastline contains OS data © Crown copyright and database right (2016).

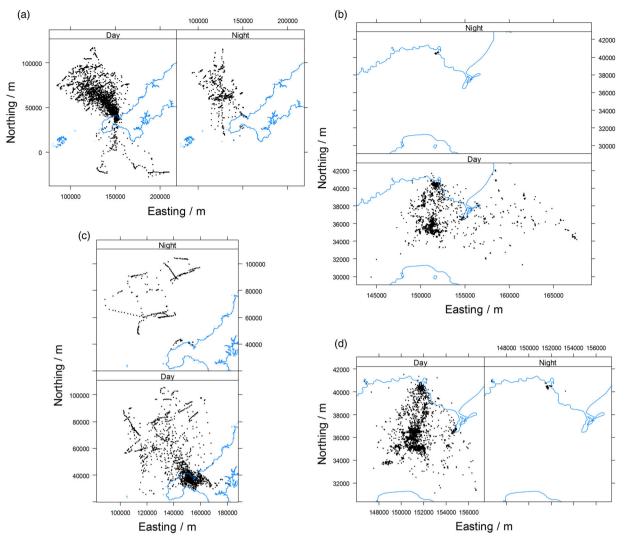


Figure A4. Locations of GPS fixes (ten-minute intervals) for the full study period split into daytime (two hours before sunrise until two hours after sunset) and night-time. Individual Herring Gulls are plotted separately: (a) G4036, (b) G4037, (c) G4038, (d) G4039. Coastline contains OS data © Crown copyright and database right (2016).



Figure A5. GPS data in relation to the agricultural landscape. Note that the GPS data and images are not contemporaneous. We believe that it is common agricultural practice for individual fields always to be ploughed in a consistent direction according to the topography of the landscape, in order to avoid run-off. In cases where birds have consistent linear tracks running in the same direction as the plough furrows in historical images, we infer that these birds are interacting with ongoing agricultural activities such as harvesting or seed drilling etc. In other cases, where GPS data overlaid onto images of ploughed fields show non-linear patterns of movement, we infer that these fields may at the time have been fallow or with no ongoing agricultural activity. G4036 is almost absent from these areas. (a) G4037 and G4038; (b) G4037, G4038 and G4039; (c) G4037, G4038 and G4039; (d) a ploughed field where GPS fixes do not follow historical plough lines. Basemap created using ArcGIS[®] software by Esri. ArcGIS[®] and ArcMapTM are the intellectual property of Esri and are used herein under licence. Copyright © Esri. All rights reserved.