

1 **Kleptoparasitism in gulls (*Laridae*) at an urban and a coastal foraging**
2 **environment: An assessment of ecological predictors.**

3

4 Robert Spencer^a, Yvan I. Russell^a, Benjamin J. A. Dickins^b and Thomas E. Dickins^a

5

6 ^aFaculty of Science & Technology, Middlesex University, London NW4 4BT, UK; ^bSchool of
7 Science & Technology, Nottingham Trent University, Nottingham NG1 4FQ, UK.

8

9

10 CONTACT Robert Spencer, email: r.spencer@mdx.ac.uk

11

12

13 Key words: Kleptoparasitism, urban ecology, coastal ecology, *Laridae*.

14 **ABSTRACT**

15 **Capsule:** Kleptoparasitism in gulls occurred at a greater rate at an urban compared with
16 a coastal site. Population density and prey size predicted the rate of kleptoparasitism at
17 the urban site.

18 **Aims:** To investigate and assess the ecological variables associated with
19 kleptoparasitism among gulls at urban and rural sites.

20 **Methods:** Field observations were conducted at Brancaster (coastal rural) and
21 Billingsgate Market (urban) to examine differences in the rate of kleptoparasitism in
22 mixed-species flocks of gulls. Four key variables (prey size, population density, season
23 and species) were assessed as predictors of kleptoparasitism.

24 **Results:** Generalized linear models revealed significant effects on kleptoparasitism rate
25 of site, population density and prey size, and two-way interactions between these main
26 terms. Population density and prey size differed significantly between sites, but
27 population density appeared to predict the rate of kleptoparasitism.

28 **Conclusion:** Kleptoparasitism may well aid invasion and increase the range of
29 environments a gull can tolerate by helping them meet their energy needs in novel
30 environments where normal foraging behaviours are difficult to implement.

31

32

33

34 INTRODUCTION

35 Kleptoparasitism can be defined most simply as “seizing food gathered by another”
36 (Hatch 1970) and it is a foraging strategy that can reduce the costs of searching for and
37 procurement of food (Thompson 1986, Barnard 1990, Giraldeau & Caraco 2000,
38 Giraldeau & Dubois 2008). Kleptoparasitism has been observed within and between
39 species across various animal taxa (Brockmann & Barnard 1979) including insects
40 (Erlandsson 1988), spiders (Coyle *et al.* 1991), mammals (Höner *et al.* 2002), and even
41 humans (Schoe *et al.* 2009). Birds, more than other taxa, have been the focus of
42 detailed research in this area (Barnard 1990). In a seminal and exhaustive review of the
43 avian literature, Brockmann & Barnard (1979) identified gulls *Laridae* as the most
44 prevalent kleptoparasites and listed ecological factors conducive to kleptoparasitism.
45 These included large concentrations of hosts (victims) and quantities of food, and large,
46 high quality food items to steal. Here, we focus on kleptoparasitism within and between
47 gull species in two distinct ecologies.

48 Research on gulls has demonstrated that kleptoparasitism is a facultative
49 behavioural strategy that is applied flexibly as ecological conditions vary. Field research
50 conducted by Maniscalco & Ostrand (1997) found that the degree of kleptoparasitism co-
51 varies with the concentration of hosts. In mixed-species foraging flocks of seabirds the
52 rate of kleptoparasitism committed by gulls increased as the density of birds increased.
53 The distribution of food resources covaried with foraging flock density, such that food
54 distribution should directly predict rates of kleptoparasitism.

55 Hamilton (2002) explored the relationship between food availability and
56 kleptoparasitism by assessing the distribution of foragers between patches that were
57 high or low in the rate of food input. The model showed that less kleptoparasitism
58 occurred in high resource input patches and that kleptoparasitism increased with
59 decreasing resource input. Increasing the density of competitors in a patch had the
60 effect of increasing the proportion of kleptoparasites, in line with the observations of
61 Maniscalco & Ostrand (1997). Increasing the number of competitors and decreasing
62 resources increased the intensity of resource competition, thus promoting
63 kleptoparasitism.

64 The findings of Maniscalco & Ostrand (1997) and Hamilton (2002) strongly
65 indicate that kleptoparasitism is a flexible behavioural strategy. However, no research
66 has yet investigated the value of kleptoparasitism in evolutionarily novel environments.
67 The increasing urbanisation of gull populations provides an opportunity to address this
68 question. Many gull species that are found in urban settings are of conservation concern
69 due to declining populations over the last 25 years or more (Eaton *et al.* 2015).

70 Understanding the behavioural strategies adopted by these species will help to further
71 understand the stresses they face (Eaton *et al.* 2015, Reid 2004, Madden & Newton
72 2004).

73 Gulls are found in a variety of habitats (Pons *et al.* 2005) and have been noted
74 for their tendency to colonise novel environments (Rock 2005). As members of the sub-
75 order *Charadrii* they are part of only two groups of modern birds known to have been
76 present since the Cretaceous period over 65 million years ago (Proctor & Lynch 1993).
77 Their significant investment in kleptoparasitism highlights the importance of this strategy
78 to gull species, and suggests kleptoparasitic behaviours may have played an important
79 role in aiding the radiation and longevity of this family. For any animal, invading an
80 urban environment entails finding solutions to a number of survival problems, the most
81 pressing of which is acquiring food. Kleptoparasitism is a foraging strategy that can be
82 used by gulls when very few conditions are met. The only essential conditions are the
83 availability of opportunistic food sources and the presence of other foragers, of any
84 species, to provide cues as to the location of food.

85 In this study, we investigated the predictors of the rate of kleptoparasitism in
86 foraging gull populations across two environments with contrasting parameters: 1) a
87 coastal environment, assumed to be typical of the shoreline foraging ecologies
88 encountered by gulls throughout much of their evolutionary history and 2) an urban
89 environment. Our predictions were: 1) that population density would be positively
90 related to the rate of kleptoparasitism, 2) that large prey items would be more
91 susceptible to theft, so that prey size should covary with kleptoparasitism rate, 3) that
92 kleptoparasitism would vary between breeding (March to August) and non-breeding
93 seasons, 4) that gull species would differ in their use of kleptoparasitic behaviour and 5)
94 that there would be a higher rate of kleptoparasitism at the urban site, where food was
95 predicted to be a rapidly decreasing resource.

96

97

98 **METHODS**

99 **Study Sites**

100 Research was conducted at two sites in the UK, between July 2014 and June 2015. Three
101 days of observations were conducted at each site in all calendar months. Site 1 was
102 Brancaster Beach, Norfolk, UK (52°58'30"N 0°38'11"E); a public beach situated within a
103 saltmarsh environment, managed by the National Trust. The low tide at Brancaster
104 exposes a large area of sand beach where numerous bird species forage for prey items
105 exposed by the receding tide. The study area was a section of beach demarcated by two
106 water channels where the outflow of water draining from the saltmarsh joins the sea.
107 These two channels marked the eastern and western boundaries of the study area. At its
108 maximum, when the tide was at its lowest point, the study area covered 1.6 km². Site 2
109 was an urban location at Billingsgate Market, east London (51°30'20"N 0°00'43"W); a
110 commercial fish market. Research was conducted in a car park used by fish merchants to
111 process and load stock onto vans, and covered an area of 0.0104 km². The size of study
112 areas was calculated using scaled aerial photographs from Google Maps.

113

114 **Study species**

115 Large numbers of gulls aggregated daily to forage at both sites. At Brancaster, gulls
116 aggregated to forage in mixed-species groups over a period of about four hours; two
117 hours either side of the low tide mark. The most numerous gull species present at this
118 site were Great Black-backed Gull *Larus marinus*, Herring Gull *Larus argentatus*, Black-
119 headed Gull *Chroicocephalus ridibundus* and Common Gull *Larus canus*. These four
120 species were the focus of research at Brancaster throughout the year. However, the
121 numbers of Common Gulls and Black-headed Gulls were lower during the summer
122 months as birds were mostly away breeding elsewhere. The foraging population of gulls
123 at Brancaster had a mean daily population size of 176 (Range: 0 - 924) gulls. The daily
124 mean number (and % of population) of each species at the site was: Herring Gull 75
125 (42%), Black-headed Gull 64 (37%), Common Gull 31 (18%) and Great Black-backed
126 Gull 6 (3%).

127 Gulls aggregated at Billingsgate to exploit seafood waste and food leftovers
128 discarded in the car park areas. The population consisted of Great Black-backed, Herring
129 and Black-headed Gulls, and all three species were the focus of research. Great Black-
130 backed and Herring Gulls were present at Billingsgate all year round, with some birds
131 nesting on the surrounding market buildings. Black-headed Gulls were largely absent
132 from the site between the April and July when they were away breeding elsewhere. The

133 foraging population at Billingsgate had a mean daily population size of 40 (Range: 24 -
134 79) gulls. The daily mean number (and % of population) of each species at Billingsgate
135 was: Herring Gull 28 (70%), Black-headed Gull 7 (19%) and Great Black-backed Gull 4
136 (11%).

137

138 **Measuring kleptoparasitism**

139 Population size and composition were calculated using scan samples at 30 minute
140 intervals. All attempts at kleptoparasitism, both successful and unsuccessful, were
141 counted. Kleptoparasitic behaviours included the use of force to take items from another
142 bird, theft without any interaction with the host and simultaneous theft (or attempted
143 theft) from a host, by two or more competitors (Giraldeau & Caraco 2000). Size of food
144 items was estimated visually in relation to bill lengths. The Herring Gull bill length was
145 used as a standard comparative measurement to assess the length of food items (Table
146 1). Food items contested by the smaller or larger species of gulls were calibrated in
147 relation to the mean size of Herring Gull bills. Prey sizes were assigned to increasingly
148 large categories in relation to Herring Gull bill size (0.5, 0.75, 1, 2, 3, 4, 5 or 6).

149

150 [INSERT TABLE 1 ABOUT HERE]

151

152 **Field observations**

153 *Brancaster*: The majority of field sessions were conducted at low tide to coincide with the
154 presence of the largest numbers of birds. Field sessions had a mean duration of 120
155 minutes (range: 90 – 220 minutes) and a total of 74 hours 28 minutes of observations
156 were conducted at Brancaster over 34 days. Field sessions were conducted during
157 daylight between 04:45 hours and 17:00 hours, to permit behaviour to be recorded on
158 video.

159 An observer (RS) scanned the beach for gulls, using binoculars, and then
160 approaching to within a distance from which foraging patches could be identified, the
161 gulls counted and their foraging behaviour recorded on video. Patches were classified as
162 discrete clusters of two or more birds exploiting a food source or searching for food in a
163 given area. The location of patches was constantly shifting around the beach. Once a
164 patch was identified, video recording was carried out from a fixed position with a Sony
165 8.9 megapixel HD camcorder mounted on a tripod. The distance from which a patch was
166 filmed varied and was contingent on how closely the researcher could approach without

167 disrupting the foraging birds. Recording of a patch was concluded when the gulls in that
168 patch dispersed. The duration of recordings ranged from 32 seconds to 40 minutes 47
169 seconds, and 142 patches were recorded in total. Videos were analysed at a later date
170 for incidents of kleptoparasitism.

171 Gull counts were conducted every 30 minutes from the start of a field session,
172 using a series of digital images (Nikon Coolpix P510 42x zoom) taken to record all gulls
173 in the study area. These images were analysed at a later date to calculate the population
174 size and composition.

175 *Billingsgate:* Observations at Billingsgate were conducted between 07:00 hours and
176 15:00 hours. The trading hours for the market were 03:00 hours to 08:30 hours. After
177 08:30 hours, the main activity at the site is the clean-up of the market and car park.
178 Prior to 07:00 hours it was not possible to conduct observations due to the large number
179 of vehicles at the site. Field sessions were conducted on days when the market was
180 operational (Tuesday to Saturday) and when it was closed (Sunday and Monday).

181 Observations and recordings were conducted from a vehicle placed to give the
182 best vantage point on the day and the position varied between observation days. Gull
183 activity at foraging patches was video recorded by the observer (RS) until the resource
184 in the patch had depleted and the birds dispersed. Over the study, 183 foraging patches
185 were recorded and these ranged in duration from 25 seconds to 29 minutes 36 seconds.
186 For each recording we noted the number of each species and ages of the gulls present.
187 Patch videos were analysed at a later date for incidents of kleptoparasitism.

188 Gull counts were conducted at 30 minute intervals from the start of a field
189 session. As at Brancaster, a series of digital images were taken of the study area, and
190 later analysed to calculate the population at the time of the sample, including the
191 species and ages of gulls present. The same recording and photographic equipment used
192 at Brancaster was used at Billingsgate.

193

194 **Statistical analysis**

195 All statistical analyses were conducted using R version 3.3.1 (R Core Team, 2016).
196 Figures were produced in R using the base package or ggplot2 version 2.1.0 (Wickham,
197 2009).

198 RESULTS

199 In total, there were 595 kleptoparasitic events recorded at Billingsgate and 99 at
200 Brancaster. A single event involving a Lesser Black-backed Gull *Larus fuscus* was
201 excluded from the analysis. There were 15 missing data points for prey size and all data
202 associated with these observations were also removed.

203 Data were analysed using a series of generalized linear models (GLM). The
204 response variable was the rate of kleptoparasitism (events per minute) for each patch
205 observed. This variable was \log_n transformed to improve the dispersion of data. The
206 predictor variables were population density (daily mean population density (birds.km⁻²)
207 over each study area), prey size, season (breeding/non-breeding), species of
208 kleptoparasite and site (Billingsgate/Brancaster). The population density, prey size and
209 response variables were each centred and scaled in order to standardize them.
210 Standardizing continuous variables facilitated meaningful comparisons between model
211 coefficients. All variables were entered as main effects into a GLM using a Gaussian
212 function with identity link (Table 2).

213 To avoid over-fitting a relatively small dataset, we next adopted a subtractive
214 approach using a backward `step()` function. This is a sequential approach to model
215 fitting using the Akaike Information Criterion corrected for finite sample sizes (AICc).
216 Models with AICc values which differ by less than 2 are regarded as being similarly good
217 fits, whereas differences (Δ AICc) over 2 suggest the model with the higher AICc is a
218 poorer fit (Burnham & Anderson 2001). This approach led to the removal of season and
219 species from the best fitting model, leaving a minimal main effects model with site,
220 standardized population density and standardized prey size as significant predictors of
221 kleptoparasitism rate (Table 2).

222

223 [INSERT FIGURES 1 & 2 AND TABLE 2 ABOUT HERE]

224

225 A positive correlation was apparent between population density and standardized \log_n
226 kleptoparasitism rate at Billingsgate, and to a lesser extent at Brancaster (Figure 1). A
227 positive correlation was also seen between prey size and standardized \log_n
228 kleptoparasitism rate at Billingsgate, but this correlation appears to be negative at
229 Brancaster (Figure 2).

230 Owing to the trend differences noted between sites (Figures 1 and 2), a second
231 (Gaussian) GLM was constructed which included the main effects and all pairwise

232 interactions between site, standardized prey size and standardized population density.
233 This model suggested that the interactions were significant (Table 2). Notably, however,
234 the coefficients for the main effects of site, standardized prey size and standardized
235 population density remained approximately the same (Table 2) indicating that the data
236 collected at Brancaster did not evidence a trend reversal.

237 Data from Brancaster showed a smaller range of values for prey size and
238 population density than Billingsgate, and in the case of population density the data
239 ranges for the two sites were non-overlapping (x axes in Figures 1 and 2, Table 3). This
240 suggests that additional data may be needed to be collected at Brancaster (or an
241 equivalent site) to capture the influence of these variables on kleptoparasitism across
242 this reduced ranges. Prey sizes and population densities were both significantly greater
243 at Billingsate (Table 3).

244

245 [INSERT TABLE 3 ABOUT HERE]

246 Returning to the response variable and to explore the relative importance of pairwise
247 interactions in the interactions model we again adopted a subtractive ΔAICc approach
248 (using the `drop1()` function). All three pairwise interactions between the three entered
249 variables could be removed while lowering the AICc with one exception: the site \times prey
250 size interaction. Removing only this interaction from the model resulted in an increased
251 AICc. The reasonable fit offered by models of kleptoparasitism that include interactions
252 and the significant differences between the two key continuous predictor variables
253 support the view that the two sites show a core ecological difference.

254 **DISCUSSION**

255 Our results show that rates of kleptoparasitism in gulls are affected by bird population
256 density and prey size. While these two predictors seem to be robustly positively
257 correlated with increased rates of kleptoparasitism, differences between the sites in the
258 predictors and the response variable support a more cautious interpretation. It is
259 possible that the population density measure may under-estimate the search time
260 entailed for would-be kleptoparasites at Brancaster, in contrast to Billingsgate.

261 Maniscalco & Ostrand (1997) demonstrated how a shift in the foraging conditions
262 in a single environment resulted in an increase in kleptoparasitic behaviour by gulls.
263 Our results complement that finding and describe clear frequency differences between a
264 rural and an urban site. Our study gave focus to the role that kleptoparasitism might
265 play in helping gulls meet their energy needs when invading urban environments. Our
266 sample size is small – one rural and one urban environment only – and so we must be
267 cautious in generalizing any findings. However, here we consider the mechanism by
268 which urban invasion might occur when birds initially encounter those spaces. As
269 Marzluff *et al.* (2001) have described, the foraging environment changes on a gradient
270 between wildland environments and heavily urbanised spaces. As a gull moves along this
271 gradient it will encounter fewer aspects of the foraging environment with which it is
272 familiar. At one extreme of this gradient are heavily urbanised spaces containing lots of
273 anthropogenic novelty with few of the characteristics of a natural food web. Billingsgate
274 is such a site, as all the food there is waste provisioned by human activities. A gull, or
275 small founder population of gulls, invading an urban environment must either obtain
276 food through: innovation by exploring the novel foraging space; learning what things are
277 edible and where to find them by copying other foragers; or stealing food from other
278 individuals.

279 Previous research has emphasised the importance of innovative behaviour in
280 species that invade novel environments (Sol *et al.* 2005, Sol *et al.* 2008). Some
281 proportion of innovators, who explore the environment, are essential in any population
282 otherwise there would be no one to copy, however, rates of innovation in any natural
283 population are quite low (Page 2008), making the second two options, copying or
284 stealing, more likely for invasive gulls. Of these, copying other foragers to learn the
285 locations of food is necessary, but stealing can be efficient as it avoids the cost of the full
286 foraging cycle by acquiring food discovered by another's effort. To this end, we can think
287 of stealing information and stealing food as on a continuum; the cost of stealing the food
288 is actually the marginal cost of stealing conditional on already observing the victim.

289 As gulls can range over large areas they can occupy different habitats on the
290 gradient described above in a single foraging bout or day. This suggests a plausible

291 alternative mechanism to the one described above by which gulls can invade urban
292 spaces. They can forage in environments where they encounter conditions with which
293 they are familiar, and then make forays and encroachments into urban spaces in search
294 of supplemental food and other foraging populations. Foraging in the littoral zone of
295 rivers and estuaries that pass near or through cities is an example of how this might
296 work. In our argument regarding the utility of kleptoparasitism we have made the
297 assumption that while this second mechanism would undoubtedly occur, the additional
298 travel and foraging costs involved would make it energetically more expensive than
299 exploiting other foragers through kleptoparasitism. These costs would not be prohibitive
300 of this foraging approach but we suggest that these additional costs would make it
301 secondary to the kleptoparasitic strategies considered above. At present little is known
302 about the foraging habits and ranges of urban gull populations, and tracking of
303 individuals to see the extent of their foraging ranges was not undertaken in our study.
304 Further work of this nature would be useful to assess whether urban gull populations,
305 such as the one at Billingsgate, obtain their food exclusively at that site or exploit a
306 variety of habitats.

307 Comparing the range and diversity of environments occupied by different gull
308 species may also provide insights into the role of kleptoparasitism in supporting invasion.
309 As described by Brockmann & Barnard (1979) 23 of 88 gull species are reported to use
310 kleptoparasitism. A comparison between kleptoparasitic and non-kleptoparasitic gull
311 species of the diversity of habitats that these species routinely breed and forage in, and
312 the extent of their ranges, may provide indirect evidence for the proposed role of
313 kleptoparasitism as a strategy that buffers against environmental change. If this
314 proposed function of kleptoparasitism is plausible we should expect to see kleptoparasitic
315 gull species occupying a broader diversity of habitats than non-kleptoparasitic gull
316 species.

317

318 *Ecological predictors of kleptoparasitism*

319 Birds are dispersed widely at Brancaster and population density was positively correlated
320 with kleptoparasitism. This finding is consistent with empirical research that shows
321 foragers are more likely to encounter each other at high population densities and
322 interact aggressively (Colwell 2010). It also lends support to the theoretical model of
323 Hamilton (2002) demonstrating increased kleptoparasitism with increasing competitor
324 density.

325 In addition, King *et al.* (2009), in research on baboon troops, found that the
326 distribution of resources influenced the rate of kleptoparasitism, with small tightly

327 clustered patches prompting more kleptoparasitism. The resources in the study
328 environments at Brancaster and Billingsgate were clearly distributed in different ways
329 that provided a useful test of the pattern of behaviour described by King *et al.* (2009).
330 The food at Brancaster was naturally more widely dispersed throughout the environment
331 and it was a much larger study area than Billingsgate, permitting gulls to be more
332 spaced out whilst foraging. Our results support the finding of King *et al.* (2009) with
333 more kleptoparasitism in high density areas where gulls were forced to forage closer
334 together, perhaps making it easier to take advantage of opportunities to try and steal.

335 The finding that larger food items were more likely to be targeted for theft is in
336 accord with the findings of several empirical studies (Hopkins & Wiley 1972, Ens &
337 Cayford 1996, Leeman *et al.* 2001). Large prey items provide a conspicuous visual cue
338 to the presence of food, and a large prey item requires longer handling time, which
339 increases the likelihood that other foragers can approach and try to steal the item. Our
340 use of an ordinal scale to measure the size of prey items in terms of bill lengths was a
341 limitation of this study that may have resulted in a loss of additional data of value.
342 Ordinal measures of this kind result in a lack of precision that may mask useful patterns
343 of behaviour. A more finely grained measure would have been beneficial, but the ordinal
344 measure of bill lengths used represented the most practical way to assess the size of
345 food items from the observational data obtained.

346 *Concluding remarks:* Kleptoparasitism was higher in the urban environment. Large prey
347 items that take longer to handle, and high population densities that increase competition
348 for available resources were the critical aspects of the urban environment at Billingsgate
349 that promoted kleptoparasitism. Kleptoparasitism may well aid invasion and increase the
350 range of environments a gull can tolerate by helping them meet their energy needs in
351 novel environments where normal foraging behaviours are difficult to implement.

352 **Acknowledgements**

353 The authors should like to thank the National Trust for permission to conduct field work
354 at Brancaster, the City of London Corporation for permitting field work at Billingsgate
355 Market and two anonymous reviewers and the editor for useful commentary on previous
356 drafts.

357 **References**

- 358 **Barnard, C.J.** 1990. Parasitic relationships. In C.J. Barnard & J.M. Behnke (eds.).
359 *Parasitism and Host Behaviour* pp. 1-33. Taylor & Francis, London.
- 360 **Brockmann, H.J. & Barnard, C.J.** 1979. Kleptoparasitism in birds. *Animal Behaviour*
361 **27**: 487-514.
- 362 **Burnham, K.P. & Anderson, D.R.** 2001. Kullback-Leibler information as a basis for
363 strong inference in ecological studies. *Wildlife Research* **28**: 111-119.
- 364 **Cohen, J.E., Jonsson, T. & Carpenter, S.R.** 2003. Ecological community description
365 using the food web, species abundance, and body size. *Proceedings of the National*
366 *Academy of Sciences* **100**: 1781-1786.
- 367 **Colwell, M.A.** 2010. *Shorebird Ecology, Conservation, and Management*. University of
368 California Press, Berkeley, USA.
- 369 **Coyle, F.A., O'Shields, T.C. & Perlmutter, D.G.** 1991. Observations on the behaviour
370 of the kleptoparasitic spider, *Mysmenopsis furtive* (Araneae, Mysmenidea). *Journal of*
371 *Arachnology* **19**: 62-66.
- 372 **Eaton, M.A., Aebischer, N.J., Brown, A.F., Hearn, R., Lock, L., Noble, D.G.,**
373 **Musgrave, A.J., Noble, D.G., Stroud, D. & Gregory, R.D.** 2015. Birds of conservation
374 concern 4. *British Birds* **108**: 708-746.
- 375 **Ens, B.J. & Cayford, J.T.** 1996. Feeding with other oystercatchers. In J.D. Goss-
376 Custard (ed). *The Oystercatcher: From Individuals to Populations* pp. 77- 104. Oxford
377 University Press, Oxford.
- 378 **Erlandsson, A.** 1988. Food sharing vs monopolising prey: a form of kleptoparasitism in
379 *Velia Caprai* (Heteroptera). *Oikos* **53**: 203-206.
- 380 **Giraldeau, L.-A., & Dubois, F.** 2008. Social foraging and the study of exploitative
381 behaviour. *Advances in the Study of Behavior* **38**: 59-104.
- 382 **Giraldeau, L.-A. & Caraco, T.** 2000. *Social Foraging Theory*. Princeton University Press,
383 Princeton.
- 384 **Hatch, J.J.** 1970. Predation and piracy by gulls at a ternery in Maine. *The Auk* **87**: 244-
385 254.

- 386 **Hamilton, I.M.** 2002. Kleptoparasitism and the distribution of unequal competitors.
387 *Behavioural Ecology* **13**: 260-267.
- 388 **Höner, O.P., Wachter, B., East, M.L. & Hofer, H.** 2002. The response of spotted
389 hyaenas to long-term changes in prey populations: functional response and interspecific
390 kleptoparasitism. *Journal of Animal Ecology* **71**: 236–246.
- 391 **Hopkins, C.D. & Wiley, R.H.** 1972. Food parasitism and competition in two terns. *The*
392 *Auk* **89**: 583-594.
- 393 **King, A.J., Isaac, N.J.B. & Cowlshaw, G.** 2009. Ecological, social and reproductive
394 factors shape producer-scrounger dynamics in baboons. *Behavioural Ecology* **20**: 1039-
395 1049.
- 396 **Leeman, L.W., Colwell, M.A., Leeman, T.S. & Mathis, R.L.** 2001. Diets, energy
397 intake, and kleptoparasitism of nonbreeding Long-billed Curlews in a northern California
398 estuary. *Wilson Bulletin* **113**: 194-201.
- 399 **Madden, B. and Newton, S.F.** 2004. Herring Gull *Larus argentatus*. In: P.I. Mitchell,
400 S.F. Newton, N. Ratcliffe, and T.E. Dunn, (eds.). *Seabird Populations of Britain and*
401 *Ireland* pp 242-262. T. & A.D. Poyser, London.
- 402 **Malling Olsen, K. & Larsson, H.** 2003. *Gulls of Europe, Asia, and North America*.
403 Christopher Helm, London.
- 404 **Maniscalco, J.M. & Ostrand, W.D.** 1997. Seabird behaviors at forage fish schools in
405 Prince William Sound, Alaska. In *Forage Fishes in Marine Ecosystems. Proceedings of the*
406 *International Symposium on the Role of Forage Fishes in Marine Ecosystems*. Alaska Sea
407 Grant College Program Report No. 97-01 pp 175-190. University of Alaska Fairbanks.
- 408 **Marzluff, J.M., Bowman, R. & Donnelly, R.** 2001. *Avian Ecology and Conservation in*
409 *an Urbanising World*. Kluwer Academic Publishers, Norwell, USA.
- 410 **Pons, J.-M., Hassanin, A. & Crochet, P.-A.** 2005. Phylogenetic relationships within
411 the *Laridae (Charadriiformes:Aves)* inferred from mitochondrial markers. *Molecular*
412 *Phylogenetics and Evolution* **37**: 686-699.
- 413 **Proctor, N.S. & Lynch, P.J.** 1993. *Manual of Ornithology: Avian Structure and*
414 *Function*. Yale, New Haven, USA.
- 415 **R Core Team.** 2016. R: A language and environment for statistical computing. R
416 Foundation for Statistical Computing, Vienna, Austria. URL: <https://www.R-project.org/>

- 417 **Reid, J.B.** 2004. Great Black-backed Gull *Larus marinus*. Pp 263-276 in Mitchell, P.I.,
418 Newton, S.F., Ratcliffe, N. and Dunn, T.E. (eds.). *Seabird Populations of Britain and*
419 *Ireland*. T. & A.D. Poyser, London.
- 420 **Rock, P.** 2005. Urban gulls: problems and solutions, *British Birds* **98**: 338-355.
- 421 **Schoe, M., De Iongh, H.H. & Croes, B.M.** 2009. Humans displacing lions and stealing
422 their food in Bénoué National Park, North Cameroon. *African Journal of Ecology* **47**: 445-
423 447.
- 424 **Sol, D., Duncan, R.P., Blackburn, T.M., Cassey, P. & Lefebvre, L.** 2005. Big brains,
425 enhanced cognition, and response of birds to novel environments. *Proceedings of the*
426 *National Academy of Science*. **102**: 5460–5465.
- 427 **Sol, D., Bacher, S., Reader, S.M. & Lefebvre, L.** 2008. Brain size predicts the success
428 of mammal species introduced into novel environments. *American Naturalist* **172**: 63–
429 71.
- 430 **Thompson, D.B.A.** 1986. The economics of kleptoparasitism: optimal foraging, host
431 and prey selection by gulls. *Animal Behaviour* **34**: 1189-1205.
- 432 **Wickham, H.** 2009. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag, New
433 York.

434 **Tables**

435

436 **Table 1.** Data used to obtain a standardised bill length measurement. Calculated by taking the mean bill
 437 length for both sexes for each species (from Malling Olsen & Larsson 2003), and then taking the mean of all
 438 four species' means. This averaging across species returned a figure of 45mm. This was closest to the bill
 439 length of Herring Gull (difference of 7mm). The Herring Gull bill length was therefore used to assess the size of
 440 food items in the field.

s	m	bill	bill	species bill	s
	length (mm)	length (mm)	length (mm)	length (mm)	bill length (mm)
Common Gull	36.10	32.70	34.40	11	
Black-headed Gull	33.60	31.60	32.60	12	
Herring Gull	55.20	49.70	52.45	-7	
Great Black-backed Gull	63.10	57.60	60.35	-15	

441

442

443

444 **Table 2.** Summary of generalised linear models exploring the effects on \log_n kleptoparasitism rate (events per
 445 minute) of site (with Billingsgate as reference), standardised population density, standardised prey size,
 446 species of kleptoparasite and season.

447

Model	terms	coefficients	AICc	Δ AICc
a. Main effects model	all		1474.182	6.687
b. Minimal main effects model	site	-0.86128	1468.817	1.322
	population density	+0.45983		
	prey size	+0.08091		
c. Interactions model (two-way interactions)	site	-1.35673	1467.495	0
	population density	+0.43881		
	prey size	+0.08240		

448

449

450

451 **Table 3.** Differences in prey size and population density between Billingsgate (N = 593) and Brancaster (N =
 452 86). Differences between site were tested using Mann-Whitney tests.

453

Site	median	range	statistic
a) Population density (birds.km ⁻²)			
Billingsgate	1.730	0.380 - 4.330	U = 50998, <i>P</i> < 0.0001
Brancaster	0.0190	0.0025 - 0.1250	
b) Prey size (bill lengths)			
Billingsgate	8.00	0.75 - 20.00	U = 46575, <i>P</i> < 0.0001
Brancaster	0.75	0.50 - 6.00	

454

455

456

457 **Figure Legends**

458 **Figure 1.** Population density plotted against standardized \log_n kleptoparasitism rate at both sites, with fitted
459 regression line and shading indicating 95% confidence intervals.

460 **Figure 2.** Prey size plotted against standardized \log_n kleptoparasitism rate at both sites, with fitted regression
461 line and shading indicating 95% confidence intervals.

462