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**Citation:** Spencer, R. & Broom, M. (2018). A game-theoretical model of kleptoparasitic behavior in an urban gull (*Laridae*) population. *Behavioral Ecology*, 29(1), pp. 60-78. doi: 10.1093/beheco/arx125

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1 **A game-theoretical model of kleptoparasitic behaviour in an urban gull (*Laridae*)**  
2 **population**

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8 **Running title: Game theory and urban gull kleptoparasitism.**

9  
10 **Acknowledgements**

11 The authors thank the City of London Corporation for permission to conduct the fieldwork  
12 aspects of this research at Billingsgate Market. RS also thanks Tom Dickins (Middlesex  
13 University) and Paul Roper of ntgg.org for supervision and advice on various aspects of  
14 fieldwork.

15  
16 **Data Accessibility**

Analyses reported in this article can be reproduced using the data and supplementary material  
appendices provided by Spencer & Broom (2017).

15 **A game-theoretical model of kleptoparasitic behaviour in an urban gull (*Laridae*)**  
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18

19 **Abstract**

20 Kleptoparasitism (food stealing) is a significant behaviour for animals that forage in social  
21 groups as it permits some individuals to obtain resources whilst avoiding the costs of  
22 searching for their own food. Evolutionary game theory has been used to model  
23 kleptoparasitism, with a series of differential equation based compartmental models  
24 providing significant theoretical insights into behaviour in kleptoparasitic populations. In this  
25 paper we apply this compartmental modelling approach to kleptoparasitic behaviour in a real  
26 foraging population of urban gulls (*Laridae*). Field data was collected on kleptoparasitism  
27 and a model developed that incorporated the same kleptoparasitic and defensive strategies  
28 available to the study population. Two analyses were conducted: 1. An assessment of whether  
29 the density of each behaviour in the population was at an equilibrium. 2. An investigation of  
30 whether individual foragers were using *Evolutionarily Stable Strategies* (ESS) in the correct  
31 environmental conditions. The results showed the density of different behaviours in the  
32 population could be at an equilibrium at plausible values for handling time and fight duration.  
33 Individual foragers used aggressive kleptoparasitic strategies effectively in the correct  
34 environmental conditions but some individuals in those same conditions failed to defend food  
35 items. This was attributed to the population being composed of three species that differed in  
36 competitive ability. These competitive differences influenced the strategies that individuals  
37 were able to use. Rather than gulls making poor behavioural decisions these results suggest a  
38 more complex three-species model is required to describe the behaviour of this population.

39 *Key words:* evolutionary game theory, ESS, urban gulls, *Laridae*, kleptoparasitism, social  
40 foraging.

## 41 Introduction

42 Kleptoparasitism is defined as the theft of already procured food by one individual from  
43 another (Brockmann & Barnard, 1979). It is one of the most widespread forms of exploitation  
44 found in nature having been observed across several taxonomic groups, including spiders  
45 (Coyle et al. 1991), insects (Erlandsson, 1988), mammals (Janson, 1985; Carbone et al. 2005)  
46 and birds (Barnard, 1990; Brockmann & Barnard, 1979). The significance of kleptoparasitic  
47 behaviour is that it allows individuals to avoid some of the costs of the foraging cycle  
48 (searching for, acquiring and handling food items) by exploiting food discovered by another  
49 individual's effort (Giraldeau & Caraco, 2000).

50 As a behaviour with a potentially significant impact on fitness, kleptoparasitism has  
51 attracted the interest of researchers and, due to the prevalence of kleptoparasitic species  
52 within the class *Aves*, research effort has focused on birds more than other taxa. Amongst the  
53 birds, some species specialise in an almost entirely parasitic lifestyle, such as the skuas  
54 (*Stercorariidae*) and frigatebirds (*Fregatidae*). In other species kleptoparasitism is just one of  
55 a number of foraging strategies used. Brockmann & Barnard (1979) conducted a review of  
56 kleptoparasitic incidents reported in the ornithological literature over a forty-year period.  
57 From this they identified the taxonomic families containing the largest number of  
58 kleptoparasitic species. The families of birds with the highest numbers of kleptoparasites  
59 were the *Falconidae* (falcons, kestrels, caracaras), *Accipitridae* (hawks, eagles, harriers, old  
60 world vultures), and the *Laridae* (gulls). The presence of kleptoparasitism in the *Laridae*  
61 being much more pronounced than in the other families with 23 of the 88 species of gull  
62 making use of kleptoparasitic strategies. The significant investment of gulls in  
63 kleptoparasitism highlights the value of this strategy to those species making them an  
64 important family of birds for research into kleptoparasitism (Verbeek, 1977a; Verbeek,  
65 1977b; Barnard & Thompson, 1985; Spencer et al. 2017).

66 Kleptoparasitic interactions occur when individuals forage socially (Barnard, 1984),  
67 and gulls are highly gregarious (Perrins, 2009). Much of the sociality of gulls outside the  
68 breeding season consists of mixed-species feeding aggregations around ephemeral food  
69 sources (Tinbergen, 1953; Perrins, 2009). These aggregations are complex competitive  
70 situations of the type likely to encourage kleptoparasitism as a foraging strategy. In gulls,  
71 kleptoparasitism has also been shown to be a facultative response to changing environmental  
72 conditions (Maniscalco & Ostrand, 1997). High levels of kleptoparasitism are more likely  
73 when certain environmental conditions prevail (Brockmann & Barnard, 1979), these include  
74 high densities of foragers and high concentrations of larger food items (Spencer et al. 2017).

75 Further, kleptoparasitism is not a unitary concept (Giraldeau & Caraco, 2000) and  
76 theft can be enacted through one of three kleptoparasitic strategies that have been described.  
77 These are *aggressive kleptoparasitism* (use of force or threat to steal food – Hansen, 1986;  
78 Liker & Barta, 2002), *stealth kleptoparasitism* (sneaky theft with limited interaction between  
79 kleptoparasite and host – Hockey et al. 1989) and *scramble kleptoparasitism* (theft by  
80 multiple individuals – Erlandsson, 1988). The quantity and divisibility of food items, as well  
81 as competitive differences between foragers will clearly influence which of these strategies  
82 are used when a kleptoparasitic population exploits a finite patch of resources. The fact that  
83 gulls frequently forage in mixed-species flocks, differ in size and competitive ability between  
84 species and are opportunistic foragers with a diverse diet suggests that all three of these  
85 strategies may be utilised if the correct social and environmental circumstances are  
86 encountered.

87 Following Giraldeau & Caraco (2000) we define a behaviour to be *social foraging* if  
88 two or more individuals associate and the functional consequences of their foraging  
89 behaviours are interdependent. Kleptoparasitism can be considered a social foraging strategy,  
90 a consequence of this is that the best foraging decision an individual can make depends on

91 what other individuals in the population are doing. Giraldeau & Caraco (2000) defined this as  
92 the “concurrent economic interdependence among different individuals’ payoffs and  
93 penalties” (p.3). A critical implication of this is that the analysis of kleptoparasitic behaviours  
94 requires the use of game theory. Indeed, contests over resources of this nature were among  
95 the foundational questions initially addressed by evolutionary game theory (Maynard Smith,  
96 1982). Several approaches have been taken to modelling kleptoparasitism using game theory,  
97 these include *Producer-Scrounger (P-S) Models* (Barnard & Sibly, 1981) and  
98 *Kleptoparasitism Models* (Broom & Ruxton, 1998).

99 P-S models identify the equilibrium or stable level of kleptoparasitism that should  
100 occur in a given population. A key feature of such models is that food items, or the items of  
101 food within a patch, are highly divisible. This can be a realistic assumption when studying  
102 certain species, for example, the patches exploited by many seed feeding passerines often  
103 contain many small items that can be shared between numerous foragers (Barnard & Sibly,  
104 1981). However, frequently food patches will contain fewer items that have only limited  
105 divisibility. This was true of the foraging environment exploited by the gull population that  
106 was the focus of this research.

107 The Kleptoparasitism Models developed by Broom and colleagues (Broom & Ruxton,  
108 1998; Broom et al., 2004) model foraging situations where food items come in single units  
109 that have limited divisibility and are often completely consumed by an individual forager.  
110 These Kleptoparasitism Models can be used to analyse the frequency of producing to  
111 scrounging behaviour, much like P-S models, but have an advantage over P-S models in that  
112 they can also be used to investigate the conditions that promote the theft of food and to assess  
113 the best decision individual foragers can make given those conditions. In this research we  
114 considered all three of these analyses when investigating the kleptoparasitic behaviours of a



115 foraging gull population, so we adopted Kleptoparasitism Models as the most appropriate  
116 modelling technique.

117 Kleptoparasitism Models (Broom & Ruxton, 1998; Broom & Ruxton, 2003; Broom et  
118 al. 2004; Broom & Rychtar, 2007; Broom & Rychtar, 2009; Hadjichrysanthou & Broom,  
119 2012) have systematically explored the kleptoparasitic foraging space, often changing key  
120 variables of the model one at a time to examine how this influenced behaviour. For example,  
121 the initial model in this series by Broom & Ruxton (1998), based on a mechanistic model by  
122 Ruxton & Moody (1997), considered a population of foragers where a searcher, upon  
123 encountering another forager handling a food item, was faced with the decision whether to  
124 ignore that handler and keep searching for food items or attempt to steal food from the  
125 handler. The handler was assumed always to defend its food item from attempts to steal it. In  
126 a later model (Broom et al. 2004) the assumption that the handler always defends was relaxed  
127 and the handler was given the option of whether to defend the food item or surrender it  
128 without a fight. The key features of the models developed by Broom and colleagues are: a  
129 foraging population of a fixed density; a compartmental approach to modelling the population  
130 where individuals can be in only one behavioural state at a time (e.g.. handling, searching or  
131 fighting) and the rates of change between those behavioural states are described by a system  
132 of differential equations; the assumption, previously mentioned, that food items come in  
133 single units that have limited divisibility and are consumed completely by an individual  
134 forager; as well as the use of time to model all foraging costs. Here, searching for food items,  
135 handling a food item, and engaging in a fight to either try to steal or keep hold of a food item  
136 all have a cost in terms of time. The costs incurred by the forager for making the incorrect  
137 behavioural decision accumulate over time because, whilst it is engaged in the wrong  
138 behaviour, it loses the opportunity to be doing something else that could more quickly lead to  
139 the acquisition of a food item and is thereby more profitable.

140           The kleptoparasitism modelling approach can be extended in many ways to consider  
141 various constraints and assumptions in relation to the environment and foragers. For example,  
142 the complexity of the basic model can be increased by introducing competitive differences  
143 between foragers in the population and by increasing the number of behavioural strategies  
144 they can use. These models, whilst more complex to find solutions for, still assume a forager  
145 seeks to maximise its rate of food or energy intake whilst foraging and this is achieved by  
146 choosing the behaviours that minimise the amount of time needed to obtain and consume  
147 food items.

148           The complexity of organisms, particularly when studied in wild populations means we  
149 must often rely on simple measurements that act as proxies for fitness (Hunt & Hodgson,  
150 2010). An animal's food intake rate can be seen as a proxy for fitness mediated through  
151 survivorship. Survivorship is a key component of fitness (Hunt & Hodgson, 2010), so an  
152 animal that maximises its long-term rate of food intake will, on average, have higher  
153 survivorship relative to other foragers in the population with whom it is competing. This  
154 higher feeding rate is assumed to translate into a fitness advantage for that individual and the  
155 genes that encode for the successful strategy it uses (Grafen, 1991).

156           Kleptoparasitism Models developed by Broom and colleagues have provided many  
157 theoretical insights into the behaviours we should expect to be prevalent in a population,  
158 however, little empirical work has been conducted to test these models or to compare their  
159 predictions against the behaviour of real foragers. This is because it is difficult to find real  
160 foraging populations that match all the simplifying assumptions necessary for comparison  
161 against a mathematical model.

162           In this research the compartmental kleptoparasitism modelling approach was used to  
163 investigate the behaviours of a real population of gulls foraging in an urban environment.

164 This was a population at Billingsgate Market, London, UK. The population at Billingsgate  
165 consists of three gull species all competing to exploit food resources in the car park area of  
166 the market.

167 A number of features of the foraging environment and the gull population at  
168 Billingsgate made it a useful candidate for using mathematical modelling as a study tool.  
169 First, the site is an anthropogenic environment and not a complex natural food web. This  
170 allowed us to consider Billingsgate as a kind of natural laboratory. The foraging area at  
171 Billingsgate is discrete and of a fixed size (the car park area), so travel time costs between  
172 patches in the foraging area could be largely discounted. In addition, the population at  
173 Billingsgate consists of three gull species all competing to exploit the same anthropogenic  
174 food discards, there are no other trophic levels involved, no other competitor species from  
175 outside the *Laridae* family and no predator species that might affect foraging behaviour that  
176 needed to be considered. The gulls show high levels of habituations to humans and their  
177 vehicles at this site; we noted this during field observations through the birds' short flight  
178 initiation distances. The presence of humans clearly influences foraging behaviour but this is  
179 largely through these birds having associated humans and their vehicles with the presence of  
180 food at the site. Humans were viewed primarily as an opportunity for food as opposed to a  
181 perceived predatory risk. All of the above factors made it easier to meet some of the  
182 simplifying assumptions necessary when trying to model behaviour mathematically.

183 Second, as all three study species were gull species they effectively have the same  
184 behavioural abilities and design with which to manipulate their environment when foraging,  
185 despite differing in competitive ability due to size differences. Having a standardised model  
186 forager again simplified the mathematics needed to model the foraging situation.

187           Third, the population at Billingsgate is stable. Birds are able to arrive and leave but on  
188 the whole the size and composition of the population exploiting food resources at the site  
189 remained fairly constant. Headcounts for the population, over the year of study, showed that  
190 the mean population size varied very little from month to month, having a small standard  
191 deviation relative to the mean. The population consisted of only the three study species and  
192 comparisons of headcounts for the total population and headcounts for patches showed a  
193 great deal of correspondence between the proportion of each species engaged in foraging and  
194 the proportion of each species in the population as a whole. This stability made the  
195 boundaries of the Billingsgate study population more clearly demarcated than is often  
196 possible for a wild population of birds. This fits with the assumption of a foraging population  
197 of fixed density used in this modelling approach.

198           Fourth, the real foraging data recorded at Billingsgate was obtained using  
199 observational field methods. This meant that it was not possible to directly measure the  
200 energetic costs of fighting over a food item or any possible injury costs to the individuals  
201 involved. However, the observational methods used did permit the costs of fights and  
202 searching for food items to be measured in terms of the duration of time they took, this  
203 matched the method for assessing costs used in the various models developed by Broom and  
204 colleagues.

205           Fieldwork was conducted at Billingsgate Market to record the kleptoparasitic  
206 interactions occurring between the gulls in that environment. The compartmental modelling  
207 approach was then used to develop a model of that population using the population  
208 parameters and strategies available to the foraging gulls at Billingsgate. The model was  
209 compared to the foraging behaviour recorded at Billingsgate to assess whether different  
210 behaviours were at equilibrium densities in the population and to conduct an analysis of

211 whether individuals in the Billingsgate population are making the best behavioural responses  
212 in their use of kleptoparasitism.

213           As natural selection is expected to produce foragers that are efficient and make  
214 effective behavioural decisions, it was predicted that the density of distinct foraging  
215 behaviours at Billingsgate would be at or close to equilibrium densities predicted by the  
216 model. As food at this site is limited in divisibility and quantity and the population is stable,  
217 we can expect there to be a minimum level of competition below which the population rarely  
218 falls, even if the composition of individual patches varies. Although we were unable to mark  
219 individual birds, the few colour ringed birds and birds with plumage aberrations or old  
220 injuries that were distinctive were sighted repeatedly suggesting that some of the birds  
221 foraging at Billingsgate were there consistently. In addition, the food that is available at the  
222 site is regularly scheduled, it occurs between certain hours of the day in predictable locations  
223 and in some cases is provided by the same individuals, parked in the same place, disposing of  
224 their discards at about the same time, making the competitions individuals engage in  
225 iterations of very similar contests over resources. Based on these factors we expected gulls at  
226 Billingsgate to be effective at making economic decisions regarding when to attempt  
227 kleptoparasitism and when to not. Foragers at Billingsgate were thereby expected to have  
228 converged over time to equilibrium densities of the different foraging behaviours present in  
229 the population.

230           Further, it was predicted that individual gulls in the foraging population would also be  
231 effective at deciding which behavioural strategy was the best in different environmental  
232 conditions and at adjusting their behaviour accordingly as environmental parameters in  
233 individual patches, such as food availability and population density, changed (Sirot, 2000).  
234 This was expected as kleptoparasitic strategies in wild gull populations have in previous  
235 research been shown to be facultative responses to changing environmental conditions

236 (Maniscalco & Ostrand, 1997) and as kleptoparasitism is ubiquitous among these species,  
237 that are highly mobile and encounter varied environmental conditions, it is assumed to be a  
238 beneficial foraging strategy with significant adaptive value.

239

240

## Methods

### *Study Site and Species*

242 *Study Site:* Billingsgate Market, London (Lat: 51°30'20.40"N; Long: 0°00'43.90"W) is a  
243 seafood market in the Canary Wharf area of East London. Research at this location was  
244 conducted in a car park area used by fishmongers to process and load their stock onto vans,  
245 called the Trader's Car Park. The Trader's Car Park covered an area of 0.0104 square  
246 kilometres (10,400m<sup>2</sup>). The size of this area was calculated using scaled aerial photographs  
247 from google maps. Figure 1 shows the boundaries of the Trader's Car Park from an aerial  
248 position.

249

### INSERT FIGURE 1 ABOUT HERE

250 *Study Species:* Gulls aggregate at Billingsgate to exploit seafood waste and leftovers  
251 discarded in the car park areas. The population of gulls found at this site consists of the Great  
252 Black-backed gull (GBB: *Larus marinus*), Herring gull (HG: *Larus argentatus*) and Black-  
253 headed gull (BHG: *Chroicocephalus ridibundus*). The exact history of the presence of a  
254 foraging gull population at Billingsgate is unknown; however, the site has been operating as a  
255 fish market in its current location since 1982. It is likely that gulls have been exploiting  
256 resources at this site for much of this time. The only other species' that occasionally exploit  
257 food opportunities at this site are small numbers of visitors from the *Corvidae* and  
258 *Columbidae* bird families. However, these species are infrequent visitors that largely avoid  
259 foraging groups of gulls.

260 *Measures*

261 *Population size and composition:* The size and composition of the population at Billingsgate  
262 was calculated using two methods. The first used headcount photos to count the total size and  
263 composition of the population present at the site. The size of the gull population at  
264 Billingsgate was calculated using headcounts from scan samples at 30 minute intervals. The  
265 number and species of gulls at the site were recorded. The second used headcounts at  
266 foraging patches to calculate the number and species of gulls engaged in foraging behaviour.  
267 Videos of foraging patches were viewed and a record made of the number and species of all  
268 individuals that attended the patch to forage.

269 *Kleptoparasitism:* Kleptoparasitism was recorded as frequency counts. Kleptoparasitic  
270 behaviours were deemed to have taken place if the strategies of *aggressive* or *stealth*  
271 kleptoparasitism, described by Giraldeau & Caraco (2000), were used. These were  
272 operationalised as follows:

273 *Aggressive kleptoparasitism:* Aggressive kleptoparasitism occurred if the parasite used force  
274 or threats to attempt kleptoparasitism through any of the behaviours described in Table 1. The  
275 use of threats constituted attempted kleptoparasitism without the incident necessarily  
276 escalating to physical contact between the parasite and the host as the host could choose to  
277 surrender the food item rather than defend it. Successful use of aggressive kleptoparasitism  
278 occurred only if the parasite obtained the whole of the food item being contested, either by  
279 physically taking it or if the host surrendered the item following one of the threats described  
280 (Table 1).

281 *Stealth kleptoparasitism:* Stealth kleptoparasitism was typified by the use of speed to  
282 approach, grab the food item and try to make off without directly confronting the handler for  
283 the item. Behaviours constituting stealth kleptoparasitism are described in Table 1. If the

284 parasite managed to obtain any proportion of the food item being contested successful use of  
285 stealth kleptoparasitism had occurred.

286 *Host responses to kleptoparasitism:* Analysis was conducted to evaluate the response of hosts  
287 when attacked by kleptoparasites. Hosts could either try to defend the food item they were  
288 handling or surrender the item to the kleptoparasite. Of the 577 kleptoparasitic attempts  
289 recorded, a strategy (surrender or defend) could be attributed to the host on 321 occasions. A  
290 conservative criterion was used to avoid misattributing defensive strategies. On the 256  
291 occasions where it was not possible to attribute a strategy this was often because the  
292 observer's view of the handler became obstructed at the crucial moment. This was common  
293 due to the frantic nature of the foraging activity in patches.

294 **INSERT TABLE 1 ABOUT HERE**

#### 295 *Procedure*

296 Observations at Billingsgate were conducted between the hours of 7am and 3pm. The trading  
297 hours for the market are 3am to 8:30am. After 8:30am the main activity at the site is the  
298 clean-up of the market and car park areas. Prior to 7am it was not possible to conduct  
299 observations as the large number of vehicles at the site made unobstructed observations of the  
300 study area unfeasible. After 7am the car park emptied considerably making it easier to  
301 conduct observations. This was the time that the largest number of gulls foraged in the car  
302 park. Field sessions had a mean duration of 2 hours 52 minutes (Range: 2h – 5h 05m) and  
303 were conducted on days when the market was operational (Tuesday – Saturday) and when it  
304 was closed (Sunday, Monday). A total of 80 hours 15 minutes of field observations were  
305 conducted over 33 field days across the course of a calendar year between July 2014 and June  
306 2015.



307 Observations were conducted from a vehicle. On each study day the location that  
308 would give the best unobstructed view of the study area was identified and used as the  
309 observation position for that field session. It was not always possible to use the same position  
310 as the unpredictable nature of vehicular traffic at the site meant a good observation point one  
311 day may have a view obstructed by a large vehicle the next. Food resources at the site were  
312 located in discrete patches where they were either spilled or discarded on the ground. When  
313 patches of food were discovered by gulls they were filmed from inside the vehicle using a  
314 Sony 8.9 megapixel HD camcorder. Using the vehicle as a hide in this way meant that the  
315 presence of the researcher did not disturb foraging behaviour in the study area. Patches were  
316 filmed until the resource in the patch had depleted and the birds dispersed. Over the year of  
317 study 183 foraging patches were recorded and the time taken to deplete these patches ranged  
318 in duration from 0 minutes 25 seconds to 29 minutes 36 seconds. The location of patches  
319 within the study area, the start and end time of the patch and the headcount and species of the  
320 gulls present at the patch were recorded. Patch videos were analysed at a later time for  
321 kleptoparasitic incidents, where the species, strategy and outcome of the interaction were  
322 noted. Patch videos were also analysed to assess the rate of food intake through foraging at  
323 the site. This involved counting all occasions when foragers in a patch sampled the ground  
324 for a food item, and all occasions when they actually obtained a food item. The species and  
325 number of individuals exploiting a foraging patch was also recorded.

326 To identify the strategies used by foragers at Billingsgate, focal animal observations  
327 were conducted using video recordings of foraging patches. Individual foragers were  
328 observed as they moved around the patch and a continuous record was made of their foraging  
329 behaviours, indicating whether they sampled for food items, attacked using AGG, attacked  
330 using ST and, when handling, whether they defended, resisted or surrendered against attacks  
331 by other foragers. These focal animal observations were used to build up a picture of the

332 forager's behaviour and to attribute a strategy to the forager based on the ESS strategies  
333 outlined in Table 4.

334 Headcounts of the total population were conducted at 30 minute intervals from the  
335 start of a field session. A series of photographs was taken using a Nikon Coolpix P510 (42x  
336 zoom) bridge camera, to capture all gulls in the study area. These photographs were later  
337 analysed to calculate the population size and composition.

338

339

### **The model**

340 The foraging behaviours considered in this model are: searching for food items, handling  
341 food items, and two kleptoparasitic strategies, aggressive kleptoparasitism and stealth  
342 kleptoparasitism. A forager encountering a handler can choose to ignore the handler and keep  
343 searching or attack the handler using either aggressive or stealth kleptoparasitism. Similarly,  
344 a handler attacked by another forager can choose to defend or surrender its food item. These  
345 interactions effectively encapsulated the behaviours of interest present in the Billingsgate  
346 population. Although there is potentially a third type of kleptoparasitic strategy described by  
347 Giraldeau & Caraco (2000) that gulls can use, 'scramble kleptoparasitism', where multiple  
348 foragers simultaneously steal portions of a food item, it was not included in the model due to  
349 its lack of occurrence at Billingsgate.

350 The model developed here considers a population containing one species of forager.  
351 This single-species model reduced the complexity of the mathematics needed to model the  
352 foraging population and the model was compared against the averaged foraging data obtained  
353 for the whole population at Billingsgate. Although the Billingsgate population contained 3  
354 species, with kleptoparasitism occurring both within and between species, the assumption  
355 was made that averaging the data over the whole year of study would smooth out any

356 asymmetries in competitive ability between individuals and species and permit the population  
357 to be viewed as a large population containing just one-species.

358         Broom et al. (2004) considered a population of foragers that can either attack or  
359 ignore handlers and defend or surrender food items. The model developed here extends this  
360 by considering two types of kleptoparasitic strategy and we retain and extend the notation and  
361 parameters used in Broom et al. (2004) where necessary. The foraging population consists of  
362 a population density of  $P$  individuals. That foraging population ( $P$ ) consists of groups of  
363 individuals in different behavioural states or compartments. A forager can only be engaged in  
364 one behavioural state and thereby can only be in one compartment at a time. At any time a  
365 proportion of the foraging population are searching ( $S$ ) for food items and a proportion are  
366 handling ( $H$ ) a food item. An average density  $f$  of food items is available and a forager can  
367 search the foraging area at a rate  $v_f$  for food items. The rate at which food items are  
368 discovered is therefore  $v_f f$ . Similarly, the rate at which a forager can search the foraging area  
369 for handlers is  $v_h$ , so the rate at which searchers encounter handlers of food items is  $v_h H$ .  
370 Following Broom et al. (2004), the time that food items take to handle is modelled using an  
371 exponential probability distribution with mean  $t_h$ . Additionally, a proportion of the foraging  
372 population are engaged in fights over food items, either as kleptoparasites trying to steal an  
373 item or handlers trying to keep hold of that food item. As stated previously, two  
374 kleptoparasitic strategies are possible within this population: aggressive kleptoparasitism or  
375 stealth kleptoparasitism. At any given time a proportion of the foraging population ( $P$ ) will  
376 be attempting to steal items using aggressive kleptoparasitism ( $A$ ) and a proportion of  
377 handlers will be fighting against those kleptoparasites by trying to defend ( $D$ ) their food item  
378 from being stolen. Likewise, a proportion of the foraging population will be attempting to  
379 steal using stealth kleptoparasitism ( $C$ ) and an equal proportion of handlers will be fighting  
380 to resist ( $R$ ) their food item being stolen by stealth kleptoparasites. Defending and resisting

381 are terms that both describe the defensive behaviour of handlers that are under attack,  
 382 separate terms were used, for defending against aggressive kleptoparasitism and resisting  
 383 against stealth kleptoparasitism, to differentiate the two behaviours as the probability of  
 384 defensive behaviour against one type of kleptoparasitism might differ from that of the other  
 385 type. Defenders ( $D$ ) and Resisters ( $R$ ) are therefore separate behavioural states in the  
 386 foraging population ( $P$ ). The composition of the total foraging population by compartments  
 387 that capture the different behavioural states is described by equation (1),

388

$$389 \quad P = S + H + A + D + C + R. \quad (1)$$

390

391         Once a searcher encounters a handler it either attacks the handler using aggressive  
 392 kleptoparasitism, it does this with probability  $p_1$ , or it attacks the handler using stealth  
 393 kleptoparasitism, this occurs with probability  $p_2$ , otherwise it ignores the handler and  
 394 continues searching for undiscovered food items, this occurs with probability  $1 - p_1 - p_2$   
 395 (note that this means  $p_1 + p_2 \leq 1$ , e.g. see Table 4). Conversely, a handler that is found and  
 396 attacked with aggressive kleptoparasitism can either defend against the attack, which it does  
 397 with probability  $p_3$ , or surrender the food item without a fight, which occurs with probability  
 398  $1 - p_3$ . Likewise, a handler that is attacked by a searcher using stealth kleptoparasitism  
 399 resists the attack with probability  $p_4$  or surrenders the food item without a fight with  
 400 probability  $1 - p_4$ . If a searcher attacks using aggressive or stealth kleptoparasitism and the  
 401 handler defends or resists then a fight occurs. The fight lasts for a time duration that is  
 402 modelled using an exponential probability distribution. In the case of aggressive  
 403 kleptoparasitism the duration of the fight is drawn from an exponential distribution with  
 404 mean  $t_a/2$ , the attacker wins the fight with probability  $\alpha$  and the defender wins the fight with

405 probability  $1 - \alpha$ . The duration of a stealth kleptoparasitism fight is also drawn from an  
 406 exponential distribution with mean  $t_c/2$ . The stealth attacker wins the fight with probability  
 407  $\beta$  and the resistor wins the fight with probability  $1 - \beta$ . The mean duration of stealth and  
 408 aggressive fights differs as a stealth fight involves less of an interaction between attacker and  
 409 handler than an aggressive fight so on average  $t_c < t_a$ . At the end of a fight of either type the  
 410 winner begins handling the contested food item and the loser resumes searching, either for  
 411 food items or other handlers. The notation used for the strategies and parameters described  
 412 above is summarised in Table 2.

413 **INSERT TABLE 2 ABOUT HERE**

414 If the foraging population described above and encapsulated in equation (1) is assumed to  
 415 consist of only one species then the dynamics of that population are captured by the  
 416 compartmental model outlined in Figure 2.

417 **INSERT FIGURE 2 ABOUT HERE**

418 The change in the density of each behavioural compartment as described by the rates  
 419 of inflow and outflow along the arrows shown in Figure 2, within the closed system defined  
 420 by equation (1), is described by the following system of 6 differential equations (2-7):

$$421 \quad \frac{dS}{dt} = \frac{1}{t_h}H + \frac{2}{t_c}(1 - \beta)C + \frac{2}{t_c}\beta R + \frac{2}{t_a}(1 - \alpha)A + \frac{2}{t_a}\alpha D - v_f f S - p_1 p_3 v_h S H - p_2 p_4 v_h S H, \quad (2)$$

$$422 \quad \frac{dH}{dt} = v_f f S + \frac{2}{t_c}\beta C + \frac{2}{t_c}(1 - \beta)R + \frac{2}{t_a}\alpha A + \frac{2}{t_a}(1 - \alpha)D - \frac{1}{t_h}H - p_1 p_3 v_h S H - p_2 p_4 v_h S H, \quad (3)$$

$$423 \quad \frac{dC}{dt} = p_2 p_4 v_h S H - \frac{2}{t_c}C, \quad (4)$$

$$424 \quad \frac{dR}{dt} = p_2 p_4 v_h S H - \frac{2}{t_c} R, \quad (5)$$

$$425 \quad \frac{dA}{dt} = p_1 p_3 v_h S H - \frac{2}{t_a} A, \quad (6)$$

$$426 \quad \frac{dD}{dt} = p_1 p_3 v_h S H - \frac{2}{t_a} D. \quad (7)$$

## 427 **Analysis**

428 The model was analysed and solved through three stages where equilibrium densities of the  
429 different behaviours and candidate ESS's were identified.

### 430 ***Stage 1: Equilibrium densities of the behavioural compartments:***

431 The foraging population under consideration is assumed to converge over time towards the  
432 equilibrium state (Luther & Broom (2004) provide a proof of why such an assumption is  
433 justified); this is the point at which the number of individuals in the different behavioural  
434 compartments is not changing and is found by setting each of equations 2 to 7 equal to zero  
435 and solving. So, the behavioural compartments in the population are at equilibrium densities  
436 when:

$$437 \quad \frac{dS}{dt} = \frac{dH}{dt} = \frac{dC}{dt} = \frac{dR}{dt} = \frac{dA}{dt} = \frac{dD}{dt} = 0. \quad (8)$$

438 Equations 4, 5, 6 and 7 were solved first. The solutions for these equations were then  
439 substituted for  $C, R, A$  and  $D$  in equation 2 to give the equilibrium density of searchers ( $S$ )  
440 shown in equation 9. Equation 9 was then substituted for  $S$  into the solutions for  $C, R, A$  and

441  $D$  to give equilibrium solutions for these four behavioural compartments specified in terms of  
 442 only one unknown variable  $H$ , the density of handlers (Note that  $S$  is already explicit in terms  
 443 of  $H$ ). These solutions are given in equations 10, 11, 12 and 13.

$$444 \quad S = \frac{H}{t_h v_{ff}}, \quad (9)$$

$$445 \quad C = \frac{1}{2} \frac{p_2 p_4 t_c v_h H^2}{t_h v_{ff}}, \quad (10)$$

$$446 \quad R = \frac{1}{2} \frac{p_2 p_4 t_c v_h H^2}{t_h v_{ff}}, \quad (11)$$

$$447 \quad A = \frac{1}{2} \frac{p_1 p_3 t_a v_h H^2}{t_h v_{ff}}, \quad (12)$$

$$448 \quad D = \frac{1}{2} \frac{p_1 p_3 t_a v_h H^2}{t_h v_{ff}}. \quad (13)$$

449 To find the equilibrium density of handlers, the five equilibrium solution (9-13) were  
 450 substituted into equation 1 giving equation 14, which simplifies to equation 15.

$$451 \quad P = \frac{H}{t_h v_{ff}} + H + \frac{1}{2} \frac{p_2 p_4 t_c v_h H^2}{t_h v_{ff}} + \frac{1}{2} \frac{p_2 p_4 t_c v_h H^2}{t_h v_{ff}} + \frac{1}{2} \frac{p_1 p_3 t_a v_h H^2}{t_h v_{ff}} + \frac{1}{2} \frac{p_1 p_3 t_a v_h H^2}{t_h v_{ff}}, \quad (14)$$

$$452 \quad \Rightarrow P = \frac{H}{t_h v_{ff}} + H + \frac{p_2 p_4 t_c v_h H^2}{t_h v_{ff}} + \frac{p_1 p_3 t_a v_h H^2}{t_h v_{ff}}. \quad (15)$$

453 Equation 15 was solved for  $H$  to give quadratic equation 16, and the equilibrium  
 454 density of handlers is the positive solution to equation 16 depicted using the quadratic  
 455 formula in equation 17. Appendix A gives detailed solutions for the system.

$$456 \quad -(p_1 p_3 t_a + p_2 p_4 t_c) v_h H^2 - (1 + t_h v_{ff}) H + t_h v_{ff} P = 0, \quad (16)$$

$$457 \quad \Rightarrow \frac{1 + t_h v_{ff} \pm \sqrt{(1 + t_h v_{ff})^2 - 4 \times -(p_1 p_3 t_a + p_2 p_4 t_c) v_h \times t_h v_{ff} P}}{2 \times -(p_1 p_3 t_a + p_2 p_4 t_c) v_h} = H. \quad (17)$$

458 **Stage 2: Conditions for using kleptoparasitism and defending/resisting against**

459 **kleptoparasitic attacks:**

460 This section outlines the conditions when it is advantageous for an individual forager to  
 461 attempt kleptoparasitism upon encountering a handler or to defend/resist against  
 462 kleptoparasitism when that forager is a handler that has just been challenged. The two types  
 463 of kleptoparasitism, aggressive and stealth are abbreviated to AGG and ST for convenience  
 464 hereafter.

465         Some additional assumptions of the model are introduced here. The payoffs obtained  
 466 from a fight are measured in terms of units of a food item. The assumption is made that if a  
 467 forager attacks using AGG and wins the fight it obtains the whole of the food item contested,  
 468 so the gain obtained is the probability of winning times the value of the item, which is 1  
 469 (representing one whole food item). Likewise if the handler defends the item and wins an  
 470 AGG fight it retains the whole item. It also follows that if a searcher attacks AGG and the  
 471 handler surrenders, the attacker obtains the whole food item without a fight. So the gain for  
 472 winning an AGG fight is  $1 \times \alpha = \alpha$  (where  $\alpha$  is the probability of the attacker winning the  
 473 fight as defined in Table 2).

474         In contrast, if a forager attacks using ST and wins the assumption is made that it  
 475 obtains only a portion of the food item contested if the handler defends, and the handler  
 476 retains the remaining portion. This assumption exists because this strategy is a sneaky  
 477 strategy that involved less of an interaction between forager and handler but often resulted in  
 478 the attacker obtaining only a portion ( $x$ ) of the food item (Table 2). So the gain for the  
 479 attacker from winning a stealth fight is  $x \times \beta = \beta x$ , where  $x$  is some portion less than 1, and  
 480 the proportion retained by the resisting handler even if it loses is:  $\beta(1 - x)$ . If the forager  
 481 attacks ST and loses then the handler retains the whole of the food item, and similarly if the  
 482 forager attacks ST and the handler surrenders then the forager obtains the whole food item.



483           The value of food items was measured in the way described because the field data for  
484 foraging behaviour at Billingsgate was collected using observational methods, so there was  
485 no way to directly measure the calorific value of different food items. The sizes of items in  
486 the environment also could not be controlled by the researcher. This limitation of the  
487 observational field methods meant that differences in the size and value of food items could  
488 not be accurately quantified but the method described above reduced the need to know these  
489 dimensions by assessing contested items as one unit of food that was either wholly or partly  
490 obtained. The food items at Billingsgate, being anthropogenic waste and seafood discards, are  
491 significantly larger than the food items found at coastal foraging sites (Spencer et al. 2017).  
492 This abundance of larger items meant the majority of food items at Billingsgate were big  
493 enough to make them candidates for kleptoparasitic attempts so none of the resources at  
494 Billingsgate were excluded from the model as being too small for kleptoparasitism.

495           In effect food items could be repeatedly stolen on multiple occasions; this requires  
496 some clarification of how potentially smaller and smaller items of food that have experienced  
497 some handling were treated, particularly in relation to ST kleptoparasitism where only  
498 portions of the food item are obtained. The assumption made in the model is that an item of  
499 food has the value of one whole food item regardless of whether it has previously been stolen  
500 or been part of a larger item of food. If a forager sees fit to challenge for the item then it is  
501 treated as one unit of food. It will be noted that this is akin to assuming that food items cannot  
502 be stolen multiple times and are only subject to one kleptoparasitic attempt, after which they  
503 are immediately consumed by the kleptoparasite or handler. The validity of this assumption  
504 was investigated by comparing the simplest cases possible in the population involving partial  
505 food items: whether a handler should resist against ST when attacked by a mutant  
506 kleptoparasite in a population that does not use kleptoparasitism. It was found that the  
507 conditions when it was optimal to resist were the same regardless of whether the

508 kleptoparasitic incident was the first attempt or a subsequent attempt to steal the food. This  
509 indicated that it was valid to treat each food item as one unit of food regardless of previous  
510 handling or whether it had been subject to previous kleptoparasitic attempts (Appendix B).

511 A further assumption of the model, mentioned previously, is that the duration of an  
512 AGG fight ( $t_a/2$ ) is on average longer than the duration of a ST fight ( $t_c/2$ ). So, an ST fight  
513 is less protracted and has a lower time cost but results in a lower payoff in terms of the  
514 portion of the food item gained on average by the attacker. This makes ST a less risky and  
515 less time costly strategy but one with a lower payoff than AGG when both strategies are  
516 successful.

517 The behavioural strategies being used by the population as a whole need to be  
518 considered when trying to identify when it is advantageous for a searcher to use  
519 kleptoparasitism or for a handler to defend/ resist against kleptoparasitic attacks. In the  
520 population being modelled the various population dynamics that are possible result in twelve  
521 situations that need to be considered to identify advantageous conditions for searchers to  
522 attack and handlers to defend/ resist.

523 *Searchers:*

524 Following Broom & Ruxton (1998) and Broom et al. (2004), to assess when it is  
525 advantageous for a searcher to attack a handler it is sufficient to consider the instantaneous  
526 rate at which a searcher becomes a handler after encountering a handler. When a searcher  
527 encounters a handler it must decide whether to ignore the handler and continue searching for  
528 food items or attack the handler using either AGG or ST. The strategy it should use is the one  
529 that minimises the amount of time until it becomes the handler of a food item. This is the  
530 strategy that maximises the forager's rate of gain per time foraging. If it ignores the handler  
531 then it is just a searcher and has a rate of gain of  $v_{ff}$ ; if it attacks it has a rate of gain that is

532 influenced by the time costs of the fight and, if it loses, the rate at which it finds other food  
 533 items or handlers to challenge. The rates at which other food items or handlers are found and  
 534 challenged by foragers are given by the foraging pathways  $T_s$  for AGG attackers (Figure 3)  
 535 and  $T_s^*$  for ST attackers (Figure 4). In this model the following situations need to be  
 536 considered when a searcher encounters a handler:

537 When it is advantageous to attack, when the population resists/defends against attacks.

538 1. When to use AGG (handler defends & population defends).

539 2. When to use ST (handler resists & population resists).

540 When it is advantageous not to attack the handler:

541 3. When to ignore the handler and continue searching for food (population defends/  
 542 resists).

543 When to attack if the population does not resist/defend against attacks.

544 4. Searcher should always attack and the kleptoparasitic strategy used does not matter as  
 545 both AGG and ST have the same payoff when the population surrenders. Both  
 546 strategies obtain 1 whole food item.

547 *Handlers:*

548 When a handler is discovered by a searcher and attacked it can choose either to resist/defend  
 549 the food item it is handling or surrender the item and resume searching for a new food item.

550 The strategy it should use is the one that minimises the amount of time until it resumes

551 handling a food item. If it resists/ defends the food item the time to resume handling is

552 influenced by the duration of the fight and if it loses, the rate at which it encounters other

553 food items or handlers to challenge, as stated above this search path is denoted by  $T_s$  or  $T_s^*$   
 554 (Figures 3 and 4), which shows the time to acquire a food item from the start of searching.  
 555 Likewise if it surrenders the food item it becomes a searcher again and resumes handling at  
 556 the rate at which it finds a new food item or encounters another handler and successfully  
 557 challenges them, again  $T_s$  or  $T_s^*$ . The following situations need to be considered when a  
 558 handler is discovered by a searcher:

559 When it is advantageous for a handler to resist/defend in a population where searchers attack  
 560 and the rest of the handling population resists/defends:

- 561 5. When to defend against AGG (population defends and handler's searching strategy is  
 562 AGG).
- 563 6. When to defend against AGG (population defends and handler's searching strategy is  
 564 ST).
- 565 7. When to resist against ST (population resists and handler's searching strategy is ST).
- 566 8. When to resist against ST (population resists and handler's searching strategy is  
 567 AGG).

568 When it is advantageous for a handler to resist/defend in a population where searchers attack  
 569 and the rest of the handling population does not resist:

- 570 9. When to defend against AGG (population surrenders).
- 571 10. When to resist against ST (population surrenders).

572 (In these two cases the handler's searching pathways are identical as the payoff for  
 573 both AGG and ST is equal when the population surrenders food items.  $T_s$  and  $T_s^*$   
 574 simplify to  $1/(v_f f + v_h H)$ ).

575 When it is advantageous for a handler to resist/defend in a population where searchers do not  
 576 attack but the forager is attacked by a mutant challenger:

577 11. When to defend AGG against a mutant AGG challenger.

578 12. When to resist ST against a mutant ST challenger.

579 (In these two cases the handler's searching pathways are identical as the population  
580 does not attack, so all individuals acquire food at the rate  $v_f f$ . The simplification of  
581  $T_s$  and  $T_s^*$  to this rate is given by  $1/v_f f$ .

582 **INSERT FIGURE 3 ABOUT HERE**

583 **INSERT FIGURE 4 ABOUT HERE**

584 Working through situations 1-12 in turn results in a series of inequality conditions for  
585 a forager's behaviour to be advantageous against the background population strategies  
586 described. These conditions outlining when the use of kleptoparasitism by a searcher and  
587 defending/ resisting against kleptoparasitism by a handler are optimal strategies are  
588 summarised in Table 3 (column 4) and are labelled A1a – A10 (Table 3, column 5).  
589 Appendix C outlines the steps by which conditions A1a – A10 were derived.

590 **INSERT TABLE 3 ABOUT HERE**

591 ***Stage 3: Candidate evolutionarily stable strategies (ESS's):***

592 To fully specify the behaviour of foragers in the population we must consider what decisions  
593 they make at the three decision points described by the four probabilities shown in Table 2,  
594 that is, the probability with which they attack AGG ( $p_1$ ) together with the probability with  
595 which they attack ST ( $p_2$ ) (recall that this is a single decision point with  $p_1 + p_2 \leq 1$ ), the  
596 probability with which a forager defends against AGG ( $p_3$ ) and the probability with which  
597 they defend against ST ( $p_4$ ). Following Hadjichrysanthou and Broom (2012), if the  
598 population is at or near to an equilibrium and all members follow strategy profile

599  $(p_1, p_2, p_3, p_4)$  that population can be invaded by foragers that use a different foraging  
600 strategy which results in a higher food consumption rate, as this would translate into a higher  
601 fitness payoff for those foragers. To consider whether a mutant playing a slightly different  
602 strategy to the rest of the population can invade the population playing strategy profile  
603  $(p_1, p_2, p_3, p_4)$  it is sufficient to consider whether the mutant uses a different strategy at any  
604 one of the three decision points. A different strategy at any one decision point that gives a  
605 higher payoff will result in an overall higher payoff for the mutant and it is sufficient to  
606 consider differences in pure strategies at each of the three decision points. Hadjichrysanthou  
607 and Broom (2012) provided proofs for some generic parameters and conducted extensive  
608 numerical investigation of why there are no mixed-strategy ESS's. Following those  
609 arguments, consideration of the use of only pure strategies in this model means that the  
610 searcher will either always use AGG, always use ST, or always ignore the opportunity to  
611 attack. The working assumption in the current model therefore is that there are twelve  
612 candidates for pure strategy ESS's that need to be considered as outlined below. Here the four  
613 probabilities  $(p_1, p_2, p_3, p_4)$  take the value 1 or 0, meaning the associated behaviour is always  
614 used (1) or never used (0), respectively.

- 615 - Strategy (1,0,1,0) (AGG Defender): The forager always attacks AGG and always  
616 defends against AGG, but never uses or resists against ST.
- 617 - Strategy (0,1,0,1) (ST Resistor): The forager always attacks ST and always resists ST  
618 attacks, but never uses or defends against AGG.
- 619 - Strategy (1,0,0,1) (AGG Resistor): The forager always attacks AGG but only ever  
620 resists against ST attacks.
- 621 - Strategy (1,0,0,0) (AGG Marauder): The forager always attacks AGG but never  
622 resists or defends against attack.

- 623 - Strategy (0,1,1,0) (ST Defender): The forager always attacks ST and only defends  
624 against AGG.
- 625 - Strategy (0,1,0,0) (ST Marauder): The forager always attacks ST but never resists or  
626 defends against attacks.
- 627 - Strategy (1,0,1,1) (AGG Hawk): The forager always attacks AGG and always defends  
628 and resists against both types of attack.
- 629 - Strategy (0,1,1,1) (ST Hawk): The forager always attacks ST and always defends and  
630 resists against both types of attack.
- 631 - Strategy (0,0,1,1) (Retaliator): The forager never attacks but it always defends and  
632 resists against both types of attack.
- 633 - Strategy (0,0,0,0) (Dove): The forager always searches for its own food, it never  
634 attacks and never defends or resists.
- 635 - Strategy (0,0,0,1) (ST Retaliator): The forager never attacks using either strategy and  
636 never defends against AGG but always resists against ST.
- 637 - Strategy (0,0,1,0) (AGG Retaliator): The forager never attacks using either strategy, it  
638 always defends against AGG but never against ST attacks.

639 The twelve possible strategies listed will be evolutionarily stable (ESS's) when different  
640 combinations of the conditions A1a to A10 (Table 3) are met. The combinations of  
641 conditions that result in a strategy being an ESS are shown in Table 4. Where an asterisk is  
642 shown there are no conditions in which the strategy is evolutionarily stable and a population  
643 using that strategy can always be invaded by a mutant playing a different strategy.

644 **INSERT TABLE 4 ABOUT HERE**

## Results

645

646 *Fieldwork results:*

647 *Population size and composition:* The population at Billingsgate had a mean daily size of 40  
648 (Range: 29, 53; standard deviation: ~8) gulls. Foraging patches consisted of a mean of 12  
649 gulls (Range: 9, 20; standard deviation: ~3). A comparison was made of whether the  
650 proportions of each species engaged in foraging differed from the proportion of each species  
651 in the population as a whole, using headcounts for the total population and headcounts at  
652 patches. This comparison showed a great deal of correspondence between the composition of  
653 the total population and the composition of foraging patches (Population Composition: GBB  
654 11%, HG 70%, BHG 19%; Foraging Patch Composition: GBB 12%, HG 72%, BHG: 16%),  
655 which provided some reassurance regarding the stability of the population. As the  
656 kleptoparasitic behaviours of interest occurred within foraging patches, the data obtained  
657 from patches were used for analyses.

658 *Kleptoparasitism:* Kleptoparasitic interactions were recorded in 112/183 foraging patches at  
659 Billingsgate. This gives a ratio of 61% of patches where at least one kleptoparasitic attack  
660 occurred and 39% of patches where no kleptoparasitism was observed. A total of 577  
661 kleptoparasitic incidents were recorded at Billingsgate, 362 (63%) of these occurrences were  
662 AGG kleptoparasitism and 215 (37%) were instances of ST kleptoparasitism. The success  
663 rates for the use of these strategies were AGG:  $286/362 = 79\%$  and ST  $152/215 = 71\%$ .

664 Analysis of host responses to kleptoparasitism showed that on average the population  
665 defended 45% of the time and surrendered 55% of the time. By strategy the population  
666 defended against AGG for 73/209 (35%) attacks and resisted against ST on 72/112 (64%) of  
667 occasions.



668 *Foraging:* Foraging patch videos were analysed to assess how many times foragers sampled  
669 for food and how often they obtained food items. The total number of foragers at Billingsgate  
670 recorded over all foraging patches was 2327. Analyses showed that these foragers sampled  
671 but didn't obtain food on 5605 occasions and sampled and acquired food items on 1641  
672 occasions. These behaviours mirror the foraging behaviours of interest outlined in this model  
673 (Figure 2) where individuals sampling are searchers and individuals acquiring a food item are  
674 handlers. Foraging behaviour at Billingsgate can be summarised as: searchers 5605 (~71%),  
675 handlers 1641 (~21%) and kleptoparasitism 577 (~8%).

676 *Analysis and treatment of Billingsgate foraging data (Obtaining values for the model):*

677 The data from Billingsgate provided values for a number of the model parameters and  
678 strategies. The probability of an attacker winning a fight was given by the mean success rate  
679 of each kleptoparasitic strategy in the population. This was 79% for AGG giving a  
680 probability of success ( $\alpha$ ) of 0.79, and 71% for ST giving a success probability ( $\beta$ ) of 0.71.  
681 The rate at which food was discovered at Billingsgate was calculated as the total number of  
682 items discovered divided by the total number of foragers. This gave a mean rate at which  
683 food items were discovered ( $v_{ff}$ ) as 0.71 items per forager per minute. The rate at which  
684 foragers searched for handlers ( $v_h$ ) was calculated as the rate at which foragers were  
685 discovered to challenge as a proportion of the rate at which food items were discovered, this  
686 returned a value of 0.83 per minute.

687 To calculate the probability of a searcher using a kleptoparasitic strategy, either  
688 attacking AGG or ST upon discovering a handler, ( $p_1$ ) and ( $p_2$ ) respectively, it was  
689 necessary to find some way of accounting for the proportion of occasions that foragers  
690 ignored a handler and continued searching for food items, as there is no direct way of  
691 knowing whether a searcher had the opportunity to attack and did not it was necessary to

692 estimate ignored opportunities. This was done using the percentage of foraging patches where  
693 no kleptoparasitism occurred as a measure of ignored opportunities. Kleptoparasitism was  
694 possible in all foraging patches and the percentage of patches where no kleptoparasitism took  
695 place, 39% of patches, was viewed as a crude index of the rate at which foragers ignored  
696 opportunities to steal. The probability that a searcher attacked using either AGG or ST was  
697 then calculated by multiplying the percentage with which the particular kleptoparasitic  
698 strategy was used by the percentage of patches within which kleptoparasitism occurred  
699 (61%). This gave a probability of attacking AGG ( $p_1$ ) of 0.38 and the probability of attacking  
700 ST ( $p_2$ ) of 0.23. The probability that a handler defended ( $p_3$ ) or resisted ( $p_4$ ) was simply the  
701 proportion of attacks recorded at Billingsgate where the handler defended or resisted.  
702 Handlers at Billingsgate defended against AGG 35% of the time making  $p_3$  0.35 and resisted  
703 against ST 64% of the time making  $p_4$  0.64.

704 Values were unknown for three parameters that were approximated using exponential  
705 probability distributions: mean handling time ( $t_h$ ), mean ST fight duration ( $t_c$ ), and mean  
706 AGG fight duration ( $t_a$ ). Plausible values for these parameters were investigated numerically  
707 using the solutions for the density of each behavioural compartment in the population at  
708 equilibrium and the known parameter values and behavioural compartment densities from the  
709 foraging data for Billingsgate. Table 5 summarises the parameter values and probabilities for  
710 strategy use in the Billingsgate population that were inputted into the model to investigate  
711 equilibrium densities of behaviours.

#### 712 **INSERT TABLE 5 ABOUT HERE**

713 The densities of behaviours in the population were obtained from the real foraging  
714 data for Billingsgate. The mean patch size at Billingsgate was 12 birds per patch. The data  
715 showed that on average the densities of individuals in each behavioural category were: 71%

716 searchers ( $S$ ) (this equates to  $\sim 8.52$  birds/patch), 21% handlers ( $H$ ) ( $\sim 2.52$  birds/patch) and  
 717 8% were engaged in kleptoparasitic fights over food ( $\sim 0.96$  birds/patch). As previously stated  
 718 63% of the observed fights at Billingsgate involved AGG and 37% were ST fights. This gives  
 719 values of approximately 0.6 birds per patch engaged in AGG fights and 0.36 birds per patch  
 720 engaged in ST fights. As fights involved exactly one kleptoparasite and host, the  $\sim 0.6$  birds  
 721 engaged in AGG fights is split 50:50 between aggressive attackers ( $A$ ) ( $\sim 0.3$  birds/patch) and  
 722 defenders ( $D$ ) ( $\sim 0.3$  birds/patch) and the remaining  $\sim 0.36$  birds engaged in ST is split 50:50  
 723 between stealth attackers ( $C$ ) ( $\sim 0.18$  birds/patch) and resistors ( $R$ ) ( $\sim 0.18$  birds/patch).

724 *Testing for equilibrium densities:*

725 The parameter values listed in Table 5 were used to investigate whether the density of  
 726 individuals that occurred in behavioural compartments at Billingsgate could be at an  
 727 equilibrium. Numerical investigation showed that in order for the densities of individuals  
 728 observed in the foraging population at Billingsgate (Table 6, column 3) to be at an  
 729 equilibrium, using the known parameter values and strategy probabilities for that population,  
 730 then the mean handling time for food items ( $t_h$ ), mean duration of ST fights ( $t_c$ ) and mean  
 731 duration of AGG fights ( $t_a$ ) per minute would be:  $t_h = 0.42$ ,  $t_c = 0.14$ ,  $t_a = 0.26$ . Appendix  
 732 D outlines detailed algebraic solutions that gave the parameter values for  $t_h$ ,  $t_c$  and  $t_a$ .

733 Assuming a foraging population of 12 individuals at patches, the above values for  $t_h$ ,  
 734  $t_c$ , and  $t_a$  along with the parameter values shown in Table 5, were inputted into equations 9,  
 735 10, 11, 12, 13 and 17. The quadratic formula (17) giving the equilibrium number of handlers  
 736 was solved first, followed by 9 giving the equilibrium number of searchers and then 10, 11,  
 737 12 and 13 giving the equilibrium number of ST attackers, resistors, AGG attackers and  
 738 defenders respectively. The solutions resulted in equilibrium densities close to the densities  
 739 of individuals in each compartment observed in the Billingsgate population (Table 6).

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**INSERT TABLE 6 ABOUT HERE**

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The results in Table 6 for parameter values  $t_h = 0.42$ ,  $t_c = 0.14$ ,  $t_a = 0.26$  not only gave equilibrium densities close to the densities observed in the Billingsgate foraging population but returned ratios of AGG to ST in line with the rates with which these strategies were used by foragers at Billingsgate. This indicated that the duration of an ST fight to an AGG fight, at the values of  $t_h$ ,  $t_c$  and  $t_a$  identified through numerical investigation, accurately captured the ratio of these two strategies in the real foraging population, this being that the mean duration of an AGG fight was nearly twice that of an ST fight.

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*Ecological conditions for ESS's:*

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An investigation of the regions of parameter space where each of the candidate ESS's shown in Table 4 occur was conducted. Each ESS occurs when a system of inequalities made up by various combinations of conditions A1a to A10 are satisfied (Table 4). Varying the values of different ecological parameters contained in the inequalities had a direct influence on when those inequalities were satisfied. Although all of conditions A1a to A10 were strict inequalities, the boundary conditions where they are satisfied were obtained by setting the left and right-hand sides of the inequalities equal to each other.

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The values for parameters obtained from the Billingsgate data and the values for  $t_h$ ,  $t_c$ , and  $t_a$ , described in the above section, were used in this analysis. Two parameters were allowed to vary when investigating the ecological conditions in which the ESS's occur. These were the rate at which foragers find food ( $v_f f$ ) and the total number of individuals in foraging patches (P) (Table 7).

761

**INSERT TABLE 7 ABOUT HERE**

762 These varied parameters were plotted on a Cartesian plane to create a visual  
763 parameter space of ESS's for different values of the two ecological conditions. None of the  
764 inequalities (A1a – A10) explicitly contain the parameter P. Values for P were obtained by  
765 substituting equation 17 for H in conditions A3 to A8. These were then solved for P using  
766 Wolfram Alpha mathematical software (Wolfram Alpha©, 2016). Conditions A1a, A1b, A1c,  
767 A2, A9 and A10 do not contain the variable H. These inequalities were solved using the  
768 known values from the data recorded at Billingsgate for the various parameters making up  
769 those inequalities, this gave a value of  $v_{ff}$  for all P values.

770 Inputting the real data from Billingsgate into the inequality conditions revealed that 5  
771 of the remaining 7 candidate ESS's shown in Table 4 were actually possible in the parameter  
772 space of the Billingsgate environment. These 5 strategies were AGG Resistor, AGG  
773 Marauder, ST Marauder, AGG Hawk and ST Hawk. It was found that there were no regions  
774 of the foraging parameter space at Billingsgate where all the inequality conditions for the  
775 other two ESS candidates (ST Defender and Retaliator) were met, indicating that, although  
776 they were possible as ESS's, for the values of ecological parameters occurring at Billingsgate  
777 they were not ESS strategies. For the Retaliator strategy this may be explained by the fact  
778 that the probability of success for both AGG and ST,  $\alpha$  and  $\beta$  respectively, were very high at  
779 Billingsgate ( $\alpha = 0.79, \beta = 0.71$ ) making some sort of attacking strategy worthwhile.

780 The inequality conditions that were set as equations and solved for P, described  
781 above, were plotted as boundary conditions in foraging parameter space using MATLAB  
782 (Mathworks©, version R2015b). The regions of parameter space occupied by the five ESS  
783 strategies for Billingsgate are shown in Figure 5.

784 **INSERT FIGURE 5 ABOUT HERE**

785 *Comparing strategy use at Billingsgate with ecological conditions for ESS's:*

786 A total of 189 focal animal observations were completed, as far as could be ascertained these  
787 were conducted on 189 different birds (HG: 102; GBB: 57; BHG: 30). As these focal animal  
788 analyses were observations of wild foraging birds there was considerable variation in how  
789 long a bird could be observed before it was lost from view. The duration for which an  
790 individual was observed was recorded in seconds and varied from 3 seconds to 650 seconds  
791 (Range: 647). A Shapiro Wilk test of normality on the data for duration of focal animal  
792 observations showed that it was significantly non-normally distributed ( $W=0.76$ ,  $p<0.001$ ), so  
793 the median of 60 seconds was the measure of central tendency that probably best reflected the  
794 duration of the focal animal observations conducted.

795         Successfully attributing a strategy to an individual forager required the observation of  
796 interactions by that forager as both a searcher and handler. For a strategy where the forager  
797 never engages in a type of behaviour, such as Retaliator where the searcher never attacks, a  
798 minimum observation period of 300 seconds was used. This was viewed as a sufficiently long  
799 period of time to allow the focal animal's behaviour to be observed in multiple interactions.  
800 None of the individuals observed met this threshold for duration so strategies such as Dove or  
801 Retaliator were not attributed to any birds. As neither of these strategies are ESS's in the  
802 ecological conditions at Billingsgate this was essentially a moot point but is reported here as  
803 it formed part of the method used for attributing strategies. From the 189 observations  
804 conducted it was possible to confidently attribute a strategy to 52 foragers. The strategies  
805 used by these 52 foragers were considered against the ecological conditions (rate of food  
806 discovery ( $v_{ff}$ ) and population density ( $P$ )) in the patches in which they were observed. This  
807 permitted the strategies of our 52 individual foragers to be plotted against ecological  
808 conditions in the parameter space described for Billingsgate in Figure 5.

809         All of the five strategies that could possibly be ESS's at Billingsgate were recorded  
810 from the focal animal observations. Of the 52 foragers attributed strategies it was found that

811 12 of those foragers were using strategies in the correct region of parameter space to make  
812 them ESS strategies and 40 foragers were using their strategies in non-ESS regions of  
813 parameter space; thus ~23% of foragers were making optimal foraging decisions and  
814 individually using an ESS strategy. Figure 6 shows the ESS foraging strategies plotted in  
815 parameter space and Figure 7 shows the location of the foraging strategies used in non-ESS  
816 regions of parameter space.

817 **INSERT FIGURE 6 ABOUT HERE**

818 **INSERT FIGURE 7 ABOUT HERE**

819 Considerable variation was seen between strategies in the rates with which they were  
820 used and the rates with which those strategies were correctly and incorrectly used. Of the 52  
821 foragers to whom strategies could be attributed, ST Hawk (SH) was the least used strategy  
822 being used on only 2 occasions. The most used strategy was AGG Marauder (AM). This  
823 strategy was used on 22 occasions. AGG Resistor (AR), ST Marauder (SM) and AGG Hawk  
824 (AH) were each observed 9, 10 and 9 times respectively.

825 The Marauder strategies (AGG Marauder and ST Marauder) were the strategies used  
826 least effectively by foragers, on all occasions these were observed being used in areas of  
827 parameter space where they were not an ESS strategy. In most of these cases (AM: 14; SM:  
828 10) these strategies occurred in the region of parameter space where AGG Hawk and ST  
829 Hawk were ESS's, indicating that foragers using Marauder strategies were correctly attacking  
830 handlers using AGG or ST, but not defending their food items when attacked in a region of  
831 parameter space where food was scarce and defensive strategies were optimal.

832 AGG Resistor was used in an ESS region on one occasion and in a non-ESS region on  
833 8 occasions. All observations of AGG Resistor in a non-ESS region also occurred in the  
834 region where AGG Hawk and ST Hawk were the ESS's. Foragers using this strategy

835 appeared to make the error of not defending against AGG attacks by other foragers, despite  
836 attacking AGG and resisting against ST.

837 Hawk strategies were used most effectively by foragers. ST Hawk and AGG Hawk  
838 were used in the correct regions of parameter space in which they were ESS's on all  
839 occasions (SH: 2; AH: 9), indicating that individuals using these strategies were making  
840 optimal foraging decisions given the environmental conditions in which they found  
841 themselves. Table 8 shows the frequencies with which strategies were used in ESS and non-  
842 ESS regions of parameter space.

843 Although not considered explicitly in the model the breakdown of strategy use by  
844 species showed that all 12 of the strategies used correctly were used by the larger gull  
845 species, HG and GBB. It was possible to attribute strategies to 24 GBB, 26 HG and only 2  
846 BHG. The results showed that 25% of GBB (6/24 individuals) were using an ESS, 23% of  
847 HG (6/26 individuals) were using an ESS, and neither of the smaller BHG used an ESS.

848 **INSERT TABLE 8 ABOUT HERE**

## 849 **Discussion**

850 This model was developed to try and capture the kleptoparasitic behaviours of a population of  
851 foraging gulls at Billingsgate Market and to investigate what the model could tell us about the  
852 optimality and stability of the behavioural decisions made by individuals in that population.

853 This was pursued in two ways: 1. By considering the density of individuals engaged in each  
854 behaviour of interest in the population and investigating the possibility that these behaviours  
855 were at equilibrium densities. 2. Through assessing the optimality of the behavioural



856 decisions of individual foragers when compared against the ecological conditions in the  
857 patches in which they were foraging. Were foragers using ESS strategies?

858 *Equilibrium densities:* The values of a number of the model parameters were known from the  
859 real foraging behaviour at Billingsgate. The values for handling time ( $t_h$ ), ST fight duration  
860 ( $t_c$ ) and AGG fight duration ( $t_a$ ) were unknown and were varied to investigate numerically at  
861 what values of these parameters the model produced equilibrium densities that matched the  
862 densities of behaviours observed at Billingsgate. The values arrived at were:  $t_h=0.42$ ,  
863  $t_c=0.14$ ,  $t_a=0.26$  minutes. The important question to ask about these values is whether they  
864 are plausible values for the parameters they represent.

865         Considering first the fight duration variables  $t_c$  and  $t_a$ . At the reported values the  
866 duration of an AGG fight ( $t_a$ ) was twice that of an ST fight ( $t_c$ ). This fits with our  
867 understanding of these two kleptoparasitic strategies. Stealth kleptoparasitism by definition is  
868 a sneaky strategy that involves less of an interaction between attacker and handler (Giraldeau  
869 & Caraco, 2000; Vollrath, 1984) and in many cases that interaction was over before the  
870 handler could respond effectively and escalate to a protracted fight. In contrast AGG as a  
871 strategy actually required the attacker to engage in a fight with the handler to try and take the  
872 food item by force. In light of this, the finding that the duration of an AGG fight was twice  
873 that of an ST fight was reasonable and the fact that the values that produced the equilibrium  
874 densities ( $t_c=0.14$ ,  $t_a=0.26$ ) delivered the correct ratio of AGG (~65%) to ST (~35%) as  
875 observed in the Billingsgate population was reassuring.

876         When considering whether these values accurately represent the mean duration of  
877 fights within the Billingsgate population it was noted that fights at Billingsgate, even AGG  
878 fights, whilst variable, were on average short in duration. We estimated from field  
879 observations that ST fights had mean duration of approximately 5 seconds and AGG fights

880 had mean duration of just under 10 seconds. However, we did not rely on these estimates as  
881 they were obtained during fieldwork by glancing at a wristwatch and making a quick note for  
882 an opportunistic sample of incidents, essentially those in close proximity to the observer,  
883 when other recording tasks permitted.

884 Later analysis of foraging videos proved no more effective at providing reliable  
885 estimates of fight duration. There was a large amount of aggression between individuals in  
886 this population and numerous fights, most of which were unrelated to kleptoparasitism.  
887 Fights relating to kleptoparasitic incidents frequently overlapped with and were lost in the  
888 melee of more general aggressive interactions in and around foraging patches. An example of  
889 this we termed “jockeying for position”, which was often seen in patches where a dominant  
890 individual, such as a large GBB, had taken control of a significant item of food. Rather than  
891 challenge the individual for the item a number of birds would fight amongst themselves,  
892 apparently seeking to stay close to the handler waiting for them to finish with and discard the  
893 item. Whilst it was often possible to identify kleptoparasitic attempts on the handler in these  
894 situations accurately keeping track of the individuals for the full duration of the  
895 kleptoparasitic fight in the surrounding melee proved difficult. For this reason we treated  
896 AGG and ST fight duration as unknown variables and followed the approach of investigating  
897 them numerically. When considered as proportions of a minute, the values arrived at through  
898 numerical investigation would make ST fights approximately 4 seconds ( $t_c/2 \times 60 = 0.07 \times$   
899  $60$ ) and AGG fights approximately 8 seconds ( $t_a/2 \times 60 = 0.13 \times 60$ ), both of which sit  
900 close to the level we estimated for the duration of these fights.

901 Over the year of study no significant injuries were sustained by birds engaged in  
902 fights over food. Gulls often sustain injuries whilst fighting and fights can last for a  
903 considerable length of time particularly during the breeding season when they are generally  
904 more aggressive (Tinbergen, 1953; personal obs.). The fact that no observations of injuries

905 were made over the period of study at Billingsgate may reflect that, on the whole, there is no  
906 shortage of food at the site so the conditions that would make staying in a lengthy fight a  
907 good economic decision might not have existed. This interpretation would agree with the  
908 short fight durations produced by the model for both strategies.

909         The value arrived at for mean handling time,  $t_h=0.42$ , is considerably longer than the  
910 mean fight durations. This fits with what is known about food resources in the Billingsgate  
911 environment, which contained an abundance of larger food items most of which required  
912 some handling time before they could be consumed. This longer handling time relative to  
913 fight duration also presents the necessary window of opportunity required for a forager to  
914 identify and challenge handlers before they finished handling and consumed food items. We  
915 did not attempt to obtain a comprehensive estimate of the handling time of food items from  
916 the data. There were very many handling episodes, and estimation could be seriously biased  
917 by two key factors. Firstly, the handling time for food items in general includes the time spent  
918 before and after contests for that item; concentrating only on non-contested items would bias  
919 the results. Similarly there was a great deal of variation in the size of food items available at  
920 Billingsgate and thereby the amount of time we might expect these items to be handled.  
921 Using field observations it would be easy to bias an estimate of handling time as long bouts  
922 of handling are more likely to be noticed and smaller handling bouts easily missed. An  
923 analysis of a sample of the data showed a mean handling time of somewhat over 30 seconds.  
924 The value for mean handling time arrived at through numerical investigation, when  
925 considered as a proportion of a minute gives a value of about 25 seconds ( $0.42 \times 60$ ). This  
926 value is a little lower than our crude estimate but not unrealistically so, suggesting the value  
927  $t_h = 0.42$  is plausible and may accurately reflect the mean times for which birds handled  
928 food items.

929           Using the values for  $t_h$ ,  $t_c$  and  $t_a$  to accurately draw conclusions about whether the  
930 densities of behavioural compartments at Billingsgate were at an equilibrium depends on  
931 whether the system of dynamical equations, set out in the model (equations 2, 3, 4, 5, 6 and  
932 7), included and captured all variables that influenced behaviour in that environment. As  
933 stated in the introduction, the lack of competitor species and other trophic levels at  
934 Billingsgate made it a good natural laboratory in which to try and meet the simplifying  
935 assumptions needed for a mathematical model. None of the values arrived at by numerical  
936 investigation were at unrealistic levels and the differences between  $t_c$  and  $t_a$  accurately  
937 captured the ratio of AGG to ST use at Billingsgate, meaning the model may provide a good  
938 approximation of the densities of behaviours seen in the real foraging population.

939           The fact that there has been a foraging population at this site since the early 1980's  
940 and over that time the population, and the availability and scheduling of food, is likely to  
941 have remained relatively stable makes it a realistic possibility that the population may have  
942 settled at some equilibrium of searchers to handlers to individuals involved in kleptoparasitic  
943 interactions. The model developed and tested here has improved our understanding of and  
944 accurately described the density of behaviours in the Billingsgate foraging population.

945 *Use of ESS strategies:* The focal animal analyses conducted to assess individual use of ESS's  
946 showed that all five of the ESS's that were possible at Billingsgate were actually observed in  
947 the foraging population. The fact that these were exactly the five strategies we observed is  
948 notable given that there are potentially 12 different strategies (Table 4) available to a  
949 population that can utilise the kleptoparasitic behaviours we modelled here. The presence of  
950 multiple strategies in the population adds a further strand of support to research showing that  
951 kleptoparasitism in gull species is a flexible foraging strategy and a facultative response to  
952 changing environmental conditions (Maniscalco & Ostrand, 1997; Spencer et al. 2017).

953 Further, these five strategies involved two of the types of kleptoparasitism described  
954 by Giraldeau & Caraco (2000) (Stealth and Aggressive). Our data has demonstrated the use  
955 of more than one of these kleptoparasitism types within species in the Billingsgate  
956 population. Although other research has established the existence of these different types of  
957 kleptoparasitism through their individual use by a species (e.g. Aggressive: Bald Eagles  
958 *Haliaeetus leucocephalus* (Hansen, 1986); Stealth: Eastern chipmunks *Tamias striatus*  
959 (Elliott, 1978)) no work has given particular focus to the presence of more than one of these  
960 kleptoparasitism types in a single population. We hope that the way we have recorded and  
961 analysed these behaviours has added some value to the literature for those interested in  
962 investigating how the ability to use multiple types of kleptoparasitism influences behavioural  
963 dynamics.

964 When distinguishing which of the five possible ESS strategies to use in different  
965 environmental conditions, we found that 23% of the foragers to whom strategies could be  
966 attributed were actually playing an ESS. This seems to indicate that gulls at Billingsgate were  
967 on the whole not making good behavioural decisions. There are, however, a number of  
968 possible explanations for this result.

969 First, time was used to model all the costs of the different foraging activities in this  
970 population. The model assumed we can ignore the potential energetic and injury costs of  
971 different kleptoparasitic strategies. The results showed that gulls were using Marauder  
972 strategies more than predicted by the model and thereby fighting less than they should have  
973 to match ESS predictions. This suggests that there may be additional costs to fighting beyond  
974 the time costs that were the focus of our model. If we had added an extra penalty to the  
975 model, to represent risk of injury or use of energy, making fighting more costly, this would  
976 have moved the regions of parameter space occupied by different strategies and we may have

977 found that more individuals were using ESS strategies in the appropriate environmental  
978 conditions.

979         Second, as Billingsgate provides a stable and consistent food source, it is possible that  
980 individuals in the population have learned the scheduling and have a good knowledge of  
981 quantities and regularity of food resources at the site. For example, the gulls may have  
982 learned to pay attention to certain cues associated with routines at the site. It was noted that  
983 all the bins are gathered together and washed out at the same time each day and this  
984 frequently generated food patches. In such a case we may conclude that what appeared to be  
985 non-optimal behaviours, of using Marauder strategies in patches where there were few  
986 resources and the model predicted defending food items, may actually reflect knowledge  
987 amongst members of the population of the frequency with which patches appear and an  
988 expectation that resources will not be scarce for long. Indeed, the mean number of patches  
989 per day of fieldwork at Billingsgate was 5.54, indicating that within the hours available to  
990 forage at the market the possibility of further patches appearing was often likely. A logical  
991 conclusion that could be drawn from this line of argument is that behaviour may change over  
992 the course of the day as the daily foraging window of opportunity at this site draws to a close  
993 and further patches become less and less likely. This would match previous findings in the  
994 risk-sensitive foraging literature which have shown that foragers will take greater risks as the  
995 time available to meet their daily energy needs runs out (Caraco et al., 1980). This may result  
996 in riskier aggressive and defensive strategies being more likely later in the day at  
997 Billingsgate. This is not something that was assessed in our model but suggests a potentially  
998 fruitful area for further research. Anecdotally it was noted that the population spends more  
999 time loafing as the morning progresses suggesting there are sufficient resources at the site for  
1000 the majority of birds to become satiated, however, this may change seasonally as the energy  
1001 demands of these gulls change.

1002 Third, the one-species approach used to model this population assumed that all  
1003 foragers were essentially identical and that averaging the data for the whole year of study  
1004 would successfully smooth out the influence of competitive asymmetries between individuals  
1005 and between the three study species. The one-species approach was used to keep the model as  
1006 simple as possible and make the necessary mathematics more tractable. The regions of  
1007 parameter space predicted by the model make intuitive sense and agree with previous models  
1008 (Broom et al. 2004; Hadjichrysanthou & Broom, 2012), with ESS regions for Hawk strategies  
1009 in low food availability patches and Marauder strategies in areas of higher food availability  
1010 where defensive behaviour is less necessary as new food items are encountered frequently.  
1011 The model did not fully predict individual foraging decisions. This may be because additional  
1012 factors such as injury and energetic costs, not included in the model, may have influenced  
1013 strategy choice. However, gull species differ considerably in morphology and potentially  
1014 thereby in competitive ability. Despite being frequently found together in mixed-species  
1015 foraging flocks, the three species found at Billingsgate differ considerably in size and  
1016 dominance. GBB and HG are amongst the largest of gull species, being both predatory and  
1017 aggressive with large powerful bills. The BHG in contrast is a much smaller species of gull.  
1018 Beyond the ecological parameters of food discovery rate ( $v_{ff}$ ) and density of the population  
1019 in a patch ( $P$ ) that were the focus of this analysis, asymmetries between foragers of the  
1020 different species clearly did affect the foraging decisions made. For example, the more  
1021 aggressive Hawk strategies (AGG Hawk and ST Hawk) were the strategies used effectively  
1022 and played as ESS's on all occasions. These are likely to be strategies used by the larger,  
1023 more dominant species. In contrast, the Marauder strategies (ST Marauder and AGG  
1024 Marauder) were strategies used in the non-ESS regions of parameter space. These strategies  
1025 were seen most frequently in the region where AGG Hawk and ST Hawk were ESS's,  
1026 indicating that foragers were failing to defend food items when such behaviour would have

1027 been optimal. What appeared to be sub-optimal behaviour of surrendering food in a region  
1028 where food was scarce and defensive behaviours were predicted by the model, in most cases  
1029 will have been the best behavioural decision for some handlers, given the competitive  
1030 advantages of the bird that was attacking it. For example, due to differences in size and  
1031 strength it would never be optimal for a BHG handler to defend against a GBB or HG, indeed  
1032 the data from Billingsgate showed that BHG never defended when attacked by either of these  
1033 larger species. The asymmetries between these two species are based on size dimorphism and  
1034 are clear for all individuals to see. As argued by Maynard Smith (1982), when individuals are  
1035 aware of asymmetries those asymmetries will affect behaviour. The one-species model  
1036 developed here did not reflect the fact that the optimal behaviour in a given region of  
1037 parameter space would differ between the three study species due to differences in  
1038 competitive ability; and the modelling assumption of only considering pure strategies  
1039 overlooked the fact that the best decision a handler can make may change as a function of the  
1040 species of opponent.

1041       Mixed strategies were not observed in the focal animal observations conducted. This  
1042 may be because an animal that has a best strategy should use that strategy. However, we  
1043 know from analysis of the patterns of kleptoparasitic behaviour in the data at Billingsgate that  
1044 larger species used AGG against smaller species, smaller species used ST against larger  
1045 species and that gulls used both AGG and ST against conspecifics (75% AGG, 25% ST).  
1046 This leaves a number of possible scenarios: Individuals specialise in one type of  
1047 kleptoparasitism and select their opponents based on this, so the population consists of a mix  
1048 of individuals using pure strategies. Alternatively, individuals use both types of  
1049 kleptoparasitism and will change which one they use based on the competitive ability of their  
1050 opponent. Although this second type was not observed in the focal observations it seems  
1051 likely that there will be individuals in the population that do switch strategies based on



1052 opponent. Perhaps none of the focal observations were of sufficiently long duration to  
1053 observe all the necessary interactions to show this. If it had been possible to mark/identify  
1054 individuals, this picture could have been developed by observing individuals across foraging  
1055 patches building up a more comprehensive picture of foraging strategies of individuals.  
1056 Examination of the focal animal data showed that all 12 individuals that correctly used ESS's  
1057 were larger gull species, either GBB or HG, indicating that the parameter space shown in  
1058 Figure 5 may best capture the ESS regions for more dominant individuals in the population.

1059         Despite the above argument, closer examination of the focal animal data showed that  
1060 between GBB and HG these larger species did not differ significantly in their successful use  
1061 of ESS's, with 25% of GBB and 23% of HG using the correct strategy. The GBB is larger  
1062 and more dominant than the HG, if the regions of parameter space better suit dominant  
1063 individuals we might expect the majority of birds using ESS's to be GBB, however, this was  
1064 not the case. Individuals of both species ineffectively used Marauder strategies at a high rate  
1065 with 46% of GBB and 73% of HG not defending food items in environmental conditions  
1066 where they should have. The GBB did show a slightly greater tendency to engage in some  
1067 sort of defensive behaviour, with 33% of individuals using the Aggressive Resistor (AR)  
1068 strategy compared to only 4% of HG using this strategy, but the majority of this use (88%)  
1069 was in the wrong region of parameter space. The much smaller BHG used only Marauder  
1070 strategies which fits the argument that competitive differences influenced behaviour, but as it  
1071 was only possible to attribute a strategy to 2 foraging BHG, with so few data points, this adds  
1072 little evidence to support the idea that the parameter space generated by the model depicts  
1073 strategies for dominant individuals.

1074         When assessing the amount of error in the model's ability to predict individual  
1075 behaviour the picture appears to be more complicated than species level differences in  
1076 competitive ability can account for. However, there is a further dimension upon which

1077 foragers in this population can differ in competitive ability and that is age-class. Within  
1078 species the foraging abilities of gulls increase with age up to maturity (Verbeek, 1977a;  
1079 Bertellotti & Yorio, 2000). We can expect this dimension to influence behaviour with  
1080 juvenile gulls perhaps investing more in certain types of kleptoparasitic strategies due to their  
1081 lesser competitive abilities or poorer foraging decisions due to inexperience. Juvenile gulls  
1082 made up 48% of the foraging population at Billingsgate, however, juveniles were  
1083 overrepresented in the group of 52 gulls to whom a foraging strategy could be attributed,  
1084 which consisted of 69% juvenile birds. This heavy bias towards juveniles in the population of  
1085 individuals used to assess individual foraging decisions highlights further that the division of  
1086 parameter space regions for Billingsgate may be complex and that the sample of gulls to  
1087 whom a strategy could be attributed to test the model may not generalise to the population as  
1088 a whole.

1089         The results indicate that due to competitive differences the regions of ESS parameter  
1090 space will differ between species and possibly by age-class. Rather than foragers at  
1091 Billingsgate making poor foraging decisions it is actually the case that the optimal  
1092 behavioural decision will differ by species and age-class throughout the parameter space and  
1093 as a function of opponent. A more complex model incorporating these factors is required to  
1094 investigate the optimality of individual foraging decisions in the population at Billingsgate.

1095         Further, discussion is also required of a more fundamental limitation of the approach  
1096 taken in this research. Values for model parameters were extracted from field data. Using this  
1097 approach it was necessary to find some meaningful way of aggregating field data that  
1098 captured behaviour in the Billingsgate population. This was achieved by working out  
1099 probabilities for certain behaviours based on data for the whole population over the year of  
1100 study. This gave single probabilities for behaviours such as winning fights and attempting  
1101 kleptoparasitic attacks that remained constant. Just as calculating the average for any rate is

1102 of limited value in identifying the instantaneous rate at any single point over the period of  
1103 measurement, the method for calculating probabilities for certain behaviours at Billingsgate  
1104 ignored the fact that these probabilities may change with environmental conditions over time.  
1105 The alternative approach would have required generating a model for each of the 183 patches  
1106 recorded. This would have resulted in excessive model fitting when trying to capture  
1107 something general about kleptoparasitism in this population. This limitation is of most  
1108 relevance when considering the behaviours of individual foragers. The parameter estimates  
1109 that generated the regions of parameter space for different ESS's (Figure 5) will not have  
1110 been appropriate for all foragers; this was certainly true at the level of species and age-class,  
1111 and at the finest level of granularity each forager may have had its own unique parameter  
1112 space division for ESS's. However, all methods of sampling and data collation result in some  
1113 loss of precision, so, despite these limitations, the approach taken was viewed as a valid way  
1114 to summarise kleptoparasitic behaviours and arrive at parameter estimates for this population  
1115 at the most general level.

1116         The application of theoretical models to the behaviour of wild foraging populations is  
1117 a neglected area of research. Empirical work in this area has frequently focused on using  
1118 captive populations of foragers to test the frequency-dependent payoffs predicted by P-S  
1119 models, often using aviary populations of seed-feeding passerines (Giraldeau et al., 1994;  
1120 Mottley & Giraldeau, 2000). Studies using natural populations are rare (Beauchamp, 2014).  
1121 Hansen (1986) settled for a qualitative assessment of the extent to which kleptoparasitic and  
1122 producing strategies matched game-theoretic equilibrium predictions when studying foraging  
1123 interactions between Bald eagles. Work by Beauchamp (2014) went further by assessing  
1124 whether producing and scrounging tactics provided the same mean payoffs in foraging  
1125 aggregations of Semipalmated sandpipers (*Calidris pusilla*). Behavioural cues of time spent  
1126 exploiting a patch in the Beauchamp (2014) study were used to measure intake, this was used

1127 to calculate payoffs and assess the fitness of different strategies through comparison of time  
1128 spent exploiting produced versus scrounged patches. A comparable approach in our model  
1129 would have been to try to use handling time to calculate payoffs for different strategies  
1130 relative to different sized food items that were stolen. However, in the Billingsgate  
1131 population, birds competed for discrete hard to divide food items where contest times were  
1132 integral to foraging efficiency. As a result the differential equation based method we used,  
1133 whereby minimisation of time costs in acquiring food items was used to compare the fitness  
1134 of behaviours was, we believe, the most practical approach at Billingsgate.

1135         Beauchamp (2014) found that scrounging increased when individuals had difficulty  
1136 finding patches and may function to reduce the variance in payoffs they experience. This  
1137 would be an appropriate conclusion for that study system, as sandpipers were exploiting  
1138 highly divisible patches containing numerous minute prey items and kleptoparasitism is  
1139 assumed to be a risk-averse strategy. Our population and model differed from this in that  
1140 there was a finite quantity of only partially divisible food items and gulls had no problem  
1141 locating these food items but all food items were likely to be quickly taken possession of by  
1142 other gulls. The decision to engage in kleptoparasitic behaviour then became a potentially  
1143 risky strategy often involving the cost of having to fight for the item.

1144         Research by Morand-Ferron et al., (2007) investigated kleptoparasitism in a wild  
1145 population of Carib grackles (*Quiscalus lugubris*) by using provisioning studies. Each item of  
1146 food was indivisible and required some handling before it could be exploited and Carib  
1147 grackles used aggressive and stealth kleptoparasitism to obtain these food items. They found  
1148 that scrounging was negatively frequency dependent in line with P-S model predictions, but  
1149 were unable to provide insight into how the use of different types of kleptoparasitism shaped  
1150 patterns of behaviour in their study population. This may be because, with only one study  
1151 species, there was no easy way to discern differences in competitive ability between foragers,

1152 so identifying the relationship between how differences in competitive ability influenced the  
1153 use of different types of kleptoparasitism may not have been possible. Our model, by  
1154 considering a population of one species, suffered a similar limitation and further work to  
1155 investigate the dynamics of strategy use and competitive ability, as discussed above, seems  
1156 worthwhile. Mixed-species flocks of gulls provide a good study system for addressing these  
1157 questions as they can use all three of the kleptoparasitism strategies described and differences  
1158 in competitive ability can also be readily identified through size differences between species  
1159 and age differences within species, recognised through plumage.

1160         A key aim of our model was to investigate the extent to which it is possible to  
1161 adequately specify the parameters of real populations of foragers and assess the optimality of  
1162 behaviour within those populations. This was achieved through an analysis of the equilibrium  
1163 density of kleptoparasitic behaviours as well as the optimality of individual foraging  
1164 decisions. The results suggest that in populations that can be demarcated, such as the one at  
1165 Billingsgate, applying evolutionary game theory models to study behaviour could be an  
1166 effective research tool. The model reported here proved effective at investigating the  
1167 equilibrium density of different behavioural compartments in the population and in  
1168 identifying the ESS strategies expected to be present in the population. Increasing the  
1169 complexity of this model should further increase its utility for investigating the optimality of  
1170 individual foraging behaviour, so the prospects for applying this modelling approach to real  
1171 foraging populations seem good.

1172         This research focused on modelling the behavioural decisions of a population of urban  
1173 gulls. Gull populations in the UK have declined significantly over the last century resulting in  
1174 a number of species being listed as conservation priorities (Eaton et al., 2015).  
1175 Simultaneously gull populations have been growing in urban areas (Rock, 2005) by  
1176 exploiting an abundance of food resources from anthropogenic waste as well as secure nest

1177 sites on buildings. This has generated considerable research interest regarding the  
1178 conservation and changing ecology of these species (Scott et al., 2014; Rock & Vaughan,  
1179 2013; Spencer et al., 2017; Ross-Smith et al., 2014). We hope that the research reported here  
1180 will convince researchers of the utility of evolutionary game theory as a tool for investigating  
1181 how good the behavioural decisions of urban gulls are. Knowledge of the optimality of their  
1182 behaviour and foraging abilities will be essential to their conservation and will be important  
1183 in predicting the likely population trajectory of these species.

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### Figure Legends

**Figure 1. Trader's Car Park, Billingsgate Market.** Boundaries of study area are outlined in black. Distances are shown in metres. Image taken from Google maps 24/11/15.

**Figure 2. Flow diagram showing the dynamics of the Billingsgate foraging population for the single-species model.** The arrows show the inflows and outflows of the different behavioural compartments and the rates at which these occur are shown along the arrows. Rates are given by combinations of the model notation (Table 2). Dashed arrows show the rates at which challenged handlers surrender food items without a fight and thereby change compartments with searchers.

**Figure 3. Searching pathway for an AGG forager.**  $T_s$  is the time required, from the start of searching, to either find a food item or successfully steal from another handler using AGG. Zero (0) indicates the searcher successfully acquires food and exits the searching pathway.

**Figure 4. Searching pathway for an ST forager.**  $T_s^*$  is the time required from the start of searching to either find a new food item or successfully steal from another handler using ST. Zero (0) indicates the searcher successfully finds food and exits the searching pathway. When

successful in using ST the forager still has only acquired a portion  $x$  of a food item and still has a search time of  $(1 - x)T_s^*$  before it obtains food to the value of a whole food item.

**Figure 5. Regions of the foraging parameter space at Billingsgate where each of the 5 possible ESS's occurs for different population density values (P) and food discovery rates ( $v_f f$ ).** The five possible ESS's represented are AGG Hawk (AH), ST Hawk (SH), AGG Resistor (AR), AGG Marauder (AM) and ST Marauder (SM). Lines represent the boundaries of parameter space regions where different strategies are ESS's. Labels for the strategies are shown in their ESS region. Note that it is possible for more than one strategy to be an ESS in the same region of parameter space and ESS regions for different strategies overlap in some cases.

**Figure 6. Foraging strategies used in the region of parameter space in which they are ESS's.** Each symbol plotted represents one of the 12 foragers making the optimal foraging decision. Foragers are depicted by symbols based on the strategy used: AR (O), AH (X), SH (#). Lines and labels on the figure show the boundaries for regions where different strategies are ESS's.

**Figure 7. Foraging strategies used in the region of parameter space in which they are not an ESS.** Each symbol represents a forager that is using a strategy other than the ESS strategy for that region of parameter space (N=40). Foragers are depicted by symbols based on the strategy used: AR (X), AM (O), SM (#). Lines and labels on the figure show the boundaries for regions where different strategies are ESS's.

### Tables & Table Legends

**Table 1. Behaviours constituting strategies of aggressive and stealth kleptoparasitism**

Strategy	Behaviour
<b>Aggressive</b>	Force Kleptoparasite uses of bill to make contact with host's body in order to effect theft.
	Attempt to physically pull or tear food item from host.
	Threat <i>Upright threat posture</i> – Bird stands upright with head tilted forward, and holds wings out from body so they are clearly defined and no longer partly-concealed by the contour feathers of mantle and body (Tinbergen, 1953).
	<i>Wings spread</i> – Kleptoparasite charges the host with wings spread.
	<i>Charge</i> – (BHG only) Kleptoparasite drops its head forward, flattens out its body and then charges at the host.
<b>Stealth</b>	Food stolen from the floor in front of the host.
	Food stolen whilst the host is distracted and not in contact with the food item.

**Table 2. Model notation.**

<b>Population Densities</b>	<b>Definition</b>
$P$	Density of the total foraging population
$S$	Density of searchers
$H$	Density of handlers
$A$	Density of aggressive kleptoparasites
$D$	Density of defenders against aggressive kleptoparasitism
$C$	Density of stealth kleptoparasites
$R$	Density of resistors against stealth kleptoparasitism
 <b>Model Parameters</b>	
$v_{ff}$	Rate at which foragers find food items
$v_hH$	Rate at which searchers encounter handlers
$t_h$	Expected time needed for a handler to consume a food item
$t_a/2$	Expected duration of an aggressive fight
$t_c/2$	Expected duration of a stealth fight
$\alpha$	Probability that the attacker wins an aggressive fight
$\beta$	Probability that the attacker wins a stealth fight
$x$	Avg. proportion of a food item obtained using strategy $p_2$
 <b>Strategies</b>	
$p_1$	Probability that a searcher attacks using aggressive kleptoparasitism upon encountering a handler
$p_2$	Probability that a searcher attacks using stealth kleptoparasitism upon encountering a handler
$p_3$	Probability that a handler attacked using aggressive kleptoparasitism defends its food item
$p_4$	Probability that a handler attacked using stealth

kleptoparasitism resists the attack for its food item

**Table 3. Conditions under which it is advantageous to challenge and resist/ defend in the model of the Billingsgate population.**

Situation	Situation Description	Decision	Solution	Inequality
<b>Searcher</b>				
1	Handler defends & pop'n defends	When to use AGG?	$\frac{2\alpha}{t_a} > \max\left(\frac{2\beta x}{t_c}, v_{ff}\right)$	A1a
2	Handler resists & pop'n resists	When to use ST?	$\frac{2\beta x}{t_c} > \max\left(\frac{2\alpha}{t_a}, v_{ff}\right)$	A1b
3	Handler & pop'n resists/ defends	When to ignore handler	$v_{ff} > \max\left(\frac{2\alpha}{t_a}, \frac{2\beta x}{t_c}\right)$	A1c
4	Handler surrenders & pop'n surrenders	When to use AGG or ST?	$\infty > v_{ff}$	A2
<b>Handler</b>				
5	Pop'n defends & handler is an AGG forager	When to defend against AGG?	$v_{ff} < \frac{2(1-\alpha)}{t_a} + (1 - 2\alpha)v_h H$	A3
6	Pop'n defends & handler is an ST forager	When to defend against AGG?	$v_{ff} < \frac{(1-\alpha)(2 + v_h t_c H)}{t_a - \beta v_h H}$	A4
7	Pop'n resists & handler is an ST forager	When to resist against ST?	$v_{ff} < \frac{2(1-\beta x)}{t_c} + (1 - \beta - \beta x)v_h H$	A5
8	Pop'n resists & handler is an AGG forager	When to resist against ST?	$v_{ff} < \frac{(1-\beta x)(2 + v_h t_a H)}{t_c - \alpha v_h H}$	A6
9	Pop'n surrenders	When to defend against AGG?	$v_{ff} < \frac{2(1-\alpha)}{t_a} - v_h H$	A7
10	Pop'n surrenders	When to resist against ST?	$v_{ff} < \frac{2(1-\beta x)}{t_c} - v_h H$	A8
11	Pop'n doesn't attack & mutant AGG attacker	When to defend against AGG?	$v_{ff} < \frac{2(1-\alpha)}{t_a}$	A9
12	Pop'n doesn't attack &	When to resist against ST?	$v_{ff} < \frac{2(1-\beta x)}{t_c}$	A10



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mutant ST  
attacker

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**Table 4. Conditions that need to be satisfied for each of the twelve candidate foraging strategies to be an ESS.**

Strategy	Strategy Name	ESS Conditions <sup>†</sup>
(1,0,1,0)	AGG Defender	*
(0,1,0,1)	ST Resistor	*
(1,0,0,1)	AGG Resistor	$A2 \cap A8 \cap A7^c$
(1,0,0,0)	AGG Marauder	$A2 \cap A8^c \cap A7^c$
(0,1,1,0)	ST Defender	$A2 \cap A7 \cap A8^c$
(0,1,0,0)	ST Marauder	$A2 \cap A7^c \cap A8^c$
(1,0,1,1)	AGG Hawk	$A1a \cap A3 \cap A6$
(0,1,1,1)	ST Hawk	$A1b \cap A4 \cap A5$
(0,0,1,1)	Retaliator	$A1c \cap A9 \cap A10$
(0,0,0,0)	Dove	*
(0,0,0,1)	ST Retaliator	*
(0,0,1,0)	AGG Retaliator	*

<sup>†</sup> – Systems of inequalities (A1a to A10, Table 3) that need to be satisfied for a strategy to be an ESS. Conditions with a superscript means the complement of that particular condition needs to be satisfied as part of the ESS combination. An asterisk indicates there are no conditions in which the strategy is an ESS.

**Table 5. Mean values for model parameters obtained from Billingsgate foraging data.**

<b>Parameter/ Strategy</b>	<b>Meaning of Parameter</b>	<b>Value</b>
$\alpha$	Probability of winning AGG fight	0.79
$\beta$	Probability of winning ST fight	0.71
$p_1$	Probability of using aggressive (AGG) kleptoparasitism	0.38
$p_2$	Probability of using stealth (ST) kleptoparasitism	0.23
$p_3$	Probability of defending	0.35
$p_4$	Probability of resisting	0.64
$v_{ff}$	Rate at which an individual discovers food items	0.71
$v_h$	Rate at which a forager discovers handlers	0.83
$t_h$	Mean handling time for a food item	0.42
$t_c$	Twice the duration of a stealth (ST) fight	0.14
$t_a$	Twice the duration of an aggressive (AGG) fight	0.26
$x$	Avg. portion of item obtained by ST	0.63

**Table 6. Equilibrium density results for the Billingsgate population at parameter values of  $t_h = 0.42$ ,  $t_c = 0.14$ ,  $t_a = 0.26$ .**

<b>Behavioural Compartment</b>	<b>Equilibrium Density*</b>	<b>Billingsgate Density†</b>
<b>Handlers (<i>H</i>)</b>	$\approx 2.53$	2.52
<b>Searchers (<i>S</i>)</b>	$\approx 8.5$	8.52
<b>ST attackers (<i>C</i>)</b>	$\approx 0.18$	0.18
<b>Resistors (<i>R</i>)</b>	$\approx 0.18$	0.18
<b>AGG attackers (<i>A</i>)</b>	$\approx 0.31$	0.30
<b>Defenders (<i>D</i>)</b>	$\approx 0.31$	0.30

\*Column 2 shows the density of each compartment at equilibrium for these parameter values. †Column 3 shows the density of each compartment actually observed at Billingsgate.

**Table 7. Values used to investigate the regions of parameter space occupied by different ESS's at Billingsgate.**

<b>Parameter/ Strategy</b>	<b>Meaning of Parameter</b>	<b>Value</b>
$\alpha$	Probability of winning AGG fight	0.79
$\beta$	Probability of winning ST fight	0.71
$v_{ff}$	Rate at which an individual discovers food items	Varied
$v_h$	Rate at which a forager discovers handlers	0.83
$t_h$	Mean handling time for a food item	0.42
$t_c$	Twice the duration of a stealth (ST) fight	0.14
$t_a$	Twice the duration of an aggressive (AGG) fight	0.26
$P$	Population Density	Varied

**Table 8. Frequency with which strategies at Billingsgate were used in the region of parameter space where they were an ESS and regions where they were not an ESS.**

<b>Strategy</b>	<b>ESS region</b>	<b>Non-ESS region</b>
<b>AGG Resistor</b>	1	8
<b>AGG Marauder</b>	0	22
<b>ST Marauder</b>	0	10
<b>AGG Hawk</b>	9	0
<b>ST Hawk</b>	2	0

