

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

3 **Robert Spencer – Department of Psychology, Faculty of Science & Technology,**
4 **Middlesex University, London. NW4 4BT.**

5 **Mark Broom – Department of Mathematics, City, University of London, Northampton**
6 **Square, London. EC1V 0HB.**

7 **Corresponding author: Email: r.spencer@mdx.ac.uk, Tel: 0208 411 4588**

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

9

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Data Accessibility

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

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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 (10,400m²). 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 α 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 β 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 α 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

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Fieldwork results:

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

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

Analysis of host responses to kleptoparasitism showed that on average the population defended 45% of the time and surrendered 55% of the time. By strategy the population defended against AGG for 73/209 (35%) attacks and resisted against ST on 72/112 (64%) of 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 (α) of 0.79, and 71% for ST giving a success probability (β) 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 ~ 8.52 birds/patch), 21% handlers (H) (~ 2.52 birds/patch) and
 717 8% were engaged in kleptoparasitic fights over food (~ 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 ~ 0.6 birds
 721 engaged in AGG fights is split 50:50 between aggressive attackers (A) (~ 0.3 birds/patch) and
 722 defenders (D) (~ 0.3 birds/patch) and the remaining ~ 0.36 birds engaged in ST is split 50:50
 723 between stealth attackers (C) (~ 0.18 birds/patch) and resistors (R) (~ 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).

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INSERT TABLE 7 ABOUT HERE

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 (0.42×60). 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.

Table 2. Model notation.

Population Densities	Definition
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
Model Parameters	
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
α	Probability that the attacker wins an aggressive fight
β	Probability that the attacker wins a stealth fight
x	Avg. proportion of a food item obtained using strategy p_2
Strategies	
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
Searcher				
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
Handler				
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

mutant ST
attacker

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 [†]
(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	*

[†] – 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.

Parameter/ Strategy	Meaning of Parameter	Value
α	Probability of winning AGG fight	0.79
β	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 $t_h = 0.42$, $t_c = 0.14$, $t_a = 0.26$.

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

Parameter/ Strategy	Meaning of Parameter	Value
α	Probability of winning AGG fight	0.79
β	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.

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

