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

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

9

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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).

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

19 **Abstract**

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

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

41 Introduction

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

239

240

Methods

Study Site and Species

242 *Study Site:* Billingsgate Market, London (Lat: 51°30'20.40"N; Long: 0°00'43.90"W) is a
243 seafood market in the Canary Wharf area of East London. Research at this location was
244 conducted in a car park area used by fishmongers to process and load their stock onto vans,
245 called the Trader's Car Park. The Trader's Car Park covered an area of 0.0104 square
246 kilometres (10,400m²). 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

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

389

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

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

412 **INSERT TABLE 2 ABOUT HERE**

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

416 **INSERT FIGURE 2 ABOUT HERE**

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

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

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

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

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

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

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

420

Analysis

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

423 *Stage 1: Equilibrium densities of the behavioural compartments:*

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

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

430

Equations 4, 5, 6 and 7 were solved first. The solutions for these equations were then

431

substituted for C, R, A and D in equation 2 to give the equilibrium density of searchers (S)

432

shown in equation 9. Equation 9 was then substituted for S into the solutions for C, R, A and

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

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

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

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

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

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

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

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

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

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

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

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

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

442 **kleptoparasitic attacks:**

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

448 Some additional assumptions of the model are introduced here. The payoffs obtained
449 from a fight are measured in terms of units of a food item. The assumption is made that if a
450 forager attacks using AGG and wins the fight it obtains the whole of the food item contested,
451 so the gain obtained is the probability of winning times the value of the item, which is 1
452 (representing one whole food item). Likewise if the handler defends the item and wins an
453 AGG fight it retains the whole item. It also follows that if a searcher attacks AGG and the
454 handler surrenders, the attacker obtains the whole food item without a fight. So the gain for
455 winning an AGG fight is $1 \times \alpha = \alpha$ (where α is the probability of the attacker winning the
456 fight as defined in Table 2).

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

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

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

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

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

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

506 *Searchers:*

507 Following Broom & Ruxton (1998) and Broom et al. (2004), to assess when it is
508 advantageous for a searcher to attack a handler it is sufficient to consider the instantaneous
509 rate at which a searcher becomes a handler after encountering a handler. When a searcher
510 encounters a handler it must decide whether to ignore the handler and continue searching for
511 food items or attack the handler using either AGG or ST. The strategy it should use is the one
512 that minimises the amount of time until it becomes the handler of a food item. This is the
513 strategy that maximises the forager's rate of gain per time foraging. If it ignores the handler
514 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

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

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

- 521 1. When to use AGG (handler defends & population defends).
- 522 2. When to use ST (handler resists & population resists).

523 When it is advantageous not to attack the handler:

- 524 3. When to ignore the handler and continue searching for food (population defends/
 525 resists).

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

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

530 *Handlers:*

531 When a handler is discovered by a searcher and attacked it can choose either to resist/defend
 532 the food item it is handling or surrender the item and resume searching for a new food item.
 533 The strategy it should use is the one that minimises the amount of time until it resumes
 534 handling a food item. If it resists/ defends the food item the time to resume handling is
 535 influenced by the duration of the fight and if it loses, the rate at which it encounters other

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

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

- 544 5. When to defend against AGG (population defends and handler's searching strategy is
 545 AGG).
- 546 6. When to defend against AGG (population defends and handler's searching strategy is
 547 ST).
- 548 7. When to resist against ST (population resists and handler's searching strategy is ST).
- 549 8. When to resist against ST (population resists and handler's searching strategy is
 550 AGG).

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

- 553 9. When to defend against AGG (population surrenders).
- 554 10. When to resist against ST (population surrenders).

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

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

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

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

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

565 **INSERT FIGURE 3 ABOUT HERE**

566 **INSERT FIGURE 4 ABOUT HERE**

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

573 **INSERT TABLE 3 ABOUT HERE**

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

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

582 (p_1, p_2, p_3, p_4) that population can be invaded by foragers that use a different foraging
 583 strategy which results in a higher food consumption rate, as this would translate into a higher
 584 fitness payoff for those foragers. To consider whether a mutant playing a slightly different
 585 strategy to the rest of the population can invade the population playing strategy profile
 586 (p_1, p_2, p_3, p_4) it is sufficient to consider whether the mutant uses a different strategy at any
 587 one of the three decision points. A different strategy at any one decision point that gives a
 588 higher payoff will result in an overall higher payoff for the mutant and it is sufficient to
 589 consider differences in pure strategies at each of the three decision points. Hadjichrysanthou
 590 and Broom (2012) provided proofs for some generic parameters and conducted extensive
 591 numerical investigation of why there are no mixed-strategy ESS's. Following those
 592 arguments, consideration of the use of only pure strategies in this model means that the
 593 searcher will either always use AGG, always use ST, or always ignore the opportunity to
 594 attack. The working assumption in the current model therefore is that there are twelve
 595 candidates for pure strategy ESS's that need to be considered as outlined below. Here the four
 596 probabilities (p_1, p_2, p_3, p_4) take the value 1 or 0, meaning the associated behaviour is always
 597 used (1) or never used (0), respectively.

- 598 - Strategy (1,0,1,0) (AGG Defender): The forager always attacks AGG and always
 599 defends against AGG, but never uses or resists against ST.
- 600 - Strategy (0,1,0,1) (ST Resistor): The forager always attacks ST and always resists ST
 601 attacks, but never uses or defends against AGG.
- 602 - Strategy (1,0,0,1) (AGG Resistor): The forager always attacks AGG but only ever
 603 resists against ST attacks.
- 604 - Strategy (1,0,0,0) (AGG Marauder): The forager always attacks AGG but never
 605 resists or defends against attack.

- 606 - Strategy (0,1,1,0) (ST Defender): The forager always attacks ST and only defends
607 against AGG.
- 608 - Strategy (0,1,0,0) (ST Marauder): The forager always attacks ST but never resists or
609 defends against attacks.
- 610 - Strategy (1,0,1,1) (AGG Hawk): The forager always attacks AGG and always defends
611 and resists against both types of attack.
- 612 - Strategy (0,1,1,1) (ST Hawk): The forager always attacks ST and always defends and
613 resists against both types of attack.
- 614 - Strategy (0,0,1,1) (Retaliator): The forager never attacks but it always defends and
615 resists against both types of attack.
- 616 - Strategy (0,0,0,0) (Dove): The forager always searches for its own food, it never
617 attacks and never defends or resists.
- 618 - Strategy (0,0,0,1) (ST Retaliator): The forager never attacks using either strategy and
619 never defends against AGG but always resists against ST.
- 620 - Strategy (0,0,1,0) (AGG Retaliator): The forager never attacks using either strategy, it
621 always defends against AGG but never against ST attacks.

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

627 **INSERT TABLE 4 ABOUT HERE**

Results

628

629 *Fieldwork results:*

630 *Population size and composition:* The population at Billingsgate had a mean daily size of 40
631 (Range: 29, 53; standard deviation: ~8) gulls. Foraging patches consisted of a mean of 12
632 gulls (Range: 9, 20; standard deviation: ~3). A comparison was made of whether the
633 proportions of each species engaged in foraging differed from the proportion of each species
634 in the population as a whole, using headcounts for the total population and headcounts at
635 patches. This comparison showed a great deal of correspondence between the composition of
636 the total population and the composition of foraging patches (Population Composition: GBB
637 11%, HG 70%, BHG 19%; Foraging Patch Composition: GBB 12%, HG 72%, BHG: 16%),
638 which provided some reassurance regarding the stability of the population. As the
639 kleptoparasitic behaviours of interest occurred within foraging patches, the data obtained
640 from patches were used for analyses.

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

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

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

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

660 The data from Billingsgate provided values for a number of the model parameters and
661 strategies. The probability of an attacker winning a fight was given by the mean success rate
662 of each kleptoparasitic strategy in the population. This was 79% for AGG giving a
663 probability of success (α) of 0.79, and 71% for ST giving a success probability (β) of 0.71.
664 The rate at which food was discovered at Billingsgate was calculated as the total number of
665 items discovered divided by the total number of foragers. This gave a mean rate at which
666 food items were discovered (v_{ff}) as 0.71 items per forager per minute. The rate at which
667 foragers searched for handlers (v_h) was calculated as the rate at which foragers were
668 discovered to challenge as a proportion of the rate at which food items were discovered, this
669 returned a value of 0.83 per minute.

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

675 estimate ignored opportunities. This was done using the percentage of foraging patches where
 676 no kleptoparasitism occurred as a measure of ignored opportunities. Kleptoparasitism was
 677 possible in all foraging patches and the percentage of patches where no kleptoparasitism took
 678 place, 39% of patches, was viewed as a crude index of the rate at which foragers ignored
 679 opportunities to steal. The probability that a searcher attacked using either AGG or ST was
 680 then calculated by multiplying the percentage with which the particular kleptoparasitic
 681 strategy was used by the percentage of patches within which kleptoparasitism occurred
 682 (61%). This gave a probability of attacking AGG (p_1) of 0.38 and the probability of attacking
 683 ST (p_2) of 0.23. The probability that a handler defended (p_3) or resisted (p_4) was simply the
 684 proportion of attacks recorded at Billingsgate where the handler defended or resisted.
 685 Handlers at Billingsgate defended against AGG 35% of the time making p_3 0.35 and resisted
 686 against ST 64% of the time making p_4 0.64.

687 Values were unknown for three parameters that were approximated using exponential
 688 probability distributions: mean handling time (t_h), mean ST fight duration (t_c), and mean
 689 AGG fight duration (t_a). Plausible values for these parameters were investigated numerically
 690 using the solutions for the density of each behavioural compartment in the population at
 691 equilibrium and the known parameter values and behavioural compartment densities from the
 692 foraging data for Billingsgate. Table 5 summarises the parameter values and probabilities for
 693 strategy use in the Billingsgate population that were inputted into the model to investigate
 694 equilibrium densities of behaviours.

695 **INSERT TABLE 5 ABOUT HERE**

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

699 searchers (S) (this equates to ~ 8.52 birds/patch), 21% handlers (H) (~ 2.52 birds/patch) and
 700 8% were engaged in kleptoparasitic fights over food (~ 0.96 birds/patch). As previously stated
 701 63% of the observed fights at Billingsgate involved AGG and 37% were ST fights. This gives
 702 values of approximately 0.6 birds per patch engaged in AGG fights and 0.36 birds per patch
 703 engaged in ST fights. As fights involved exactly one kleptoparasite and host, the ~ 0.6 birds
 704 engaged in AGG fights is split 50:50 between aggressive attackers (A) (~ 0.3 birds/patch) and
 705 defenders (D) (~ 0.3 birds/patch) and the remaining ~ 0.36 birds engaged in ST is split 50:50
 706 between stealth attackers (C) (~ 0.18 birds/patch) and resistors (R) (~ 0.18 birds/patch).

707 *Testing for equilibrium densities:*

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

716 Assuming a foraging population of 12 individuals at patches, the above values for t_h ,
 717 t_c , and t_a along with the parameter values shown in Table 5, were inputted into equations 9,
 718 10, 11, 12, 13 and 17. The quadratic formula (17) giving the equilibrium number of handlers
 719 was solved first, followed by 9 giving the equilibrium number of searchers and then 10, 11,
 720 12 and 13 giving the equilibrium number of ST attackers, resistors, AGG attackers and
 721 defenders respectively. The solutions resulted in equilibrium densities close to the densities
 722 of individuals in each compartment observed in the Billingsgate population (Table 6).

723

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).

744

INSERT TABLE 7 ABOUT HERE

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

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

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

767 **INSERT FIGURE 5 ABOUT HERE**

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

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

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

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

794 12 of those foragers were using strategies in the correct region of parameter space to make
795 them ESS strategies and 40 foragers were using their strategies in non-ESS regions of
796 parameter space; thus ~23% of foragers were making optimal foraging decisions and
797 individually using an ESS strategy. Figure 6 shows the ESS foraging strategies plotted in
798 parameter space and Figure 7 shows the location of the foraging strategies used in non-ESS
799 regions of parameter space.

800 **INSERT FIGURE 6 ABOUT HERE**

801 **INSERT FIGURE 7 ABOUT HERE**

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

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

815 AGG Resistor was used in an ESS region on one occasion and in a non-ESS region on
816 8 occasions. All observations of AGG Resistor in a non-ESS region also occurred in the
817 region where AGG Hawk and ST Hawk were the ESS's. Foragers using this strategy

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

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

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

831 **INSERT TABLE 8 ABOUT HERE**

832 **Discussion**

833 This model was developed to try and capture the kleptoparasitic behaviours of a population of
834 foraging gulls at Billingsgate Market and to investigate what the model could tell us about the
835 optimality and stability of the behavioural decisions made by individuals in that population.
836 This was pursued in two ways: 1. By considering the density of individuals engaged in each
837 behaviour of interest in the population and investigating the possibility that these behaviours
838 were at equilibrium densities. 2. Through assessing the optimality of the behavioural

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

841 *Equilibrium densities:* The values of a number of the model parameters were known from the
842 real foraging behaviour at Billingsgate. The values for handling time (t_h), ST fight duration
843 (t_c) and AGG fight duration (t_a) were unknown and were varied to investigate numerically at
844 what values of these parameters the model produced equilibrium densities that matched the
845 densities of behaviours observed at Billingsgate. The values arrived at were: $t_h=0.42$,
846 $t_c=0.14$, $t_a=0.26$ minutes. The important question to ask about these values is whether they
847 are plausible values for the parameters they represent.

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

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

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

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

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

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

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

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

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

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

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

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

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

960 found that more individuals were using ESS strategies in the appropriate environmental
961 conditions.

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

985 Third, the one-species approach used to model this population assumed that all
986 foragers were essentially identical and that averaging the data for the whole year of study
987 would successfully smooth out the influence of competitive asymmetries between individuals
988 and between the three study species. The one-species approach was used to keep the model as
989 simple as possible and make the necessary mathematics more tractable. The regions of
990 parameter space predicted by the model make intuitive sense and agree with previous models
991 (Broom et al. 2004; Hadjichrysanthou & Broom, 2012), with ESS regions for Hawk strategies
992 in low food availability patches and Marauder strategies in areas of higher food availability
993 where defensive behaviour is less necessary as new food items are encountered frequently.
994 The model did not fully predict individual foraging decisions. This may be because additional
995 factors such as injury and energetic costs, not included in the model, may have influenced
996 strategy choice. However, gull species differ considerably in morphology and potentially
997 thereby in competitive ability. Despite being frequently found together in mixed-species
998 foraging flocks, the three species found at Billingsgate differ considerably in size and
999 dominance. GBB and HG are amongst the largest of gull species, being both predatory and
1000 aggressive with large powerful bills. The BHG in contrast is a much smaller species of gull.
1001 Beyond the ecological parameters of food discovery rate (v_{ff}) and density of the population
1002 in a patch (P) that were the focus of this analysis, asymmetries between foragers of the
1003 different species clearly did affect the foraging decisions made. For example, the more
1004 aggressive Hawk strategies (AGG Hawk and ST Hawk) were the strategies used effectively
1005 and played as ESS's on all occasions. These are likely to be strategies used by the larger,
1006 more dominant species. In contrast, the Marauder strategies (ST Marauder and AGG
1007 Marauder) were strategies used in the non-ESS regions of parameter space. These strategies
1008 were seen most frequently in the region where AGG Hawk and ST Hawk were ESS's,
1009 indicating that foragers were failing to defend food items when such behaviour would have

1010 been optimal. What appeared to be sub-optimal behaviour of surrendering food in a region
1011 where food was scarce and defensive behaviours were predicted by the model, in most cases
1012 will have been the best behavioural decision for some handlers, given the competitive
1013 advantages of the bird that was attacking it. For example, due to differences in size and
1014 strength it would never be optimal for a BHG handler to defend against a GBB or HG, indeed
1015 the data from Billingsgate showed that BHG never defended when attacked by either of these
1016 larger species. The asymmetries between these two species are based on size dimorphism and
1017 are clear for all individuals to see. As argued by Maynard Smith (1982), when individuals are
1018 aware of asymmetries those asymmetries will affect behaviour. The one-species model
1019 developed here did not reflect the fact that the optimal behaviour in a given region of
1020 parameter space would differ between the three study species due to differences in
1021 competitive ability; and the modelling assumption of only considering pure strategies
1022 overlooked the fact that the best decision a handler can make may change as a function of the
1023 species of opponent.

1024 Mixed strategies were not observed in the focal animal observations conducted. This
1025 may be because an animal that has a best strategy should use that strategy. However, we
1026 know from analysis of the patterns of kleptoparasitic behaviour in the data at Billingsgate that
1027 larger species used AGG against smaller species, smaller species used ST against larger
1028 species and that gulls used both AGG and ST against conspecifics (75% AGG, 25% ST).
1029 This leaves a number of possible scenarios: Individuals specialise in one type of
1030 kleptoparasitism and select their opponents based on this, so the population consists of a mix
1031 of individuals using pure strategies. Alternatively, individuals use both types of
1032 kleptoparasitism and will change which one they use based on the competitive ability of their
1033 opponent. Although this second type was not observed in the focal observations it seems
1034 likely that there will be individuals in the population that do switch strategies based on

1035 opponent. Perhaps none of the focal observations were of sufficiently long duration to
1036 observe all the necessary interactions to show this. If it had been possible to mark/identify
1037 individuals, this picture could have been developed by observing individuals across foraging
1038 patches building up a more comprehensive picture of foraging strategies of individuals.
1039 Examination of the focal animal data showed that all 12 individuals that correctly used ESS's
1040 were larger gull species, either GBB or HG, indicating that the parameter space shown in
1041 Figure 5 may best capture the ESS regions for more dominant individuals in the population.

1042 Despite the above argument, closer examination of the focal animal data showed that
1043 between GBB and HG these larger species did not differ significantly in their successful use
1044 of ESS's, with 25% of GBB and 23% of HG using the correct strategy. The GBB is larger
1045 and more dominant than the HG, if the regions of parameter space better suit dominant
1046 individuals we might expect the majority of birds using ESS's to be GBB, however, this was
1047 not the case. Individuals of both species ineffectively used Marauder strategies at a high rate
1048 with 46% of GBB and 73% of HG not defending food items in environmental conditions
1049 where they should have. The GBB did show a slightly greater tendency to engage in some
1050 sort of defensive behaviour, with 33% of individuals using the Aggressive Resistor (AR)
1051 strategy compared to only 4% of HG using this strategy, but the majority of this use (88%)
1052 was in the wrong region of parameter space. The much smaller BHG used only Marauder
1053 strategies which fits the argument that competitive differences influenced behaviour, but as it
1054 was only possible to attribute a strategy to 2 foraging BHG, with so few data points, this adds
1055 little evidence to support the idea that the parameter space generated by the model depicts
1056 strategies for dominant individuals.

1057 When assessing the amount of error in the model's ability to predict individual
1058 behaviour the picture appears to be more complicated than species level differences in
1059 competitive ability can account for. However, there is a further dimension upon which

1060 foragers in this population can differ in competitive ability and that is age-class. Within
1061 species the foraging abilities of gulls increase with age up to maturity (Verbeek, 1977a;
1062 Bertellotti & Yorio, 2000). We can expect this dimension to influence behaviour with
1063 juvenile gulls perhaps investing more in certain types of kleptoparasitic strategies due to their
1064 lesser competitive abilities or poorer foraging decisions due to inexperience. Juvenile gulls
1065 made up 48% of the foraging population at Billingsgate, however, juveniles were
1066 overrepresented in the group of 52 gulls to whom a foraging strategy could be attributed,
1067 which consisted of 69% juvenile birds. This heavy bias towards juveniles in the population of
1068 individuals used to assess individual foraging decisions highlights further that the division of
1069 parameter space regions for Billingsgate may be complex and that the sample of gulls to
1070 whom a strategy could be attributed to test the model may not generalise to the population as
1071 a whole.

1072 The results indicate that due to competitive differences the regions of ESS parameter
1073 space will differ between species and possibly by age-class. Rather than foragers at
1074 Billingsgate making poor foraging decisions it is actually the case that the optimal
1075 behavioural decision will differ by species and age-class throughout the parameter space and
1076 as a function of opponent. A more complex model incorporating these factors is required to
1077 investigate the optimality of individual foraging decisions in the population at Billingsgate.

1078 Further, discussion is also required of a more fundamental limitation of the approach
1079 taken in this research. Values for model parameters were extracted from field data. Using this
1080 approach it was necessary to find some meaningful way of aggregating field data that
1081 captured behaviour in the Billingsgate population. This was achieved by working out
1082 probabilities for certain behaviours based on data for the whole population over the year of
1083 study. This gave single probabilities for behaviours such as winning fights and attempting
1084 kleptoparasitic attacks that remained constant. Just as calculating the average for any rate is

1085 of limited value in identifying the instantaneous rate at any single point over the period of
1086 measurement, the method for calculating probabilities for certain behaviours at Billingsgate
1087 ignored the fact that these probabilities may change with environmental conditions over time.
1088 The alternative approach would have required generating a model for each of the 183 patches
1089 recorded. This would have resulted in excessive model fitting when trying to capture
1090 something general about kleptoparasitism in this population. This limitation is of most
1091 relevance when considering the behaviours of individual foragers. The parameter estimates
1092 that generated the regions of parameter space for different ESS's (Figure 5) will not have
1093 been appropriate for all foragers; this was certainly true at the level of species and age-class,
1094 and at the finest level of granularity each forager may have had its own unique parameter
1095 space division for ESS's. However, all methods of sampling and data collation result in some
1096 loss of precision, so, despite these limitations, the approach taken was viewed as a valid way
1097 to summarise kleptoparasitic behaviours and arrive at parameter estimates for this population
1098 at the most general level.

1099 The application of theoretical models to the behaviour of wild foraging populations is
1100 a neglected area of research. Empirical work in this area has frequently focused on using
1101 captive populations of foragers to test the frequency-dependent payoffs predicted by P-S
1102 models, often using aviary populations of seed-feeding passerines (Giraldeau et al., 1994;
1103 Mottley & Giraldeau, 2000). Studies using natural populations are rare (Beauchamp, 2014).
1104 Hansen (1986) settled for a qualitative assessment of the extent to which kleptoparasitic and
1105 producing strategies matched game-theoretic equilibrium predictions when studying foraging
1106 interactions between Bald eagles. Work by Beauchamp (2014) went further by assessing
1107 whether producing and scrounging tactics provided the same mean payoffs in foraging
1108 aggregations of Semipalmated sandpipers (*Calidris pusilla*). Behavioural cues of time spent
1109 exploiting a patch in the Beauchamp (2014) study were used to measure intake, this was used

1110 to calculate payoffs and assess the fitness of different strategies through comparison of time
1111 spent exploiting produced versus scrounged patches. A comparable approach in our model
1112 would have been to try to use handling time to calculate payoffs for different strategies
1113 relative to different sized food items that were stolen. However, in the Billingsgate
1114 population, birds competed for discrete hard to divide food items where contest times were
1115 integral to foraging efficiency. As a result the differential equation based method we used,
1116 whereby minimisation of time costs in acquiring food items was used to compare the fitness
1117 of behaviours was, we believe, the most practical approach at Billingsgate.

1118 Beauchamp (2014) found that scrounging increased when individuals had difficulty
1119 finding patches and may function to reduce the variance in payoffs they experience. This
1120 would be an appropriate conclusion for that study system, as sandpipers were exploiting
1121 highly divisible patches containing numerous minute prey items and kleptoparasitism is
1122 assumed to be a risk-averse strategy. Our population and model differed from this in that
1123 there was a finite quantity of only partially divisible food items and gulls had no problem
1124 locating these food items but all food items were likely to be quickly taken possession of by
1125 other gulls. The decision to engage in kleptoparasitic behaviour then became a potentially
1126 risky strategy often involving the cost of having to fight for the item.

1127 Research by Morand-Ferron et al., (2007) investigated kleptoparasitism in a wild
1128 population of Carib grackles (*Quiscalus lugubris*) by using provisioning studies. Each item of
1129 food was indivisible and required some handling before it could be exploited and Carib
1130 grackles used aggressive and stealth kleptoparasitism to obtain these food items. They found
1131 that scrounging was negatively frequency dependent in line with P-S model predictions, but
1132 were unable to provide insight into how the use of different types of kleptoparasitism shaped
1133 patterns of behaviour in their study population. This may be because, with only one study
1134 species, there was no easy way to discern differences in competitive ability between foragers,

1135 so identifying the relationship between how differences in competitive ability influenced the
1136 use of different types of kleptoparasitism may not have been possible. Our model, by
1137 considering a population of one species, suffered a similar limitation and further work to
1138 investigate the dynamics of strategy use and competitive ability, as discussed above, seems
1139 worthwhile. Mixed-species flocks of gulls provide a good study system for addressing these
1140 questions as they can use all three of the kleptoparasitism strategies described and differences
1141 in competitive ability can also be readily identified through size differences between species
1142 and age differences within species, recognised through plumage.

1143 A key aim of our model was to investigate the extent to which it is possible to
1144 adequately specify the parameters of real populations of foragers and assess the optimality of
1145 behaviour within those populations. This was achieved through an analysis of the equilibrium
1146 density of kleptoparasitic behaviours as well as the optimality of individual foraging
1147 decisions. The results suggest that in populations that can be demarcated, such as the one at
1148 Billingsgate, applying evolutionary game theory models to study behaviour could be an
1149 effective research tool. The model reported here proved effective at investigating the
1150 equilibrium density of different behavioural compartments in the population and in
1151 identifying the ESS strategies expected to be present in the population. Increasing the
1152 complexity of this model should further increase its utility for investigating the optimality of
1153 individual foraging behaviour, so the prospects for applying this modelling approach to real
1154 foraging populations seem good.

1155 This research focused on modelling the behavioural decisions of a population of urban
1156 gulls. Gull populations in the UK have declined significantly over the last century resulting in
1157 a number of species being listed as conservation priorities (Eaton et al., 2015).
1158 Simultaneously gull populations have been growing in urban areas (Rock, 2005) by
1159 exploiting an abundance of food resources from anthropogenic waste as well as secure nest

1160 sites on buildings. This has generated considerable research interest regarding the
1161 conservation and changing ecology of these species (Scott et al., 2014; Rock & Vaughan,
1162 2013; Spencer et al., 2017; Ross-Smith et al., 2014). We hope that the research reported here
1163 will convince researchers of the utility of evolutionary game theory as a tool for investigating
1164 how good the behavioural decisions of urban gulls are. Knowledge of the optimality of their
1165 behaviour and foraging abilities will be essential to their conservation and will be important
1166 in predicting the likely population trajectory of these species.

References

- Barnard, C.J. 1984. The evolution of food scrounging strategies within and between species. In C. J. Barnard (Ed.). *Producers and Scroungers: Strategies of exploitation and parasitism* (pp. 95-126). London, Croom Helm.
- Barnard, C. J. 1990. Parasitic relationships. In C. J. Barnard & J. M. Behnke (eds.). *Parasitism and Host Behaviour* (pp. 1-33). London, Taylor & Francis.
- Barnard, C.J. & Sibly, R.M. 1981. Producers and scroungers: a general model and its application to captive flocks of house sparrows. *Animal Behaviour*, 29, 543-550.
- Barnard, C.J. & Thompson, D.B.A. 1985. *Gulls and plovers: the ecology of mixed-species feeding groups*, London, Croom Helm.
- Beauchamp, G. 2014. A field investigation of scrounging in semipalmated sandpipers. *Behavioural Ecology & Sociobiology*. 68, 1473-1479.
- Bertellotti M. & P. Yorio 2000. Age-related feeding behaviour and foraging efficiency in Kelp Gulls *Larus dominicanus* attending coastal trawlers in Argentina. *Ardea*, 88(2): 207-214.
- Brockmann, H. J. & Barnard, C. J. 1979. Kleptoparasitism in birds. *Animal Behaviour*, 27, 487-514.
- Broom, M., Luther, R. M. & Ruxton, G.D. 2004. Resistance is useless? Extensions to the game theory of kleptoparasitism. *Bulletin of mathematical biology*, 66, 1645-1658, doi:10.1016/j.bulm.2004.03.009
- Broom, M. & Ruxton, G.D. 1998. Evolutionarily stable stealing: game theory applied to kleptoparasitism. *Behavioural Ecology*, 9 (4), 397-405.

- Broom, M. and Ruxton, G.D. 2003. Evolutionarily stable kleptoparasitism: Consequences of different prey types. *Behavioral Ecology*, 14(1), 23-33. doi: [10.1093/beheco/14.1.23](https://doi.org/10.1093/beheco/14.1.23)
- Broom, M. and Rychtár, J. 2007. The evolution of a kleptoparasitic system under adaptive dynamics. *Journal of Mathematical Biology*, 54(2), 151-177. doi: [10.1007/s00285-006-0005-2](https://doi.org/10.1007/s00285-006-0005-2)
- Broom, M. and Rychtár, J. 2009. A game theoretical model of kleptoparasitism with incomplete information. *Journal of Mathematical Biology*, 59(5), 631-649. doi: [10.1007/s00285-008-0247-2](https://doi.org/10.1007/s00285-008-0247-2)
- Caraco, T., Martindale, S. & Whittam, T.S. 1980. An empirical demonstration of risk-sensitive foraging preferences. *Animal Behaviour*, 28, 820-830.
- Carbone, C., Frame, L., Frame, G., Malcolm, J., Fanshawe, J., FitzGibbon, C., Schaller, G., Gordon, I.J., Rowcliffe, J.M., Du Toit, J.T. 2005. Feeding success of African wild dogs (*Lycaon pictus*) in the Serengeti: the effects of group size and kleptoparasitism. *Journal of Zoology*, 266, 153–161.
- Coyle, F. A., O’Shields, T. C., & Perlmutter, D. G. 1991. Observations on the behaviour of the kleptoparasitic spider, *Mysmenopsis furtive* (Araneae, Mysmenidae). *Journal of Arachnology*, 19, 62-66.
- Eaton, M.A., Aebischer, N.J., Brown, A.F., Hearn, R., Lock, L., Noble, D.G., Musgrave, A.J., Noble, D.G., Stroud, D., & Gregory, R.D. 2015. Birds of conservation concern 4. *British Birds*, 108, 708-746.
- Elliott, L. 1978. Social behaviour and foraging ecology of the eastern chipmunk (*Tamias striatus*) in the Adirondack Mountains. *Smithsonian Contributions to Zoology*, 265.
- Erlandsson, A. 1988. Food sharing vs monopolising prey: a form of kleptoparasitism in *Velia Caprai* (Heteroptera). *Oikos*, 53, 203-206.

- Giraldeau, L-A. & Caraco, T. 2000. *Social Foraging Theory*. Princeton. Princeton University Press.
- Giraldeau, L-A., Soos, C., & Beauchamp, G. 1994. A test of the producer-scrouter foraging game in captive flocks of spice finches, *Lonchura punctulata*. *Behavioural Ecology and Sociobiology*, 34, 251-256.
- Grafen, A. 1991. Modelling in behavioural ecology. In J.R. Krebs & N.B. Davies (Eds.). *Behavioural ecology: An evolutionary approach* (3rd ed.), p.5-31, Oxford. Blackwell.
- Hadjichrysanthou, C. and Broom, M. 2012. When should animals share food? Game theory applied to kleptoparasitic populations with food sharing. *Behavioral Ecology*, 23(5), 977-991. doi: [10.1093/beheco/ars061](https://doi.org/10.1093/beheco/ars061)
- Hansen, A.J. 1986. Fighting behaviour in bald eagles: A test of game theory. *Ecology*, 67 (3), 787-797.
- Hockey, P.A.R., Ryan, P.G. & Bosman, A.L. 1989. Age-related intraspecific kleptoparasitism and foraging success of kelp gulls, *Larus domenicanus*. *Ardea*, 77, 205-210.
- Hunt, J. & Hodgson, D. 2010. What is fitness, and how do we measure it? In D. F. Westneat & C. W. Fox (Eds.), *Evolutionary Behavioural Ecology*, p.46-70, New York, Oxford University Press.
- Luther, R.M. and Broom, M. 2004. Rapid convergence to an equilibrium state in kleptoparasitic populations. *Journal of Mathematical Biology*, 48(3), 325-339. doi: [10.1007/s00285-003-0237-3](https://doi.org/10.1007/s00285-003-0237-3)
- Janson, C.H. 1985. Aggressive competition and animal food consumption in wild brown capuchin monkeys (*Cebus apella*). *Behavioral Ecology & Sociobiology*, 18, 125–138.
- Maniscalco, J. M. & Ostrand, W. D. 1997. Seabird behaviors at forage fish schools in Prince William Sound, Alaska. In Forage Fishes in Marine Ecosystems. *Proceedings of the*

International Symposium on the Role of Forage Fishes in Marine Ecosystems. Alaska Sea Grant College Program Report No. 97-01, p.175-190, University of Alaska Fairbanks, 1997.

MATLAB and Statistics Toolbox Release 2015b. 2015. The MathWorks, Inc., Natick, Massachusetts, UnitedStates [computer software].

Maynard Smith, J. 1982. *Evolution and the theory of games*. Cambridge. Cambridge University Press.

Morand-Ferron, J., Giraldeau, L-A., Lefebvre, L. (2007). Wild Carib grackles play a producer-scrourer game. *Behavioural Ecology*, 916-921, doi:10.1093/beheco/arm058

Mottley, K. & Giraldeau, L-A. 2000. Experimental evidence that group foragers can converge on predicted producer-scrourer equilibria. *Animal Behaviour*, 60 (3), 341-350.

Perrins, C. 2009. *The Encyclopedia of Birds*. Oxford. Oxford University Press.

Rock, P. 2005. Urban gulls: problems and solutions, *British Birds*, 98, 338-355.

Rock, P. & Vaughan, I.P. 2013. Long-term estimates of adult survival rates of urban Herring Gulls *Larus argentatus* and Lesser Black-backed Gulls *Larus fuscus*. *Ringing & Migration*, 28, 21-29.

Ross-Smith, V.H., Robinson, R.A., Banks, A.N., Frayling, T.D., Gibson, C.C. & Clark, J.A. 2014. The Lesser Black-backed Gull *Larus fuscus* in England: How to resolve a conservation conundrum. *Seabird*, 27, 41-61.

- Ruxton, G.D. & Moody, A.L. 1997. The ideal free distribution with kleptoparasitism. *Journal of theoretical biology*, 186, 449-458.
- Scott, P., Duncan, P., & Green, J.A. 2014. Food preferences of the black-headed gull *Chroicocephalus ridibundus* differs along a rural-urban gradient. *Bird Study*, DOI: 10.1080/00063657.2014.984655
- Sirof, E. 2000. An evolutionarily stable strategy for aggressiveness in feeding groups. *Behavioural Ecology*, 11, 351-356.
- Spencer, R., & Broom, M. 2017. Data from: A game-theoretical model of kleptoparasitic behaviour in an urban gull (*Laridae*) population. *Behavioural Ecology*. doi:10.5061/dryad.cp423
- Spencer, R., Russell, Y.I., Dickins, B.J.A., & Dickins, T.E. 2017. Kleptoparasitism in gulls (*Laridae*) at an urban and a coastal foraging environment: an assessment of ecological predictors, *Bird Study*, 64, 1, 12-19.
- Tinbergen, N. 1953. *The Herring Gull's World*. London. Collins.
- Verbeek, N.A.M. 1977a. Comparative feeding behaviour of immature and adult herring gulls. *The Wilson Bulletin*, 89, 415-421.
- Verbeek, N. A. M. 1977b. Comparative feeding ecology of Herring gulls (*Larus argentatus*) and Lesser Black-backed gulls (*Larus fuscus*). *Ardea*, 65, 25-42.
- Vollrath, F. 1984. Kleptobiotic interactions in vertebrates. In C.J. Barnard (Ed.), *Producers and Scroungers: Strategies of exploitation and parasitism*, p. 61-94, Beckenham, Croom Helm.
- Wolfram Alpha LLC. 2016. Wolfram|Alpha. <http://www.wolframalpha.com> (access November 11, 2016) [computer software].

Figure Legends

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

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

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

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

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

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

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

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

Tables & Table Legends

Table 1. Behaviours constituting strategies of aggressive and stealth kleptoparasitism

Strategy	Behaviour
Aggressive	<p data-bbox="528 663 1375 808">Force Kleptoparasite uses of bill to make contact with host's body in order to effect theft.</p> <hr/> <p data-bbox="528 808 1375 887">Attempt to physically pull or tear food item from host.</p> <hr/> <p data-bbox="528 887 1375 1256">Threat <i>Upright threat posture</i> – Bird stands upright with head tilted forward, and holds wings out from body so they are clearly defined and no longer partly-concealed by the contour feathers of mantle and body (Tinbergen, 1953).</p> <hr/> <p data-bbox="528 1256 1375 1402"><i>Wings spread</i> – Kleptoparasite charges the host with wings spread.</p> <hr/> <p data-bbox="528 1402 1375 1621"><i>Charge</i> – (BHG only) Kleptoparasite drops its head forward, flattens out its body and then charges at the host.</p>
Stealth	<p data-bbox="528 1621 1375 1700">Food stolen from the floor in front of the host.</p> <hr/> <p data-bbox="528 1700 1375 1841">Food stolen whilst the host is distracted and not in contact with the food item.</p>

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 resisters 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 & mutant ST attacker	When to resist against ST?	$v_{ff} < \frac{2(1 - \beta x)}{t_c}$	A10
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Table 4. Conditions that need to be satisfied for each of the twelve candidate foraging strategies to be an ESS.

Strategy	Strategy Name	ESS Conditions [†]
(1,0,1,0)	AGG Defender	*
(0,1,0,1)	ST Resistor	*
(1,0,0,1)	AGG Resistor	$A2 \cap A8^c \cap A7^c$
(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

