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.**

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Data Accessibility

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

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Abstract

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

Introduction

41   Kleptoparasitism is defined as the theft of already procured food by one individual from

42   another (Brockmann & Barnard, 1979). It is one of the most widespread forms of exploitation

43   found in nature having been observed across several taxonomic groups, including spiders

44   (Coyle et al. 1991), insects (Erlandsson, 1988), mammals (Janson, 1985; Carbone et al. 2005)

45   and birds (Barnard, 1990; Brockmann & Barnard, 1979). The significance of kleptoparasitic

46   behaviour is that it allows individuals to avoid some of the costs of the foraging cycle

47   (searching for, acquiring and handling food items) by exploiting food discovered by another

48   individual's effort (Giraldeau & Caraco, 2000).

49

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   (*Sterciraridae*) 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**

241 *Study Site and Species*

242 *Study Site:* Billingsgate Market, London (Lat: 51°30'20.40"N; Long: 0°00'43.90"W) is a

243 seafood market in the Canary Wharf area of East London. Research at this location was

244 conducted in a car park area used by fishmongers to process and load their stock onto vans,

245 called the Trader's Car Park. The Trader's Car Park covered an area of 0.0104 square

246 kilometres (10,400m^2). 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 Resistors (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

$$P = S + H + A + D + C + R. \tag{1}$$

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):

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

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

$$\frac{dC}{dt} = p_2 p_4 v_h SH - \frac{2}{t_c}C, \tag{4}$$

$$\frac{dR}{dt} = p_2 p_4 v_h SH - \frac{2}{t_c} R, \tag{5}$$

$$\frac{dA}{dt} = p_1 p_3 v_h SH - \frac{2}{t_a} A, \tag{6}$$

$$\frac{dD}{dt} = p_1 p_3 v_h SH - \frac{2}{t_a} D. \tag{7}$$

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:

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

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.

$$S = \frac{H}{t_h v_f f}, \tag{9}$$

$$C = \frac{1}{2}\frac{p_2 p_4 t_c v_h H^2}{t_h v_f f}, \tag{10}$$

$$R = \frac{1}{2}\frac{p_2 p_4 t_c v_h H^2}{t_h v_f f}, \tag{11}$$

$$A = \frac{1}{2}\frac{p_1 p_3 t_a v_h H^2}{t_h v_f f}, \tag{12}$$

$$D = \frac{1}{2}\frac{p_1 p_3 t_a v_h H^2}{t_h v_f f}. \tag{13}$$

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.

$$P = \frac{H}{t_h v_f f} + H + \frac{1}{2}\frac{p_2 p_4 t_c v_h H^2}{t_h v_f f} + \frac{1}{2}\frac{p_2 p_4 t_c v_h H^2}{t_h v_f f} + \frac{1}{2}\frac{p_1 p_3 t_a v_h H^2}{t_h v_f f} + \frac{1}{2}\frac{p_1 p_3 t_a v_h H^2}{t_h v_f f}, \tag{14}$$

$$\Rightarrow P = \frac{H}{t_h v_f f} + H + \frac{p_2 p_4 t_c v_h H^2}{t_h v_f f} + \frac{p_1 p_3 t_a v_h H^2}{t_h v_f f}. \tag{15}$$

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.

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

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

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 $v_f f$; 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

food items or handlers to challenge, as stated above this search path is denoted by T_s or T_s^*

(Figures 3 and 4), which shows the time to acquire a food item from the start of searching.

Likewise if it surrenders the food item it becomes a searcher again and resumes handling at

the rate at which it finds a new food item or encounters another handler and successfully

challenges them, again T_s or T_s^*. The following situations need to be considered when a

handler is discovered by a searcher:

When it is advantageous for a handler to resist/defend in a population where searchers attack

and the rest of the handling population resists/defends:

5. When to defend against AGG (population defends and handler's searching strategy is

    AGG).

6. When to defend against AGG (population defends and handler's searching strategy is

    ST).

7. When to resist against ST (population resists and handler's searching strategy is ST).

8. When to resist against ST (population resists and handler's searching strategy is

    AGG).

When it is advantageous for a handler to resist/defend in a population where searchers attack

and the rest of the handling population does not resist:

9. When to defend against AGG (population surrenders).

10. When to resist against ST (population surrenders).

    (In these two cases the handler's searching pathways are identical as the payoff for

    both AGG and ST is equal when the population surrenders food items. T_s and T_s^*

    simplify to $1/(v_f f + v_h H)$.

When it is advantageous for a handler to resist/defend in a population where searchers do not

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**

<center>**Results**</center>

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 ($v_f f$) 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**

724   The results in Table 6 for parameter values $t_h = 0.42, t_c = 0.14, t_a = 0.26$ not only

725   gave equilibrium densities close to the densities observed in the Billingsgate foraging

726   population but returned ratios of AGG to ST in line with the rates with which these strategies

727   were used by foragers at Billingsgate. This indicated that the duration of an ST fight to an

728   AGG fight, at the values of t_h, t_c and t_a identified through numerical investigation,

729   accurately captured the ratio of these two strategies in the real foraging population, this being

730   that the mean duration of an AGG fight was nearly twice that of an ST fight.

731   *Ecological conditions for ESS's:*

732   An investigation of the regions of parameter space where each of the candidate ESS's shown

733   in Table 4 occur was conducted. Each ESS occurs when a system of inequalities made up by

734   various combinations of conditions A1a to A10 are satisfied (Table 4). Varying the values of

735   different ecological parameters contained in the inequalities had a direct influence on when

736   those inequalities were satisfied. Although all of conditions A1a to A10 were strict

737   inequalities, the boundary conditions where they are satisfied were obtained by setting the left

738   and right-hand sides of the inequalities equal to each other.

739   The values for parameters obtained from the Billingsgate data and the values for t_h,

740   t_c, and t_a, described in the above section, were used in this analysis. Two parameters were

741   allowed to vary when investigating the ecological conditions in which the ESS's occur. These

742   were the rate at which foragers find food $(v_f f)$ and the total number of individuals in

743   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 $v_f f$ 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 ($v_f f$) 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 ($v_f f$) 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.

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Figure Legends

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

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

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

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

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

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

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

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

Tables & Table Legends

Table 1. Behaviours constituting strategies of aggressive and stealth kleptoparasitism

Strategy		Behaviour
Aggressive	Force	Kleptoparasite uses of bill to make contact with host's body in order to effect theft.
		Attempt to physically pull or tear food item from host.
	Threat	*Upright threat posture* – 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).
		Wings spread – Kleptoparasite charges the host with wings spread.
		Charge – (BHG only) Kleptoparasite drops its head forward, flattens out its body and then charges at the host.
Stealth		Food stolen from the floor in front of the host.
		Food stolen whilst the host is distracted and not in contact with the food item.

Table 2. Model notation.

Population Densities	Definition
P	Density of the total foraging population
S	Density of searchers
H	Density of handlers
A	Density of aggressive kleptoparasites
D	Density of defenders against aggressive kleptoparasitism
C	Density of stealth kleptoparasites
R	Density of resistors against stealth kleptoparasitism
Model Parameters	
$v_f f$	Rate at which foragers find food items
$v_h H$	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?	$\dfrac{2\alpha}{t_a} > \max\left(\dfrac{2\beta x}{t_c}, v_f f\right)$	A1a
2	Handler resists & pop'n resists	When to use ST?	$\dfrac{2\beta x}{t_c} > \max(\dfrac{2\alpha}{t_a}, v_f f)$	A1b
3	Handler & pop'n resists/ defends	When to ignore handler	$v_f f > \max\left(\dfrac{2\alpha}{t_a}, \dfrac{2\beta x}{t_c}\right)$	A1c
4	Handler surrenders & pop'n surrenders	When to use AGG or ST?	$\infty > v_f f$	A2
		Handler		
5	Pop'n defends & handler is an AGG forager	When to defend against AGG?	$v_f f < \dfrac{2(1-\alpha)}{t_a} + (1 - 2\alpha)v_h H$	A3
6	Pop'n defends & handler is an ST forager	When to defend against AGG?	$v_f f < \dfrac{(1-\alpha)(2 + v_h t_c H)}{t_a} - \beta v_h H$	A4
7	Pop'n resists & handler is an ST forager	When to resist against ST?	$v_f f < \dfrac{2(1-\beta x)}{t_c} + (1 - \beta - \beta x)v_h H$	A5
8	Pop'n resists & handler is an AGG forager	When to resist against ST?	$v_f f < \dfrac{(1-\beta x)(2 + v_h t_a H)}{t_c} - \alpha v_h H$	A6
9	Pop'n surrenders	When to defend against AGG?	$v_f f < \dfrac{2(1-\alpha)}{t_a} - v_h H$	A7
10	Pop'n surrenders	When to resist against ST?	$v_f f < \dfrac{2(1-\beta x)}{t_c} - v_h H$	A8
11	Pop'n doesn't attack & mutant AGG attacker	When to defend against AGG?	$v_f f < \dfrac{2(1-\alpha)}{t_a}$	A9

12	Pop'n doesn't attack & mutant ST attacker	When to resist against ST?	$v_f f < \dfrac{2(1 - \beta x)}{t_c}$	A10

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

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

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

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

Parameter/ Strategy	Meaning of Parameter	Value
α	Probability of winning AGG fight	0.79
β	Probability of winning ST fight	0.71
p_1	Probability of using aggressive (AGG) kleptoparasitism	0.38
p_2	Probability of using stealth (ST) kleptoparasitism	0.23
p_3	Probability of defending	0.35
p_4	Probability of resisting	0.64
$v_f f$	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 (H)	≈2.53	2.52
Searchers (S)	≈8.5	8.52
ST attackers (C)	≈0.18	0.18
Resistors (R)	≈0.18	0.18
AGG attackers (A)	≈0.31	0.30
Defenders (D)	≈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
$v_f f$	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