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

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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.

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

Introduction

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

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

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

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

Following Giraldeau & Caraco (2000) we define a behaviour to be *social foraging* if two or more individuals associate and the functional consequences of their foraging behaviours are interdependent. Kleptoparasitism can be considered a social foraging strategy, a consequence of this is that the best foraging decision an individual can make depends on what other individuals in the population are doing. Giraldeau & Caraco (2000) defined this as the “concurrent economic interdependence among different individuals’ payoffs and penalties” (p.3). A critical implication of this is that the analysis of kleptoparasitic behaviours requires the use of game theory. Indeed, contests over resources of this nature were among the foundational questions initially addressed by evolutionary game theory (Maynard Smith, 1982). Several approaches have been taken to modelling kleptoparasitism using game theory, these include *Producer-Scrounger (P-S) Models* (Barnard & Sibly, 1981) and *Kleptoparasitism Models* (Broom & Ruxton, 1998).

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

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

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

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

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

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

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

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

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

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

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

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

Fieldwork was conducted at Billingsgate Market to record the kleptoparasitic interactions occurring between the gulls in that environment. The compartmental modelling approach was then used to develop a model of that population using the population parameters and strategies available to the foraging gulls at Billingsgate. The model was compared to the foraging behaviour recorded at Billingsgate to assess whether different behaviours were at equilibrium densities in the population and to conduct an analysis of whether individuals in the Billingsgate population are making the best behavioural responses in their use of kleptoparasitism.

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

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

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

Methods

Study Site and Species

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

INSERT FIGURE 1 ABOUT HERE

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

Measures

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

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

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

Stealth kleptoparasitism: Stealth kleptoparasitism was typified by the use of speed to approach, grab the food item and try to make off without directly confronting the handler for the item. Behaviours constituting stealth kleptoparasitism are described in Table 1. If the parasite managed to obtain any proportion of the food item being contested successful use of stealth kleptoparasitism had occurred.

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

INSERT TABLE 1 ABOUT HERE

Procedure

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

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

To identify the strategies used by foragers at Billingsgate, focal animal observations were conducted using video recordings of foraging patches. Individual foragers were observed as they moved around the patch and a continuous record was made of their foraging behaviours, indicating whether they sampled for food items, attacked using AGG, attacked using ST and, when handling, whether they defended, resisted or surrendered against attacks by other foragers. These focal animal observations were used to build up a picture of the forager's behaviour and to attribute a strategy to the forager based on the ESS strategies outlined in Table 4.

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

The model

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

The model developed here considers a population containing one species of forager. This single-species model reduced the complexity of the mathematics needed to model the foraging population and the model was compared against the averaged foraging data obtained for the whole population at Billingsgate. Although the Billingsgate population contained 3 species, with kleptoparasitism occurring both within and between species, the assumption was made that averaging the data over the whole year of study would smooth out any asymmetries in competitive ability between individuals and species and permit the population to be viewed as a large population containing just one-species.

Broom et al. (2004) considered a population of foragers that can either attack or ignore handlers and defend or surrender food items. The model developed here extends this by considering two types of kleptoparasitic strategy and we retain and extend the notation and parameters used in Broom et al. (2004) where necessary. The foraging population consists of a population density of P individuals. That foraging population (P) consists of groups of individuals in different behavioural states or compartments. A forager can only be engaged in one behavioural state and thereby can only be in one compartment at a time. At any time a proportion of the foraging population are searching (S) for food items and a proportion are handling (H) a food item. An average density f of food items is available and a forager can search the foraging area at a rate v_f for food items. The rate at which food items are discovered is therefore $v_f f$. Similarly, the rate at which a forager can search the foraging area for handlers is v_h, so the rate at which searchers encounter handlers of food items is $v_h H$. Following Broom et al. (2004), the time that food items take to handle is modelled using an exponential probability distribution with mean t_h. Additionally, a proportion of the foraging population are engaged in fights over food items, either as kleptoparasites trying to steal an item or handlers trying to keep hold of that food item. As stated previously, two kleptoparasitic strategies are possible within this population: aggressive kleptoparasitism or stealth kleptoparasitism. At any given time a proportion of the foraging population (P) will be attempting to steal items using aggressive kleptoparasitism (A) and a proportion of handlers will be fighting against those kleptoparasites by trying to defend (D) their food item from being stolen. Likewise, a proportion of the foraging population will be attempting to steal using stealth kleptoparasitism (C) and an equal proportion of handlers will be fighting to resist (R) their food item being stolen by stealth kleptoparasites. Defending and resisting are terms that both describe the defensive behaviour of handlers that are under attack, separate terms were used, for defending against aggressive kleptoparasitism and resisting against stealth kleptoparasitism, to differentiate the two behaviours as the probability of defensive behaviour against one type of kleptoparasitism might differ from that of the other type. Defenders (D) and Resistors (R) are therefore separate behavioural states in the foraging population (P). The composition of the total foraging population by compartments that capture the different behavioural states is described by equation (1),

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

Once a searcher encounters a handler it either attacks the handler using aggressive kleptoparasitism, it does this with probability p_1, or it attacks the handler using stealth kleptoparasitism, this occurs with probability p_2, otherwise it ignores the handler and continues searching for undiscovered food items, this occurs with probability $1 - p_1 - p_2$ (note that this means $p_1 + p_2 \leq 1$, e.g. see Table 4). Conversely, a handler that is found and attacked with aggressive kleptoparasitism can either defend against the attack, which it does with probability p_3, or surrender the food item without a fight, which occurs with probability $1 - p_3$. Likewise, a handler that is attacked by a searcher using stealth kleptoparasitism resists the attack with probability p_4 or surrenders the food item without a fight with probability $1 - p_4$. If a searcher attacks using aggressive or stealth kleptoparasitism and the handler defends or resists then a fight occurs. The fight lasts for a time duration that is modelled using an exponential probability distribution. In the case of aggressive kleptoparasitism the duration of the fight is drawn from an exponential distribution with mean $t_a/2$, the attacker wins the fight with probability α and the defender wins the fight with probability $1 - \alpha$. The duration of a stealth kleptoparasitism fight is also drawn from an exponential distribution with mean $t_c/2$. The stealth attacker wins the fight with probability β and the resistor wins the fight with probability $1 - \beta$. The mean duration of stealth and aggressive fights differs as a stealth fight involves less of an interaction between attacker and handler than an aggressive fight so on average $t_c < t_a$. At the end of a fight of either type the winner begins handling the contested food item and the loser resumes searching, either for food items or other handlers. The notation used for the strategies and parameters described above is summarised in Table 2.

INSERT TABLE 2 ABOUT HERE

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

INSERT FIGURE 2 ABOUT HERE

The change in the density of each behavioural compartment as described by the rates of inflow and outflow along the arrows shown in Figure 2, within the closed system defined 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

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

Stage 1: Equilibrium densities of the behavioural compartments:

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Stage 2: Conditions for using kleptoparasitism and defending/resisting against kleptoparasitic attacks:

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

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

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

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

In effect food items could be repeatedly stolen on multiple occasions; this requires some clarification of how potentially smaller and smaller items of food that have experienced some handling were treated, particularly in relation to ST kleptoparasitism where only portions of the food item are obtained. The assumption made in the model is that an item of food has the value of one whole food item regardless of whether it has previously been stolen or been part of a larger item of food. If a forager sees fit to challenge for the item then it is treated as one unit of food. It will be noted that this is akin to assuming that food items cannot be stolen multiple times and are only subject to one kleptoparasitic attempt, after which they are immediately consumed by the kleptoparasite or handler. The validity of this assumption was investigated by comparing the simplest cases possible in the population involving partial food items: whether a handler should resist against ST when attacked by a mutant kleptoparasite in a population that does not use kleptoparasitism. It was found that the conditions when it was optimal to resist were the same regardless of whether the kleptoparasitic incident was the first attempt or a subsequent attempt to steal the food. This indicated that it was valid to treat each food item as one unit of food regardless of previous handling or whether it had been subject to previous kleptoparasitic attempts (Appendix B).

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

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

Searchers:

Following Broom & Ruxton (1998) and Broom et al. (2004), to assess when it is advantageous for a searcher to attack a handler it is sufficient to consider the instantaneous rate at which a searcher becomes a handler after encountering a handler. When a searcher encounters a handler it must decide whether to ignore the handler and continue searching for food items or attack the handler using either AGG or ST. The strategy it should use is the one that minimises the amount of time until it becomes the handler of a food item. This is the strategy that maximises the forager’s rate of gain per time foraging. If it ignores the handler 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 influenced by the time costs of the fight and, if it loses, the rate at which it finds other food items or handlers to challenge. The rates at which other food items or handlers are found and challenged by foragers are given by the foraging pathways T_s for AGG attackers (Figure 3) and T_s^* for ST attackers (Figure 4). In this model the following situations need to be considered when a searcher encounters a handler:

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

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

When it is advantageous not to attack the handler:

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

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

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

Handlers:

When a handler is discovered by a searcher and attacked it can choose either to resist/defend the food item it is handling or surrender the item and resume searching for a new food item. The strategy it should use is the one that minimises the amount of time until it resumes handling a food item. If it resists/ defends the food item the time to resume handling is 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:

11. When to defend AGG against a mutant AGG challenger.
12. When to resist ST against a mutant ST challenger.

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

INSERT FIGURE 3 ABOUT HERE

INSERT FIGURE 4 ABOUT HERE

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

INSERT TABLE 3 ABOUT HERE

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

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

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

- Strategy (1,0,1,0) (AGG Defender): The forager always attacks AGG and always defends against AGG, but never uses or resists against ST.
- Strategy (0,1,0,1) (ST Resistor): The forager always attacks ST and always resists ST attacks, but never uses or defends against AGG.
- Strategy (1,0,0,1) (AGG Resistor): The forager always attacks AGG but only ever resists against ST attacks.
- Strategy (1,0,0,0) (AGG Marauder): The forager always attacks AGG but never resists or defends against attack.

- Strategy (0,1,1,0) (ST Defender): The forager always attacks ST and only defends against AGG.
- Strategy (0,1,0,0) (ST Marauder): The forager always attacks ST but never resists or defends against attacks.
- Strategy (1,0,1,1) (AGG Hawk): The forager always attacks AGG and always defends and resists against both types of attack.
- Strategy (0,1,1,1) (ST Hawk): The forager always attacks ST and always defends and resists against both types of attack.
- Strategy (0,0,1,1) (Retaliator): The forager never attacks but it always defends and resists against both types of attack.
- Strategy (0,0,0,0) (Dove): The forager always searches for its own food, it never attacks and never defends or resists.
- Strategy (0,0,0,1) (ST Retaliator): The forager never attacks using either strategy and never defends against AGG but always resists against ST.
- Strategy (0,0,1,0) (AGG Retaliator): The forager never attacks using either strategy, it always defends against AGG but never against ST attacks.

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

INSERT TABLE 4 ABOUT HERE

Results

Fieldwork results:

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

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

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

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

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

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

To calculate the probability of a searcher using a kleptoparasitic strategy, either attacking AGG or ST upon discovering a handler, (p_1) and (p_2) respectively, it was necessary to find some way of accounting for the proportion of occasions that foragers ignored a handler and continued searching for food items, as there is no direct way of knowing whether a searcher had the opportunity to attack and did not it was necessary to estimate ignored opportunities. This was done using the percentage of foraging patches where no kleptoparasitism occurred as a measure of ignored opportunities. Kleptoparasitism was possible in all foraging patches and the percentage of patches where no kleptoparasitism took place, 39% of patches, was viewed as a crude index of the rate at which foragers ignored opportunities to steal. The probability that a searcher attacked using either AGG or ST was then calculated by multiplying the percentage with which the particular kleptoparasitic strategy was used by the percentage of patches within which kleptoparasitism occurred (61%). This gave a probability of attacking AGG (p_1) of 0.38 and the probability of attacking ST (p_2) of 0.23. The probability that a handler defended (p_3) or resisted (p_4) was simply the proportion of attacks recorded at Billingsgate where the handler defended or resisted. Handlers at Billingsgate defended against AGG 35% of the time making p_3 0.35 and resisted against ST 64% of the time making p_4 0.64.

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

INSERT TABLE 5 ABOUT HERE

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

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

Testing for equilibrium densities:

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

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

INSERT TABLE 6 ABOUT HERE

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

Ecological conditions for ESS's:

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

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

INSERT TABLE 7 ABOUT HERE

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

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

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

INSERT FIGURE 5 ABOUT HERE

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

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

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

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

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

INSERT FIGURE 6 ABOUT HERE

INSERT FIGURE 7 ABOUT HERE

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

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

AGG Resistor was used in an ESS region on one occasion and in a non-ESS region on 8 occasions. All observations of AGG Resistor in a non-ESS region also occurred in the region where AGG Hawk and ST Hawk were the ESS's. Foragers using this strategy appeared to make the error of not defending against AGG attacks by other foragers, despite attacking AGG and resisting against ST.

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

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

INSERT TABLE 8 ABOUT HERE

Discussion

This model was developed to try and capture the kleptoparasitic behaviours of a population of foraging gulls at Billingsgate Market and to investigate what the model could tell us about the optimality and stability of the behavioural decisions made by individuals in that population. This was pursued in two ways: 1. By considering the density of individuals engaged in each behaviour of interest in the population and investigating the possibility that these behaviours were at equilibrium densities. 2. Through assessing the optimality of the behavioural decisions of individual foragers when compared against the ecological conditions in the patches in which they were foraging. Were foragers using ESS strategies?

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

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

When considering whether these values accurately represent the mean duration of fights within the Billingsgate population it was noted that fights at Billingsgate, even AGG fights, whilst variable, were on average short in duration. We estimated from field observations that ST fights had mean duration of approximately 5 seconds and AGG fights had mean duration of just under 10 seconds. However, we did not rely on these estimates as they were obtained during fieldwork by glancing at a wristwatch and making a quick note for an opportunistic sample of incidents, essentially those in close proximity to the observer, when other recording tasks permitted.

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

Over the year of study no significant injuries were sustained by birds engaged in fights over food. Gulls often sustain injuries whilst fighting and fights can last for a considerable length of time particularly during the breeding season when they are generally more aggressive (Tinbergen, 1953; personal obs.). The fact that no observations of injuries were made over the period of study at Billingsgate may reflect that, on the whole, there is no shortage of food at the site so the conditions that would make staying in a lengthy fight a good economic decision might not have existed. This interpretation would agree with the short fight durations produced by the model for both strategies.

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

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

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

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

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

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

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

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

Third, the one-species approach used to model this population assumed that all foragers were essentially identical and that averaging the data for the whole year of study would successfully smooth out the influence of competitive asymmetries between individuals and between the three study species. The one-species approach was used to keep the model as simple as possible and make the necessary mathematics more tractable. The regions of parameter space predicted by the model make intuitive sense and agree with previous models (Broom et al. 2004; Hadjichrysanthou & Broom, 2012), with ESS regions for Hawk strategies in low food availability patches and Marauder strategies in areas of higher food availability where defensive behaviour is less necessary as new food items are encountered frequently. The model did not fully predict individual foraging decisions. This may be because additional factors such as injury and energetic costs, not included in the model, may have influenced strategy choice. However, gull species differ considerably in morphology and potentially thereby in competitive ability. Despite being frequently found together in mixed-species foraging flocks, the three species found at Billingsgate differ considerably in size and dominance. GBB and HG are amongst the largest of gull species, being both predatory and aggressive with large powerful bills. The BHG in contrast is a much smaller species of gull. Beyond the ecological parameters of food discovery rate ($v_f f$) and density of the population in a patch (P) that were the focus of this analysis, asymmetries between foragers of the different species clearly did affect the foraging decisions made. For example, the more aggressive Hawk strategies (AGG Hawk and ST Hawk) were the strategies used effectively and played as ESS's on all occasions. These are likely to be strategies used by the larger, more dominant species. In contrast, the Marauder strategies (ST Marauder and AGG Marauder) were strategies used in the non-ESS regions of parameter space. These strategies were seen most frequently in the region where AGG Hawk and ST Hawk were ESS's, indicating that foragers were failing to defend food items when such behaviour would have been optimal. What appeared to be sub-optimal behaviour of surrendering food in a region where food was scarce and defensive behaviours were predicted by the model, in most cases will have been the best behavioural decision for some handlers, given the competitive advantages of the bird that was attacking it. For example, due to differences in size and strength it would never be optimal for a BHG handler to defend against a GBB or HG, indeed the data from Billingsgate showed that BHG never defended when attacked by either of these larger species. The asymmetries between these two species are based on size dimorphism and are clear for all individuals to see. As argued by Maynard Smith (1982), when individuals are aware of asymmetries those asymmetries will affect behaviour. The one-species model developed here did not reflect the fact that the optimal behaviour in a given region of parameter space would differ between the three study species due to differences in competitive ability; and the modelling assumption of only considering pure strategies overlooked the fact that the best decision a handler can make may change as a function of the species of opponent.

Mixed strategies were not observed in the focal animal observations conducted. This may be because an animal that has a best strategy should use that strategy. However, we know from analysis of the patterns of kleptoparasitic behaviour in the data at Billingsgate that larger species used AGG against smaller species, smaller species used ST against larger species and that gulls used both AGG and ST against conspecifics (75% AGG, 25% ST). This leaves a number of possible scenarios: Individuals specialise in one type of kleptoparasitism and select their opponents based on this, so the population consists of a mix of individuals using pure strategies. Alternatively, individuals use both types of kleptoparasitism and will change which one they use based on the competitive ability of their opponent. Although this second type was not observed in the focal observations it seems likely that there will be individuals in the population that do switch strategies based on opponent. Perhaps none of the focal observations were of sufficiently long duration to observe all the necessary interactions to show this. If it had been possible to mark/identify individuals, this picture could have been developed by observing individuals across foraging patches building up a more comprehensive picture of foraging strategies of individuals. Examination of the focal animal data showed that all 12 individuals that correctly used ESS's were larger gull species, either GBB or HG, indicating that the parameter space shown in Figure 5 may best capture the ESS regions for more dominant individuals in the population.

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

When assessing the amount of error in the model's ability to predict individual behaviour the picture appears to be more complicated than species level differences in competitive ability can account for. However, there is a further dimension upon which foragers in this population can differ in competitive ability and that is age-class. Within species the foraging abilities of gulls increase with age up to maturity (Verbeek, 1977a; Bertellotti & Yorio, 2000). We can expect this dimension to influence behaviour with juvenile gulls perhaps investing more in certain types of kleptoparasitic strategies due to their lesser competitive abilities or poorer foraging decisions due to inexperience. Juvenile gulls made up 48% of the foraging population at Billingsgate, however, juveniles were overrepresented in the group of 52 gulls to whom a foraging strategy could be attributed, which consisted of 69% juvenile birds. This heavy bias towards juveniles in the population of individuals used to assess individual foraging decisions highlights further that the division of parameter space regions for Billingsgate may be complex and that the sample of gulls to whom a strategy could be attributed to test the model may not generalise to the population as a whole.

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

Further, discussion is also required of a more fundamental limitation of the approach taken in this research. Values for model parameters were extracted from field data. Using this approach it was necessary to find some meaningful way of aggregating field data that captured behaviour in the Billingsgate population. This was achieved by working out probabilities for certain behaviours based on data for the whole population over the year of study. This gave single probabilities for behaviours such as winning fights and attempting kleptoparasitic attacks that remained constant. Just as calculating the average for any rate is of limited value in identifying the instantaneous rate at any single point over the period of measurement, the method for calculating probabilities for certain behaviours at Billingsgate ignored the fact that these probabilities may change with environmental conditions over time. The alternative approach would have required generating a model for each of the 183 patches recorded. This would have resulted in excessive model fitting when trying to capture something general about kleptoparasitism in this population. This limitation is of most relevance when considering the behaviours of individual foragers. The parameter estimates that generated the regions of parameter space for different ESS's (Figure 5) will not have been appropriate for all foragers; this was certainly true at the level of species and age-class, and at the finest level of granularity each forager may have had its own unique parameter space division for ESS's. However, all methods of sampling and data collation result in some loss of precision, so, despite these limitations, the approach taken was viewed as a valid way to summarise kleptoparasitic behaviours and arrive at parameter estimates for this population at the most general level.

The application of theoretical models to the behaviour of wild foraging populations is a neglected area of research. Empirical work in this area has frequently focused on using captive populations of foragers to test the frequency-dependent payoffs predicted by P-S models, often using aviary populations of seed-feeding passerines (Giraldeau et al., 1994; Mottley & Giraldeau, 2000). Studies using natural populations are rare (Beauchamp, 2014). Hansen (1986) settled for a qualitative assessment of the extent to which kleptoparasitic and producing strategies matched game-theoretic equilibrium predictions when studying foraging interactions between Bald eagles. Work by Beauchamp (2014) went further by assessing whether producing and scrounging tactics provided the same mean payoffs in foraging aggregations of Semipalmated sandpipers (*Calidris pusilla*). Behavioural cues of time spent exploiting a patch in the Beauchamp (2014) study were used to measure intake, this was used to calculate payoffs and assess the fitness of different strategies through comparison of time spent exploiting produced versus scrounged patches. A comparable approach in our model would have been to try to use handling time to calculate payoffs for different strategies relative to different sized food items that were stolen. However, in the Billingsgate population, birds competed for discrete hard to divide food items where contest times were integral to foraging efficiency. As a result the differential equation based method we used, whereby minimisation of time costs in acquiring food items was used to compare the fitness of behaviours was, we believe, the most practical approach at Billingsgate.

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

Research by Morand-Ferron et al., (2007) investigated kleptoparasitism in a wild population of Carib grackles (*Quiscalus lugubris*) by using provisioning studies. Each item of food was indivisible and required some handling before it could be exploited and Carib grackles used aggressive and stealth kleptoparasitism to obtain these food items. They found that scrounging was negatively frequency dependent in line with P-S model predictions, but were unable to provide insight into how the use of different types of kleptoparasitism shaped patterns of behaviour in their study population. This may be because, with only one study species, there was no easy way to discern differences in competitive ability between foragers, so identifying the relationship between how differences in competitive ability influenced the use of different types of kleptoparasitism may not have been possible. Our model, by considering a population of one species, suffered a similar limitation and further work to investigate the dynamics of strategy use and competitive ability, as discussed above, seems worthwhile. Mixed-species flocks of gulls provide a good study system for addressing these questions as they can use all three of the kleptoparasitism strategies described and differences in competitive ability can also be readily identified through size differences between species and age differences within species, recognised through plumage.

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

This research focused on modelling the behavioural decisions of a population of urban gulls. Gull populations in the UK have declined significantly over the last century resulting in a number of species being listed as conservation priorities (Eaton et al., 2015). Simultaneously gull populations have been growing in urban areas (Rock, 2005) by exploiting an abundance of food resources from anthropogenic waste as well as secure nest sites on buildings. This has generated considerable research interest regarding the conservation and changing ecology of these species (Scott et al., 2014; Rock & Vaughan, 2013; Spencer et al., 2017; Ross-Smith et al., 2014). We hope that the research reported here will convince researchers of the utility of evolutionary game theory as a tool for investigating how good the behavioural decisions of urban gulls are. Knowledge of the optimality of their behaviour and foraging abilities will be essential to their conservation and will be important 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?	$\frac{2\alpha}{t_a} > \max\left(\frac{2\beta x}{t_c}, v_f f\right)$	A1a
2	Handler resists & pop'n resists	When to use ST?	$\frac{2\beta x}{t_c} > \max(\frac{2\alpha}{t_a}, v_f f)$	A1b
3	Handler & pop'n resists/ defends	When to ignore handler	$v_f f > \max\left(\frac{2\alpha}{t_a}, \frac{2\beta x}{t_c}\right)$	A1c
4	Handler surrenders & pop'n surrenders	When to use AGG or ST?	$\infty > v_f f$	A2
		Handler		
5	Pop'n defends & handler is an AGG forager	When to defend against AGG?	$v_f f < \frac{2(1-\alpha)}{t_a} + (1 - 2\alpha)v_h H$	A3
6	Pop'n defends & handler is an ST forager	When to defend against AGG?	$v_f f < \frac{(1-\alpha)(2+v_h t_c H)}{t_a} - \beta v_h H$	A4
7	Pop'n resists & handler is an ST forager	When to resist against ST?	$v_f f < \frac{2(1-\beta x)}{t_c} + (1 - \beta - \beta x)v_h H$	A5
8	Pop'n resists & handler is an AGG forager	When to resist against ST?	$v_f f < \frac{(1-\beta x)(2+v_h t_a H)}{t_c} - \alpha v_h H$	A6
9	Pop'n surrenders	When to defend against AGG?	$v_f f < \frac{2(1-\alpha)}{t_a} - v_h H$	A7
10	Pop'n surrenders	When to resist against ST?	$v_f f < \frac{2(1-\beta x)}{t_c} - v_h H$	A8
11	Pop'n doesn't attack & mutant AGG attacker	When to defend against AGG?	$v_f f < \frac{2(1-\alpha)}{t_a}$	A9
12	Pop'n doesn't attack &	When to resist against ST?	$v_f f < \frac{2(1-\beta x)}{t_c}$	A10

mutant ST attacker

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

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

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

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

Parameter/ Strategy	Meaning of Parameter	Value
α	Probability of winning AGG fight	0.79
β	Probability of winning ST fight	0.71
p_1	Probability of using aggressive (AGG) kleptoparasitism	0.38
p_2	Probability of using stealth (ST) kleptoparasitism	0.23
p_3	Probability of defending	0.35
p_4	Probability of resisting	0.64
$v_f f$	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 $\boldsymbol{t_h = 0.42, t_c = 0.14, t_a = 0.26}$.

Behavioural Compartment	**Equilibrium Density***	**Billingsgate Density†**
Handlers ($\boldsymbol{H}$)	≈2.53	2.52
Searchers ($\boldsymbol{S}$)	≈8.5	8.52
ST attackers ($\boldsymbol{C}$)	≈0.18	0.18
Resistors ($\boldsymbol{R}$)	≈0.18	0.18
AGG attackers ($\boldsymbol{A}$)	≈0.31	0.30
Defenders ($\boldsymbol{D}$)	≈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
$\boldsymbol{\alpha}$	Probability of winning AGG fight	0.79
$\boldsymbol{\beta}$	Probability of winning ST fight	0.71
$\boldsymbol{v_f f}$	Rate at which an individual discovers food items	Varied
$\boldsymbol{v_h}$	Rate at which a forager discovers handlers	0.83
$\boldsymbol{t_h}$	Mean handling time for a food item	0.42
$\boldsymbol{t_c}$	Twice the duration of a stealth (ST) fight	0.14
$\boldsymbol{t_a}$	Twice the duration of an aggressive (AGG) fight	0.26
$\boldsymbol{P}$	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