

1 **The effect of kleptoparasite and host numbers on the risk of food-stealing in an avian**
2 **assemblage**

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17

18 **Abstract**

19 Kleptoparasitism involves the theft of resources such as food items from one individual by
20 another. Such food-stealing behaviour can have important consequences for birds, in terms of
21 individual fitness and population sizes. In order to understand avian host-kleptoparasite
22 interactions, studies are needed which identify the factors which modulate the risk of
23 kleptoparasitism. In temperate European intertidal areas, Eurasian oystercatchers
24 (*Haematopus ostralegus*) feed primarily on bivalve molluscs, which may be stolen by
25 kleptoparasitic species such as carrion crows (*Corvus corone*) and herring gulls (*Larus*
26 *argentatus*). In this study we combined overwinter foraging observations of oystercatchers
27 and their kleptoparasites on the Exe Estuary, UK, with statistical modelling to identify the
28 factors that influence the likelihood of successful food stealing behaviour occurring. Across
29 the winter, 16.4 % of oystercatcher foraging attempts ended in successful kleptoparasitism;
30 the risk of theft was lowest in February (10.8 %) and highest in December (36.3 %). Using an
31 information theoretic approach to compare multiple logistic regression models we present
32 evidence that the outcome of host foraging attempts varied with the number of
33 kleptoparasites per host within the foraging patch for two out of five individual months, and
34 for all months grouped. Successful, kleptoparasitism was more likely to occur when the total
35 number of all kleptoparasites per host was greater. Across the entire winter study period,
36 oystercatcher foraging attempts that resulted in kleptoparasitism were associated with a mean
37 number of kleptoparasites per host that was more than double that for foraging attempts that
38 ended in the oystercatcher successfully consuming the mussel. Conversely, the stage of the
39 tidal cycle within the estuary did not affect the outcome of oystercatcher foraging attempts.
40 Our study provides evidence that bird numbers influence the risk of kleptoparasitism within
41 avian assemblages.

42

43 **Introduction**

44 Kleptoparasitism, whereby individuals steal food from others, is a commonly observed
45 phenomenon in nature (Brockman and Barnard 1979, Ens and Goss-Custard 1984, Amat
46 1990). The occurrence of kleptoparasitism can have important individual- and population-
47 level consequences for both species involved. Individuals subject to kleptoparasitism (termed
48 ‘hosts’) suffer reduced intake of energy and nutrient due to the loss of prey, which can lead to
49 reduced individual survival and breeding success, and ultimately to smaller populations in
50 areas with high risk of kleptoparasitism (Gorman et al. 1998). Conversely, food-stealing
51 individuals might increase their reproductive success due to greater food intake from
52 kleptoparasitism (García et al. 2011, García et al. 2013). Kleptoparasite populations can be
53 highly responsive to changes in population size of the host species that they steal from. For
54 example Phillips et al. (1996) reported that over a 21 year period around the coast of Shetland
55 (UK), inter-annual fluctuations in the population size of Arctic terns (*Sterna paradisaea*
56 Pontoppidan 1763) were closely matched by changes in the population size of their main
57 kleptoparasite species, the Arctic skua (*Stercorarius parasiticus* Linnaeus 1758). Subsequent
58 research has shown substantial declines in Arctic skua numbers in response to collapses in the
59 breeding populations of the host species that the skuas steal from (Caldow and Furness 2000).
60 Kleptoparasitism can also cause the host species to increase the number of prey harvested to
61 compensate for stolen prey, leading to greater reductions in prey populations (García et al.
62 2011, Dekker et al. 2012).

63 Given the influence of kleptoparasitic interactions on individual animal fitness and
64 population sizes, as well as trophic interactions and food webs, knowledge of
65 kleptoparasitism is vital if the population dynamics of avian communities are to be
66 understood. Numerous studies have documented food stealing behaviour across a wide range
67 of avian species (e.g. Brockman and Barnard 1979, Amat 1990, Iyengar 2008). In order to

68 understand host-kleptoparasite interactions, studies are needed which identify the factors
69 which modulate the risk of kleptoparasitism within avian assemblages (e.g. Amat and
70 Aguilera 1990, García et al. 2010).

71 Within avian assemblages, corvids and gulls have been reported to steal food items from
72 smaller-bodied wading bird species (Källander 1977, Thompson 1983, Ens et al. 1990, Taylor
73 and Taylor, 2005). Wading birds such as the Eurasian oystercatcher (*Haematopus ostralegus*
74 Linnaeus 1758) that feed on shellfish in intertidal areas represent a useful study system in
75 which kleptoparasitism can be studied. The relatively simple habitat structure, unobscured
76 views, and large, distinct food items ensure that foraging interactions can be observed clearly,
77 even from distance. Oystercatchers feed primarily on mussels (*Mytilus edulis* Linnaeus
78 1758), which may be stolen by carrion crows (*Corvus corone* Linnaeus 1758) or herring gulls
79 (*Larus argentatus* Pontoppidan 1763) whilst the oystercatcher is engaged in the process of
80 opening and consuming the mussel (Ens and Goss-Custard 1984). Both crows and gulls are
81 known to feed on mussels directly (e.g. Whiteley et al. 1990, Norris et al. 2000) and thus
82 kleptoparasitism is a facultative feeding strategy in these species. Individuals may reduce
83 searching and handling costs by stealing a food item from another individual (Stillman et al.
84 1997, Flower et al. 2013). Whilst intraspecific food-stealing behaviour among oystercatchers
85 has been well-studied (e.g. Goss-Custard et al. 1982, Ens and Goss-Custard 1984, Stillman et
86 al. 1997, Goss-Custard et al. 1999), interspecific interactions have received little attention.
87 Consequently, to address this knowledge gap we focus on interspecific kleptoparasitism in
88 this study.

89 In this study we combined overwinter foraging observations of oystercatchers and their
90 kleptoparasites with statistical modelling to test two predictions related to factors that may
91 influence the occurrence of successful food stealing behaviour. Our first prediction was that,
92 among the range of potential measures of relative kleptoparasite pressure on host individuals,

93 the number of kleptoparasite individuals per host would be the best predictor of increased
94 kleptoparasitism risk. The relationship between kleptoparasitism risk and the relative
95 numbers of kleptoparasites and hosts is not well understood for most kleptoparasitic
96 interactions. Typically, host numbers have been reported, but the evidence for a relationship
97 between host numbers and kleptoparasitism risk is mixed. Some studies have reported that
98 the risk of kleptoparasitism rises with host numbers (Garrido et al. 2002, Mahendiran and
99 Urfi 2010). However, other studies have reported that the numbers of hosts and
100 kleptoparasites were poor predictors of kleptoparasitism risk (Woodall 1984, Varpe 2010).
101 Therefore, to examine the effect of host and kleptoparasite numbers on kleptoparasitism risk,
102 we sequentially tested the relationships between 12 potential measures of relative
103 kleptoparasite pressure, incorporating host and/or kleptoparasite numbers, and the outcome of
104 oystercatcher foraging attempts (i.e. consumed by oystercatcher or stolen by kleptoparasite).
105 The 12 potential measures of kleptoparasite pressure represented a comprehensive range used
106 across a range of different studies of kleptoparasitic interactions (Woodall 1984, Garrido et
107 al. 2002, Mahendiran and Urfi 2010, Varpe 2010): (1) Number of oystercatchers; (2) Number
108 of feeding oystercatchers; (3) Percentage of oystercatchers feeding; (4) Number of crows; (5)
109 Number of gulls; (6) Number of crows and gulls (*i.e.* all kleptoparasites); (7) Number of
110 crows per oystercatcher; (8) Number of gulls per oystercatcher; (9) Number of all
111 kleptoparasites per oystercatcher; (10) Number of crows per feeding oystercatcher; (11)
112 Number of gulls per feeding oystercatcher; (12) Number of all kleptoparasites per feeding
113 oystercatcher.

114 Our second prediction was that the outcome of oystercatcher foraging attempts on mussels
115 would vary in association with two variables. Firstly, the relative kleptoparasite pressure on
116 host individuals, which as stated above was expected to be synonymous with the number of
117 kleptoparasite individuals per host. Secondly, the timing of when, both within a day and a

118 season, the host foraging attempt occurs, may affect the relative value of the food item for
119 both the forager and kleptoparasite (Baglione and Canestrari 2009). Animal foraging
120 decisions are known to be sensitive to seasonal changes in food quantity, quality and
121 exploitation costs (e.g. Wood et al. 2013). Previous observations of many kleptoparasitic
122 interactions have suggested that the risk of kleptoparasitism can vary temporally (Hulsman
123 1976, Oro and Martinez-Vilalta 1994, Dies and Dies 2005).

124

125 **Materials and methods**

126 *Study system*

127 The Exe estuary in south-west England is 10 km long and ranges between 1 and 2 km wide
128 ($50^{\circ}36'N$ $03^{\circ}25'W$; **Figure 1**). The peak overwinter counts of oystercatchers within the
129 estuary have declined progressively from 4733 individuals in the 1995/6 winter to 2126 in the
130 2012/3 winter, although the causes of this apparent decline are unclear (Austin et al. 2014).
131 The overwintering oystercatcher population of the Exe estuary has been well-studied, and the
132 birds known to feed predominantly upon mussels in intertidal areas (Goss-Custard and Durell
133 1983, Ens and Goss-Custard 1984, Stillman and Wood 2015).

134

135 *Foraging observations*

136 Each month between November 2013 and March 2014 inclusive, each of the nine mussel
137 beds were surveyed for foraging oystercatchers over a complete spring tidal cycle. In order to
138 achieve a standardised sampling effort across different months, our observations were made
139 continuously over the tidal cycle, rather than within an arbitrary time-frame. During each
140 survey, we scanned the mussel bed, using a Swarovski STS 80HD (20×60) tripod-mounted

141 telescope (Swarovski AG, Austria), looking for an oystercatcher in the process of seizing a
142 mussel. We then followed that individual until the outcome of the foraging attempt was
143 observed. We recorded whether the mussel was successfully opened and consumed, or
144 whether the individual lost the mussel due to kleptoparasitism by a carrion crow or herring
145 gull. If the individual abandoned the mussel without opening it, was attacked by another
146 oystercatcher, or was lost from view, then the observation was terminated and no record was
147 made. For each individual foraging observation, we recorded the numbers of oystercatchers,
148 carrion crows and herring gulls present on the mussel bed. Furthermore, we noted the
149 proportion of oystercatchers on the focal mussel bed that were actively foraging. For each
150 observation we also calculated the relative stage of the tidal cycle (T) as follows:

$$151 \quad T = (t_x / t_{max}) \cdot 100,$$

152 where t_x was the number of minutes elapsed since the first exposure of the mussel bed on the
153 receding tide, and t_{max} was the total number of minutes for which the mussel bed was exposed
154 during that tidal cycle. Thus each of our individual foraging observations was associated with
155 corresponding values for host and kleptoparasite abundance, month, and stage of the tidal
156 cycle.

157

158 *Statistical analyses*

159 To address our first prediction, we used logistic regressions with binomial error structures to
160 test the relationships between 12 potential measures of kleptoparasite pressure and the
161 outcome of oystercatcher foraging attempts. A separate regression was carried out for each of
162 the 12 potential measures of kleptoparasite pressure (in addition to the null model). Our
163 response variable, the outcome of oystercatcher foraging attempts, was a binary variable with

164 the following levels: 0 = oystercatcher consumed mussel, 1 = mussel was stolen by
165 kleptoparasite. The 12 potential measures of kleptoparasite pressure were as follows: (1)
166 Number of oystercatchers; (2) Number of feeding oystercatchers; (3) Percentage of
167 oystercatchers feeding; (4) Number of crows; (5) Number of gulls; (6) Number of crows and
168 gulls (*i.e.* all kleptoparasites); (7) Number of crows per oystercatcher; (8) Number of gulls
169 per oystercatcher; (9) Number of all kleptoparasites per oystercatcher; (10) Number of crows
170 per feeding oystercatcher; (11) Number of gulls per feeding oystercatcher; (12) Number of all
171 kleptoparasites per feeding oystercatcher. Each parameter was tested independently in
172 separate logistic regression analyses in order to find the best-fitting parameter. After
173 McFadden (1974) we used McFadden's R^2 as our measure of the variance explained for each
174 relationship, calculated as: $R^2_{McFadden} = 1 - (\ln(L_{fit}) / \ln(L_{null}))$, where $\ln(L_{fit})$ refers to the
175 natural logarithm of the maximised likelihood of the fitted model, whilst $\ln(L_{null})$ refers to the
176 natural logarithm of the maximised likelihood of the null model.

177 To address our second prediction, we used logistic regressions with binomial error structures
178 to test all combinations of the following variables on the binary outcome of oystercatcher
179 foraging attempts: N = number of all kleptoparasites per oystercatcher; M = Month of the
180 winter period (1 to 5 corresponding to November to March); T = % of tidal cycle elapsed at
181 time of observation. N, M and T were treated as continuous variables. We carried out full
182 subset model selection in order to test all possible combinations of additive and two-way
183 interaction terms. To prevent issues with collinearity we used Pearson's product-moment
184 correlations to test for correlations between our explanatory variables; significantly correlated
185 variables were not permitted together within candidate models (Graham 2003). We modelled
186 all combinations of variables and from these selected the model with the lowest Akaike's
187 Information Criteria (AIC) value as our best model (Burnham et al. 2011).

188 We carried out all of our statistical analyses using R version 3.1.2 (R Development Core
189 Team 2015), with data and residual exploration performed according to the established
190 protocol of Zuur et al. (2010), which confirmed that model assumptions were met. For all
191 comparisons a significant effect was attributed where $p < 0.05$.

192

193 **Results**

194 We recorded 997 observations of oystercatcher feeding attempts on mussels between
195 November and March. Overall oystercatchers successfully consumed mussels on 833 (83.6
196 %) occasions, whilst kleptoparasitism by crows and gulls accounted for 104 (10.4 %) and 60
197 (6.0 %) foraging attempts respectively (Table 1). Oystercatcher foraging success, defined as
198 the percentage of mussels found by oystercatchers that were consumed rather than stolen, was
199 lowest in December (63.7 %; $n = 102$) and greatest in February (89.3 %; $n = 233$). In each
200 month a greater percentage of the observed kleptoparasitic events were carried out by crows
201 than gulls (Table 1). However, the difference between the percentages of kleptoparasitism for
202 which crows and gulls were responsible ranged from 0.4 % in February to 12.7 % in
203 December (Table 1).

204 Logistic regression analyses indicated that, of our different measures of relative
205 kleptoparasite pressure, the total number of all kleptoparasites per oystercatcher best
206 explained the outcome of oystercatcher foraging attempts (Table 2). Indeed, the total number
207 of all kleptoparasites per oystercatcher had a McFadden's R^2 value of 0.056 compared with
208 the 0.046 value associated with the next best measure, the total number of all kleptoparasites
209 per feeding oystercatcher. Of our different measures of relative kleptoparasite pressure, only
210 the percentage of oystercatchers feeding and the number of gulls were not found to have
211 significant effects on the outcome of oystercatcher foraging attempts.

212 We found evidence of a significant negative correlation between the number of
213 kleptoparasites per oystercatcher and the month in which that observation was made (Table
214 3); hence, the numbers of kleptoparasites per oystercatcher were typically lower in later
215 winter months relative to early winter months. Accordingly, the number of kleptoparasites
216 per oystercatcher and month were not permitted in the same model during all subsequent
217 analyses. No other significant correlations between potential explanatory variables were
218 detected (Table 3).

219 Multiple logistic regression analyses indicated that a model comprised of the number of
220 kleptoparasites per oystercatcher best explained the outcome of oystercatcher foraging
221 attempts (Table 4). Indeed, the best model had an Δ AIC value of 48.1 greater than the null
222 model composed of an intercept alone. Combined data from all months indicated a significant
223 relationship between the total number of all kleptoparasites per oystercatcher and the binary
224 outcome of oystercatcher foraging attempts (Table 5). However, performing logistic
225 regression analyses for each month separately indicated that significant relationships between
226 the total number of all kleptoparasites per oystercatcher and the binary outcome of
227 oystercatcher foraging attempts were detected for November and March only (Figure 2; Table
228 5). Across all months, the mean (\pm 95 % CI) number of kleptoparasites per oystercatcher was
229 0.8 ± 0.1 where oystercatchers successfully consumed mussels and 1.9 ± 0.4 where
230 kleptoparasitic crows or gulls successfully stole the mussel from the oystercatcher (Figure 3).

231 Whilst a model containing the number of kleptoparasites per oystercatcher and stage of the
232 tidal cycle had an Δ AIC value of only 1.7 greater than our best model, the stage of the tidal
233 cycle was not a significant term and so this model was not considered further (Table 4).

234 Similarly, a model containing the number of kleptoparasites per oystercatcher, the stage of
235 the tidal cycle, and the two-way interaction between these two variables had an Δ AIC value
236 of 3.2 greater than our best model, but again the stage of the tidal cycle and the interaction

237 were not significant terms. A model composed of month alone indicated that the month of
238 observation had a significant effect on the outcome of oystercatcher foraging attempts, yet
239 this model had an ΔAIC value of 34.2 greater than our best model (Table 4). Conversely, we
240 found no support that the stage of the tidal cycle had any significant effect on the outcome of
241 oystercatcher foraging attempts in any of our models.

242

243 **Discussion**

244 In order to understand interactions between kleptoparasites and their hosts, researchers need
245 to quantify the factors which influence the risk of kleptoparasitism (Brockman and Barnard
246 1979, Amat 1990, LeSchack and Hepp 1995, Iyengar 2008). In this study, we found evidence
247 that the outcome of foraging attempts by a molluscivorous wading bird on bivalve molluscs
248 varied with the number of kleptoparasites per host on the mussel bed, supporting our first
249 prediction. In particular, for the whole winter period as well as for two out of the five
250 individual months studied, successful kleptoparasitism was more likely to occur when the
251 total numbers of all kleptoparasites per host were high, offering partial support for our second
252 prediction. Across the entire winter study period, oystercatcher foraging attempts that were
253 ended by kleptoparasitism were associated with a mean number of kleptoparasites per host
254 that was more than double that for foraging attempts that ended in the oystercatcher
255 successfully consuming the mussel. More broadly, our findings concur with research that
256 demonstrates that the numbers of organisms within a patch is a key regulator of biotic
257 processes across taxa and ecosystems. A growing number of studies have found that greater
258 numbers or biomasses of organisms within an area are associated with greater magnitudes of
259 biological processes including herbivore impacts on plants (Wood et al. 2012), predator

260 impacts on prey (Vucetich et al. 2002), rates of decomposition (Parkyn et al. 1997), and
261 parasite impacts on hosts (Cotgreave and Clayton 1994).

262 We have documented kleptoparasitism of mussel-feeding oystercatchers by two species:
263 carrion crows and herring gulls. Kleptoparasitic attacks typically involved one oystercatcher
264 and one crow or gull, but on some occasions multiple kleptoparasites were involved in
265 opportunistic attacks; this was similar to the observations of Oro (1996) for kleptoparasitic
266 Audouin's gulls (*Larus audouinii* Payraudeau 1826). In our study up to 36.3 % of
267 oystercatcher feeding attempts ended in the theft of the food item by a kleptoparasite. Our
268 study suggests higher kleptoparasitism risk for oystercatchers from crows and gulls than
269 during previous research carried out in the 1979-1980 winter. Goss-Custard et al (1982)
270 reported that oystercatchers would have just 3 % of mussels stolen by crows, whilst gull
271 kleptoparasitism was not documented. Indeed, we are not aware of any previous studies
272 which have quantified kleptoparasitism risk for oystercatchers from herring gulls.
273 Oystercatcher populations are currently declining at the flyway level, as well as at many
274 individual sites including the Exe estuary (Austin et al. 2014). In order to inform
275 oystercatcher conservation, it is important to quantify biotic interactions which may be
276 impacting on demographic parameters (e.g. survival) through reduced food intake, increased
277 energy expenditure avoiding kleptoparasites, and physical injuries suffered during
278 kleptoparasitism. We have presented evidence in this study that the levels of food-stealing
279 among an intertidal avian community have increased in the last 34 years. Further research is
280 now needed to understand the costs of these higher levels of kleptoparasitism on
281 oystercatchers, as well as the potential benefits to crows and gulls.

282 Previous research has suggested that large concentrations of host individuals appears to be a
283 prerequisite for the evolution of kleptoparasitic behaviour among avian communities (Iyengar
284 2008). In our study we found that high numbers of kleptoparasites per host, rather than

285 numbers of hosts *per se*, best determined the risk of successful kleptoparasitism. Whilst we
286 found evidence of a relationship between the occurrence of food-stealing by crows and gulls
287 and their combined numbers on the mussel beds, the numbers of gulls alone was a relatively
288 poor predictor of kleptoparasitism risk. In particular, kleptoparasite risk appeared unrelated to
289 the numbers of gulls present on the mussel bed. Only when the number of oystercatcher hosts
290 was accounted for, and the measure of kleptoparasite pressure expressed as ‘gulls per
291 oystercatcher’, did we detect a significant relationship with kleptoparasite success. This
292 finding is in apparent contrast to the findings of Tuckwell and Nol (1997), who reported that
293 kleptoparasitism by gulls on American oystercatchers (*Haematopus palliatus* Temminck
294 1820) increased as the number of gulls on the shellfish beds increased. However, a key
295 difference between our study and Tuckwell and Nol (1997) is that in our study gulls were not
296 the only kleptoparasites present. Indeed, in every month of our study oystercatchers were
297 robbed more frequently by crows than by gulls. These findings suggest that all of the key
298 kleptoparasite species must be accounted for in any measure of kleptoparasitism pressure.

299 In our study we have measured the probability of successful kleptoparasitism as a feature of a
300 given environment at a given time. However, the probability of successful kleptoparasitism
301 can also depend on intrinsic factors such as host behaviour (e.g. Blackburn et al. 2009) and
302 age (e.g. Carroll and Cramer 1985, Ridley and Child 2009). Such intrinsic factors may
303 account for at least part of the unexplained variance in our results. Oystercatchers are known
304 to use vigilance behaviours whilst feeding, including periodic pauses and visual scans of their
305 surroundings, to attempt to reduce their chance of being the victim of kleptoparasitism (Goss-
306 Custard et al. 1999). Anti-kleptoparasite vigilance is likely to be more effective in the
307 presence of lower numbers of kleptoparasites, as there would be fewer threats to identify and
308 monitor. Thus in the presence of fewer kleptoparasites, hosts would have more time to devote
309 to evaluating the potential threat posed by each individual in the vicinity. For greater numbers

310 of kleptoparasites, in particular where there are 1.9 kleptoparasites per host or greater, our
311 study suggests that oystercatcher vigilance behaviours is insufficient to avoid being targeted
312 by kleptoparasites. Furthermore, in other species researchers have observed a number of other
313 behavioural responses used to reduce the risk of kleptoparasitism, including changes in
314 microhabitat use, and switches to less vulnerable prey items such as those with shorter
315 handling times (e.g. Rice 1987, Blackburn et al. 2009, Suraci and Dill 2011). During our
316 foraging observations, we noted that on a number of occasions oystercatchers held mussels
317 underwater whilst opening them, which may have been a strategy to prevent food stealing.
318 Similar behaviours have been reported for other avian species attempting to reduce the risk of
319 kleptoparasitism (e.g. Amat and Aguilera 1989). Future research should aim to identify the
320 range of anti-kleptoparasite behaviours shown by the oystercatcher, and quantify their role in
321 reducing the chance of successful kleptoparasitism.

322 For logistical reasons we unable to measure distances between individuals in our study. Yet,
323 we know from previous research that the density of birds on the mussel beds is strongly
324 influenced by the stage of the tidal cycle; towards low tide the area of exposed mussel beds
325 increases and the birds can spread themselves over a larger area, resulting in lower densities
326 (Sutherland and Koene 1982). Given that we tested for the effect of stage of the tidal cycle on
327 kleptoparasitism success, and found no such effect, we are confident that changes in the
328 distance between kleptoparasites and hosts did not confound our results. Our finding that the
329 stage of the tidal cycle, and thus the relative inundation of the mussel bed, had no effect on
330 the outcome of oystercatcher foraging attempts is consistent with previous research that
331 found no effect of environmental conditions on risk of kleptoparasitism. For example García
332 et al. (2010) reported that the direction and intensity of the wind, as well as the tide, did not
333 significantly affect the risk of kleptoparasitism by kelp gulls (*Larus dominicanus* Lichtenstein
334 1823) within a seabird colony.

335 Kleptoparasitic behaviour has long been of interest to ornithologists and numerous examples
336 within avian communities have been documented (Brockman and Barnard 1979, Amat 1990).
337 Yet these disparate examples and case studies have not allowed researchers to achieve a more
338 general understanding of the conditions which modulate the risk of kleptoparasitism. In this
339 study we have shown through field observations and statistical modelling how the factors
340 which promote kleptoparasitism within avian communities can be identified. Improving our
341 knowledge of how kleptoparasitism varies in space and time, and with biotic and abiotic
342 factors, will help ornithologists understand when and where the impacts of kleptoparasitism
343 on individual fitness, population sizes, trophic interactions, and food webs will occur.

344

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350

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478 **Tables**

479 Table 1: Monthly observations of successful oystercatcher foraging and successful

480 kleptoparasitism by carrion crows and herring gulls.

Month	Total observations	Oystercatcher successes		Thefts by carrion crows		Thefts by herring gulls	
		<i>n</i>	%	<i>n</i>	%	<i>n</i>	%
November	214	171	79.9	30	14.0	13	6.1
December	102	65	63.7	25	24.5	12	11.8
January	163	140	85.9	13	8.0	10	6.1
February	233	208	89.3	13	5.6	12	5.2
March	285	249	87.4	23	8.1	13	4.6
All months	997	833	83.6	104	10.4	60	6.0

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484 Table 2: Comparison of the independent fit of different measures of relative kleptoparasite
485 pressure on the binary outcome of oystercatcher foraging attempts on mussels (consumed by
486 oystercatcher or stolen by kleptoparasites). All models were comprised of one parameter and
487 were tested sequentially. The best fitting model is indicated in bold. For each test d.f. = 996.
488 All bird numbers refer to total number of a given species present on the focal mussel bed at
489 the time of observation. After McFadden (1974) we used McFadden's R^2 as our measure of
490 the variance explained for each relationship, calculated as: $R^2_{McFadden} = 1 - (\ln(L_{fit}) / \ln(L_{null}))$,
491 where $\ln(L_{fit})$ refers to the natural logarithm of the maximised likelihood of the fitted model,
492 whilst $\ln(L_{null})$ refers to the natural logarithm of the maximised likelihood of the null model.

Measure of kleptoparasite pressure	Z value	p value	$R^2_{McFadden}$
No. of oystercatchers	3.691	0.001	0.018
No. of feeding oystercatchers	3.648	0.001	0.018
Percentage of oystercatchers feeding	-1.011	0.312	0.001
No. of crows	-5.808	< 0.001	0.036
No. of gulls	0.575	0.565	0.001
No. of crows and gulls	-3.297	0.001	0.012
No. of crows per oystercatcher	-5.249	< 0.001	0.033
No. of gulls per oystercatcher	-4.199	< 0.001	0.039
No. of crows and gulls per oystercatcher	-6.399	< 0.001	0.056
No. of crows per feeding oystercatcher	-5.168	< 0.001	0.032
No. of gulls per feeding oystercatcher	-4.136	< 0.001	0.026
No. of crows and gulls per feeding oystercatcher	-6.148	< 0.001	0.046
Intercept only (null model)	-19.02	< 0.001	0.000

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496 Table 3: A summary of the results of the Pearson's product-moment correlations associated
 497 with our potential explanatory variables: N = number of all kleptoparasites per oystercatcher;
 498 M = month of the winter period; T = % of tidal cycle elapsed at time of observation.
 499 Statistically significant correlations are indicated in bold.

Variable	M	N	T
M	-	$r = -0.203$; $t_{995} = -6.529$; $p < 0.001$	$r = -0.006$; $t_{995} = 0.195$; $p = 0.846$
N	$r = -0.203$; $t_{995} = -6.529$; $p < 0.001$	-	$r = -0.062$; $t_{995} = -1.947$; $p = 0.052$
T	$r = -0.006$; $t_{995} = 0.195$; $p = 0.846$	$r = -0.062$; $t_{995} = -1.947$; $p = 0.052$	-

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502 Table 4: Comparison of the Akaike Information Criteria (AIC) and McFadden's R^2 values
503 associated with each of our explanatory models. We also indicate which of the following
504 terms in each model had a significant effect ($p < 0.05$) on the outcome of oystercatcher
505 foraging attempts. N = number of all kleptoparasites per oystercatcher; M = month of the
506 winter period; T = % of tidal cycle elapsed at time of observation.

Model tested	Significant terms	AIC	ΔAIC	Relative likelihood	Akaike weight	$R^2_{McFadden}$
N	N	845.3	0.0	1.00	0.61	0.056
N+T	N	847.0	1.7	0.43	0.26	0.057
N+T + (N*T)	N	848.5	3.2	0.20	0.12	0.057
M+T + (M*T)	M, T, M*T	877.1	31.8	0.00	0.00	0.025
M	M	879.5	34.2	0.00	0.00	0.018
M+T	M	881.4	36.1	0.00	0.00	0.018
Null (intercept only)	-	893.4	48.1	0.00	0.00	0.000
T	-	895.4	50.1	0.00	0.00	0.000

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510 Table 5: The values associated with the logistic regression relationships between the number
 511 of kleptoparasites per oystercatcher (N) and the probability of an oystercatcher foraging
 512 attempt resulting in successful kleptoparasitism (P). Each of these relationships had the form:
 513 $P = e^{a+bN} / (1 + e^{a+bN})$, where $e = 2.718$, equivalent to the base of the natural logarithm.

Month	a (± SE)	b (± SE)	Z value	p value	d.f.	$R^2_{McFadden}$
November	-1.73 (± 0.22)	0.18 (± 0.64)	2.77	0.006	214	0.040
December	-0.79 (± 0.32)	0.14 (± 0.15)	0.96	0.338	102	0.010
January	-1.82 (± 0.28)	0.02 (± 0.34)	0.07	0.945	163	0.000
February	-2.50 (± 0.35)	1.03 (± 0.66)	1.54	0.123	233	0.010
March	-2.67 (± 0.26)	0.61 (± 0.14)	4.21	< 0.001	285	0.180
All Months	-1.99 (± 0.11)	0.31 (± 0.05)	6.40	< 0.001	997	0.056

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517 **Figures**

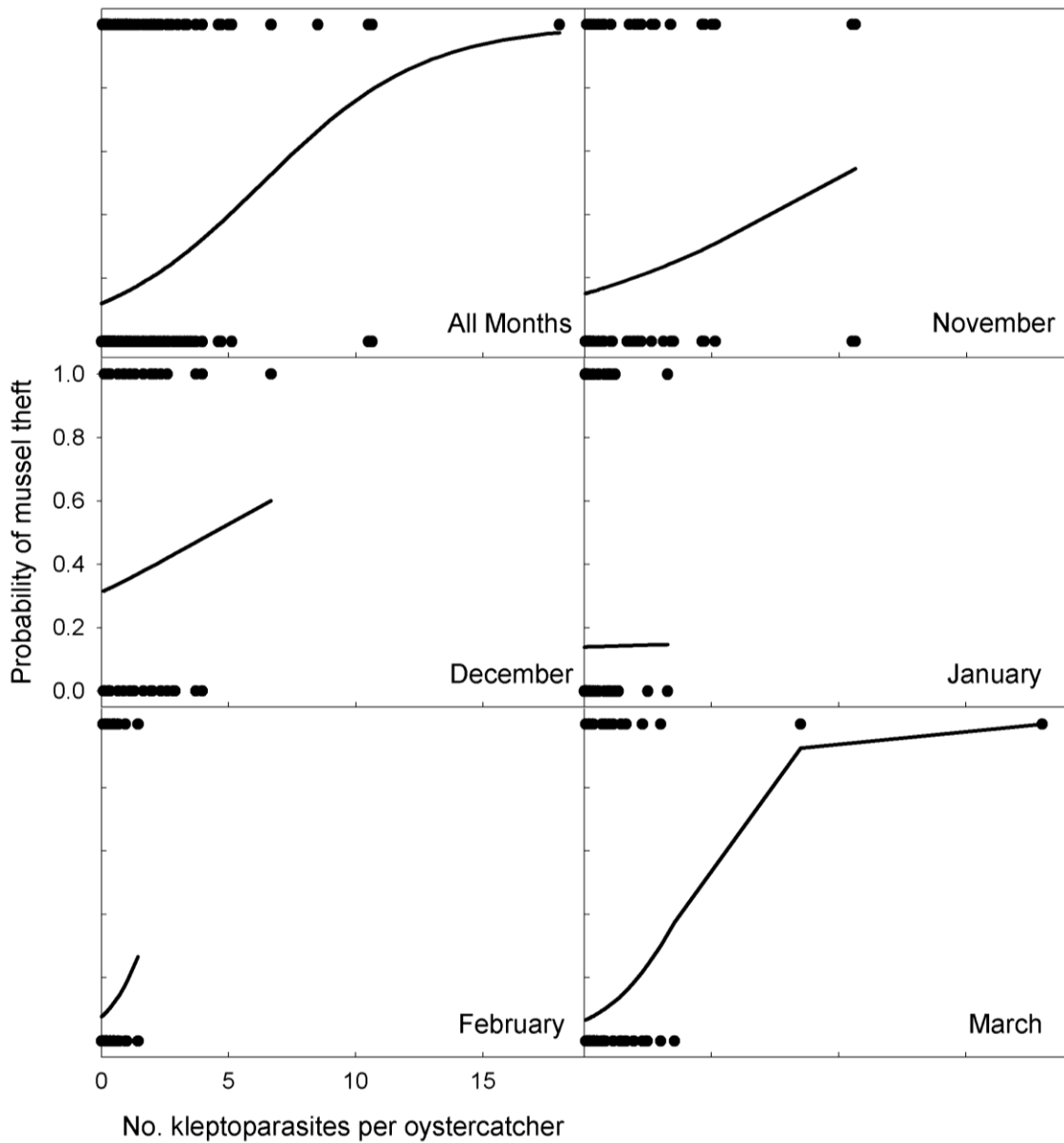
518 **Figure 1:** A map of the Exe estuary, including the full extent of mussel beds available to
519 oystercatchers and their kleptoparasites at low tide (shown in dark grey). Brown, yellow and
520 dark green patches indicate areas of intertidal mud, sand and eelgrass (*Zostera* sp.)
521 respectively.



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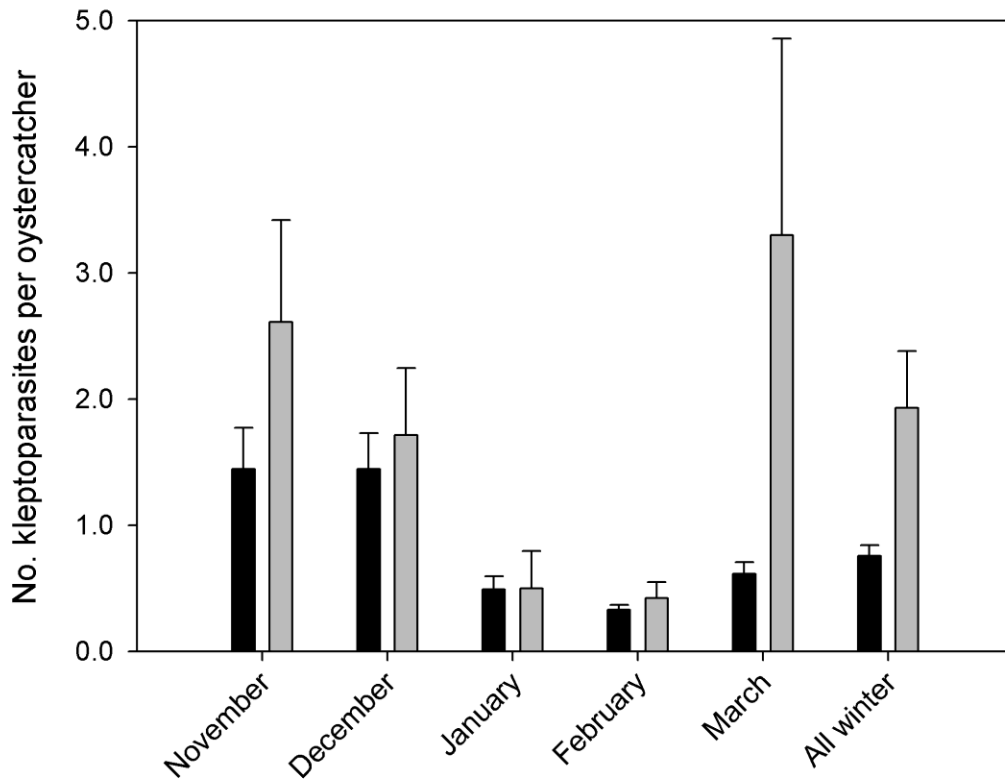
524 **Figure 2:** The relationships between the number of kleptoparasites per oystercatcher and the
525 probability of an oystercatcher foraging attempt resulting in loss of the mussel due to
526 kleptoparasitism, as indicated by logistic regression analyses. The equation that describes
527 each relationship is given in Table 5.



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530 **Figure 3:** Comparisons of the mean (\pm 95 % CI) number of kleptoparasites per oystercatcher
531 for observations of successful oystercatcher foraging (black bars) and successful
532 kleptoparasitism by carrion crows and herring gulls (grey bars).



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