

The joint evolution of movement and competition strategies

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1 **Abstract**

2 Competition typically takes place in a spatial context, but eco-evolutionary models rarely ad-
3 dress the the joint evolution of movement and competition strategies. Here we investigate a
4 spatially explicit producer-scrounger model where consumers can either forage on a hetero-
5 geneous resource landscape or steal prey from conspecifics (kleptoparasitism). We compare
6 different scenarios for the interaction of movement and competition strategies. In all cases,
7 movement strategies evolve rapidly and consistently across replicate simulations. At equilib-
8 rium, foragers do not match the prey input rate, contrary to 'ideal free' predictions. We show
9 that this is related to the intrinsic difficulty of moving effectively on a depleted landscape
10 with few reliable cues for movement. The evolved movement strategies of kleptoparasites dif-
11 fer markedly from those of foragers. Even within each competition strategy, polymorphisms
12 emerge, corresponding to individual differences in movement rules. Our study emphasises
13 the advantages of a mechanistic approach when studying competition in a spatial context.

1 Introduction

Intraspecific competition is an important driver of population dynamics and the spatial distribution of organisms (Krebs and Davies, 1978), and can be broadly classified into two main types, ‘exploitation’ and ‘interference’. In exploitation competition, individuals compete indirectly by depleting a common resource, while in interference competition, individuals compete directly by interacting with each other (Birch, 1957; Case and Gilpin, 1974; Keddy, 2001). A special case of interference competition which is widespread among animal taxa is ‘kleptoparasitism’, in which an individual steals a resource from its owner (Iyengar, 2008). Experiments with foraging birds have shown that competition, including kleptoparasitism, can affect the spatial distribution of individuals across resource patches (Goss-Custard, 1980; Vahl et al., 2005a,b, 2007; Rutten et al., 2010a). The avoidance of competitive interactions can also affect the distribution and behaviour of animals foraging in groups (Rutten et al., 2010b; Bijleveld et al., 2012). At larger scales, competition among different behavioural types in a species can strongly influence species distributions and animal movement decisions (e.g. Duckworth and Badyaev, 2007; Schlägel et al., 2020). The fine-scale mechanisms and evolutionary consequences of competition are difficult to study in free-living animals, yet their knowledge is central to evolutionary ecology. It is nearly impossible to study competition and its coevolution with movement strategies at evolutionary time-scales in most animals, due to a lack of long-term data (Clutton-Brock and Sheldon, 2010) — this necessitates the use of models.

Competition is key to paradigms of animal space-use, including the ideal free distribution (IFD, Fretwell and Lucas, 1970), information-sharing based local enhancement (also called conspecific aggregation Giraldeau and Beauchamp, 1999; Folmer et al., 2012), and producer-scrounger dynamics (Barnard and Sibly, 1981; Vickery et al., 1991; Beauchamp, 2008). Yet these paradigms often treat competition in highly simplified ways. Most IFD models, for instance, assume that resource depletion is either negligible, or that resources have a constant influx rate, where standing stock densities are effectively zero due to immediate consumption (continuous input/ immediate consumption models, Tregenza, 1995; van der Meer and Ens, 1997). Other IFD models that do include resource depletion make simplifying assumptions about the importance of interference competition, considering it unimportant, or even modelling a ben-

43 efit of grouping (e.g. Amano et al., 2006). Producer-scrounger models are primarily concerned
44 with the benefits of choosing either a producer or scrounger strategy in relation with local
45 conditions, such as the number of conspecifics (Vickery et al., 1991), or the order of arrival on
46 a patch (Beauchamp, 2008). While models such as Beauchamp (2008) and Tania et al. (2012)
47 allow for individuals to either search for food or scrounge off exploited patches, they simplify
48 the mechanisms by which this decision is made (see also Holmgren, 1995; Garay et al., 2020).
49 Few foraging ecology models — either IFD or producer-scrounger — allow for realistic move-
50 ment strategies, often assuming omniscient animals with no travel costs (Vickery et al., 1991;
51 Tregenza, 1995; van der Meer and Ens, 1997, *but see* Amano et al. 2006; Cressman and Křivan
52 2006).

53 On the contrary, competition occurs in a spatial context, and spatial structure is key to for-
54 aging (competition) decisions (Beauchamp, 2008). Consequently, the abundance of resources
55 and their depletion, as well as the presence of potential competitors is of obvious importance
56 to individuals' movement decisions (resource selection, *sensu* Manly et al., 2007). How an-
57 imals are assumed to integrate the costs (and potential benefits) of competition into their
58 movement decisions has important consequences for theoretical expectations of population
59 distributions (van der Meer and Ens, 1997; Hamilton, 2002; Beauchamp, 2008). In addition to
60 short-term, ecological effects, competition should also have evolutionary consequences for in-
61 dividual *movement strategies*, as it does for so many other aspects of behaviour (Baldauf et al.,
62 2014), setting up feedback loops between ecology and evolution. Modelling competition and
63 movement decisions jointly is thus a major challenge. A number of models take an entirely
64 ecological view, assuming that individuals move or compete ideally, or according to some
65 fixed strategies (Vickery et al., 1991; Holmgren, 1995; Tregenza, 1995; Amano et al., 2006, but
66 see Hamilton 2002). Models that include evolutionary dynamics in the movement (de Jager
67 et al., 2011, 2020) and foraging competition strategies (Beauchamp, 2008; Tania et al., 2012) are
68 more plausible, but they too make arbitrary assumptions about the functional importance of
69 environmental cues to individual decisions. Ideally, both movement and competition strate-
70 gies should be the joint outcomes of selection, allowing for different competition strategies to
71 be associated with different movement rules (see the approach in Getz et al., 2015).

72 Here, we present a first mechanistic, model of intraspecific competition in a spatially explicit

73 context, where competition is shaped by the *joint evolution* of foraging competition and move-
74 ment strategies. As foraging and movement decisions are taken by individuals, we study the
75 joint evolution of both types of decision-making by means of a simulation model. Such mod-
76 els are well suited to modelling the ecology and evolution of complex behaviours (Guttal and
77 Couzin, 2010; Kuijper et al., 2012; Getz et al., 2015, 2016; White et al., 2018; Long and Weiss-
78 ing, 2020; Netz et al., 2020, for conceptual underpinnings see Huston et al. (1988); DeAngelis
79 and Diaz (2019)). This allows us to both focus more closely on the interplay of exploitation
80 and interference competition, and to examine the feedback between movement and foraging
81 behaviour at ecological and evolutionary timescales. In our model, foraging individuals move
82 on a spatially fine-grained resource landscape with discrete, depletable food items that need
83 to be processed ('handled') before consumption. Foragers make movement decisions using an
84 inherited (and evolvable) strategy which integrates local cues, such as the local resource and
85 competitor densities. After each move, individuals choose between two foraging strategies:
86 whether to search for a food item or steal from another individual; the mechanism underly-
87 ing this foraging choice is also inherited. We take lifetime resource consumption as a proxy
88 for fitness, such that more successful individuals produce more offspring, and thus are more
89 successful in transmitting their movement and foraging strategies to future generations (sub-
90 ject to small mutations). We consider three scenarios: in the first scenario, we examine only
91 exploitation competition. In the second scenario, we introduce kleptoparasitic interference as
92 an inherited strategy, fixed through an individual's life. In the third scenario, we model klep-
93 toparasitism as a behavioural strategy conditioned on local environmental and social cues.

94 Our model allows us to examine the evolution of individual movement strategies, population-
95 level resource intake, and the spatial structure of the resource landscape. The model enables
96 us to take ecological snapshots of consumer-resource dynamics (animal movement, resource
97 depletion, and competition) proceeding at evolutionary time-scales. Studying these snapshots
98 from all three scenarios allows us to check whether, when, and to what extent the spatial dis-
99 tribution of competitors resulting from the co-evolution of competition and movement strate-
100 gies corresponds to standard IFD predictions. Using this model, we investigate three primary
101 questions: (1) Under what conditions does kleptoparasitic interference evolve and persist in
102 the population? How do the movement strategies of kleptoparasites differ from those of the

103 foragers? (2) What are the eco-evolutionary implications of conditional kleptoparasitism? Do
104 conditional strategies evolve under broader conditions than a polymorphism of fixed pure
105 strategies, and do they lead to a different spatial distribution of competitors? (3) To what ex-
106 tent does the spatial distribution of competitors and resources in space correspond to an ideal
107 free distribution?

108 **2 The Model**

109 We implement an individual-based evolutionary simulation model whose most basic compo-
110 nents — the environment’s gridded structure, and each cell’s capacity to hold multiple in-
111 dividuals, as well as the discrete conception of time within and between generations — are
112 inspired by the behaviour of waders (*Charadrii*). Waders are extensively studied in the context
113 of foraging competition, both empirically (e.g. Vahl et al., 2005*a,b*, 2007; Rutten et al., 2010*a,b*),
114 and using IBMs (reviewed in Stillman and Goss-Custard, 2010) — but few, if any, models
115 consider the interplay of ecology and evolution when studying wader movement and compe-
116 tition. We simulated a population with a fixed size moving on a landscape of 512^2 grid cells,
117 with the landscape wrapped at the boundaries so that individuals passing beyond the bounds
118 at one end re-appear on the diametrically opposite side. The model has two time scales, first,
119 an ecological (or behavioural) time scale of T timesteps, during which individuals move, make
120 foraging decisions, and handle prey items they find or steal. Individuals are modelled as being
121 immobile while handling food items, creating the conditions for kleptoparasitism (Brockmann
122 and Barnard, 1979; Holmgren, 1995). On the second, evolutionary time scale, individuals re-
123 produce and pass on their movement and foraging strategies to their offspring, the number of
124 which is proportional to their intake at the behavioural time scale. By default, we set T to 400,
125 and simulated 1,000 generations of a population of 10,000 individuals; thus there are about 26
126 times more grid cells than individuals.

127 **2.1 Resource Landscape**

128 **Prey Abundance** We considered a resource landscape that is heterogeneous in its productiv-
129 ity of discrete resources, but with strong spatial clustering of grid cells of similar productivity

130 (see Fig. 1C; panel *gen: 1*, showing a subset of 60^2 grid cells). We assigned each cell a constant
131 probability of generating a new prey item per timestep, which we refer to as the cell-specific
132 growth rate r . We modelled clustering in landscape productivity by having the distribution of
133 r across the grid take the form of 1,024 resource peaks, placed at regular distances of 16 grid
134 cells from the peaks around them; r declines from the centre of each peak (called r_{max}) to its pe-
135 riphery (see Fig. 1C). Effectively, the cell at the centre of each cluster generates a prey item five
136 times more frequently than the cells at the edges. We ran all three scenarios at a default r_{max} of
137 0.01, and also across a range of r_{max} values between 0.001 and 0.05. For an $r_{max} = 0.01$, the most
138 productive cells (at the centres of a cluster) are likely to generate one item per 100 timesteps (or
139 four items per generation, for $T = 400$), while the least productive cells (at cluster peripheries)
140 are likely to generate one item every 500 timesteps (only about one item per generation, for T
141 = 400). Since our model was conceived to represent foraging waders, we considered our re-
142 sources to represent mussels, a common prey of many waders, whose abundances are largely
143 driven by external gradients; we refer to these resources as ‘prey items’ henceforth. Cells in
144 our landscape were modelled as having a uniform carrying capacity K of 5 prey items, and
145 while a cell is at carrying capacity its r is 0.

146 **Prey Acquisition by Foragers** Foragers can perceive a cue indicating the number of all
147 prey items P in a cell, but do not know the exact locations of these prey. We model foragers as
148 having a probability q of failing to detect a prey item, and a probability q^P of not detecting any
149 of P prey items; foragers are thus successful in finding a prey item with a probability $1 - q^P$.
150 Individuals on a cell forage in a randomised sequence, and the probability of finding a prey
151 item ($1 - q^P$) is updated as individuals find prey, reducing P . Foragers that are assigned a prey
152 item in timestep t begin handling it, and are considered to be handlers from the end of the
153 timestep, i.e., for the movement and foraging decisions of other individuals. Foragers that are
154 not assigned a prey item are considered idle, and are counted as non-handlers.

155 **2.2 Movement and Competition Strategies**

156 **Movement Strategies** We model movement as a fine-scale process comprised of small, dis-
157 crete steps of fixed size. These steps are the outcome of short-term individual movement deci-

158 sions, which are made using evolved movement strategies. Movement decisions are modelled
159 as the individual selection of a destination cell, after assessing potential destinations based on
160 available cues (akin to the concept of step selection or resource selection Fortin et al., 2005;
161 Manly et al., 2007), an approach used previously by Getz et al. (2015, 2016) and White et al.
162 (2018). At the end of each timestep t , individuals scan the nine cells of their Moore neighbour-
163 hood for three environmental cues, (1) an indication of the number of discrete prey items P , (2)
164 the number of individuals handling prey H (referred to as ‘handlers’), and (3) the number of
165 individuals not handling prey N (referred to as ‘non-handlers’). Based on these cues, a ‘suit-
166 ability score’ S is assigned to each cell as $S = s_P P + s_H H + s_N N$. At the start of timestep $t + 1$,
167 each individual moves to the cell to which it assigned the highest suitability. The weighing
168 factors for each cue, s_P , s_H , and s_N , are genetically encoded and transmitted from parents
169 to their offspring. All individuals move simultaneously, and then implement their foraging
170 or kleptoparasitic behaviour to acquire prey. Individuals move and forage on the resource
171 landscape for T timesteps per generation.

172 **Scenario 1: Exploitative Competition** The first scenario simulates only exploitative com-
173 petition; individuals (henceforth called ‘foragers’) move about on the landscape and proba-
174 bilistically find and consume prey items. A forager can be either in a ‘searching’ state or in
175 a ‘handling’ state, as we assume that between finding and consuming a prey item individu-
176 als must handle each prey for a fixed handling time T_H (set at 5 timesteps by default). The
177 handling time dynamic is well known from many systems; for instance, it could be the time re-
178 quired for an oystercatcher to break through a mussel shell, or the time between catching and
179 subduing prey for raptors, with the handling action obvious to nearby individuals, and the
180 prey not fully under the control of the finder (Brockmann and Barnard, 1979). Handlers are as-
181 sumed to be fully absorbed in their processing of prey, and do not make any movements until
182 they have fully handled and consumed their prey. In scenario 1, the only evolvable properties
183 are the cue weighing factors which determine the suitability scores (s_P , s_H and s_N).

184 **Scenario 2: Fixed Interference Competition** The second scenario builds on Scenario 1,
185 but in addition to foragers there is a second category of individuals called ‘kleptoparasites’.

186 Kleptoparasites do not search for food, but rather for handlers from which they can steal
 187 prey (similar to Holmgren, 1995). Agents that steal are termed kleptoparasites. Kleptopar-
 188 asites are always successful in stealing from a handler; this may be thought of as the benefit of
 189 the element of surprise, a common observation among birds (Brockmann and Barnard, 1979).
 190 However, if multiple kleptoparasites target the same handler, only one of them, randomly
 191 selected, is considered successful — thus kleptoparasites also compete exploitatively among
 192 themselves. Individuals that have been stolen from subsequently ‘flee’ and are moved to a
 193 random cell within a Chebyshev distance of 5. Having acquired prey, a kleptoparasite con-
 194 verts into a handler, but need only handle prey for $T_H - t_h$ timesteps, where t_h is the time
 195 that the prey has already been handled by its previous owner; thus kleptoparasites save time
 196 on handling compared to a forager. Unsuccessful kleptoparasites are considered idle, and are
 197 also counted as non-handlers. Handlers that finish processing their prey in timestep t return
 198 to the non-handler state and are assessed as such by other individuals when determining their
 199 movements. In scenario 2, there are two fixed competition strategies that are inherited from
 200 parents to offspring, and each of these strategies can evolve a (separate) movement strategy.

201 **Scenario 3: Conditional Interference Competition** In scenario 3, each individual can ei-
 202 ther act as a forager, searching for food, or as a kleptoparasite, dependent on its local circum-
 203 stances. Individuals process the cell-specific environmental cues P , H , and N to determine
 204 their location in the next timestep (based on their inherited movement strategy). Additionally,
 205 individuals process the environmental cues to determine their strategy in the next timestep as

$$206 \text{strategy} = \begin{cases} \text{forager,} & \text{if } w_P P + w_H H + w_N N \geq w_0 \\ \text{kleptoparasite,} & \text{otherwise} \end{cases} \quad (1)$$

207 where the cue weights w_P , w_H and w_N , and the threshold value w_0 are also genetically encoded
 208 and heritable between generations. Apart from the ability to switch between foraging and
 209 kleptoparasitism, the foraging dynamics are the same as described in the fixed-strategy case.

210 **2.3 Reproduction and Inheritance**

211 For simplicity, our model considers a population of fixed size (10,000 individuals) with dis-
212 crete, non-overlapping generations. Individuals are haploid and reproduction is asexual. Each
213 individual has 7 gene loci that encode the decision making weights; only the weights in con-
214 trol of individual movement (s_P, s_H, s_N) are active in scenarios 1 and 2. In scenario 3, the
215 weights for foraging decisions (w_P, w_H, w_N, w_0) are also active, and are transmitted from par-
216 ent individuals to offspring. Hence the alleles at these loci correspond to real numbers that are
217 transmitted from parent individuals to their offspring.

218 We assume that the expected number of offspring per individual is proportional to the indi-
219 vidual's total lifetime intake of resources (hence resource intake is used as a proxy for fitness).
220 This is implemented as a weighted lottery (with weights proportional to lifetime resource in-
221 take) that selects a parent for each offspring in the subsequent generation (see prior implemen-
222 tation in Tania et al., 2012; Netz et al., 2020). In all scenarios, the movement decision-making
223 weights are subject to independent random mutations with a probability of 0.001. The muta-
224 tional step size (either positive or negative) is drawn from a Cauchy distribution with a scale
225 of 0.01 centred on zero. This allows for a small number of very large mutations while the
226 majority of mutations are small. In scenarios 1 and 2, the foraging-decision weights are not
227 relevant. However, in scenario 2 we allow a forager to mutate into a kleptoparasite (or *vice*
228 *versa*) with a probability of 0.001. In scenario 3, the foraging weights mutate in the same way
229 as the movement weights, described above. We initialised each offspring at a random location
230 on the landscape; this potentially forces individuals to contend with conditions very different
231 from those of their direct parent.

232 **2.4 Simulation Output and Analysis**

233 **Population Activities and Intake** We counted the number of times foragers were search-
234 ing for prey, kleptoparasites were searching for handlers, and the number of timesteps that
235 individuals of either strategy were handling a prey item. We refer to the ratio of time spent
236 foraging, stealing, and handling as the population's 'activity budget'. We examined how the
237 population activity budget developed over evolutionary time, and whether a stable ecological

238 equilibrium was reached. Furthermore, we counted the population's mean per capita intake
239 per generation as a measure of population productivity.

240 **Resource Landscape and Individual Distribution Snapshots** To visualise the effect of dif-
241 ferent foraging strategies on the resource landscape, we exported snapshots of the entire sim-
242 ulation landscape at the mid-point of each generation ($t = 200$). This snapshot contained data
243 on (1) the number of prey items, (2) the number of handling individuals, and the number of in-
244 dividuals using either a (3) searching strategy or (4) kleptoparasitic strategy, on each grid cell.
245 We used only a subset of the total landscape (60^2 of 512^2 cells) for further analyses to speed up
246 computation.

247 **Testing the Input Matching Rule** To examine whether foragers in our model achieved an
248 IFD, we used the snapshots to test a basic prediction of the IFD and the related matching rule:
249 that the number of individuals on occupied patches should be proportional with patch pro-
250 ductivity (Fretwell and Lucas, 1970; Parker, 1978; Houston, 2008). In real world systems, patch
251 productivity is challenging to measure, but not so in simulation models, where it is among
252 the model's building blocks. We calculated the correlation coefficient between the number of
253 individuals (excluding handlers) and the cell-specific productivity r , and plotted it over gen-
254 erations for each replicate.

255 **Informativeness of Resource Landscapes** Another measure of whether foragers have achieved
256 the IFD on their resource landscape is whether individuals can improve their intake by mov-
257 ing to another location; in our model, this would be to a neighbouring cell. We calculated the
258 cell-specific item gradient for each landscape snapshot, as the difference in item counts be-
259 tween each cell and its neighbouring cells. We then calculated the proportion of grid cells from
260 which it was possible to sense differences in prey items, i.e., a cell with either more or fewer
261 items. When it is impossible to sense such differences, movement informed by relative prey
262 item abundances is difficult, and achieving the IFD becomes a challenge.

263 **Visualising Decision-Making Weights** To understand the evolutionary consequences of our
264 simulation on the individual decision making weights, we exported the weights of each indi-

265 vidual in every generation of the simulation. To depict as much as possible of the typical
266 variation of weights, which could take arbitrarily large values and therefore vary by orders of
267 magnitude, we multiplied each weight by 20 and applied a hyperbolic tangent transform. This
268 scaled the weights between -1 and +1.

269 See the **Data Availability Statement** for links to the published model source code, results
270 analysis code, and the simulation data output.

271 **3 Results**

272 **3.1 Scenario 1: No Kleptoparasitism**

273 When only foragers are present in the population, individuals deplete prey items faster than
274 they can be replenished, and the overall number of prey items is drastically reduced within
275 only a few generations (Fig. 1A). The population's activity budget is split between searching
276 and handling (Fig. 1B). The proportion of time spent handling and the population's mean
277 per capita intake are both initially low, but then peak within ten generations (Fig. 1C). This
278 is because individuals can easily acquire prey items from the fully stocked landscape in the
279 first few generations. As the number of prey items reduces, handling as a share of the activ-
280 ity budget declines to a stable $\sim 45\%$ within 50 generations; this is because fewer searching
281 foragers find a prey item. This leads to a similar stabilisation in mean per capita intake (Fig.
282 1C). Though in early generations, foragers are attracted to resource peaks and tend to accu-
283 mulate on resource-rich locations (Fig. 1A), the correlation between the number of foragers
284 on a cell and the productivity of that cell is only slightly positive (Fig. 1D). This is in contrast
285 with the perfect correspondence between resource input rate and forager density (the 'input
286 matching rule'), which is a defining property of the IFD (Parker, 1978; Houston, 2008). Con-
287 trary to standard IFD assumptions, foragers cannot directly "sense" the local cell productivity
288 r ; instead they can only use the (small) number of prey items available in a cell as a cue for
289 local productivity ("cell quality").

290 **3.2 Scenario 2: Co-existence of Foragers and Kleptoparasites**

291 When both foraging and kleptoparasitism is allowed, the spatial distribution of consumers and
292 prey items at equilibrium are very different from a forager-only population. Consumers gather
293 on resource peaks in early generations, grazing them down until very few prey items remain
294 on the landscape and consumers are dispersed; however, within 50 generations the resource
295 landscape recovers with prey abundances higher than in the earliest generations (Fig. 2A).
296 This is explained by the presence of kleptoparasites (Fig. 2B), which reduces the prey intake
297 rate of the population, and accordingly lead to a higher prey abundance. In early generations,
298 kleptoparasites are very rare, and the activity budget, the population mean per capita intake,
299 and the distribution of consumers over the landscape show the same patterns as in Fig. 1.
300 Mean per capita intake also spikes in early generations as individuals successfully acquire
301 prey items from the fully stocked prey landscape (Fig. 2C). At this stage, it becomes more
302 likely for a kleptoparasite to encounter a handler than for a searching forager to find a prey
303 item, and from generation 30 onwards, as kleptoparasitism becomes the dominant strategy
304 (a stable $\sim 70\%$ of the population; see Fig. 2B), searching for handlers from whom to steal
305 becomes the dominant activity. However, the high frequency of this activity, and the low
306 frequency of handling, indicate that many kleptoparasites are actually unsuccessful at finding
307 handlers. With few searching foragers, fewer prey items are extracted from the landscape,
308 which recovers beyond its initial prey abundance within 50 generations (Fig. 2A).

309 Despite the strong spatial structure of the resource landscape within 50 generations, the
310 correlation between consumer abundance and cell productivity remains weak or zero across
311 generations (Fig. 2D). This may be explained by the dynamics of kleptoparasitism: foragers
312 fleeing a kleptoparasitic attack are displaced far from their original location, and kleptopar-
313 asites must track these foragers if they are to acquire resources. As kleptoparasites, the nu-
314 merically dominant strategy, seek to move towards handlers (rather than prey), they are not
315 strongly influenced by prey item abundances.

316 The increase of kleptoparasitism from a negligible fraction to the dominant strategy (Fig.
317 3A) is associated with the evolutionary divergence of the movement strategies in foragers and
318 kleptoparasites. While foragers and kleptoparasites respond to prey density and non-handler

319 density in a similar way (see Supplementary Figure S5), preferring higher prey density while
320 avoiding high non-handler density, the two types of competition strategy differ substantially
321 in their response to handlers (Fig. 3B, 3C). Kleptoparasites very rapidly (within 3 generations)
322 evolve a strong preference for moving towards handlers, which are their primary resource
323 (Fig. 3B). In the absence of kleptoparasites, foragers would evolve a preference for moving
324 towards handlers (see Supplementary Figure S4), because the presence of handlers is an indi-
325 rect indicator of productive cells. However, with kleptoparasites common in the population,
326 searching foragers both avoid and prefer handlers in about equal proportions (Fig. 3C). While
327 all kleptoparasites evolve to prefer moving towards handlers, the strength of the attraction to
328 handlers shows multiple, distinct values or ‘morphs’, which are remarkably persistent across
329 generations (Fig. 3B). In replicate 3, for example, the dominant movement strategy exhibits
330 only a weak attraction to handlers, but this strategy coexists with various strategies that all
331 show a much stronger attraction to handlers (Fig. 3B). The movement strategies of foragers
332 show an even higher degree of polymorphism (Fig. 3C). Typically, there are no predominant
333 movement strategies. Instead, a wide range of coexisting handler attraction/repulsion values
334 emerges. In other words, some foragers are strongly attracted by handlers, others are strongly
335 repelled by handlers, and yet others are neutral to the presence of handlers.

336 **3.3 Scenario 3: Condition-dependent Kleptoparasitism**

337 When individuals are allowed to choose their competition strategy (foraging or kleptopara-
338 sitism) based on local environmental cues, the distribution of individuals and prey items is
339 substantially different from the two previous scenarios (Fig. 4A). Initially, as in scenario 1,
340 depletion of prey items results in the degradation of the resource landscape within ten gener-
341 ations. By generation 50, the resource landscape recovers some of the spatial structure of the
342 first generation, but prey-item abundances do not reach the level of the similar recovery seen
343 in scenario 2. This too is explained by the observation that by generation 30, all individuals
344 have a propensity to steal from handlers, i.e., when handlers are present in the vicinity, con-
345 sumers will choose to target handlers for prey items, rather than forage for prey themselves
346 (“opportunistic kleptoparasitism”; Fig. 4B; *orange line*). However, unlike scenario 2, individu-
347 als search for prey more often and steal less (at or below 25%; compare with Fig. 2B), leading

348 to a sustained high mean per capita intake rate and the depletion of the resource landscape.
349 Consequently, mean per capita intake stabilises (after an initial spike, as in scenarios 1 and 2)
350 within ten generations to a level similar to scenario 1 (Fig. 4C). The reduced depletion follow-
351 ing the evolution and persistence of kleptoparasitism leads to a resource landscape recovery
352 intermediate between scenarios 1 and 2 within 50 generations (Fig. 4A). As individuals move
353 and choose foraging strategies conditionally, they are able to better choose between the payoff
354 of more prey items, more handling foragers from which to steal, and the risk of falling victim to
355 kleptoparasites. Thus, while not as strong as predicted by IFD theory, the correlations between
356 consumer abundance and cell productivity are weakly positive (Fig. 4D).

357 **3.4 Evolution, the Ideal Free Distribution, and Alternative Movement Cues**

358 Orienting movement towards resources (Nathan et al., 2008, ; *where to move*) can be a chal-
359 lenge in a system with low densities of discrete prey items, because the local prey *density* may
360 provide very limited information about local *productivity*. In fact, major parts of the resource
361 landscape may be a ‘clueless plateau’ (Perkins, 1992); on most cells, foragers cannot make di-
362 rected movement decisions based on prey-item abundances alone, as all neighbouring items
363 abundances are identical (see white areas in Fig. 5A; A1: scenario 1, A2: scenario 2, A3: sce-
364 nario 3). At the beginning of all three scenarios, about 75% of landscape cells have a different
365 number of prey-items from the cells around them; these are primarily the cells with an in-
366 termediate r , which have more prey than the lowest productivity cells at the peripheries of
367 resource peaks, but fewer prey than the peaks themselves. This proportion rapidly declines to
368 a much lower value within 10 generations in all three scenarios.

369 The scenarios differ, however, regarding the ‘cluelessness’ of the landscape on evolutionary
370 timescales (Fig. 5B). In scenario 1, the proportion of cells from which it is possible to move to
371 a neighbouring cell with more items is initially very high (Fig. 5A1). This proportion rapidly
372 declines to $\sim 25\%$ within 10 generations, as foragers deplete most cells on the landscape until
373 they are devoid of prey items, and the majority of the landscape is a clueless plateau. In this
374 context, foragers evolve to move towards handlers — with $> 75\%$ of individuals showing a
375 preference for handlers within 100 generations (Fig. 5B1 – blue line). Forager preference for
376 handlers (which do not represent a direct resource in scenario 1), may be explained as the

377 sensing of a long-term cue of local productivity. Since handlers are immobilised on the cell
378 where they find a prey item, cells with handlers are (1) certain to have a non-zero rate of
379 prey item generation, and (2) likely to border cells which can generate prey items, due to the
380 autocorrelation (spatial patterning) of the landscape.

381 Scenario 2 landscapes follow a similar pattern to scenario 1 in the first 10 generations (Fig.
382 5A2). However, within 50 generations, the reduction in prey item extraction allows most cells
383 to regenerate prey items, with differences among cells according to their productivity r (see
384 also Fig. 2A). Thus it is possible to move to a neighbouring cell with more items from $> 75\%$
385 of the landscape (Fig. 5A2 – panel *gen: 50*, 5B2). However, since the majority of foragers are
386 kleptoparasites, which seek out handlers, this recovery of the resource landscape provides only
387 indirect movement cues, as searching foragers are more likely to convert to handlers on cells
388 with more prey items. Unlike scenario 1, the rapid increase in handler preference is driven
389 by correlational selection on kleptoparasites (see subsection above). Scenario 3 is similar to
390 scenario 2, except that only about half the landscape allows movement to a neighbouring cell
391 with more prey items (Fig. 5A3, 5B3). Here, the rapid evolution of a handler preference in
392 movement decisions cannot be assigned a clear cause, since handlers are both a potential direct
393 resource as well as indirect cues to the location of productive cells.

394 **3.5 Effect of Landscape Productivity on Evolutionary Outcomes**

395 The prey-item regrowth rate that characterises the peaks of the resource landscape (r_{max}) is
396 a measure of the productivity of the resource landscape overall. Having thus far focused on
397 scenarios with $r_{max} = 0.01$ (corresponding to a peak production of 4 food times per consumer
398 lifetime), we find that, not unexpectedly, the value of r_{max} has a marked effect on evolved pop-
399 ulation activity budgets, mean per capita intake, and even evolved strategies. The frequency
400 of foraging reduces with r_{max} in scenarios 1 and 3; this is caused by more frequent acquisition
401 of prey items (as regrowth keeps pace with depletion), which results in a greater frequency of
402 handling rather than foraging.

403 In scenario 2 however, the frequency of handling is relatively unaffected by increasing r_{max}
404 (Fig. 6A). The difference between scenarios 2 and 3 has to do with the change in the frequency
405 of kleptoparasitism (Fig. 6B). In scenario 2, kleptoparasitism forms $> 75\%$ of all activities at

406 very low r_{max} , and is much more common than in scenario 3 populations at the same regrowth
407 rate. However, at relatively high r_{max} (0.03), the fixed kleptoparasitic strategy goes extinct.
408 This is because at high r_{max} , the probability of a forager finding prey is much greater than the
409 probability of a kleptoparasite finding a handler, in both initial (< 10) and later generations
410 (> 50). Consequently, kleptoparasites are responsible for only a very small fraction of the total
411 population intake, have relatively much lower fitness, and do not proliferate. Thus at these
412 regrowth rates, a scenario 2 population is nearly identical to a scenario 1 population; while
413 some kleptoparasites may be seen in later generations, these are more likely due to mutation
414 in the forager strategy, rather than longstanding lineages of kleptoparasites.

415 In scenario 3, kleptoparasitism persists at low frequencies even at the highest regrowth rates
416 (Fig. 6B); thus some foragers lose time in extracting items which are then stolen from them.
417 Consequently, while populations in all three scenarios achieve very similar mean per capita
418 intakes at low r_{max} , at intermediate regrowth rates (0.01 – 0.025), conditionally kleptoparasitic
419 populations achieve a higher mean per capita intake than populations using fixed strategies.
420 Only at high regrowth rates, when fixed strategy populations (scenario 2) effectively convert
421 to purely forager populations (scenario 1), do they achieve a higher intake than scenario 3
422 populations (Fig. 6C).

423 **4 Discussion**

424 **Summary of Results** Our spatially-explicit individual-based model implements the ecology
425 and evolution of movement and foraging decisions, as well as resource dynamics, in biologi-
426 cally plausible ways, and offers a new perspective about the distribution of animals in relation
427 to their resources under different scenarios of competition. First, we show that when mov-
428 ing with a limited perception range and competing only by exploitation, individuals evolve
429 movement strategies for both direct and indirect resource cues (prey items and handlers, re-
430 spectively). Regardless, on a resource landscape with discrete prey items, large areas may
431 become devoid of any movement cues, leading to a mismatch between individual distribu-
432 tion, prey item distribution, and landscape productivity. Second, we show that when inter-
433 ference competition in the form of kleptoparasitism is allowed as a fixed strategy, it rapidly

434 establishes itself on landscapes where stealing is more time-efficient than searching for prey.
435 This rapid increase in kleptoparasitism as a strategy is accompanied by the evolution of move-
436 ment strategies that favour moving towards handlers, which are the primary resource of the
437 kleptoparasites. In this sense, obligate kleptoparasites may be thought of as forming a higher
438 trophic level, with any handling consumers as their prey. Third, we show that when foraging
439 strategy is allowed to be conditional on local cues, (1) the population's mean per capita in-
440 take is significantly higher than that of a population with fixed strategies, and (2) unlike fixed
441 strategy populations, kleptoparasitism as a strategy does not go extinct on high-productivity
442 landscapes. However, across scenarios, individuals are broadly unable to match the produc-
443 tivity of the resource landscape, contrary to the predictions of IFD based models, which predict
444 input matching for some (Parker and Sutherland, 1986; Holmgren, 1995; Hamilton, 2002), or
445 all of the competitive types Korona (1989).

446 **Comparison with Previous Models** Existing models of competition and movement impose
447 fixed movement rules on individuals to mimic either ideal or non-ideal individuals (Vickery
448 et al., 1991; Cressman and Křivan, 2006; Amano et al., 2006; Beauchamp, 2008; Stillman and
449 Goss-Custard, 2010; White et al., 2018). When individual competitive strategies are included,
450 models consider them to represent differences in competitive ability (e.g. Parker and Suther-
451 land, 1986; Holmgren, 1995; Hamilton, 2002), or as a probabilistic switch between producing
452 and scrounging (Beauchamp, 2008). In contrast, our model allows individuals' movement (and
453 competition) decisions to be adaptive responses to local environmental cues. Similar to Getz
454 et al. (2015, 2016) and White et al. (2018), our individuals choose from among the available
455 movement options after weighing the local environmental cues; this is analogous to the move-
456 ment ecology concepts of resource or step selection functions (Fortin et al., 2005; Manly et al.,
457 2007; White et al., 2018). The local environmental cues in our model are constantly changing,
458 as we model discrete, depletable prey items on the resource landscape, contrasting with many
459 IFD models (Tregenza, 1995; Amano et al., 2006). This allows for a more plausible, fine-scale
460 consideration of exploitation competition, which is often neglected, and allows the cues sensed
461 by individuals to strongly structure the distribution of competitors (see below).

462 Adaptive responses must have an explicit evolutionary context, and consider multiple gen-

463 erations of the population. We follow Beauchamp (2008) and Getz et al. (2015) in allowing
464 the decision making weights for movement, and variation thereof, to be the outcomes of nat-
465 ural selection. However, instead of using ‘evolutionary algorithms’ (Beauchamp, 2008; Getz
466 et al., 2015, 2016) to ‘optimise’ individual movement rules, we consider a more plausible evo-
467 lutionary process: Instead of allowing the fittest 50% of the population to replicate, the number
468 of offspring are proportional to individual fitness (Hofbauer and Sigmund, 2003). The weight
469 loci are subject to mutations independently, rather than subjecting all loci of an individual to si-
470 multaneous mutation. Finally, we avoided the unrealistic assumption of ‘simulated annealing’,
471 which adapts the mutation rate or the mutational step sizes to the rate of evolutionary change.
472 Instead we drew mutation sizes from a Cauchy distribution, so that most mutations are very
473 small, but large-effect mutations do occur throughout the simulation. Similarly, rather than
474 determining foraging style (searching or stealing) probabilistically or ideally (Vickery et al.,
475 1991; Beauchamp, 2008; Tania et al., 2012), our individuals’ foraging decisions are also shaped
476 by selection (in scenarios 2 and 3).

477 **Movement Rules on Depleted Landscapes** In our scenario 1, depletion of discrete prey
478 can leave many areas empty of prey items: in such areas, movement informed by a resource
479 gradient is impossible, and individuals move randomly (‘clueless regions’: Perkins, 1992). Our
480 work suggests that this lack of movement cues and the resulting random movement might be
481 among the mechanisms by which unsuitable ‘matrix’ habitats modify animal movement on
482 heterogeneous landscapes (Kuefler et al., 2010).

483 When individuals do not sense resource gradients, the presence of successful consumers
484 (handlers) may indicate a suitable foraging spot (local enhancement; see Giraldeau and Beauchamp,
485 1999; Beauchamp, 2008; Cortés-Avizanda et al., 2014), or direction of movement (Guttal and
486 Couzin, 2010). The presence of unsuccessful individuals, meanwhile, may signal potential
487 costs from exploitation or interference competition. This selects for movement strategies in-
488 corporating the presence and condition of competitors into individual movement decisions
489 (‘social information’: Danchin et al., 2004; Dall et al., 2005). While external costs such as pre-
490 dation have been invoked to explain consumer aggregation (Krause and Ruxton, 2002; Folmer
491 et al., 2012), information on the location of productive areas alone may be a sufficient benefit to

492 promote the evolution of social information use, and consequently aggregation (Folmer et al.,
493 2010; Cortés-Avizanda et al., 2014).

494 While individuals broadly prefer prey and handlers, and avoid non-handlers, there is sub-
495 stantial individual variation in the strength of each weight within populations, as expected
496 from heterogeneous landscapes (see Supplementary Material; see Wolf and Weissing 2010 for
497 background). The persistence of multiple ‘movement morphs’ (see Getz et al., 2015) across
498 multiple generations indicates that they are alternative movement strategies of equal fitness.
499 Indeed, polymorphism in movement rules may help reduce competition as individuals make
500 subtly different movement decisions when presented with the same cues (see Wolf and Weissing,
501 2012, for a review; see also Laskowski and Bell 2013).

502 **Movement Rules and Competitive Interactions** IFD models predict that individual move-
503 ment should result in ‘input matching’: consumer distributions should track the profitability
504 of resource patches (Fretwell and Lucas, 1970; Parker, 1978), and dominant competitive types
505 (including kleptoparasites) should monopolise the best patches (Parker and Sutherland, 1986;
506 Holmgren, 1995; Hamilton, 2002, but see Korona 1989). In our scenarios 2 and 3, individuals
507 seeking to steal prey from competitors unsurprisingly and rapidly evolve to track handlers (a
508 direct resource), while avoiding non-handlers (potential competitors). However, these evolved
509 rules do not lead kleptoparasites to occupy the best cells as predicted (Parker and Sutherland,
510 1986; Holmgren, 1995; Hamilton, 2002). Across our scenarios (including sc. 1), individual
511 density is only weakly correlated with cell productivity.

512 In scenario 2, this departure from predictions is driven by the contrasting movement rules
513 of foragers, which evolve to *avoid* handlers as well as non-handlers, both of which might be
514 kleptoparasites (Folmer et al. 2010; Bijleveld et al. 2012; see Supplementary Material). Thus,
515 foragers (the subordinate competitive type) undermatch the resource landscape, as resource
516 peaks are more likely to have handlers (Parker and Sutherland, 1986; Holmgren, 1995; Hamil-
517 ton, 2002). Fixed kleptoparasites cannot extract prey themselves, and must move off resource
518 peaks to track and rob handlers (similar to Parker and Sutherland, 1986), breaking the link
519 between individual density and productivity.

520 This shows the pitfalls of simplistically linking current ecological conditions with evolved

521 behavioural responses (and emergent distributions), and shows why understanding the evo-
522 lutionary history of competitive interactions is key. In this vein, a hypothetical experiment
523 would wrongly expect that foragers from resource-rich landscapes (sc. 2) better tolerate com-
524 petitors due to less exploitation competition, while foragers from resource scarce landscapes
525 (sc. 1) might be competitor-avoidant. Furthermore, ecological conditions *may not* be a reliable
526 guide to the presence of individual variation, which is often expected as an outcome of en-
527 hanced competition. Indeed, scenario 2 shows significant within-strategy individual variation
528 in movement weights, which might help reduce within-strategy exploitation competition, or
529 help foragers better avoid kleptoparasites (Wolf and Weissing, 2012; Laskowski and Bell, 2013).

530 Interestingly, scenario 3 has the least individual variation in movement rules, potentially be-
531 cause behavioural plasticity in foraging strategy dampens individual variation (Pfennig et al.,
532 2010). Here, the non-handler avoidance shows the most morphs, but it is unclear whether this
533 variation is linked to the frequency with which individuals use either foraging strategy — po-
534 tentially leading to subtle, emergent behavioural differences that are conditioned on the local
535 environment (Wolf and Weissing, 2010, 2012).

536 **Ecological Constraints and Evolved Foraging Strategies** Foraging strategies in which
537 animals specialise on a resource type are expected to be constrained by the availability of that
538 resource; thus kleptoparasitism should be constrained by the density of targets (Spencer et al.,
539 2017; Spencer and Broom, 2018). In our scenarios 2 and 3, we would expect to see more klep-
540 toparasitism with increasing r_{max} , as prey and consequently, handlers, are more abundant. We
541 find instead that kleptoparasitism declines with increasing r_{max} , in line with Emlen (1966), who
542 predicted that the commoner food type (prey) rather than the more efficiently exploited one
543 (handlers) should be preferred.

544 This effect is especially stark in scenario 2, where kleptoparasites go extinct when prey are
545 very common at high r_{max} . At stable population densities (due to external constraints such as
546 nest-site availability), the persistence of fixed kleptoparasitism depends on their intake *relative*
547 *to foragers*. Since intake is an outcome of movement rules, and population movement rules are
548 not well adapted to their environment in early generations, foragers obtain, as a clade, more
549 intake than kleptoparasites. Modelling discrete prey items and individuals in a spatial context,

550 then, leads to the finding that obligate kleptoparasitism is only a viable strategy when the
551 probability of encountering prey is much less than the probability of encountering handlers.
552 While few taxa show such a marked foraging specialisation within populations, this might
553 explain why kleptoparasitism is frequent among seabirds, whose communal roosts are much
554 more easily targeted than unpredictable shoals of fish out at sea (Brockmann and Barnard,
555 1979).

556 Finally, comparing across regrowth rates shows why predicting the long-term effect of envi-
557 ronmental change on populations must keep unanticipated behavioural complexity in mind.
558 While both scenario 1 and 2 populations appear identical at high r_{max} , even a small decrease
559 in environmental productivity could lead to an abrupt drop in per-capita intake — and po-
560 tentially, strongly reduced growth or survival — for fixed strategy populations due to (unex-
561 pected) emergent kleptoparasitism.

562 **5 Data and Code Availability**

563 The simulation model code can be found on Github: github.com/pratikunterwegs/Kleptomove
564 and archived on Zenodo: zenodo.org/record/4905476.

565 Simulation data used in this study are available on the DataverseNL repository as a draft:
566 <https://dataverse.nl/privateurl.xhtml?token=1467641e-2c30-486b-a059-1e37be815b7c>, and will
567 be available at this persistent link after publication: doi.org/10.34894/JFSC41.

568 Code for data analysis and preparing the figures in the main text and Supplementary Mate-
569 rial is available on Github: github.com/pratikunterwegs/kleptomove-ms and archived on Zen-
570 odo: doi.org/10.5281/zenodo.4904497.

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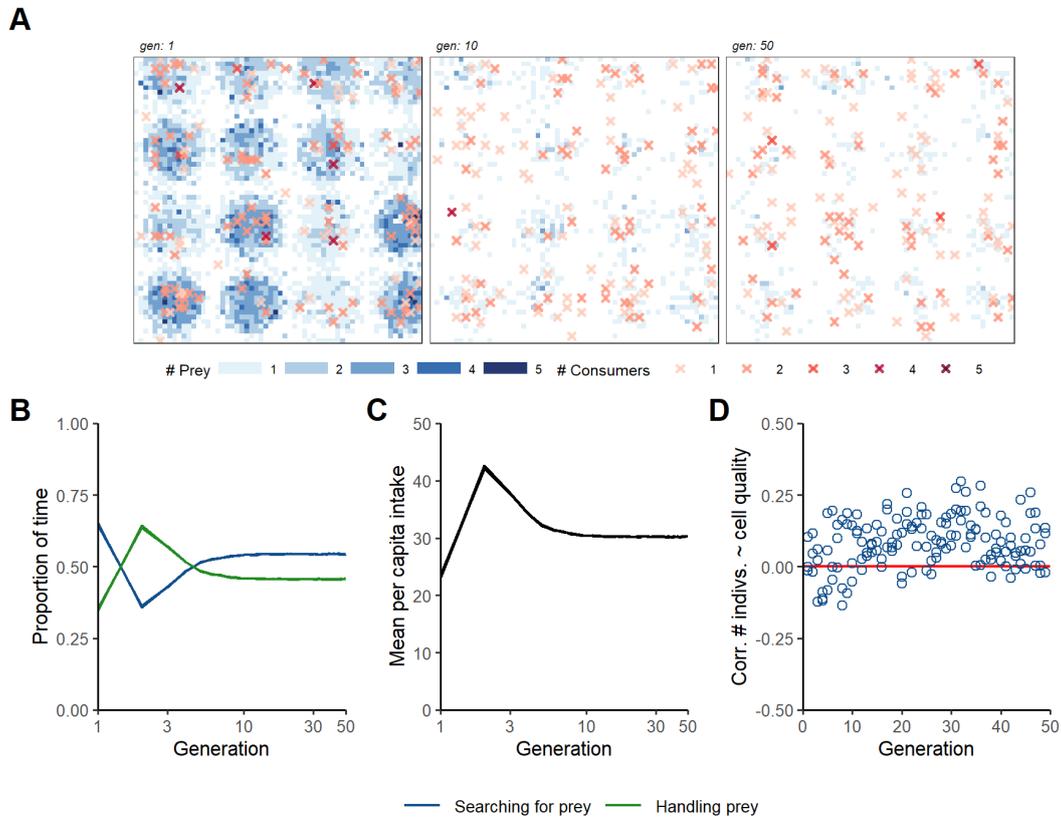


Figure 1: Eco-evolutionary implications of pure exploitation competition (scenario 1). (A) When a population is comprised solely of foragers seeking prey on a resource landscape, the initially well-stocked resource landscape is swiftly depleted within 10 generations (out of 1,000 simulated). This sparsity in prey-item abundance is maintained throughout the remaining generations of the simulation. Individuals, whose local density is shown by coloured crosses, are scattered over the landscape. These dynamics are explained by the fact that (B) within 20 generations of evolution, the population reaches an equilibrium in the relative proportion of time spent on searching prey and handling prey, and in (C) the total intake of the population. (D) In a departure from the intake matching rule of IFD theory, cell occupancy (number of foragers per cell) is only weakly correlated with cell productivity r . Panel A shows a single replicate, while panels B, C and D show three replicate simulations (lines overlap almost perfectly); all panels are for $r_{max} = 0.01$. NB: Both B, C show a log-scaled X axis to more clearly show dynamics in early generations.

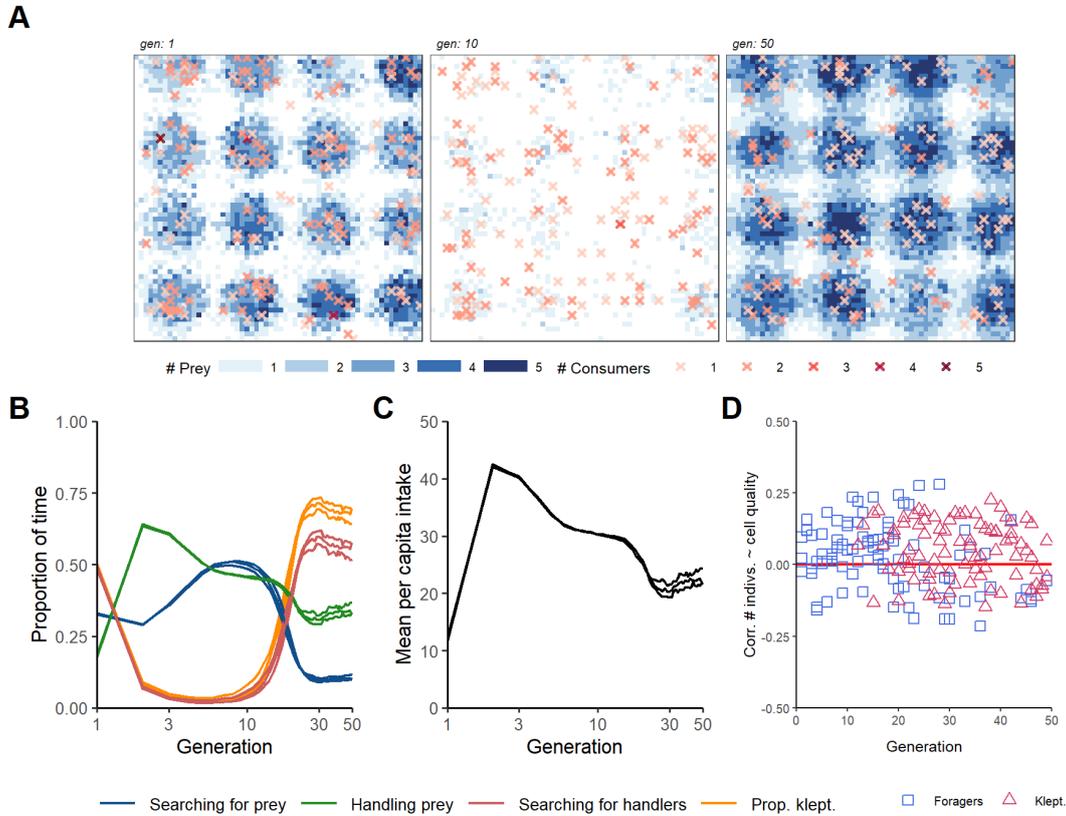


Figure 2: Eco-evolutionary implications of the coexistence of foragers and kleptoparasites (scenario 2). In populations with both foragers and kleptoparasites, **(A)** the initially well-stocked resource landscape is drastically depleted by generation 10; however, prey densities recover strongly by generation 50, even beyond the densities in generation 1. The local density of individuals on occupied cells is shown as coloured crosses. **(B)** An equilibrium between the strategies is reached within 30 generations, with the relative frequency of kleptoparasites (orange line) first dropping to very low levels but later recovering to reach a high level ($\sim 70\%$) in all three replicates. The activity budget parallels the relative frequency of kleptoparasites, and at equilibrium, about 10% of the individuals are foragers searching for prey, 50% are kleptoparasites searching for handlers, and 40% are handlers (either foragers or kleptoparasites). **(C)** In early generations, when kleptoparasites are rare, the population intake rate exhibits the same pattern as in Fig. 1B, dropping to a lower level with the emergence of kleptoparasites. This is accompanied by an increase in the proportion of time spent on stealing attempts (red line – **B**), and a corresponding decrease in prey seeking (by searching foragers; blue line – **B**), and handling (green line – **C**). **(D)** Cell occupancy (local density of foragers per cell) is only weakly correlated with cell productivity r , dropping to zero at equilibrium. Panel **A** shows a single replicate, while **B**, **C** and **D** show three replicates; all panels are for $r_{max} = 0.01$.

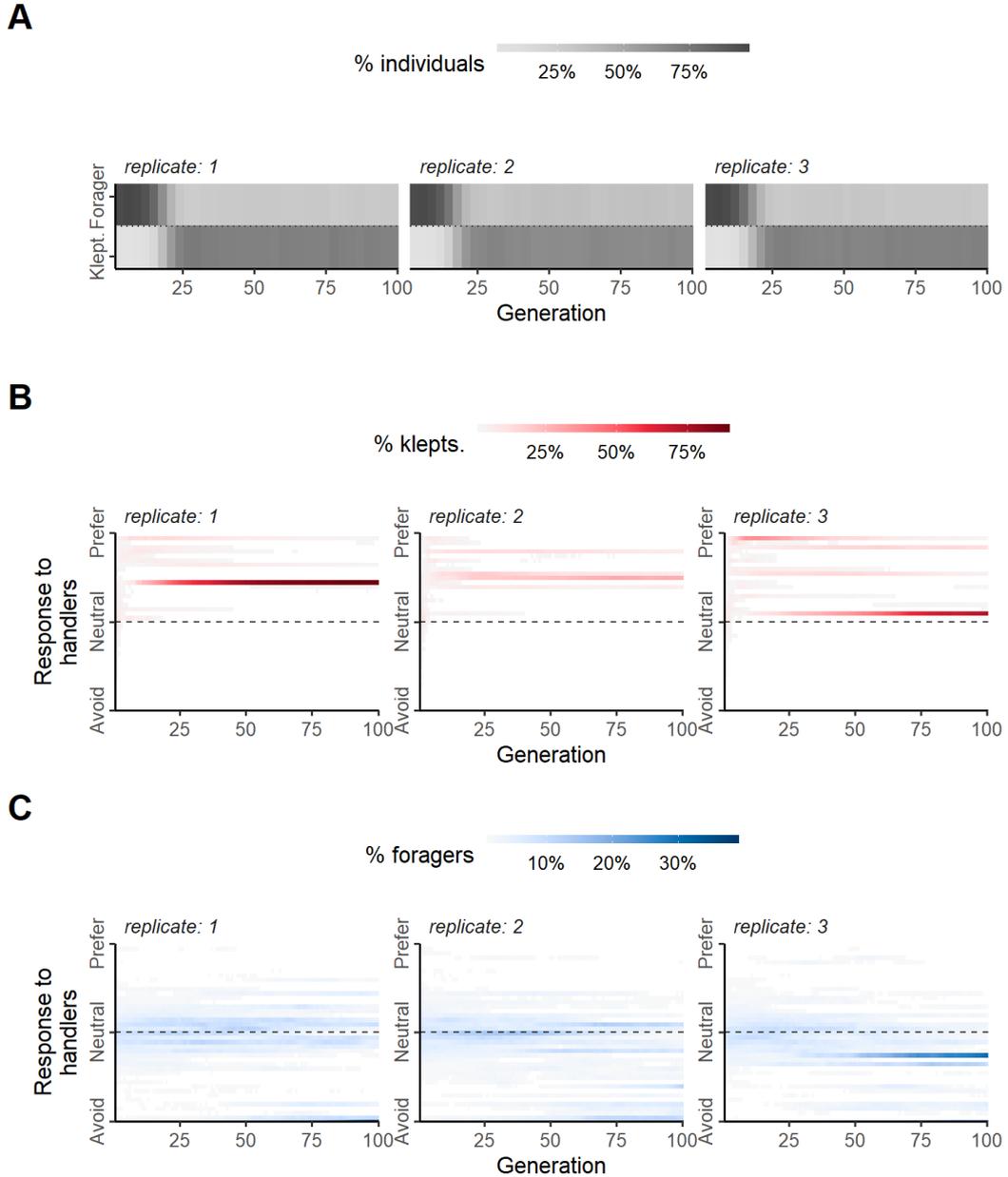


Figure 3: Divergence of movement strategies between foragers and kleptoparasites (scenario 2). (A) Kleptoparasitism rapidly becomes the more frequent strategy in scenario 2 populations for the parameters considered, with no differences across replicates. However, replicates differ considerably in the evolved movement strategies. This is illustrated by the distribution of the weighing factor s_H (describing the effect of local handler density on the movement decision) in kleptoparasites (B) and foragers (C), respectively. In kleptoparasites, the weights s_H are generally positive, indicating that kleptoparasites are attracted by handlers. However, different s_H values stably coexist, indicating that kleptoparasites are polymorphic in their movement strategy. Foragers are also polymorphic in their handler responses: foragers attracted by handlers (positive s_H) coexist with foragers repelled by handlers (negative s_H). All panels show three replicates at $r_{max} = 0.01$.

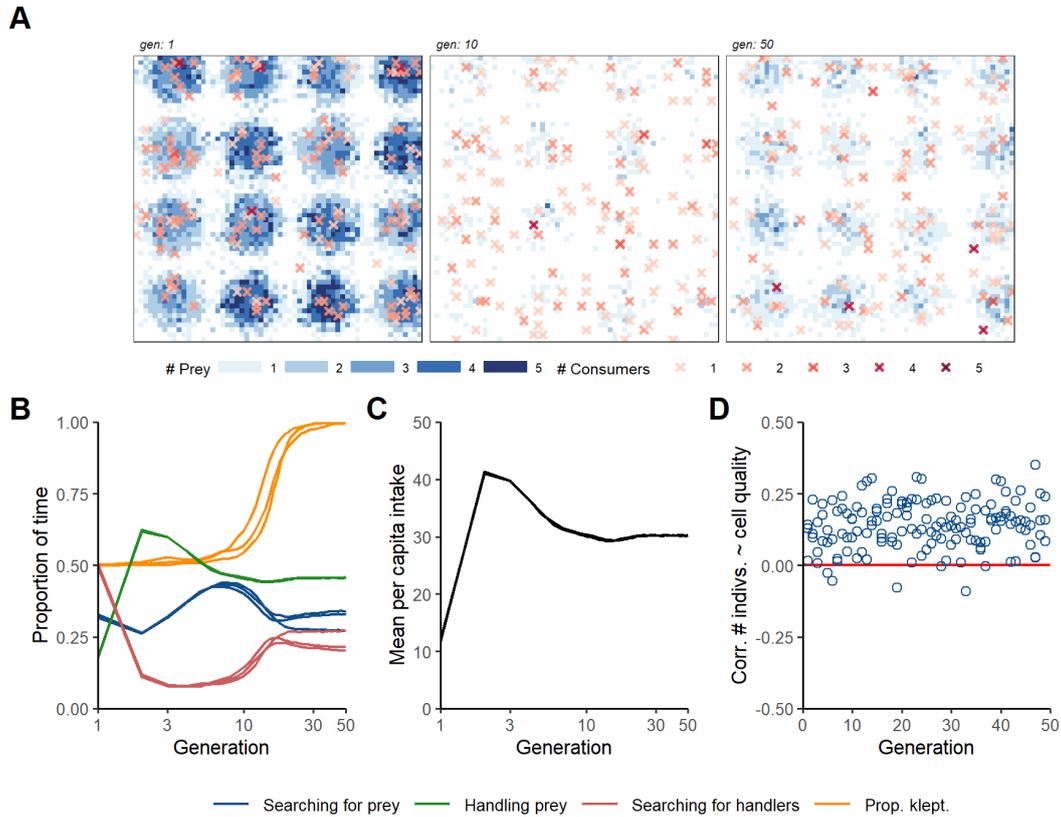


Figure 4: Eco-evolutionary implications of conditional foraging strategies (scenario 3). (A) The initially well-stocked resource landscape is rapidly depleted within 10 generations, yet within 50 generations, prey abundances recover on many cells, though not to the extent of scenario 2. The local density of individuals on occupied cells is shown as coloured crosses. (B) By generation 30, all individuals encountering handlers will choose to steal prey rather than search for prey themselves. The proportion of time spent searching (blue line), handling (green line), and stealing prey (red line) also reach an equilibrium that differs somewhat across replicates. (C) Yet, the total intake of the population reaches the same equilibrium value in all three replicates. (D) The correlation between the local density of individuals on a cell, and its productivity r is stronger than in scenario 2. Panel A shows a single replicate, while B, C and D show three replicates; all panels are for $r_{max} = 0.01$.

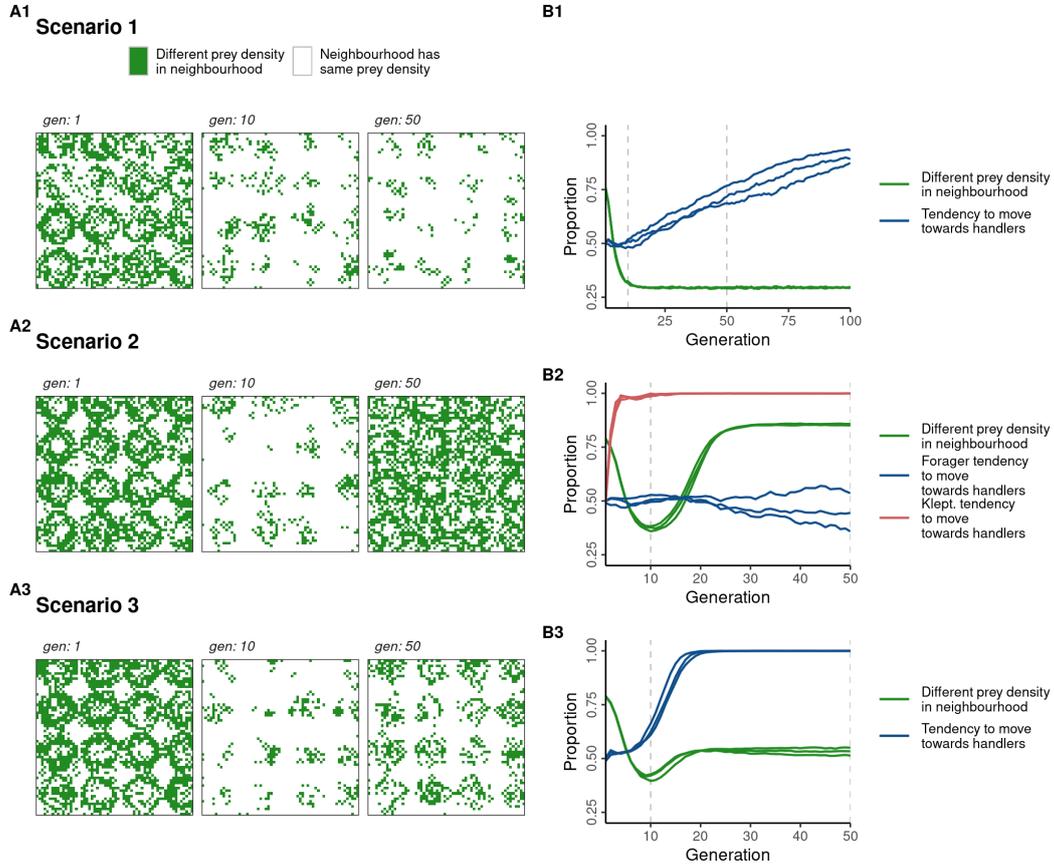


Figure 5: Uninformative prey densities and the evolution of alternative movement cues. (A1, A2, A3) On cells coloured green, local prey densities are informative for movement, as the central and neighbouring cells have different prey densities. While differences in local prey densities provide informative cues for ‘adaptive’ movement in early generations, this is much less true once the resource landscape is depleted of prey items (depending on the scenario). (B1, B2, B3) The proportion of cells where differences in local prey densities provide informative movement cues (green line), and the proportion of individuals preferring to move towards handlers (blue line), whose presence may be used as an alternative cue for movement towards higher-productivity areas of the landscape. In (B2) representing scenario 2, this proportion is shown separately for foragers (blue line) and kleptoparasites (red line). While panels in (A) show a single representative replicate for $r_{max} = 0.01$, panels in (B) show three replicates.

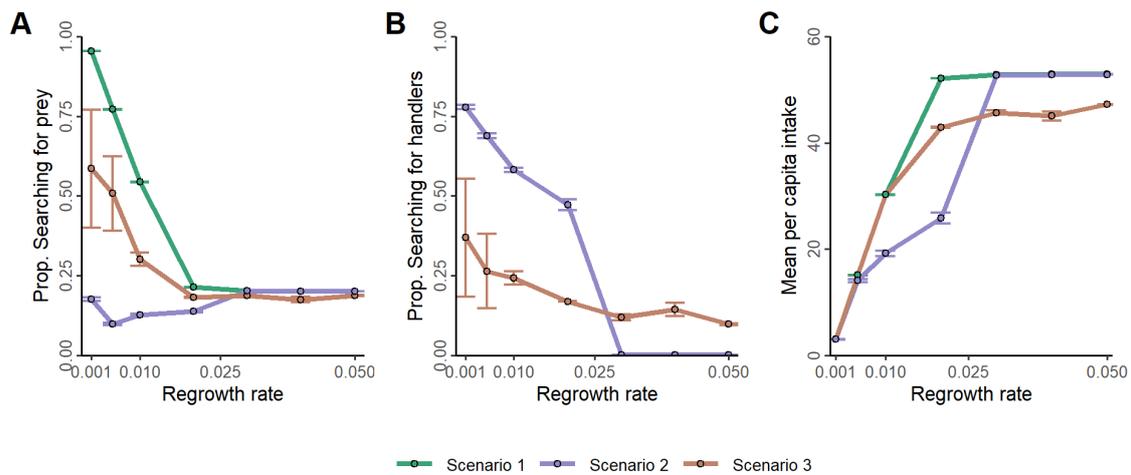


Figure 6: Landscape productivity strongly affects scenario outcomes. (A) The proportion of time spent searching for food decreases with increasing r_{max} in scenarios 1 and 3 but remains relatively stable within scenarios. This is partly due to a higher proportion of time spent handling at higher prey densities. (B) The proportion of time spent searching for handlers (in order to steal prey from them) also decreases with increasing r_{max} . In scenario 2, kleptoparasites go extinct for r_{max} values above 0.025. (C) At low productivity, the average intake is similar in all three scenarios. For higher r_{max} values the average intake rate is lowest in scenario, until r_{max} is larger than 0.025 and kleptoparasites go extinct (leading to the same kind of population as in scenario 1). At high r_{max} , the average intake rate in populations with conditional kleptoparasites (scenario 3) is substantially lower than in populations without kleptoparasitism.