

The joint evolution of animal movement and competition strategies

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Abstract

1

2 Competition typically takes place in a spatial context, but eco-evolutionary models rarely address
3 the joint evolution of movement and competition strategies. Here we investigate a spatially ex-
4 plicit producer-scrounger model where consumers can either forage on a heterogeneous resource
5 landscape or steal resource items from conspecifics (kleptoparasitism). We consider three scenar-
6 ios: (1) a population of foragers in the absence of kleptoparasites; (2) a population of consumers
7 that are either specialized on foraging or on kleptoparasitism; and (3) a population of individuals
8 that can fine-tune their behavior by switching between foraging and kleptoparasitism depend-
9 ing on local conditions. By means of individual-based simulations, we study the joint evolution
10 of movement and competition strategies, and we investigate the implications on the resource
11 landscape and the distribution of consumers over this landscape. In all scenarios and for all
12 parameters considered, movement and competition strategies evolved rapidly and consistently
13 across replicate simulations. The evolved movement and resource exploitation patterns differ
14 considerably across the three scenarios. For example, foragers are attracted by conspecifics in
15 scenario (1), while they are repelled by conspecifics in scenario (2). Generally the movement
16 strategies of kleptoparasites differ markedly from those of foragers, but even within each class
17 of consumers polymorphisms emerge, corresponding to pronounced differences in movement
18 patterns. In all scenarios, the distribution of consumers over resources differs substantially from
19 'ideal free' predictions. We show that this is related to the intrinsic difficulty of moving effectively
20 on a depleted landscape with few reliable cues for movement. Our study emphasises the advan-
21 tages of a mechanistic approach when studying competition in a spatial context, and suggests
22 how evolutionary modelling can be integrated with current work in animal movement ecology.

23

Introduction

24 Intraspecific competition is an important driver of population dynamics and the spatial distribu-
25 tion of organisms (Krebs and Davies, 1978), and can be broadly classified into two main types,
26 ‘exploitation’ and ‘interference’. In exploitation competition, individuals compete indirectly by
27 depleting a common resource, while in interference competition, individuals compete directly by
28 interacting with each other (Birch, 1957; Case and Gilpin, 1974; Keddy, 2001). A special case of
29 interference competition which is widespread among animal taxa is ‘kleptoparasitism’, in which
30 an individual steals a resource from its owner (Iyengar, 2008). Since competition has an obvious
31 spatial context, animals should account for the locations of intraspecific foraging competitors
32 when deciding where to move (Nathan et al., 2008). Experimental work shows that indeed,
33 competition, as well as the pre-emptive avoidance of competitive interactions, affects animal
34 movement decisions in taxa as far apart as waders (Goss-Custard, 1980; Vahl et al., 2005a; Rutten
35 et al., 2010b, see also Rutten et al. 2010a; Bijleveld et al. 2012), and fish (Laskowski and Bell,
36 2013). This is expected to have downstream effects on animal distributions at relatively small
37 scales, such as across resource patches (see Fretwell and Lucas, 1970), as well as at larger scales,
38 determining species distributions (e.g. Duckworth and Badyaev, 2007, see Schlägel et al. 2020 for
39 background). Animal movement decisions are thus likely to be adaptive responses to landscapes
40 of competition, with competitive strategies themselves being evolved responses to animal distri-
41 butions. Studying this joint evolution is key to understanding the spatial distribution of animals,
42 but empirical studies are nearly impossible at large spatio-temporal scales. This makes models
43 linking individual traits and behavioural decisions to population distributions necessary.

44 Contemporary individual-to-population models of animal space-use (reviewed in DeAngelis
45 and Diaz, 2019) and competition, however, are only sufficient to represent very simple move-
46 ment and prey-choice decisions, and struggle to adequately represent more complex systems
47 of consumer-resource interactions. For example, models including the ideal free distribution
48 (IFD; Fretwell and Lucas, 1970), information-sharing models (Giraldeau and Beauchamp, 1999;
49 Folmer et al., 2012), and producer-scrounger models (Barnard and Sibly, 1981; Vickery et al.,

50 1991; Beauchamp, 2008), often treat foraging competition in highly simplified ways. Most IFD
51 models, for instance, consider resource depletion unimportant or negligible (continuous input
52 models, see Tregenza, 1995; van der Meer and Ens, 1997), or make simplifying assumptions
53 about interference competition, even modelling an *ad hoc* benefit of grouping (e.g. Amano et al.,
54 2006). Producer-scrounger models primarily examine the benefits of choosing either a producer
55 or scrounger strategy given local conditions, such as the number of conspecifics (Vickery et al.,
56 1991), or the order of arrival on a patch (Beauchamp, 2008). Moreover, these models simplify the
57 mechanisms by which competitive decisions are made, often ignoring spatial structure (see also
58 Holmgren, 1995; Garay et al., 2020; Spencer and Broom, 2018).

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

75 Furthermore, populations likely contain significant individual variation in movement and
76 competition characteristics, such that individuals make different decisions given similar cues
77 (Laskowski and Bell, 2013). Capturing these differences in models is likely key to better under-

78 standing how individual decisions scale to population- and community-level outcomes (Bolnick
79 et al., 2011). Individual based models are well suited to capturing variation in responses to en-
80 vironmental cues, and also force researchers to be explicit about their modelling assumptions,
81 such as *how exactly* competition affects fitness. Similarly, rather than taking a purely ecological
82 approach and assuming such differences (e.g. in movement rules White et al., 2018), modelling
83 the evolution of movement strategies in a competitive landscape can reveal whether individual
84 variation emerges in plausible ecological scenarios (as in Getz et al., 2015). This allows the func-
85 tional importance of environmental cues to movement and competition decisions in evolutionary
86 models to be joint outcomes of selection, leading, for example, different competition strategies to
87 be associated with different movement rules (Getz et al., 2015).

88 Here, we present a mechanistic, model of intraspecific foraging competition in a spatially
89 explicit context, where competition is shaped by the joint evolution of foraging competition and
90 movement strategies. As foraging and movement decisions are taken by individuals, we study
91 the joint evolution of both types of decision-making by means of an individual-based simula-
92 tion model. Such models are well suited to modelling the ecology and evolution of complex
93 behaviours (Guttal and Couzin, 2010; Kuijper et al., 2012; Getz et al., 2015, 2016; White et al.,
94 2018; Long and Weissing, 2020; Netz et al., 2020, for conceptual underpinnings see Huston et al.
95 (1988); DeAngelis and Diaz (2019)). This allows us to both focus more closely on the interplay
96 of exploitation and interference competition, and to examine the feedback between movement
97 and foraging behaviour at ecological and evolutionary timescales. In our model, foraging indi-
98 viduals move on a spatially fine-grained resource landscape with discrete, depletable food items
99 that need to be processed ('handled') before consumption. Foragers make movement decisions
100 using an inherited (and evolvable) strategy which integrates local cues, such as the local resource
101 and competitor densities. After each move, individuals choose between two foraging strategies:
102 whether to search for a food item or steal from another individual; the mechanism underlying
103 this foraging choice is also inherited. We take lifetime resource consumption as a proxy for
104 fitness, such that more successful individuals produce more offspring, and thus are more suc-
105 cessful in transmitting their movement and foraging strategies to future generations (subject to

106 small mutations). We consider three scenarios: in the first scenario, we examine only exploita-
107 tion competition. In the second scenario, we introduce kleptoparasitic interference as an inherited
108 strategy, fixed through an individual's life. In the third scenario, we model kleptoparasitism as a
109 behavioural strategy conditioned on local environmental and social cues.

110 Our model allows us to examine the evolution of individual movement strategies, population-
111 level resource intake, and the spatial structure of the resource landscape. The model enables us
112 to take ecological snapshots of consumer-resource dynamics (animal movement, resource deple-
113 tion, and competition) proceeding at evolutionary time-scales. Studying these snapshots from all
114 three scenarios allows us to check whether, when, and to what extent the spatial distribution of
115 competitors resulting from the co-evolution of competition and movement strategies corresponds
116 to standard IFD predictions. We investigate three primary questions: (1) What movement pat-
117 terns will evolve in producer-scrounger systems? To what extent will the pattern differ between
118 producers and scroungers? (2) Does the (evolved) spatial distribution of consumers and re-
119 sources correspond to "ideal free" expectations? To what extent is the outcome dependent on the
120 modeling scenarios considered? (3) Do individuals in the same "competition" state use the same
121 movement strategy or are there indications for systematic individual differences in movement
122 patterns?

123 The Model

124 Individual-based models have the advantage and the disadvantage that they have to explicitly
125 specify numerous assumptions (e.g. on the spatial structure, the interaction structure, the timing
126 of events), while the same kind of assumptions are often hidden below the surface in analytical
127 models. As we are mainly interested in general, conceptual insights, we tried to keep our model
128 assumptions as simple and generic as possible. However, to keep the model realistic (and to
129 relate model outcomes with empirical observations) the model set-up is inspired by the foraging
130 behavior of shorebirds *Charadrii*. This is reflected by the gridded structure of the environment,
131 the capacity of each grid cell to hold multiple individuals, the discrete nature of the resources,
132 and the discrete conception of time within and between generations. Shorebirds such as oyster-

133 catchers (*Haematopus* spp.) are a convenient model system, and are extensively studied in the
134 context of foraging competition, both empirically (e.g. Vahl et al., 2005a,b, 2007; Rutten et al.,
135 2010a,b), and using individual-based models (reviewed in Stillman and Goss-Custard, 2010). We
136 simulated a population with a fixed number of individuals ($N = 10,000$), which move on a land-
137 scape of 512^2 grid cells (approx. 1 individual per 26 cells), with wrapped boundaries; individuals
138 passing beyond the bounds at one end re-appear on the opposite side. The model has two time
139 scales, first, an ecological time scale of T timesteps comprising one generation (default $T = 400$),
140 during which individuals move, make foraging decisions, and handle prey-items they find or
141 steal. Individuals are immobile while handling food items, creating the conditions for klep-
142 toparasitism (Brockmann and Barnard, 1979; Ruxton et al., 1992). On the second, evolutionary
143 time scale of 1,000 generations, individuals reproduce, transmitting their movement and foraging
144 strategies to their offspring, whose number is proportional to individual intake at the ecological
145 time scale.

146 *Resource Landscape*

147 *Prey Abundance.* We considered a resource landscape that is heterogeneous in its productivity
148 of discrete resources, but with strong spatial clustering of grid cells of similar productivity. We
149 considered our discrete resources, called ‘prey-items’ to represent mussels, a common prey of
150 many shorebirds, whose abundances are largely driven by external gradients. We assigned each
151 cell a constant probability of generating a new prey item per timestep, which we refer to as
152 the cell-specific growth rate r . We modelled clustering in landscape productivity by having the
153 distribution of r across the grid take the form of 1,024 resource peaks, placed at regular distances
154 of 16 grid cells from the peaks around them; r declines from the centre of each peak (called
155 r_{max}) to its periphery (see Fig. 1C). Thus the central cell generates prey-items five times more
156 frequently than peripheral cell: at $r_{max} = 0.01$, central cells generate one item per 100 timesteps
157 (four items/generation), while the peripheral cells generate one item only every 500 timesteps
158 ($< one\ item/generation$). All landscape cells have a uniform carrying capacity K of 5 prey-items.

159 *Prey Acquisition by Foragers.* Foragers perceive a cue indicating the number of prey-items P in
160 a cell, but fail to detect each item with a probability q , and are thus successful in finding a
161 prey-item with a probability $1 - q^P$. Individuals on a cell forage in a randomised sequence, and
162 the probability of finding a prey-item ($1 - q^P$) is updated as individuals find prey, reducing P .
163 Foragers that find a prey-item must handle it for a fixed handling time T_H (default = 5 timesteps),
164 before consuming it (Ruxton et al., 1992). Natural examples include the time required for an
165 oystercatcher to break through a mussel shell, or a raptor to subdue prey; overall, the handling
166 action is obvious, and the prey is not fully under the control of the finder (Brockmann and
167 Barnard, 1979). Foragers that do not find a prey-item are considered idle in that timestep, and
168 are counted as ‘non-handlers’. Similarly, handlers that finish processing their prey in timestep t
169 can only forage again in timestep $t + 1$, i.e., they are idle in the timestep t .

170 *Movement and Competition Strategies*

171 *Movement Strategies.* We model movement as comprised of small, discrete steps of fixed size,
172 which are the outcome of individual movement decisions made using evolved movement strate-
173 gies. Across scenarios, individuals make movement decisions by selecting a destination cell, after
174 assessing potential destinations based on available cues (similar to step selection or resource se-
175 lection; Fortin et al., 2005; Manly et al., 2007), and similar to the approach used previously by
176 Getz et al. (2015, 2016) and White et al. (2018). At the end of each timestep t , individuals scan
177 the nine cells of their Moore neighbourhood for three environmental cues, (1) an indication of
178 the number of discrete prey items P , (2) the number of individuals handling prey H (referred
179 to as ‘handlers’), and (3) the number of individuals not handling prey N (referred to as ‘non-
180 handlers’). Individuals rank potential destinations (including the current cell) by their suitability
181 S , where $S = s_P P + s_H H + s_N N$, and move to the most suitable cell in timestep $t + 1$. The
182 weighing factors for each cue, s_P , s_H , and s_N , are evolvable traits, and are genetically encoded
183 and transmitted between generations. All individuals move simultaneously, and then implement
184 their foraging or kleptoparasitic behaviour to acquire prey. However, handlers do not make any
185 movements until they have fully handled and consumed their prey.

186 *Scenario 1: Exploitative Competition.* In scenario 1, we simulate only exploitative competition;
187 individuals (henceforth called ‘foragers’) move about on the landscape and probabilistically find,
188 handle, and consume prey items. Foragers can be either in a ‘searching’ or a ‘handling’ state
189 (Holmgren, 1995). The only evolvable properties are the cue weighing factors which determine
190 the suitability scores (s_P , s_H and s_N).

191 *Scenario 2: Fixed Interference Competition.* In scenario 2, the competition strategy is genetically
192 determined and transmitted from parents to offspring: exploitative competition (by foragers), or
193 kleptoparasitic interference (by kleptoparasites). Each of these strategies can evolve a (separate)
194 movement strategy. Kleptoparasites cannot extract prey-items directly from the landscape, and
195 only steal from handlers (see Holmgren, 1995). Kleptoparasites are modelled as always being
196 successful in stealing from handlers, and such successful surprise attacks are commonly observed
197 among birds (Brockmann and Barnard, 1979). However, if multiple kleptoparasites target the
198 same handler, only one (randomly selected) is considered successful — thus kleptoparasites
199 compete exploitatively among themselves. Handlers robbed of prey subsequently ‘flee’ up to
200 5 cells away from their location. Having acquired prey, kleptoparasites become handlers, but
201 need only handle prey for $T_H - t_h$ timesteps, where t_h is the time that the prey has already
202 been handled by its previous owner. Unsuccessful kleptoparasites are considered idle, and are
203 counted as non-handlers.

204 *Scenario 3: Conditional Interference Competition.* In scenario 3, each individual can either act as a
205 forager, or as a kleptoparasite, depending on its assessment of local circumstances. Individuals
206 process the cell-specific environmental cues P , H , and N to determine their location in the next
207 timestep (based on their inherited movement strategy). Additionally, individuals process cell-
208 specific environmental cues in timestep t to determine their strategy in the next timestep as

$$209 \quad \text{strategy} = \begin{cases} \text{forager,} & \text{if } w_P P + w_H H + w_N N \geq w_0 \\ \text{kleptoparasite,} & \text{otherwise} \end{cases} \quad (1)$$

210 where the cue weights w_P , w_H and w_N , and the threshold value w_0 , are also heritable between
211 generations. Apart from the ability to switch between foraging and kleptoparasitism, the com-
212 petition dynamics are the same as in scenario 2.

213 *Reproduction and Inheritance*

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

221 Each individual's number of offspring is proportional to the individual's total lifetime intake
222 of resources; hence, resource intake is used as a proxy for fitness. A weighted lottery (with
223 weights proportional to lifetime resource intake) selects a parent for each offspring in the subse-
224 quent generation (prior implementation in Tania et al., 2012; Netz et al., 2020). Across scenarios,
225 the movement decision-making weights are subject to rare, independent mutations ($\mu = 0.001$).
226 The mutational step size (either positive or negative) is drawn from a Cauchy distribution with
227 a scale of 0.01 centred on zero, allowing for a small number of very large mutations while most
228 mutations are small. In scenarios 1 and 2, the foraging-decision weights are not relevant. How-
229 ever, in scenario 2, we allow a forager to infrequently mutate into a kleptoparasite (or *vice versa*; μ
230 = 0.001). In scenario 3, the foraging weights also mutate as described above. We initialised each
231 offspring at random locations on the landscape, leading individuals to experience conditions
232 potentially very different from those of their parent.

233 *Simulation Output and Analysis*

234 We ran all three scenarios at a default r_{max} of 0.01, which we present in the RESULTS, and also
235 across a range of r_{max} values between 0.001 and 0.05 (see Fig. 6 and Supplementary Material Figs.

236 1.1 – 1.3). We initialised the decision making weights with values uniformly distributed between
237 -1.0 and 1.0, to allow sufficient variation in the population.

238 *Population Activities and Intake.* Across scenarios, in each generation, we counted the number
239 of times foragers were searching for prey, kleptoparasites were searching for handlers, and the
240 number of timesteps that individuals of either strategy were handling a prey-item. We refer to
241 the ratio of these values as the population's 'activity budget'. We examined how the population
242 activity budget developed over evolutionary time, and whether a stable equilibrium was reached.
243 Furthermore, we counted the population's mean per-capita intake per generation as a measure
244 of population productivity.

245 *Visualising Decision-Making Weights.* To understand the evolution of individual movement and
246 competition strategies, we exported the decision-making weights of each individual in every
247 generation of the simulation. To visualise functional differences in weights, which could take
248 arbitrarily large values, we multiplied each weight by 20 and applied a hyperbolic tangent trans-
249 form. This scaled the weights between -1 and +1, and we plotted these weights to understand
250 individual variation in movement rules, as well as calculating how preference and avoidance of
251 cues evolved across scenarios.

252 *Ecological Snapshots of Consumer-Resource Distributions.* We exported snapshots of the entire sim-
253 ulation landscape at the mid-point of each generation ($t = 200$). Each snapshot contained data
254 on (1) the number of prey-items, (2) the number of handling individuals, and the number of
255 individuals using either a (3) searching forager strategy or (4) kleptoparasitic strategy, on each
256 cell. We used a subset of the total landscape (60^2 of 512^2 cells) for further analyses to speed up
257 computation. We determined the availability of direct resource cues for movement in each cell by
258 calculating the cell-specific item gradient for each landscape snapshot, as the difference in prey
259 counts between each cell and its neighbouring cells. For each generation, we calculated the pro-
260 portion of cells from which it was possible to sense differences in prey-items, i.e., a neighbouring
261 cell with either more or fewer items.

262 *Testing the Input Matching Rule.* A basic prediction of the IFD and the related matching rule is
263 that the number of individuals on occupied patches should be proportional to patch productivity
264 (Fretwell and Lucas, 1970; Parker, 1978; Houston, 2008). Patch productivity is challenging to
265 measure in real world systems, but is among our model's building blocks, and we examined
266 the correlation between the number of individuals (excluding handlers) and the cell-specific
267 productivity r , expecting large positive values.

268 **Results**

269 *Scenario 1: No Kleptoparasitism*

270 In scenario 1, foragers deplete prey-items faster than they are replenished, drastically reducing
271 the overall number of prey within 50 generations (Fig. 1A). The population activity budget is
272 split between searching and handling (Fig. 1B); while handling and the mean per-capita intake
273 are both initially low, they peak within ten generations (Fig. 1C), as individuals easily acquire
274 prey-items from the fully stocked landscape in the first few generations. With dwindling prey-
275 items, fewer searching foragers find prey, and handling as a share of the activity budget declines
276 to a stable $\sim 45\%$ within 50 generations, and mean per-capita intake also stabilises (Fig. 1C).
277 Across generations, the correlation between the number of foragers and cell productivity is only
278 slightly positive (Fig. 1D). This is in contrast with the perfect correspondence between resource
279 input rate and forager density (the 'input matching rule'), which is a defining property of the IFD
280 (Parker, 1978; Houston, 2008). Contrary to standard IFD assumptions, foragers cannot directly
281 "sense" the local cell productivity r ; instead they can only use the (small) number of prey items
282 available in a cell as a cue for local productivity ("cell quality").

283 *Scenario 2: Co-existence of Foragers and Kleptoparasites*

284 In scenario 2, with fixed foraging and kleptoparasitism allowed, the spatial distribution of prey-
285 items at equilibrium is very different from scenario 1. Consumers graze down resource peaks
286 until few prey-items remain on the landscape; however, within 50 generations the resource land-

287 scape recovers with prey abundances higher than in the earliest generations (Fig. 2A). This is
288 because of the emergence of kleptoparasites (Fig. 2B): in early generations, kleptoparasites are
289 rare, and the activity budget, the mean per-capita intake, and the distribution of consumers over
290 the landscape, are similar to scenario 1. As resources are depleted and kleptoparasite-handler
291 encounters become more common than forager-prey encounters, kleptoparasitism becomes the
292 majority strategy (a stable ~70% of the population; see Fig. 2B), and searching for handlers to
293 rob becomes the commonest activity. However, the high frequency of this activity and the low
294 frequency of handling, indicate that few kleptoparasites are successful at robbing handlers.

295 With few foragers, few prey-items are extracted from the landscape, which recovers beyond its
296 initial prey abundance within 50 generations (Fig. 2A). As fewer prey-items are extracted overall,
297 mean per-capita intake also declines from an initial peak (Fig. 2C). Despite the strong spatial
298 structure of the resource landscape within 50 generations, the correlation between consumers (of
299 either strategy) and cell productivity remains weak or zero across generations (Fig. 2D). This
300 may be explained by the dynamics of kleptoparasitism: foragers fleeing a kleptoparasitic attack
301 are displaced far from their original location, and kleptoparasites must track these foragers if
302 they are to acquire resources.

303 The increase of kleptoparasites from a negligible fraction to the majority strategy (Fig. 3A) is
304 associated with an evolutionary divergence of movement strategies between foragers and klep-
305 toparasites. While all individuals (both foragers and kleptoparasites) evolve to prefer high prey
306 density and avoid high non-handler density (see Supplementary Material Fig. 2.2), the two types
307 of competition strategy differ substantially in their response to handlers (Fig. 3B, 3C). Klep-
308 toparasites very rapidly (within 3 generations) evolve a strong preference for moving towards
309 handlers, which are their primary resource (Fig. 3B). In the absence of kleptoparasites, for-
310 agers would evolve a preference for moving towards handlers (see Supplementary Material Fig.
311 2.1), but, with kleptoparasites common in the population, searching foragers avoid and prefer
312 handlers in about equal proportions (Fig. 3C). While all kleptoparasites evolve to prefer mov-
313 ing towards handlers, the strength of the attraction to handlers shows multiple distinct values
314 ('morphs'), which are remarkably persistent across generations (Fig. 3B). In replicate 3, for ex-

315 ample, the commonest movement strategy is only weakly attracted to handlers, but this strategy
316 coexists with various strategies that are all strongly attracted to handlers (Fig. 3B). The move-
317 ment strategies of foragers show an even higher degree of polymorphism (Fig. 3C). Typically,
318 there are no predominant movement strategies. Instead, a wide range of coexisting handler at-
319 traction/repulsion values emerges: some foragers are strongly attracted by handlers, others are
320 strongly repelled by handlers, and yet others are neutral to the presence of handlers.

321 *Scenario 3: Condition-dependent Kleptoparasitism*

322 When individuals are allowed to choose their competition strategy (foraging or kleptoparasitism)
323 based on local environmental cues, the distribution of individuals and prey items is substantially
324 different from the two previous scenarios (Fig. 4A). Initially, as in scenario 1, individuals deplete
325 the resource landscape of prey-items within ten generations. By generation 50, the resource
326 landscape recovers some of the spatial structure of early generations, but prey-item abundances
327 do not match the recovery seen in scenario 2. This too is explained by the observation that by
328 generation 30, all individuals have a propensity to steal from handlers, i.e., when handlers are
329 present in the vicinity, consumers will choose to target handlers for prey items, rather than forage
330 for prey themselves (“opportunistic kleptoparasitism”; Fig. 4B; *orange line*). However, unlike
331 scenario 2, individuals search for prey more often and steal less (at or below 25%; compare Fig.
332 2B), preventing a full recovery of the resource landscape. Consequently, mean per-capita intake
333 stabilises (after an initial spike, as in scenarios 1 and 2) within ten generations to a level similar to
334 scenario 1 (Fig. 4C). Using conditional foraging strategies, individuals are able to switch between
335 resource types (prey and handlers) depending on which is more profitable (Emlen, 1966), and
336 appear to track resources. Thus, while not as strong as predicted by IFD theory, the correlations
337 between consumer abundance and cell productivity are weakly positive (Fig. 4D).

338 *Movement Rules on Depleted Landscapes*

339 Orienting movement towards resources (Nathan et al., 2008, ; *where to move*) can be a challenge
340 in a system with low densities of discrete prey items, because the local prey *density* may provide

341 very limited information about local *productivity*. In our model, prey-depletion leads parts of
342 the resource landscape to become ‘clueless regions’ (Perkins, 1992), where foragers cannot make
343 directed movements based on prey-item abundances alone, as all neighbouring item abundances
344 are identical (see white areas in Fig. 5A; A1: scenario 1, A2: scenario 2, A3: scenario 3). At
345 the beginning of all three scenarios, about 75% of landscape cells have a different number of
346 prey-items from the cells around them; these are primarily cells with an intermediate r , which
347 have more prey than peripheral cells of resource peaks, but fewer prey than the central cells. This
348 proportion rapidly declines to a much lower value within 10 generations in all three scenarios.

349 The ‘cluelessness’ of the landscapes develops differently across scenarios on evolutionary
350 timescales (Fig. 5B). In scenario 1, the proportion of cells with a different number of items in the
351 neighbourhood is initially very high (Fig. 5A1). This proportion rapidly declines to $\sim 25\%$ within
352 10 generations, as foragers deplete most prey-items, making most of the landscape a clueless
353 region. In this context, foragers evolve to move towards handlers, with $> 75\%$ of individuals
354 showing a preference for handlers within 100 generations (Fig. 5B1). Forager preference for
355 handlers may be explained as the sensing of a long-term cue of local productivity. Since handlers
356 are immobilised on the cell where they find a prey-item, handler density is an indirect indicator
357 of cell r , and due to spatial autocorrelation, also of the r of bordering cells.

358 Scenario 2 landscapes develop similarly to scenario 1 in early generations (Fig. 5A2). How-
359 ever, within 50 generations, most cells bear items as extraction is reduced, with differences among
360 cells according to their r (see also Fig. 2A). Thus $> 75\%$ of cells have a different number of items
361 from neighbouring cells (Fig. 5A2 – panel *gen: 50*, 5B2). Unlike scenario 1, the rapid increase
362 in handler preference is driven by kleptoparasites becoming the majority strategy (see above).
363 Scenario 3 is similar to scenario 2, except that only about half of all cells have a different number
364 of prey-items from neighbouring cells (Fig. 5A3, 5B3). Here, the rapid evolution of a handler
365 preference in movement decisions cannot be assigned a clear cause, since handlers are both a
366 potential direct resource as well as indirect cues to the location of productive cells.

Effect of Landscape Productivity

367

368 The prey-item regrowth rate that characterises the peaks of the resource landscape (r_{max}) is a mea-
369 sure of the productivity of the resource landscape overall. Having thus far focused on scenarios
370 with $r_{max} = 0.01$ (corresponding to a peak production of 4 food times per consumer lifetime), we
371 find that, not unexpectedly, the value of r_{max} has a marked effect on evolved population activity
372 budgets, mean per capita intake, and even evolved strategies. The frequency of foraging reduces
373 with r_{max} in scenarios 1 and 3; this is caused by more frequent acquisition of prey items (as re-
374 growth keeps pace with depletion), which results in a greater frequency of handling rather than
375 foraging.

376 In scenario 2 however, the frequency of handling is relatively unaffected by increasing r_{max}
377 (Fig. 6A). The difference between scenarios 2 and 3 has to do with the change in the frequency
378 of kleptoparasitism (Fig. 6B). In scenario 2, kleptoparasitism forms $> 75\%$ of all activities at
379 low r_{max} , and is much more common than in scenario 3 populations at the same regrowth rate.
380 However, at relatively high r_{max} (0.03), the fixed kleptoparasitic strategy goes extinct. This is
381 because at high r_{max} , forager-prey encounters are more common than kleptoparasite-handler
382 encounters, in both early (< 10) and later generations (> 50). Consequently, kleptoparasites have
383 relatively much lower fitness than foragers, and do not proliferate. Thus at high r_{max} , a scenario 2
384 population is nearly identical to a scenario 1 population; while some kleptoparasites may be seen
385 in later generations, these occur most likely due to ephemeral mutations in the forager strategy.

386 In scenario 3, kleptoparasitism persists at low frequencies even at the highest regrowth rates
387 (Fig. 6B); thus some foragers lose time in extracting items which are then stolen from them. Con-
388 sequently, while populations in all three scenarios achieve very similar mean per-capita intakes
389 at low r_{max} , at intermediate regrowth rates (0.01, 0.02), conditionally kleptoparasitic populations
390 achieve a higher mean per-capita intake than populations using fixed strategies. Only at high
391 r_{max} , when fixed strategy populations effectively convert to purely forager populations, do they
392 achieve a higher intake than conditional strategy populations (Fig. 6C).

393

Discussion

394 Our spatially-explicit individual-based model implements the ecology and evolution of move-
395 ment and foraging decisions, as well as resource dynamics, in biologically plausible ways, and
396 offers a new perspective about the distribution of animals in relation to their resources under dif-
397 ferent scenarios of competition. First, we show that when moving with a limited perception range
398 and competing only by exploitation, individuals evolve movement strategies for both direct and
399 indirect resource cues (prey items and handlers, respectively). Regardless, on a resource land-
400 scape with discrete prey items, large areas may become devoid of any movement cues, leading to
401 a mismatch between individual distribution, prey item distribution, and landscape productivity.
402 Second, we show that when interference competition in the form of kleptoparasitism is allowed
403 as a fixed strategy, it rapidly establishes itself on landscapes where stealing is more time-efficient
404 than searching for prey. This rapid increase in kleptoparasitism as a strategy is accompanied
405 by the evolution of movement strategies that favour moving towards handlers, which are the
406 primary resource of the kleptoparasites. In this sense, obligate kleptoparasites may be thought
407 of as forming a higher trophic level, with any handling consumers as their prey. Third, we show
408 that when foraging strategy is allowed to be conditional on local cues, (1) the population's mean
409 per capita intake is significantly higher than that of a population with fixed strategies, and (2)
410 unlike fixed strategy populations, kleptoparasitism as a strategy does not go extinct on high-
411 productivity landscapes. However, across scenarios, individuals are broadly unable to match the
412 productivity of the resource landscape, contrary to the predictions of IFD based models, which
413 predict input matching for some (Parker and Sutherland, 1986; Holmgren, 1995; Hamilton, 2002),
414 or all of the competitive types Korona (1989).

415

Comparison with Existing Models

416 Existing models of competition and movement impose fixed movement rules on individuals
417 to mimic either ideal or non-ideal individuals (Vickery et al., 1991; Cressman and Křivan, 2006;
418 Amano et al., 2006; Beauchamp, 2008; Stillman and Goss-Custard, 2010; White et al., 2018). When

419 individual competitive strategies are included in models, they represent differences in competi-
420 tive ability (e.g. Parker and Sutherland, 1986; Holmgren, 1995; Hamilton, 2002), or a probabilistic
421 switch between producing and scrounging (Beauchamp, 2008). In contrast, our model allows
422 individuals' movement (and competition) decisions to be adaptive responses to local environ-
423 mental cues. Similar to Getz et al. (2015, 2016) and White et al. (2018), our individuals choose
424 from among the available movement options after weighing the local environmental cues, similar
425 to resource selection functions (Manly et al., 2007; White et al., 2018). Local environmental cues
426 in our model are constantly changing, as we model discrete, depletable prey-items, contrasting
427 with many IFD models (Tregenza, 1995; Amano et al., 2006). This allows for a more plausible,
428 fine-scale consideration of exploitation competition, which is often neglected, and allows the cues
429 sensed by individuals to strongly structure the distribution of competitors (see below).

430 Adaptive responses must have an explicit evolutionary context, and consider multiple gen-
431 erations of the population. We follow Beauchamp (2008) and Getz et al. (2015) in allowing the
432 decision making weights for movement, and variation thereof, to be the outcomes of natural se-
433 lection. However, instead of using 'evolutionary algorithms' (Beauchamp, 2008; Getz et al., 2015,
434 2016) to 'optimise' individual movement rules, we consider a more plausible evolutionary pro-
435 cess: Instead of allowing the fittest 50% of the population to replicate, the number of offspring are
436 proportional to individual fitness. The weight loci are subject to mutations independently, rather
437 than subjecting all loci of an individual to simultaneous mutation. Finally, we avoided the un-
438 realistic assumption of 'simulated annealing', which adapts the mutation rate or the mutational
439 step sizes to the rate of evolutionary change. Instead we drew mutation sizes from a Cauchy
440 distribution, so that most mutations are very small, but large-effect mutations do occur through-
441 out the simulation. Similarly, rather than determining competition strategy probabilistically or
442 ideally (Vickery et al., 1991; Beauchamp, 2008; Tania et al., 2012), our individuals' competition
443 decisions are also shaped by selection (in scenarios 2 and 3).

Movement Rules on Depleted Landscapes

444
445 In scenario 1, depletion of discrete prey can leave many areas empty of prey-items: in such areas,
446 movement informed by a resource gradient is impossible, and individuals may move randomly
447 (Perkins, 1992). This lack of direct resource cues for locally optimal movement might be among
448 the mechanisms by which unsuitable ‘matrix’ habitats modify animal movement on heteroge-
449 neous landscapes (Kuefler et al., 2010). When individuals do not sense resource gradients, the
450 presence of more successful conspecifics may indicate a suitable foraging spot (local enhance-
451 ment; Giraldeau and Beauchamp, 1999; Beauchamp, 2008; Cortés-Avizanda et al., 2014). The
452 presence of unsuccessful individuals, meanwhile, may signal potential costs from exploitation
453 or interference competition. This selects for movement strategies incorporating the presence and
454 condition of competitors into individual movement decisions (‘social information’: Dall et al.,
455 2005). Consequently, consumer aggregation — often explained by invoking external costs such
456 as predation (Krause and Ruxton, 2002; Folmer et al., 2012) — could also be the outcome of move-
457 ment rules that have evolved to trade competition costs for valuable social information on the
458 underlying drivers of the spatial structure (here, r) of uninformative landscapes (Folmer et al.,
459 2010; Cortés-Avizanda et al., 2014).

Individual Variation in Movement Rules

460
461 We find substantial individual variation in the strength of movement weights within popula-
462 tions, as expected from heterogeneous landscapes (see Supplementary Material Fig. 2.1 – 2.3;
463 see Wolf and Weissing 2010 for background). The persistence of multiple ‘movement morphs’
464 across generations indicates that they are alternative movement strategies of equal fitness (see
465 Getz et al., 2015). Indeed, polymorphism in movement rules may help reduce competition as
466 individuals make subtly different movement and competition decisions when presented with the
467 same cues (Laskowski and Bell, 2013, see also Wolf and Weissing 2012). Scenario 2 also shows
468 significant within-strategy individual variation in movement weights, which might ameliorate
469 within-strategy exploitation competition, or help foragers avoid kleptoparasites (Wolf and Weiss-

470 ing, 2012; Laskowski and Bell, 2013). Interestingly, scenario 3 has the least individual variation
471 in movement rules, potentially because plasticity in competition strategy dampens such diversi-
472 fication (Pfennig et al., 2010), but also possibly because the ability to switch between prey types
473 reduces the intensity of competition. Here, non-handler avoidance shows the most morphs, but
474 it is unclear whether this variation is linked to the frequency with which individuals use ei-
475 ther foraging strategy — potentially leading to subtle, emergent behavioural differences that are
476 conditioned on the local environment (Wolf and Weissing, 2010, 2012).

477 *Competition Strategies and the IFD*

478 IFD models predict that individual movement should result in consumer distributions tracking
479 the profitability of resource patches (Fretwell and Lucas, 1970; Parker, 1978), with dominant com-
480 petitive types (including kleptoparasites) monopolising the best patches (Parker and Sutherland,
481 1986; Holmgren, 1995; Hamilton, 2002, but see Korona 1989). In scenarios 2 and 3, kleptopar-
482 asitic individuals unsurprisingly and rapidly evolve to track handlers (a direct resource), while
483 avoiding non-handlers (potential competitors). However, these evolved rules do not lead klep-
484 toparasites to occupy the best cells as predicted (Parker and Sutherland, 1986; Holmgren, 1995;
485 Hamilton, 2002). Across our scenarios (including scenario 1), individual density is only weakly
486 correlated with cell productivity. In scenario 2, this departure from predictions is driven by the
487 contrasting movement rules of foragers, which evolve to *avoid* handlers as well as non-handlers,
488 both of which might be kleptoparasites (cryptic interference; seen in interference-sensitive waders
489 Folmer et al. 2010; Bijleveld et al. 2012; see Supplementary Material). Thus, foragers likely avoid
490 resource peaks, which are more likely to have handlers (due to the higher probability of forager-
491 prey encounters Parker and Sutherland, 1986; Holmgren, 1995; Hamilton, 2002). Fixed klep-
492 toparasites cannot extract prey themselves, and must move off resource peaks to track and rob
493 handlers (similar to Parker and Sutherland, 1986), breaking the link between individual density
494 and productivity. This shows the pitfalls of simplistically linking current ecological conditions
495 with population distributions without considering competitive strategies or evolutionary history.

Constraints on Competition Strategies

496

497 Foraging strategies involving specialisation on a resource type are expected to be constrained by
498 the availability of that resource; thus kleptoparasitism, seen as a prey-choice problem, should
499 be constrained by the density of targets (Ens et al., 1990). In scenarios 2 and 3, more klep-
500 toparasitism should be expected with increasing r_{max} , as prey and consequently, handlers, are
501 expected to be more abundant. Instead, kleptoparasitism declines with increasing r_{max} , in line
502 with Emlen (1966), who predicted that the commoner food type (prey) rather than the more
503 efficiently exploited one (handlers) should be preferred. This effect is especially stark in sce-
504 nario 2, where kleptoparasites go extinct when prey are very common at high r_{max} . At stable
505 population densities, the persistence of fixed kleptoparasitism depends on their intake *relative to*
506 *foragers*. Since intake is an outcome of movement rules, and population movement rules are not
507 well adapted to the environment in early generations, foragers obtain, as a clade, more intake
508 than kleptoparasites. Modelling discrete prey-items and individuals in a spatial context, then,
509 leads to the finding that obligate kleptoparasitism is only a viable strategy when forager-prey
510 encounters are less common than kleptoparasite-handler encounters. This might explain why —
511 and is supported by the observation that — kleptoparasitism is common among seabirds, whose
512 communal roosts are much easier targets than unpredictable shoals of fish out at sea (Brockmann
513 and Barnard, 1979); in contrast, grazing geese have similar flock sizes but their resource is also
514 very easily located, hence kleptoparasitism is rare even though interference is common (Amano
515 et al., 2006). Finally, comparing across regrowth rates shows why possibly cryptic behavioral
516 complexity should be considered in predictions of the long-term effect of environmental change
517 on populations. While both scenario 1 and 2 populations appear identical at high r_{max} , even a
518 small decrease in environmental productivity could lead to an abrupt drop in per-capita intake
519 — and potentially, strongly reduced growth or survival — for fixed strategy populations due to
520 unexpected, emergent kleptoparasitism.

521 *Comparison with Conceptual Models*

522 Classical models of animal movement and foraging largely consider homogeneous populations
523 and environmental conditions, and movements that are made either optimally or at random.
524 While these models provide powerful insights, individual-based models such as ours have the
525 advantage that they can accommodate individual variation, local environmental conditions, and
526 the mechanisms of movement and decision-making. Individual-based modeling has the obvious
527 drawback that numerous specific assumptions have to be made, which might not all be founded
528 on empirical evidence, and might seem to limit the generality of the conclusions. Nevertheless,
529 as long as these models are not mistaken for attempts at faithful representations of real systems,
530 their exploration provides valuable perspectives on the conceptual models that have dominated
531 theory in the past. After all, traditional models also include numerous assumptions (the spatio-
532 temporal structure, the timing of events, the distribution and inheritance of traits) that are usually
533 not stated and therefore less visible. For the future, we envisage pluralistic approaches, where
534 both types of model are applied to the same research question. Only comparing the outcomes of
535 diverse models will reveal which conclusions and insights are robust, and which reflect peculiar-
536 ities of the model structure. Only such model comparison can tell us whether and when simple
537 models produce general insights, where simple models fail, and when mechanisms can explain
538 initially counterintuitive observations, such as the attraction to competitors that we observed in
539 our study.

540 *Individual Based Models in Movement Ecology*

541 Animal movement ecology takes an explicitly individual-based approach, centred around indi-
542 vidual decisions (Nathan et al., 2008). This makes individual-based models a reasonable choice
543 when seeking general insights into the evolutionary ecology of animal movement strategies (see
544 e.g. Getz et al., 2015), whose ultimate causes are otherwise difficult to study empirically. They can
545 incorporate local circumstances and state variables in considerable detail, and thereby promote
546 careful consideration of what we know about animal response mechanisms. Individual-based

547 models of movement decisions can also be related to existing empirical work in animal tracking.
548 For example, our model's decision making weights are likely familiar to movement ecologists in
549 the form of the individual-specific coefficients of resource-selection or step-selection functions,
550 and have been interpreted as such (White et al., 2018). By allowing selection coefficients from
551 animal-tracking studies to undergo natural selection on simulated landscapes, similar models
552 could help explore long-term changes in movement strategies. This approach would require
553 very accurate estimation of the fitness outcomes of movement — no easy task. Consequently,
554 individual-based models are not (yet) intended to be 'fit' to empirical movement data. Rather,
555 they are useful to elucidate how simple mechanisms can lead to unexpectedly complex out-
556 comes, and to help define a broad envelope of potential outcomes, given known mechanisms
557 and explicit assumptions. These outcomes can provide valuable perspective on population-level
558 models (such as the IFD), or be used to explore how movement strategies evolve in dynamic
559 environments.

560 **Data and Code Availability**

561 Simulation model code is on Github: github.com/pratikunterwegs/Kleptomove and Zenodo:
562 zenodo.org/record/4905476. Simulation data are available from DataverseNL as a draft:
563 <https://dataverse.nl/privateurl.xhtml?token=1467641e-2c30-486b-a059-1e37be815b7c>.
564 Data will be at this persistent link after publication: doi.org/10.34894/JFSC41.
565 Data analysis code is on Github: github.com/pratikunterwegs/kleptomove-ms and on Zenodo:
566 doi.org/10.5281/zenodo.4904497.

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Figures

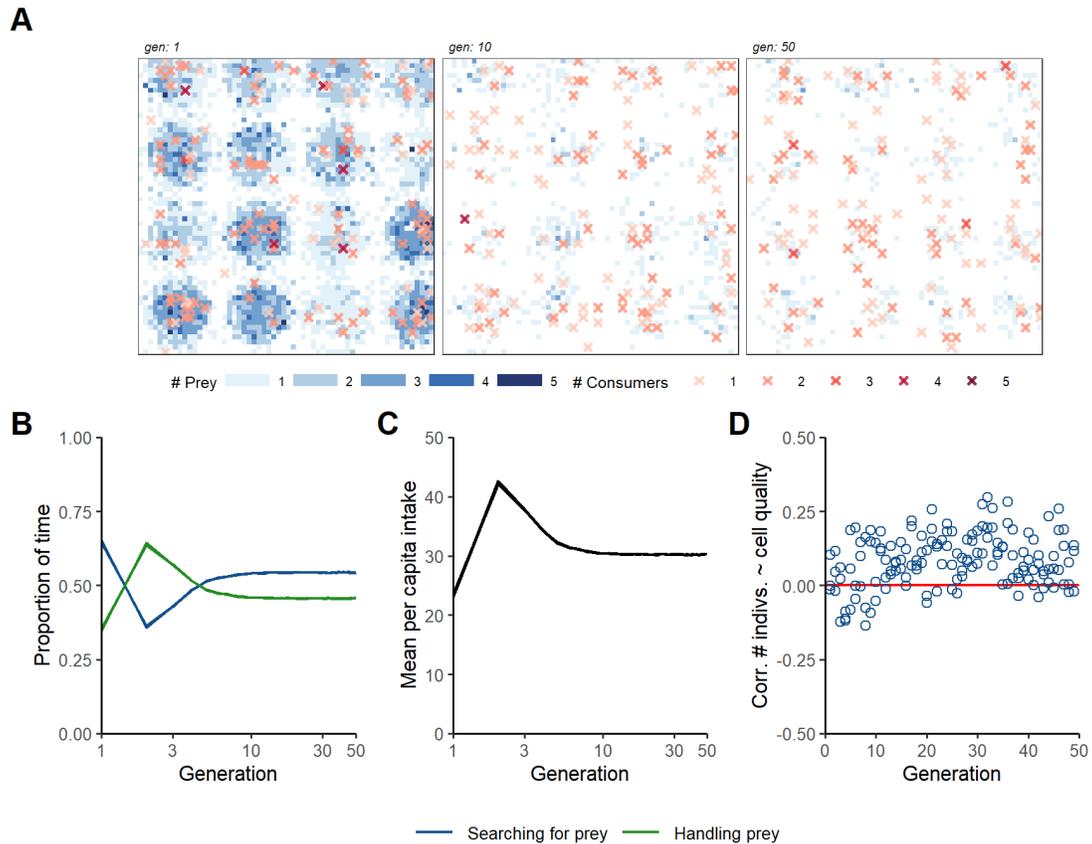


Figure 1: Eco-evolutionary implications of pure exploitation competition (scenario 1). (A) When a population is comprised solely of foragers seeking prey on a resource landscape, the initially well-stocked resource landscape is swiftly depleted within 10 generations (out of 1,000 simulated). This sparsity 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.

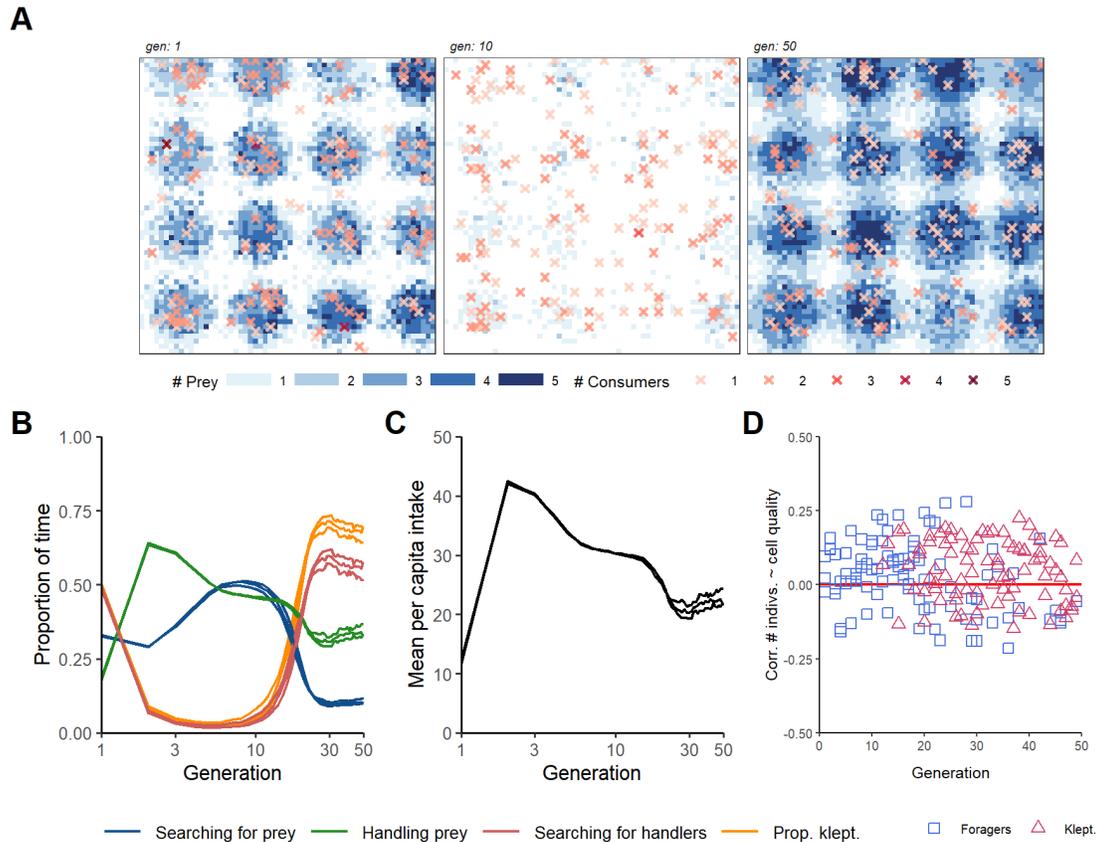


Figure 2: Eco-evolutionary implications of the coexistence of foragers and kleptoparasites (scenario 2). In populations with both foragers and kleptoparasites, **(A)** the initially well-stocked resource landscape is drastically depleted by generation 10; however, prey densities recover strongly by generation 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 $r_{max} = 0.01$.

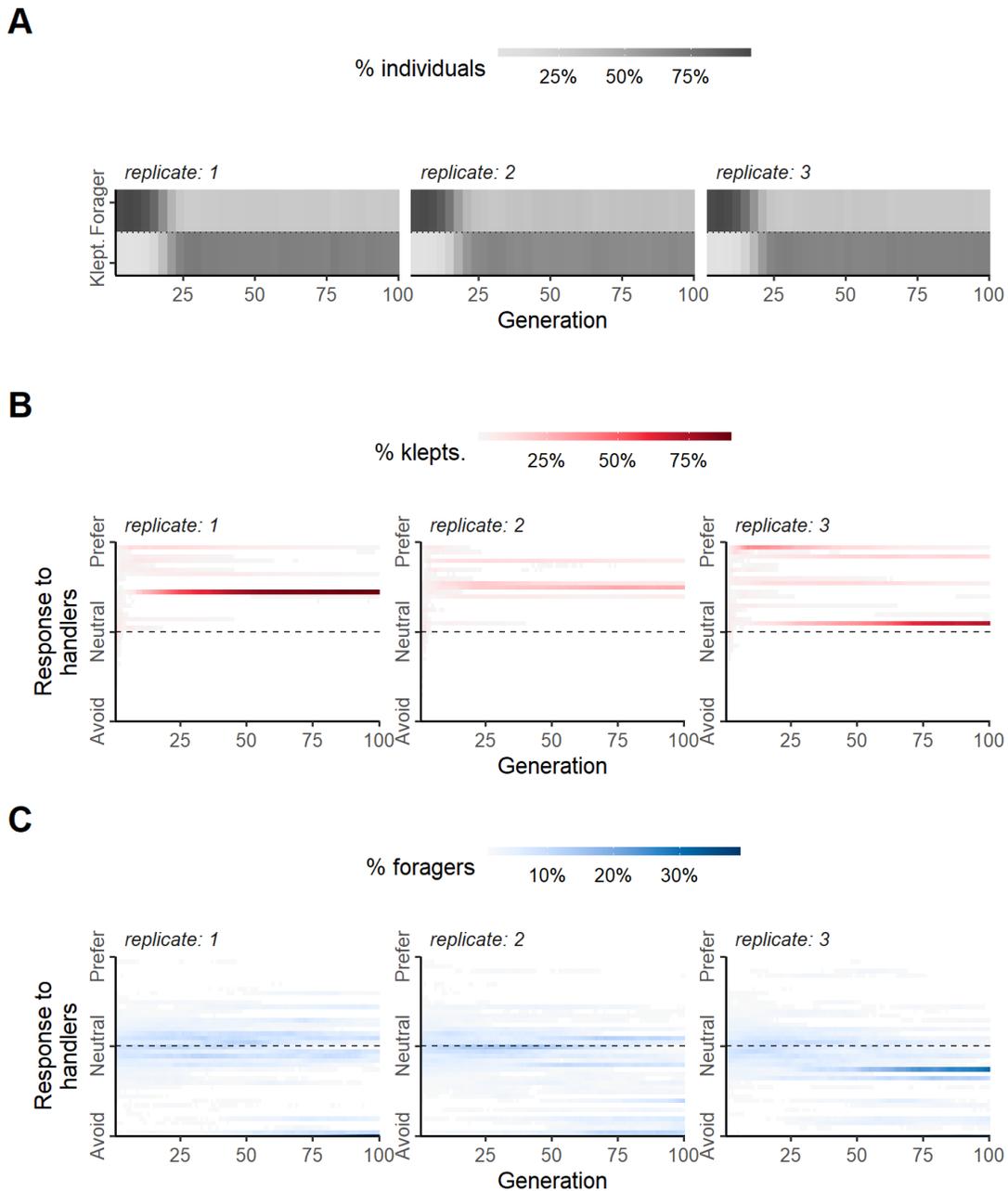


Figure 3: Divergence of movement strategies between foragers and kleptoparasites (scenario 2). (A) Kleptoparasitism rapidly becomes the more frequent strategy in scenario 2 populations for the parameters considered, with no differences across replicates. However, replicates differ considerably in the 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 $r_{max} = 0.01$.

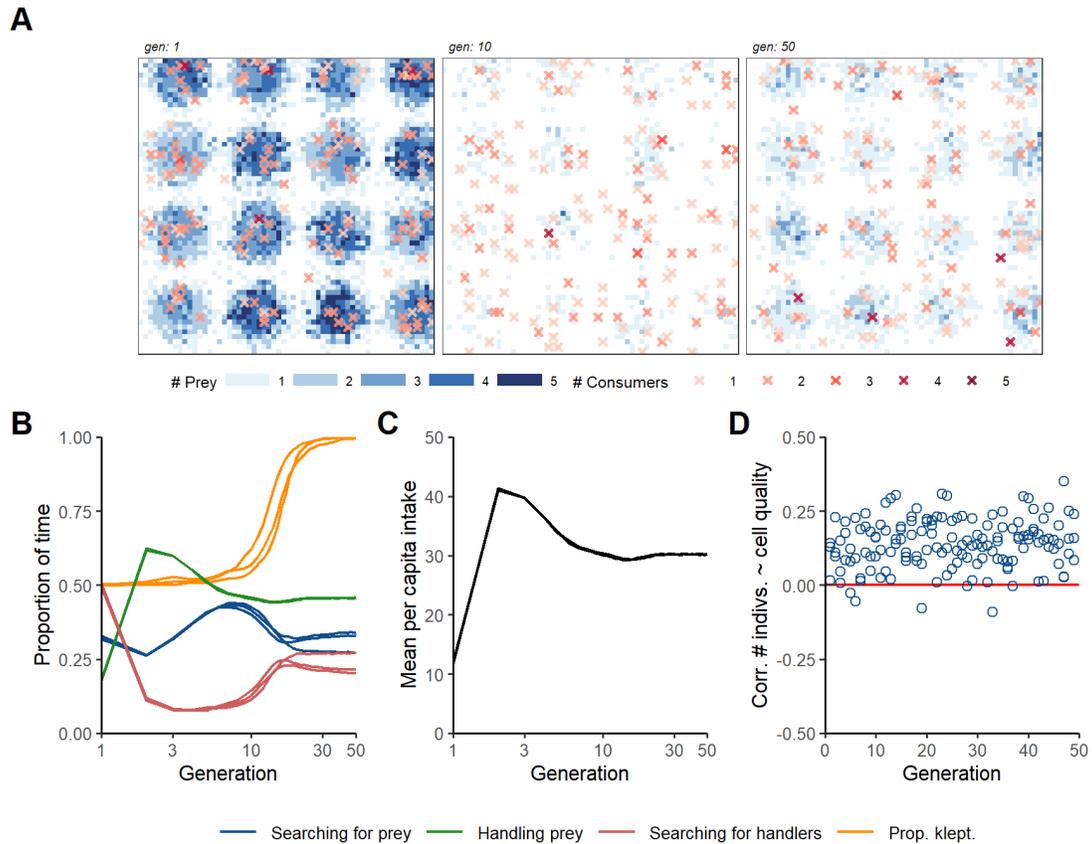


Figure 4: Eco-evolutionary implications of conditional foraging strategies (scenario 3). (A) The initially well-stocked resource landscape is rapidly depleted within 10 generations, yet within 50 generations, prey abundances recover on many cells, though not to the extent of scenario 2. The local density 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 $r_{max} = 0.01$.

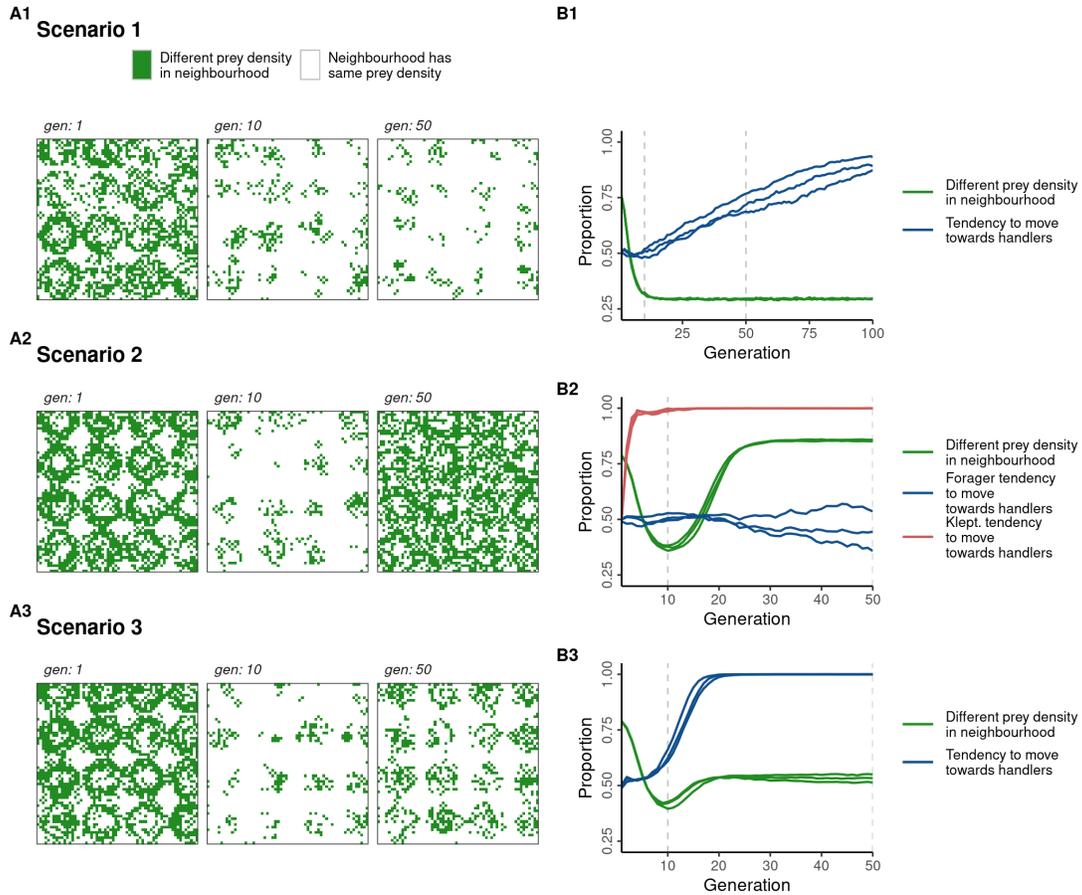


Figure 5: Uninformative prey densities and the evolution of alternative movement cues. (A1, A2, A3) On cells coloured green, local prey densities are informative for movement, as the central and neighbouring cells have different prey densities. While differences in local prey densities provide informative 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.

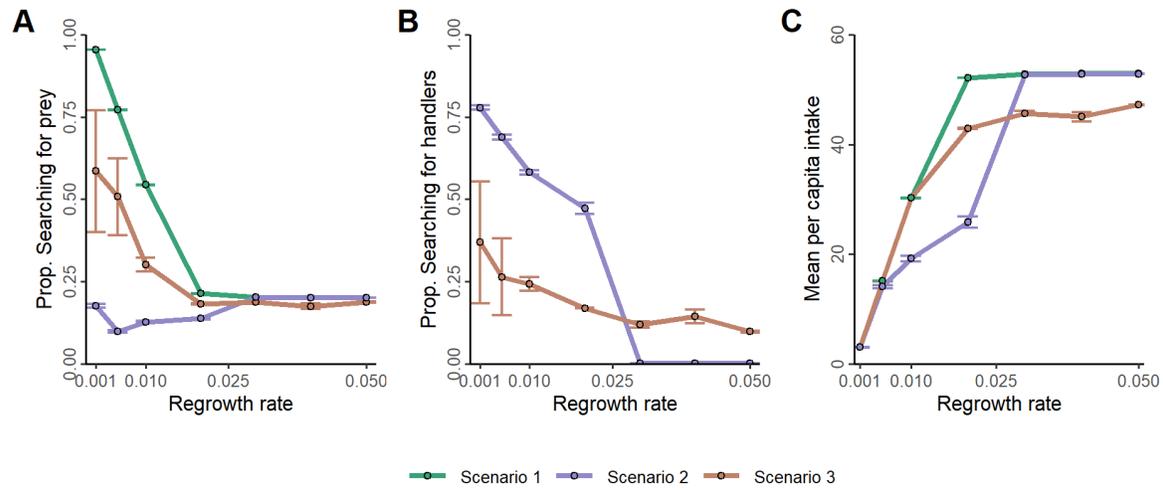


Figure 6: Landscape productivity strongly affects scenario outcomes. (A) The proportion of time spent searching for food decreases with increasing r_{max} in scenarios 1 and 3 but remains relatively stable within scenarios. This is partly due to a higher proportion of time spent handling at higher prey 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.