The joint evolution of movement and competition strategies

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Abstract

Competition typically takes place in a spatial context, but eco-evolutionary models rarely address the the joint evolution of movement and competition strategies. Here we investigate a spatially explicit producer-scrounger model where consumers can either forage on a heterogeneous resource landscape or steal prey from conspecifics (kleptoparasitism). We compare different scenarios for the interaction of movement and competition strategies. In all cases, movement strategies evolve rapidly and consistently across replicate simulations. At equilibrium, foragers do not match the prey input rate, contrary to 'ideal free' predictions. We show that this is related to the intrinsic difficulty of moving effectively on a depleted landscape with few reliable cues for movement. The evolved movement strategies of kleptoparasites differ markedly from those of foragers. Even within each competition strategy, polymorphisms emerge, corresponding to individual differences in movement rules. Our study emphasises 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., 2005*a*,*b*, 2007; Rutten et al., 2010*a*), while the avoidance of competitive interactions can also affect the distribution and behaviour of animals foraging in groups (Rutten et al., 2010*b*; 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, see Schlägel et al. 2020 for background). The fine-scale mechanisms and evolutionary consequences of competition are difficult to study in free-living animals at large spatial scales, yet their knowledge is central to evolutionary ecology, and to understanding the spatial distribution of animals. Furthermore, it is nearly impossible to study competition and its co-evolution with movement strategies at evolutionary time-scales in most animals, due to a lack of long-term data (Clutton-Brock and Sheldon, 2010) — making models necessary.

Competition has long been included in individual-to-population models of animal space-use, including the ideal free distribution (IFD, Fretwell and Lucas, 1970), information-sharing based local enhancement (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 that matches consumption (continuous input models, Tregenza, 1995; van der Meer and Ens, 1997). IFD models that do include resource depletion make simplifying assumptions about the importance of interference competition, considering it unimportant, or even modelling a

benefit of grouping (e.g. Amano et al., 2006). On the other hand, producer-scrounger models are primarily concerned with the benefits of choosing either a producer or scrounger strategy in relation with local conditions, such as the number of conspecifics (Vickery et al., 1991), or the order of arrival on a patch (Beauchamp, 2008). Models such as Beauchamp (2008) and Tania et al. (2012) simplify the mechanisms by which such decisions are made (see also Holmgren, 1995; Garay et al., 2020).

Competition occurs in a spatial context, and spatial structure is key to foraging (competition) decisions (Beauchamp, 2008). Consequently, the abundance of resources and their depletion, as well as the presence of potential competitors is of obvious importance to individuals' movement decisions (resource selection, see Manly et al., 2007). How animals are assumed to integrate the costs (and potential benefits) of competition into their movement decisions has important consequences for theoretical expectations of population distributions (van der Meer and Ens, 1997; Hamilton, 2002; Beauchamp, 2008). Yet models which include competitive interactions often assume simple movement strategies, such as omniscient animals with no travel costs (Vickery et al., 1991; Tregenza, 1995; van der Meer and Ens, 1997, *but see* Amano et al. 2006; Cressman and Křivan 2006). On the contrary, in addition to short-term, ecological effects, competition should also have evolutionary consequences for individual *movement strategies*, setting up feedback loops between competition and movement rules at ecological and evolutionary scales. Modelling competition and movement decisions jointly is thus a major challenge. A number of models take an entirely ecological view, assuming that individuals move or compete ideally, or according to some fixed strategies (Vickery et al., 1991; Holmgren, 1995; Tregenza, 1995; Amano et al., 2006, but see Hamilton 2002). Models that include evolutionary dynamics in the movement (de Jager et al., 2011, 2020) and foraging competition strategies (Beauchamp, 2008; Tania et al., 2012) are more plausible, but they too make arbitrary assumptions about the functional importance of environmental cues to individual decisions. Ideally, both movement and competition strategies should be the joint outcomes of selection, allowing for different competition strategies to be associated with different movement rules (see the approach in Getz et al., 2015).

Here, we present a first mechanistic model of intraspecific competition in a spatially explicit context, where competition is shaped by the *joint evolution* of foraging competition and move-

4

ment strategies. In our model, foraging individuals move on a spatially fine-grained resource landscape with discrete, depletable food items that need to be processed ('handled') before consumption. Foragers make movement decisions using an inherited (and evolvable) strategy which integrates local cues, such as the local resource and competitor densities. After each move, individuals choose between two foraging strategies: whether to search for a food item or steal from another individual; the mechanism underlying this foraging choice is also inherited. We take lifetime resource consumption as a proxy for fitness, such that more successful individuals produce more offspring, and thus are more successful in transmitting their movement and foraging strategies to future generations (subject to small mutations). We consider three scenarios: in the first, we examine only exploitation competition. In the second scenario, we introduce kleptoparasitic interference as an inherited strategy, fixed throughout an individual's lifetime. In the third scenario, we model kleptoparasitism as a behavioural strategy conditioned on local environmental and social cues.

Our model allows us to examine the evolution of individual movement strategies, population-level resource intake, and the spatial structure of the resource landscape. The model enables us to take ecological snapshots of consumer-resource dynamics (animal movement, resource depletion, and competition) proceeding at evolutionary time-scales. Studying these snapshots from all three scenarios allows us to check whether, when, and to what extent the spatial distribution of competitors resulting from the co-evolution of competition and movement strategies corresponds to standard IFD predictions. Using this model, we investigate three primary questions: *(1)* Under what conditions does kleptoparasitic interference evolve and persist in the population? How do the movement strategies of kleptoparasites differ from those of the foragers? *(2)* What are the eco-evolutionary implications of conditional kleptoparasitism? Do conditional strategies evolve under broader conditions than a polymorphism of fixed pure strategies, and do they lead to a different spatial distribution of competitors? *(3)* To what extent does the spatial distribution of competitors and resources in space correspond to an ideal free distribution?

2 The Model

We implement an individual-based evolutionary simulation model inspired by the behaviour of waders (*Charadrii*), which are extensively studied in the context of foraging competition, both empirically (e.g. Vahl et al., 2005*a,b*, 2007; Rutten et al., 2010*a,b*), and using IBMs (reviewed in Stillman and Goss-Custard, 2010). We simulated a population with a fixed size (N = 10,000), moving on a landscape of 512^2 grid cells (approx. 1 individual per 26 cells), with wrapped boundaries; individuals passing beyond the bounds at one end re-appear on the diametrically opposite side. The model has two time scales, first, an ecological time scale of T timesteps (by default, 400), during which individuals move, make foraging decisions, and handle prey items they find or steal. Individuals are immobile while handling food items, creating the conditions for kleptoparasitism (Brockmann and Barnard, 1979; Holmgren, 1995). On the second, evolutionary time scale of 1,000 generations, individuals reproduce and transmit their movement and foraging strategies to their offspring, whose number is proportional to individual intake at the behavioural time scale.

2.1 Resource Landscape

Prey Abundance   Resource landscape cells form 1,024 regularly spaced clusters of high-productivity areas ('resource peaks'; see Fig. 1C; panel *gen: 1*, showing a subset of 60^2 cells); each peak is approx. 16 cells away from neighbouring peaks. Since our model was conceived to represent foraging waders, we considered our discrete resources to represent mussels, a common prey of many waders, whose abundances are largely driven by external gradients; we refer to these resources as 'prey items'. Each cell has a constant probability of generating a new prey item per timestep, the cell-specific growth rate r. r declines from the centre of each peak (called r_{max}) to its periphery (see Fig. 1C), such that the centre of each peak generates a prey item five times more frequently than the cells at the edges. At r_{max} = 0.01, the most productive cells (at the centres of a cluster) are likely to generate one item per 100 timesteps (four items / generation, for T = 400), while the least productive cells (at cluster peripheries) are likely to generate one item every 500 timesteps (only about one item per generation, for T = 400). All landscape cells have a uniform carrying capacity K of 5 prey items, and while a cell

6

128 is at carrying capacity its *r* is 0.

Prey Acquisition by Foragers Foragers can perceive a cue indicating the number of prey
130 items P in a cell, but have a probability q of failing to detect individual prey items, and a
131 probability q^P of not detecting any of P prey items. Foragers are thus successful in finding
132 a prey item with a probability $1 - q^P$. Individuals on a cell forage in a randomised sequence,
133 and the probability of finding a prey item $(1 - q^P)$ is updated as individuals find prey, reducing
134 P. Foragers that find a prey item in timestep t begin handling it, and become 'handlers' from
135 the end of the timestep, i.e., for the movement and foraging decisions of other individuals.
136 Foragers that do not find a prey item are considered idle, and are counted as 'non-handlers'.

2.2 Movement and Competition Strategies

Movement Strategies We model movement as a fine-scale process comprised of small, dis-
139 crete steps of fixed size. These steps are the outcome of short-term individual movement deci-
140 sions, which are made using evolved movement strategies. Movement decisions are modelled
141 as the individual selection of a destination cell, after assessing potential destinations based on
142 available cues (similar to step selection or resource selection Fortin et al., 2005; Manly et al.,
143 2007), an approach used previously by Getz et al. (2015, 2016) and White et al. (2018). At
144 the end of each timestep t, individuals scan the nine cells of their Moore neighbourhood for
145 three environmental cues, *(1)* an indication of the number of discrete prey items P, *(2)* the
146 number of individuals handling prey H ('handlers'), and *(3)* the number of individuals not
147 handling prey N ('non-handlers'). Individuals assign a 'suitability score' S to each cell as
148 $S = s_P P + s_H H + s_N N$. At the start of timestep $t + 1$, each individual moves to the cell to
149 which it assigned the highest suitability. The weighing factors for each cue, s_P, s_H, and s_N, are
150 genetically encoded and transmitted from parents to their offspring. All individuals move si-
151 multaneously, and then implement their foraging or kleptoparasitic behaviour to acquire prey.

Scenario 1: Exploitative Competition The first scenario simulates only exploitative compe-
153 tition; individuals (called 'foragers') move on the landscape and probabilistically find, handle,
154 and consume prey items. A forager can be either in a 'searching' state or in a 'handling' state,

7

as individuals must handle each prey for a fixed handling time T_H (default = 5 timesteps), between finding and consuming it (see Ruxton and Moody, 1997; Spencer and Broom, 2018). The handling time dynamic is well known from many systems; for instance, it could be the time required for an oystercatcher to break through a mussel shell, or the time between catching and subduing prey for raptors, with the handling action obvious to nearby individuals, and the prey not fully under the control of the finder (Brockmann and Barnard, 1979). Handlers are assumed to be fully absorbed in their processing of prey, and do not make any movements until they have fully handled and consumed their prey. In scenario 1, the only evolvable properties are the cue weighing factors which determine cell suitability scores (s_P, s_H and s_N).

Scenario 2: Fixed Interference Competition The second scenario builds on Scenario 1, but there are two fixed competition strategies that are transmitted from parents to offspring: in addition to foragers there is a second category of individuals called 'kleptoparasites'. Kleptoparasites cannot extract prey items directly from the resource landscape, but only steal from handlers (similar to Holmgren, 1995). Kleptoparasites are always successful in stealing from a handler; this may be thought of as the benefit of the element of surprise, a common observation among birds (Brockmann and Barnard, 1979; Spencer and Broom, 2018). However, if multiple kleptoparasites target the same handler, only one of them, randomly selected, is considered successful — thus kleptoparasites also compete exploitatively among themselves. Handlers that have been robbed subsequently 'flee', and are moved to a random cell within a Chebyshev distance of 5. Having acquired prey, a kleptoparasite converts into a handler, but need only handle prey for $T_H - t_h$ timesteps, where t_h is the time that the prey has already been handled by its previous owner; thus kleptoparasites save time on handling compared to foragers. Unsuccessful kleptoparasites are considered idle, and are also counted as non-handlers. Handlers that finish processing their prey in timestep t return to the non-handler state and are assessed as such by other individuals when determining their movements.

Scenario 3: Conditional Interference Competition In scenario 3, each individual can either act as a forager, searching for food, or as a kleptoparasite, depending on its local circumstances. Individuals process the cell-specific environmental cues P, H, and N to determine

their location in the next timestep (based on their inherited movement strategy). Additionally, individuals process the environmental cues to determine their strategy in the next timestep as

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

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

2.3 Reproduction and Inheritance

For simplicity, we model a population of fixed size (N = 10,000 individuals) with discrete, non-overlapping generations. Individuals are haploid and reproduction is asexual. Each individual has 7 gene loci that encode the (numeric) decision making weights; only the weights controlling individual movement (s_P, s_H, s_N) are active in scenarios 1 and 2. In scenario 3, the weights for foraging decisions (w_P, w_H, w_N, w_0) are also active, and are transmitted from parent individuals to offspring.

The expected number of offspring per individual is proportional to the individual's total lifetime intake of resources, and hence resource intake is used as a proxy for fitness (Hofbauer and Sigmund, 2003). This is implemented as a weighted lottery (with weights proportional to lifetime resource intake) that selects a parent for each offspring in the subsequent generation (prior implementation in Tania et al., 2012; Netz et al., 2020). Across scenarios, the movement decision-making weights are subject to independent random mutations with a probability of 0.001. The mutational step size (either positive or negative) is drawn from a Cauchy distribution with a scale of 0.01 centred on zero. This allows for a small number of very large mutations while the majority of mutations are small. In scenarios 1 and 2, the foraging-decision weights are not relevant. However, in scenario 2 we allow a forager to mutate into a kleptoparasite (or *vice versa*) with a probability of 0.001. In scenario 3, the foraging weights mutate in the same way as the movement weights, described above. We initialised each offspring at a random location on the landscape; this leads individuals to potentially contend with conditions very

9

different from those of their parent.

2.4 Simulation Output and Analysis

We ran all three scenarios at a default r_{max} of 0.01, which we present in the RESULTS, and also across a range of r_{max} values between 0.001 and 0.05 (see Supplementary Material Figs. 1.1 – 1.3).

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

Ecological Snapshots of Resources and Individuals   To visualise the effect of different foraging strategies on the resource landscape, we exported snapshots of the entire simulation landscape at the mid-point of each generation ($t = 200$). This snapshot contained data on *(1)* the number of prey items, *(2)* the number of handling individuals, and the number of individuals using either a *(3)* searching forager strategy or *(4)* kleptoparasitic strategy, on each grid cell. We used only a subset of the total landscape (60^2 of 512^2 cells) for further analyses to speed up computation. To determine the availability of movement cues, we calculated the cell-specific item gradient for each landscape snapshot, as the difference in item counts between each cell and its neighbouring cells. We then calculated, for each generation, the proportion of grid cells from which it was possible to sense differences in prey items, i.e., a neighbouring cell with either more or fewer items.

Testing the Input Matching Rule   A basic prediction of the IFD and the related matching rule is that the number of individuals on occupied patches should be proportional to patch productivity (Fretwell and Lucas, 1970; Parker, 1978; Houston, 2008). Patch productivity is

10

challenging to measure in real world systems, but is among our model's building blocks, allowing us to examine the correlation between the number of individuals (excluding handlers) and the cell-specific productivity r.

Visualising Decision-Making Weights   To understand the evolutionary consequences of our simulation on the individual decision making weights, we exported the weights of each individual in every generation of the simulation. To depict as much as possible of the typical variation of weights, which could take arbitrarily large values and therefore vary by orders of magnitude, we multiplied each weight by 20 and applied a hyperbolic tangent transform. This scaled the weights between -1 and +1, and we plotted these weights to understand individual variation in movement rules, as well as calculating how preference and avoidance of cues evolved across scenarios.

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

3 Results

3.1 Scenario 1: No Kleptoparasitism

In scenario 1, foragers deplete prey items faster than they can be replenished, drastically reducing the overall number of prey items within only a few generations (Fig. 1A). The population activity budget is split between searching and handling (Fig. 1B). The proportion of time spent handling, and the mean per capita intake are both initially low, but peak within ten generations (Fig. 1C), as individuals can easily acquire prey items from the fully stocked landscape in the first few generations. With dwindling prey items, fewer searching foragers find a prey item, and handling as a share of the activity budget declines to a stable $\sim 45\%$ within 50 generations, and mean per capita intake also stabilises (Fig. 1C). In early generations, foragers tend to accumulate on resource peaks (Fig. 1A), but the correlation between the number of foragers and cell productivity is only slightly positive (Fig. 1D).

3.2 Scenario 2: Co-existence of Foragers and Kleptoparasites

In scenario 2, with both foraging and kleptoparasitism allowed, the spatial distribution of consumers and prey items at equilibrium are very different from scenario 1. Consumers gather on resource peaks in early generations, grazing them down until very few prey items remain on the landscape and consumers are dispersed; however, within 50 generations the resource landscape recovers with prey abundances higher than in the earliest generations (Fig. 2A). This is because of the presence of kleptoparasites (Fig. 2B), which reduces the prey intake rate of the population, and accordingly leads to a higher prey abundance. In early generations, kleptoparasites are rare, and the activity budget, the mean per capita intake, and the distribution of consumers over the landscape, are similar to scenario 1. As resources are depleted and it becomes more likely for a kleptoparasite to encounter a handler than for a searching forager to find a prey item, kleptoparasitism becomes the majority strategy (a stable ∼70% of the population; see Fig. 2B), and searching for handlers to rob becomes the commonest activity. However, the high frequency of this activity, and the low frequency of handling, indicate that many kleptoparasites are actually unsuccessful at finding handlers. With few searching foragers, few prey items are extracted from the landscape, which recovers beyond its initial prey abundance within 50 generations (Fig. 2A). Despite the strong spatial structure of the resource landscape within 50 generations, the correlation between consumers (of both strategies) and cell productivity remains weak or zero across generations (Fig. 2D).

The increase of kleptoparasitism from a negligible fraction to the majority strategy (Fig. 3A) is associated with an evolutionary divergence of the movement strategies in foragers and kleptoparasites. While foragers and kleptoparasites respond to prey density and non-handler density in a similar way (see Supplementary Material Fig. 2.2), preferring higher prey density while avoiding high non-handler density, the two types of competition strategy differ substantially in their response to handlers (Fig. 3B, 3C). Kleptoparasites very rapidly (within 3 generations) evolve a strong preference for moving towards handlers, which are their primary resource (Fig. 3B). In the absence of kleptoparasites, foragers would evolve a preference for moving towards handlers (see Supplementary Material Fig. 2.1), but, with kleptoparasites common in the population, searching foragers avoid and prefer handlers in about equal pro-

12

portions (Fig. 3C). While all kleptoparasites evolve to prefer moving towards handlers, the strength of the attraction to handlers shows multiple, distinct values or 'morphs', which are remarkably persistent across generations (Fig. 3B). In replicate 3, for example, the commonest movement strategy exhibits only a weak attraction to handlers, but this strategy coexists with various strategies that all show a much stronger attraction to handlers (Fig. 3B). The movement strategies of foragers show an even higher degree of co-existing polymorphisms (Fig. 3C), with no dominant movement strategies; some foragers strongly prefer handlers, others strongly avoid them, and yet others are neutral to handler presence.

3.3 Scenario 3: Condition-dependent Kleptoparasitism

In scenario 3, with conditional competition strategies based on local environmental cues, the distribution of individuals and prey items is substantially different from the two previous scenarios (Fig. 4A). Initially, as in scenario 1, depletion of prey items results in the degradation of the resource landscape within ten generations. By generation 50, the resource landscape recovers some of the spatial structure of the first generation, but prey-item abundances do not reach the level of the similar recovery seen in scenario 2. This too is because, by generation 30, all individuals have a propensity to steal from handlers, i.e., when handlers are present in the vicinity, all consumers choose to target them for prey items, rather than forage for prey themselves ("opportunistic kleptoparasitism"; Fig. 4B; *orange line*). However, unlike scenario 2, individuals search for prey more often and steal less (at or below 25%; compare Fig. 2B), leading to the depletion of the resource landscape. Consequently, mean per capita intake stabilises (after an initial spike, as in scenarios 1 and 2) within ten generations to a level similar to scenario 1 (Fig. 4C). The reduced depletion following the evolution and persistence of conditional kleptoparasitism leads to a resource landscape recovery intermediate between scenarios 1 and 2 within 50 generations (Fig. 4A). Using conditional foraging strategies, individuals are able to better choose between the payoff of more prey items, more handling foragers from which to steal, and the risk of falling victim to kleptoparasites. Thus, while not as strong as predicted by IFD theory, the correlations between consumer abundance and cell productivity are weakly positive (Fig. 4D).

13

3.4 Movement Rules on Depleted Landscapes

Orienting movement towards resources (Nathan et al., 2008, ; *where to move*) can be a challenge when local prey *density* may provide very limited information about local *productivity*. In our model, parts of the resource landscape may be 'clueless regions' (Perkins, 1992), where foragers cannot make directed movement decisions based on prey-item abundances alone, as all neighbouring items abundances are identical (see white areas in Fig. 5A; A1: scenario 1, A2: scenario 2, A3: scenario 3). At the beginning of all three scenarios, about 75% of landscape cells have a different number of prey-items from the cells around them; these are primarily the cells with an intermediate r, which have more prey than the lowest productivity cells at the peripheries of resource peaks, but fewer prey than the peaks themselves. This proportion rapidly declines to a much lower value within 10 generations in all three scenarios.

The scenarios differ, however, regarding the 'cluelessness' of the landscape on evolutionary timescales (Fig. 5B). In scenario 1, the proportion of cells with a different number of items in the neighbourhood is initially very high (Fig. 5A1). This proportion rapidly declines to ∼25% within 10 generations, as foragers deplete most cells on the landscape of prey items, and most of the landscape is a clueless region. In this context, foragers evolve to move towards handlers — with > 75% of individuals showing a preference for handlers within 100 generations (Fig. 5B1 – blue line). Forager preference for handlers (not a direct resource in scenario 1), may be explained as the sensing of a long-term cue of local productivity. Since handlers are immobilised on the cell where they find a prey item, handler density is an indirect indicator of cell r, and due to spatial patterning, also of the r of bordering cells.

Scenario 2 landscapes follow a similar pattern to scenario 1 in the first 10 generations (Fig. 5A2). However, within 50 generations, the reduction in prey item extraction allows most cells to regenerate prey items, with differences among cells according to their r (see also Fig. 2A). Thus > 75% of cells have a different number of items from their neighbouring cells (Fig. 5A2 – panel *gen: 50*, 5B2). However, since most consumers are kleptoparasites which seek out handlers, this regenerated resource landscape provides only indirect movement cues, as searching foragers are more likely to convert to handlers on cells with more prey items. Unlike scenario 1, the rapid increase in handler preference is driven by kleptoparasites becoming the majority

14

³⁴⁶ strategy (see subsection above). Scenario 3 is similar to scenario 2, except that only about half

³⁴⁷ of all cells have a different number of prey items from neighbouring cells (Fig. 5A3, 5B3). Here,

³⁴⁸ the rapid evolution of a handler preference in movement decisions cannot be assigned a clear

³⁴⁹ cause, since handlers are both a potential direct resource as well as indirect cues to the location

³⁵⁰ of productive cells.

3.5 Effect of Landscape Productivity

³⁵² The prey-item regrowth rate of central cells of resource peaks (r_{max}) is a proxy of the productiv-

³⁵³ ity of the resource landscape overall. Not unexpectedly, the value of r_{max} has a marked effect

³⁵⁴ on evolved population activity budgets, mean per capita intake, and even evolved strategies.

³⁵⁵ The frequency of foraging reduces with r_{max} in scenarios 1 and 3, as more frequent acquisi-

³⁵⁶ tion of prey items (as regrowth keeps pace with depletion), results in a greater frequency of

³⁵⁷ handling rather than foraging. In scenario 2 however, the frequency of handling is relatively

³⁵⁸ unaffected by increasing r_{max} (Fig. 6A).

³⁵⁹ The frequency of kleptoparasitism differs between scenarios 2 and 3 (Fig. 6B). In scenario

³⁶⁰ 2, kleptoparasitism forms $> 75\%$ of all activities at low r_{max}, and is much more common than

³⁶¹ in scenario 3 populations at the same regrowth rate. However, at relatively high r_{max} (0.03),

³⁶² the fixed kleptoparasitic strategy goes extinct. This is because at high r_{max}, the probability of a

³⁶³ forager finding prey is much greater than the probability of a kleptoparasite finding a handler,

³⁶⁴ in both initial (< 10) and later generations (> 50). Consequently, kleptoparasites are respon-

³⁶⁵ sible for only a very small fraction of the total population intake, have relatively much lower

³⁶⁶ fitness, and do not proliferate. Thus at high r_{max}, a scenario 2 population is nearly identical

³⁶⁷ to a scenario 1 population; while some kleptoparasites may be seen in later generations, these

³⁶⁸ are more likely due to mutation in the forager strategy, rather than longstanding lineages of

³⁶⁹ kleptoparasites.

³⁷⁰ In scenario 3, kleptoparasitism persists at low frequencies even at the highest regrowth rates

³⁷¹ (Fig. 6B); thus some foragers lose time in extracting items which are then stolen from them.

³⁷² Consequently, while populations in all three scenarios achieve very similar mean per capita

³⁷³ intakes at low r_{max}, at intermediate regrowth rates (0.01, 0.02), conditionally kleptoparasitic

³⁷⁴ populations achieve a higher mean per capita intake than populations using fixed strategies.

15

Only at high r_{max}, when fixed strategy populations effectively convert to purely forager populations, do they achieve a higher intake than conditional strategy populations (Fig. 6C).

4 Discussion

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

Existing models of competition and movement impose fixed movement rules on individuals to mimic either ideal or non-ideal individuals (Vickery et al., 1991; Cressman and Křivan, 2006; Amano et al., 2006; Beauchamp, 2008; Stillman and Goss-Custard, 2010; White et al., 2018). When individual competitive strategies are included, models consider them to represent dif-

16

ferences in competitive ability (e.g. Parker and Sutherland, 1986; Holmgren, 1995; Hamilton, 2002), or as a probabilistic switch between producing and scrounging (Beauchamp, 2008). In contrast, our model allows individuals' movement (and competition) decisions to be adaptive responses to local environmental cues. Similar to Getz et al. (2015, 2016) and White et al. (2018), our individuals choose from among the available movement options after weighing the local environmental cues; this is analogous to the movement ecology concepts of resource or step selection functions (Fortin et al., 2005; Manly et al., 2007; White et al., 2018). The local environmental cues in our model are constantly changing, as we model discrete, depletable prey items on the resource landscape, contrasting with many IFD models (Tregenza, 1995; Amano et al., 2006). This allows for a more plausible, fine-scale consideration of exploitation competition, which is often neglected, and allows the cues sensed by individuals to strongly structure the distribution of competitors (see below).

Adaptive responses must have an explicit evolutionary context, and consider multiple generations of the population. We follow Beauchamp (2008) and Getz et al. (2015) in allowing the decision making weights for movement, and variation thereof, to be the outcomes of natural selection. However, instead of using 'evolutionary algorithms' (Beauchamp, 2008; Getz et al., 2015, 2016) to 'optimise' individual movement rules, we consider a more plausible evolutionary process: Instead of allowing the fittest 50% of the population to replicate, the number of offspring are proportional to individual fitness (Hofbauer and Sigmund, 2003). The weight loci are subject to mutations independently, rather than subjecting all loci of an individual to simultaneous mutation. Finally, we avoided the unrealistic assumption of 'simulated annealing', which adapts the mutation rate or the mutational step sizes to the rate of evolutionary change. Instead we drew mutation sizes from a Cauchy distribution, so that most mutations are very small, but large-effect mutations do occur throughout the simulation. Similarly, rather than determining foraging style (searching or stealing) probabilistically or ideally (Vickery et al., 1991; Beauchamp, 2008; Tania et al., 2012), our individuals' foraging decisions are also shaped by selection (in scenarios 2 and 3).

In our scenario 1, depletion of discrete prey can leave many areas empty of prey items: in such areas, movement informed by a resource gradient is impossible, and individuals move randomly ('clueless regions': Perkins, 1992). Our work suggests that this lack of movement

17

cues and the resulting random movement might be among the mechanisms by which unsuitable 'matrix' habitats modify animal movement on heterogeneous landscapes (Kuefler et al., 2010).

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

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

IFD models predict that individual movement should result in 'input matching': consumer distributions should track the profitability of resource patches (Fretwell and Lucas, 1970; Parker, 1978), and dominant competitive types (including kleptoparasites) should monopolise the best patches (Parker and Sutherland, 1986; Holmgren, 1995; Hamilton, 2002, but see Korona 1989). In our scenarios 2 and 3, individuals seeking to steal prey from competitors unsurprisingly and rapidly evolve to track handlers (a direct resource), while avoiding non-handlers (potential competitors). However, these evolved rules do not lead kleptoparasites to occupy the best cells as predicted (Parker and Sutherland, 1986; Holmgren, 1995; Hamilton, 2002). Across our

scenarios (including sc. 1), individual density is only weakly correlated with cell productivity.

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

This shows the pitfalls of simplistically linking current ecological conditions with evolved behavioural responses (and emergent distributions), and shows why understanding the evolutionary history of competitive interactions is key. In this vein, a hypothetical experiment would wrongly expect that foragers from resource-rich landscapes (sc. 2) better tolerate competitors due to less exploitation competition, while foragers from resource scarce landscapes (sc. 1) might be competitor-avoidant. Furthermore, ecological conditions *may not* be a reliable guide to the presence of individual variation, which is often expected as an outcome of enhanced competition. Indeed, scenario 2 shows significant within-strategy individual variation in movement weights, which might help reduce within-strategy exploitation competition, or help foragers better avoid kleptoparasites (Wolf and Weissing, 2012; Laskowski and Bell, 2013).

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

Foraging strategies in which animals specialise on a resource type are expected to be constrained by the availability of that resource; thus kleptoparasitism should be constrained by the density of targets (Spencer et al., 2017; Spencer and Broom, 2018). In our scenarios 2 and 3, we would expect to see more kleptoparasitism with increasing r_{max}, as prey and consequently, handlers, are more abundant. We find instead that kleptoparasitism declines with increasing

19

r_{max}, in line with Emlen (1966), who predicted that the commoner food type (prey) rather than the more efficiently exploited one (handlers) should be preferred.

This effect is especially stark in scenario 2, where kleptoparasites go extinct when prey are very common at high r_{max}. At stable population densities (due to external constraints such as nest-site availability), the persistence of fixed kleptoparasitism depends on their intake *relative to foragers*. Since intake is an outcome of movement rules, and population movement rules are not well adapted to their environment in early generations, foragers obtain, as a clade, more intake than kleptoparasites. Modelling discrete prey items and individuals in a spatial context, then, leads to the finding that obligate kleptoparasitism is only a viable strategy when the probability of encountering prey is much less than the probability of encountering handlers. While few taxa show such a marked foraging specialisation within populations, this might explain why kleptoparasitism is frequent among seabirds, whose communal roosts are much more easily targeted than unpredictable shoals of fish out at sea (Brockmann and Barnard, 1979).

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

5 Data and Code Availability

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

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

Code for data analysis and preparing the figures in the main text and Supplementary Material is available on Github: github.com/pratikunterwegs/kleptomove-ms and archived on Zen-

6 Acknowledgments

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7 Figure legends

A
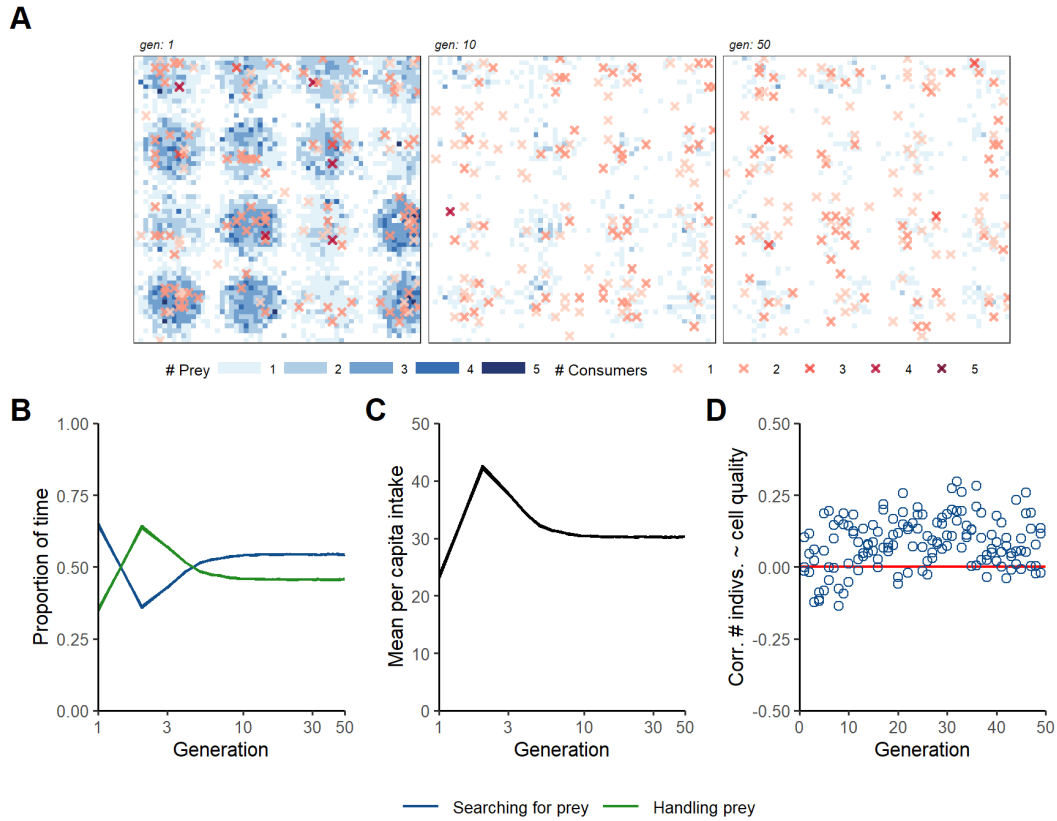
Figure 1: Eco-evolutionary implications of pure exploitation competition (scenario 1). **(A)** When a population is comprised solely of foragers seeking prey on a resource landscape, the initially well-stocked resource landscape is swiftly depleted within 10 generations (out of 1,000 simulated). This 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.
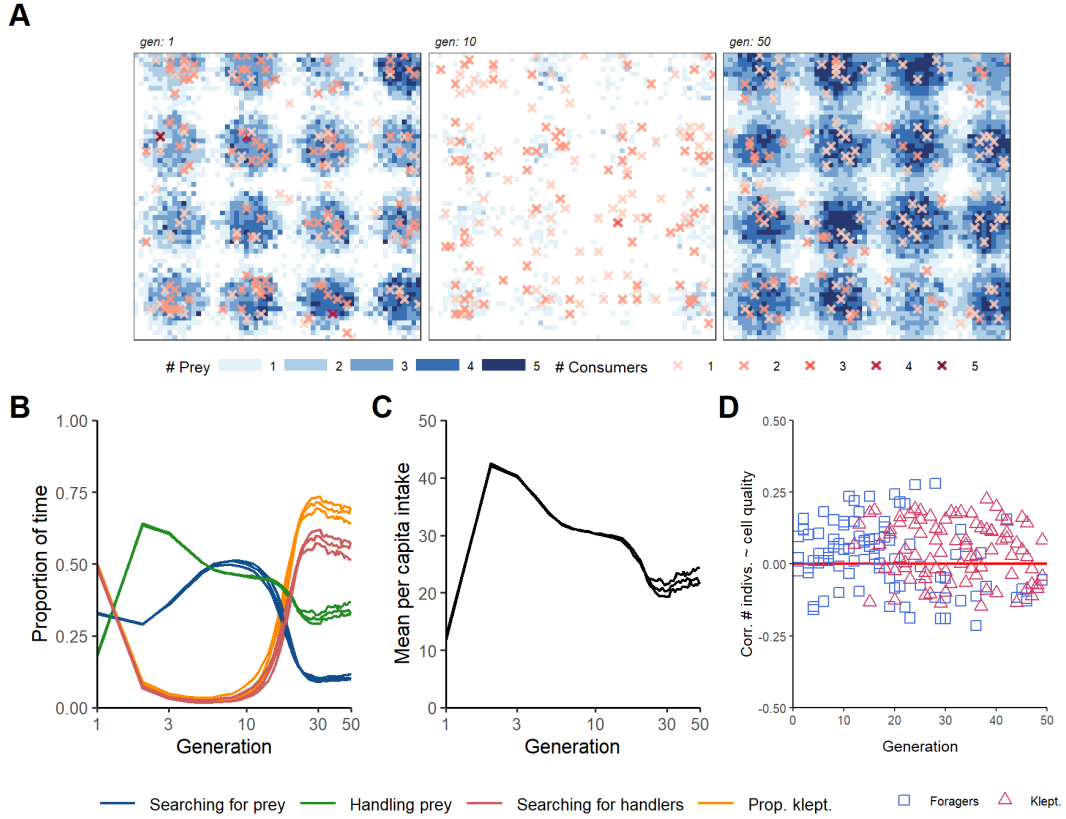
Figure 2: Eco-evolutionary implications of the coexistence of foragers and kleptoparasites (scenario 2). In populations with both foragers and kleptoparasites, **(A)** the initially well-stocked resource landscape is drastically depleted by generation 10; however, prey densities recover strongly by generation 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 $r_{max} = 0.01$.

27
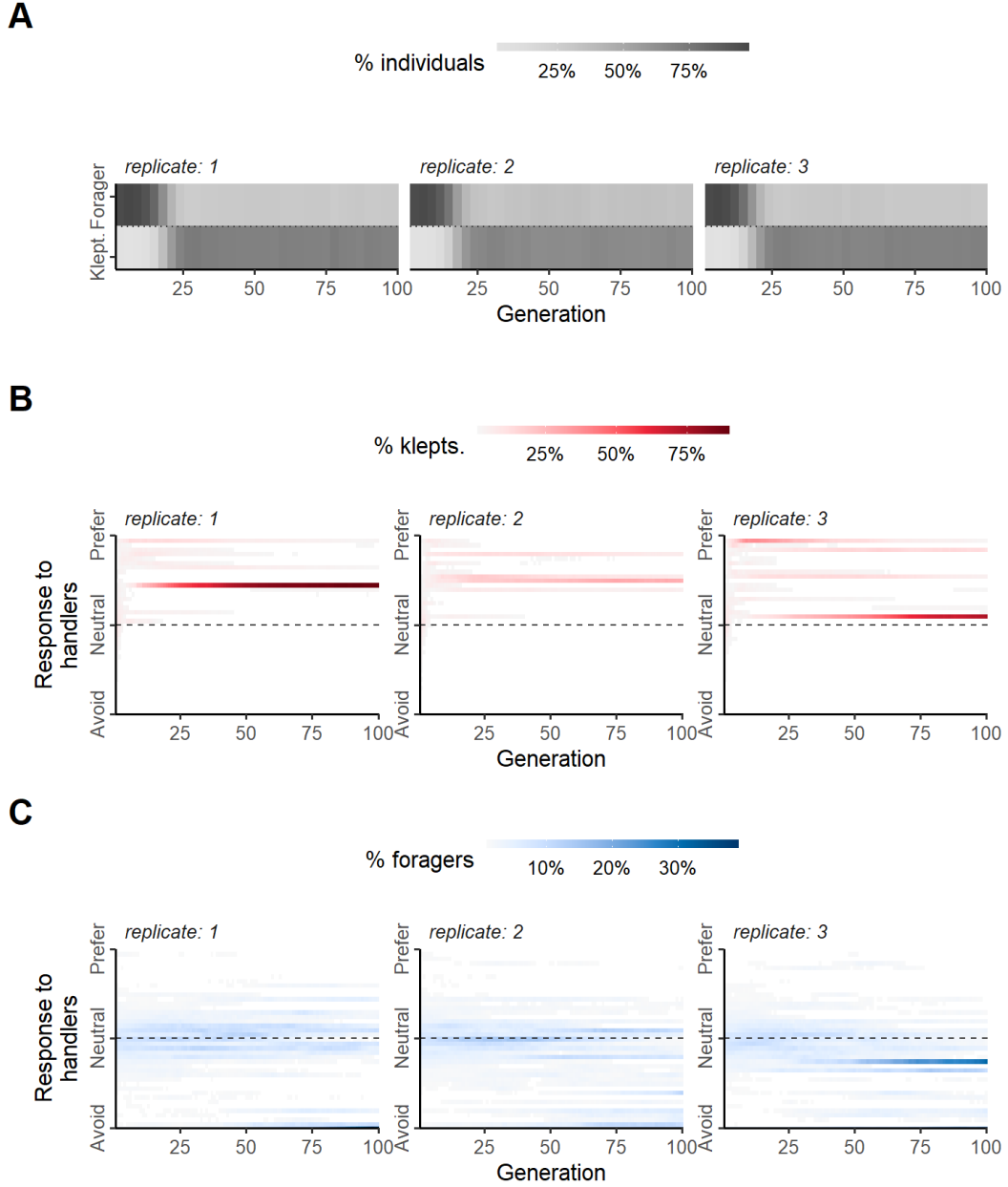
Figure 3: Divergence of movement strategies between foragers and kleptoparasites (scenario 2). **(A)** Kleptoparasitism rapidly becomes the more frequent strategy in scenario 2 populations for the parameters considered, with no differences across replicates. However, replicates differ considerably in 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 $r_{max} = 0.01$.
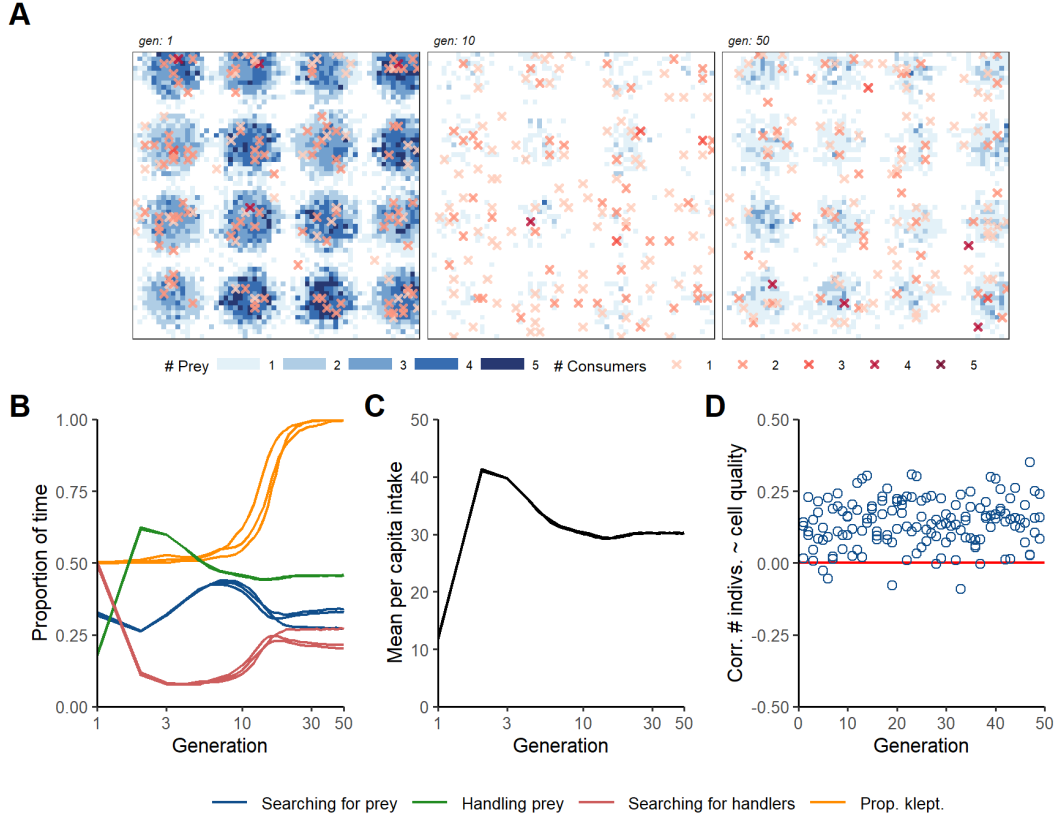
Figure 4: Eco-evolutionary implications of conditional foraging strategies (scenario 3). (A)
The initially well-stocked resource landscape is rapidly depleted within 10 generations, yet
within 50 generations, prey abundances recover on many cells, though not to the extent of
scenario 2. The local density 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 $r_{max} = 0.01$.
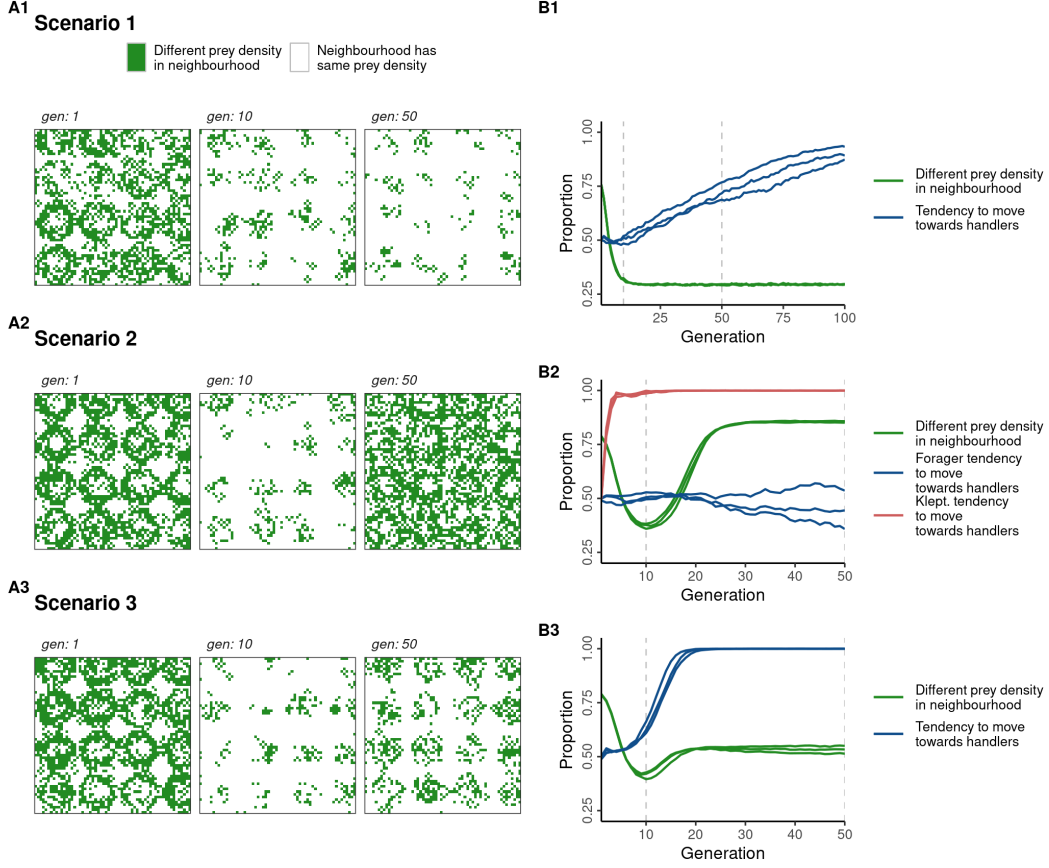
Figure 5: Uninformative prey densities and the evolution of alternative movement cues.
(A1, A2, A3) On cells coloured green, local prey densities are informative for movement, as the central and neighbouring cells have different prey densities. While differences in local prey densities provide informative 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.
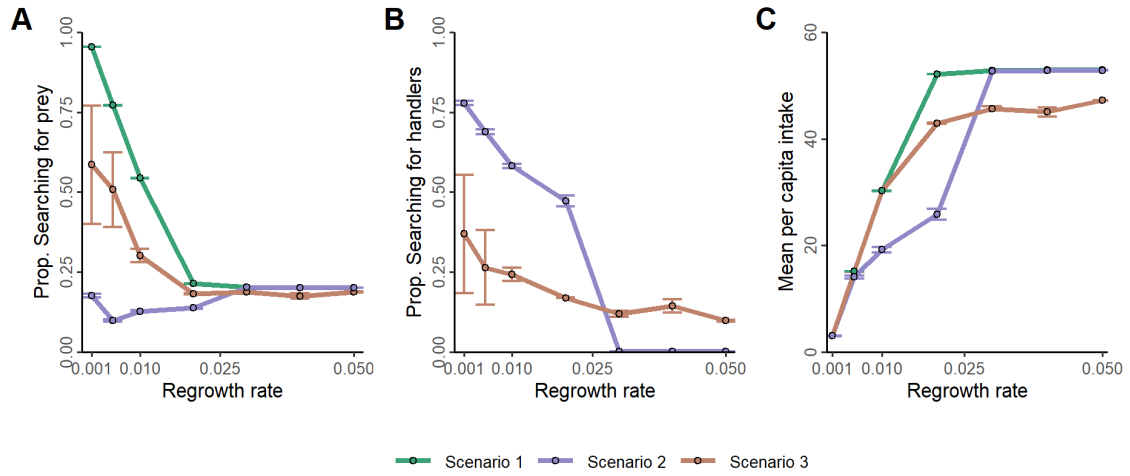
Figure 6: Landscape productivity strongly affects scenario outcomes. (A) The proportion of time spent searching for food decreases with increasing r_{max} in scenarios 1 and 3 but remains relatively stable within scenarios. This is partly due to a higher proportion of time spent handling at higher prey 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.