The joint evolution of movement and competition strategies

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1 Abstract

To be added.

2 Introduction

Intraspecific competition is a constant feature of animal ecology, and an important driver of population dynamics and the spatial distribution of organisms (Krebs and Davies, 1978). Competition 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, Rutten et al., 2010b, Vahl et al., 2005a, 2007, 2005b). The avoidance of competitive interactions can also affect the distribution and behaviour of animals foraging in groups (Bijleveld et al., 2012, Rutten et al., 2010a). At larger scales, competition among different behavioural types in a species can strongly influence species distributions and animal movement decisions (e.g. Duckworth and Badyaev, 2007, Schlägel et al., 2020). Competition is difficult to study in free living animals, yet knowledge of the fine-scale mechanisms and evolutionary consequences of competition is central to basic evolutionary ecology. For instance, it is surmised that interference is more important than exploitation under natural conditions (see Case and Gilpin, 1974), but it is difficult to establish whether interference, and especially kleptoparasitism, represents a foraging specialisation shown by part of the population, or whether it is an opportunistic strategy conditioned on local cues, that can be used by all individuals. Furthermore, it is nearly impossible to study the causes and consequences of competition — such as its coevolution with movement strategies, or the effect on resource landscapes — at evolutionary time-scales in most animals, due to a lack of long-term data (Clutton-Brock and Sheldon, 2010).

Our poor understanding of competition poses a problem, since it is key to models such as the Ideal Free

Distribution (IFD), which is a cornerstone of evolutionary ecology (Fretwell and Lucas, 1970). The IFD posits that individuals should distribute on a heterogeneous resource landscape such that their intake rate is identical at all occupied locations, after accounting for competition. As suggested by the name, the IFD assumes that competing individuals are omniscient ("ideal"), and move instantaneously, without costs, to any location on the landscape ("free"). While these evidently unrealistic assumptions have their own ramifications (Amano et al., 2006, Cressman and Křivan, 2006, Matsumura et al., 2010, Tregenza, 1995), IFD models also often implement competition in highly simplified ways that neglect the underlying mechanisms. For instance, IFD models ignore resource depletion, and model resource intake at a continuous rate rather than as the finding and processing of discrete items, implying an unrealistic, equal sharing of resources among individuals (Cressman and Křivan, 2006, Fretwell and Lucas, 1970, van der Meer and Ens, 1997). Furthermore, IFD models assume that interference is an almost inevitable part of the foraging process, i.e., that all individuals always compete with each other, regardless of their condition (for instance, handling prey items; reviewed in Tregenza, 1995, van der Meer and Ens, 1997, see also Cressman and Křivan 2006, Garay et al. 2020). On the contrary, the abundance of resources and their depletion is of obvious importance to individuals' movement decisions. Similarly, interference competition is a complex individual behaviour which is closely related to movement decisions, and even minor differences in its treatment in models can have important consequences for theoretical expectations (van der Meer and Ens, 1997). A final issue is that competition (both exploitation and interference) should have evolutionary consequences for individual movement, as it does for so many other aspects of behaviour (Baldauf et al., 2014) — and vice versa, setting up feedback loops between ecology and evolution. Contemporary models that integrate movement and competition rarely span more than a single generation; the (ideal, fitness maximising) movement rules that are assumed of foragers in these models are thus moot.

Here, we present the first mechanistic model of intraspecific competition in a spatially explicit context, where competition is shaped by the evolution of behavioural and movement strategies. This allows us to both focus more closely on the interplay of exploitation and interference competition, and to examine the feedback between movement and foraging behaviour at evolutionary scales. As foraging and movement decisions are taken by individuals, we study the joint evolution of both types of decision-making by means

of individual-based evolutionary simulation models (IBMs; see for a conceptual basis DeAngelis and Diaz, 2019, Huston et al., 1988), which are well suited to modelling the evolution of complex behaviours (Getz et al., 2015, 2016, Guttal and Couzin, 2010, Netz et al., 2020). We implement a spatially explicit IBM approach to competition and animal movement decisions, using one model with three scenarios of increasing complexity. 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 consider 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). In the first scenario, we examine how exploitation competition influences the evolution of individual movement rules, population-level resource intake, and the spatial structure of the resource landscape. In the second scenario, we introduce kleptoparasitic interference as an inherited strategy, fixed through an individual's life, and investigate how individual movement and foraging decisions coevolve. In the third scenario, we model kleptoparasitism more realistically, as a behavioural strategy conditioned on local environmental and social cues, and compare the population-level and landscape-scale outcomes between scenarios 2 and 3 to show the influence of modelling choices.

Using this model, we investigate three primary questions: *(1)* Do movement decisions, evolved in the context of exploitation competition, and based on localised cues of resource abundance and competitor presence, lead to an ideal free distribution? *(2)* Under what conditions does kleptoparasitic interference evolve and persist in a population? *(3)* Can conditional foraging strategies outperform fixed foraging strategies, and do either of them lead to ideal free distributions?

3 The Model

We implement an individual-based evolutionary simulation model with three scenarios of increasing complexity whose most basic components — the environment size and shape, its gridded structure and each cell's capacity to hold multiple individuals, as well as the discrete conception of time within and between generations — are inspired by Netz et al. (2020). We conceptualised the models around the behaviour of waders (*Charadrii*), which are extensively studied in the context of foraging competition, both empirically (e.g. Rutten et al., 2010*a*,*b*, Vahl et al., 2005*a*, 2007, 2005*b*), and using IBMs (reviewed in Stillman and Goss-Custard, 2010). We simulated a population with a fixed size moving on a landscape of 512^2 grid cells, with the landscape wrapped at the boundaries so that individuals passing beyond the bounds at one end re-appear on the diametrically opposite side. The model has two time scales, first, a behavioural time scale of T timesteps, during which individuals move, make foraging decisions, and handle prey items they find or steal. Individuals are modelled as being immobile while handling food items, creating the conditions for kleptoparasitism (Brockmann and Barnard, 1979). On the second, evolutionary time scale, individuals reproduce and pass on their movement and foraging strategies to their offspring, the number of which is proportional to their intake at the behavioural time scale. By default, we set T to 400, and simulated a population of 10,000 individuals over 1,000 generations.

3.1 Resource Landscape

Prey Abundance   We considered a resource landscape that is heterogeneous in its productivity of discrete resources, but with strong spatial clustering of grid cells of similar productivity (see Fig. 1C; panel *gen: 1*, showing a subset of 60^2 grid cells). We assigned each cell a constant probability of generating a new prey item per timestep, which we refer to as the cell-specific growth rate r. We modelled clustering by having the distribution of r across the grid take the form of 1,024 uniformly distributed resource peaks with r declining from the centre of each peak (called r_{max}) to its periphery (see Fig. 1C). Effectively, the cell at the centre of each cluster generates a prey item five times more frequently than the cells at the edges. We ran all three scenarios at a default r_{max} of 0.01, and also across a range of r_{max} values between 0.001 and 0.05. For an

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r_{max} = 0.01, the most productive cells (at the centres of a cluster) are likely to generate one item per 100 timesteps (or four times per generation, for T = 400), while the least productive cells (at cluster peripheries) are likely to generate one item every 500 timesteps (only about once per generation, for T = 400). Since our model was conceived to represent foraging waders, we considered our 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' henceforth. Cells in our landscape were modelled as having a uniform carrying capacity K of 5 prey items, and while a cell is at carrying capacity its r is 0.

Prey Acquisition by Foragers   Foragers can perceive a cue indicating the number of all prey items P in a cell, but do not know the exact locations of these prey. We model foragers as having a probability q of failing to detect a prey item, and a probability q^P of not detecting any of P prey items; foragers are thus successful in finding a prey item with a probability $1 - (q^P)$. As foraging events occur simultaneously, it is possible for more foragers to be considered successful in finding prey than there are discrete items in that cell. This simple case of exploitation competition is resolved by assigning P prey among some N successful searchers at random. Foragers that are assigned a prey item in timestep t begin handling it, and are considered to be handlers for the purposes of timestep $t + 1$ (i.e., movement and foraging decisions of other individuals). Foragers that are not assigned a prey item are considered idle during timestep t, and are counted as non-handlers for $t + 1$.

3.2   Competition and Movement Strategies

Scenario 1: Exploitative Competition   The first scenario simulates only exploitative competition; individuals move about on the landscape and probabilistically find and consume prey items. Between finding and consuming a prey item, individuals must 'handle' each prey for a fixed handling time T_H (set at 5 timesteps by default). 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). We refer to such individuals as 'handlers'

for convenience. 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.

Scenarios 2 and 3: Kleptoparasitic Interference Competition   The second scenario builds on Scenario 1, with the addition that individuals inherit a fixed strategy to either forage or to steal prey items from handlers. Agents that steal are termed kleptoparasites. 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). When the number of kleptoparasites exceeds handlers, handlers are assigned among kleptoparasites at random. Individuals that have been stolen from subsequently 'flee' and are moved to a random cell within a Chebyshev distance of 5, and do not make any further foraging decisions there. 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 a forager. Unsuccessful kleptoparasites are considered idle, and are also counted as non-handlers for timestep $t + 1$. 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 movements for $t + 1$. Scenario 3 is similar to scenario 2, except that individuals process local environmental cues and pick either the forager or kleptoparasite strategy to use in the next timestep. Apart from the frequency of the choice, the actual foraging dynamics are the same as described in the fixed-strategy case.

Movement Strategies   Movement decisions are modelled as in (Netz et al., 2020): at the end of each timestep t, individuals scan the nine cells of its Moore neighbourhood for three environmental cues, *(1)* the number of discrete prey items P, *(2)* the number of individuals handling prey H (referred to as 'handlers'), and *(3)* the number of individuals not handling prey Nh (referred to as 'non-handlers'). Based on these cues, a 'suitability score' S is assigned to each cell as $S = s_P P + s_H H + s_{Nh} Nh$. At the start of timestep $t + 1$, each individual moves to the cell to which it assigned the highest suitability. The weighing factors for each cue, s_P, s_H, and s_{Nh}, are genetically encoded and heritable between generations. All individuals move simultaneously, and then implement their foraging or kleptoparasitic behaviour to acquire prey. Individuals move and forage on the resource landscape for T timesteps per generation, and T is set at 400 by default.

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Competition Strategies Individuals in scenario 1 only search for prey, and thus are subject only to exploitation competition. Individuals in scenario 2 either search or steal based on their inherited strategy. However, individuals in scenario 3 process the cell-specific environmental cues P, H, and Nh to determine their next foraging strategy as

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

where the cue weights w_P, w_H and w_{Nh}, and the threshold value w_0 are also genetically encoded and heritable between generations.

3.3 Reproduction and Inheritance

We modelled discrete, non-overlapping generations of haploid individuals with 7 gene loci, with asexual reproduction. Population size was fixed, and each generation of individuals is considered to be replaced by its offspring. The gene loci encoding the decision making weights in control of individual movement (s_P, s_H, s_{Nh}) and foraging decisions (w_P, w_H, w_{Nh}, w_0) are transmitted from parent individuals to offspring. The total lifetime intake of individuals is used as a proxy of fitness. The number of offspring of each parent is thus proportional to the parent's share of the population intake, and this is implemented as a weighted lottery that selects a parent for each offspring (see prior implementation in Netz et al., 2020, Tania et al., 2012). The decision-making weights are subject to independent random mutations with a probability of 0.001. The size of the mutation (either positive or negative) is drawn from a Cauchy distribution with a scale of 0.01 centred on the current value of the weight to be mutated. This allows for a small number of very large mutations while the majority of mutations are small. We recognised that spatial autocorrelation in the resource landscape coupled with limited natal dispersal can lead to spatial heterogeneity in evolved movement rules, as lineages adapt to local conditions (Wolf and Weissing, 2010). To examine individual movement rules that are suitable for the global landscape, rather than adapted for local conditions, we intialised each offspring at a random location on the landscape; this potentially forces individuals to contend with conditions very different from those of their direct parent.

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3.4 Simulation Output and Analysis

Population Activities and Intake   We counted the number of times the forager or kleptoparasite strategy was used in each generation of our simulations, as well as the number of times no strategy could be used because individuals were handling a food 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 total population intake — the number of items consumed in each generation — as a measure of population productivity.

Resource Landscape and Individual Distribution Snapshot   To visualise the effect of different foraging strategies on the resource landscape, we exported snapshots of the entire simulation landscape at the midpoint 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 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.

Testing the Matching Rule   To examine whether foragers in our model achieved an IFD, we used the snapshots to test a basic prediction of the IFD and the related matching rule: that the number of individuals on a patch should be strongly positively correlated with patch quality (Fretwell and Lucas, 1970, Parker, 1978). In real world systems, patch quality is measured as a matter of convenience: either as a snapshot of the number of discrete items on a patch at a given time point, or as patch productivity, which is a more long-term predictor of item abundance. We calculated the correlation coefficient between the number of individuals (excluding handlers) and *(a)* the number of prey items, and *(b)* the cell-specific productivity r.

Resource Landscape Gradients   Another measure of whether foragers have achieved the IFD on their resource landscape is whether individuals can improve their intake by moving to another location; in our model, this would be to a neighbouring cell. 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

the proportion of grid cells from which it was possible to move to a neighbouring cell with more prey items, with the expectation that higher values indicate a more non-ideal distribution of foragers.

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, with each weight scaled separately in each simulation run.

Data Availability   Simulation data used in this study are available on the Dryad/IRODS/Zenodo repository **REPOSITORY LINK HERE**; simulation code is available on Github (https://github.com/pratikunterwegs/Kleptomove) and archived on Zenodo at **ZENODO LINK HERE**; data analysis and figure code is available on Github (https://github.com/pratikunterwegs/kleptomove-ms) and archived on Zenodo at **ZENODO LINK HERE**.

4   Results

4.1   Scenario 1: No Kleptoparasitism

In scenario 1, the population's activity budget is split among foraging and handling (Fig. 1A; $r_{max} = 0.01$). The proportion of handling in the activity budget, and the population intake are both initially low, but then peak within ten generations (Fig. 1B). This is because individuals can easily acquire prey items from the fully stocked landscape in the first few generations, as no time has to be spent on searching. As individuals deplete prey items faster than they can be replenished, the overall number of prey items is drastically reduced (Fig. 1C; panel *gen = 1, gen = 10*). As the number of prey items reduces, handling as a share of the activity budget declines to a stable $\sim 45\%$ within 50 generations; this is because fewer searching foragers find a prey item. This leads to a similar stabilisation in population intake (Fig. 1A, 1B). Furthermore, with few prey items, foragers are unable to detect useful movement cues (as they cannot detect r), and move essentially randomly on the landscape. Consequently, and contrary to expectations under the IFD, the correlation

between the number of foragers and cell productivity remains just above zero across generations (Fig. 1D). Finally, forager and prey abundances are not independent, with prey items attracting foragers to cells, and foragers reducing prey item counts; as a result, the correlation between forager and prey item abundances remains weakly negative across generations (Fig. 1E).

4.2 Scenario 2: Fixed Competition Strategies

In scenario 2, the population activity budget includes stealing, in addition to foraging, handling (Fig. 2A; r_{max} = 0.01). As in scenario 1, the most common activity in early generations is searching for prey items, with stealing attemps relatively rare and going nearly extinct as a strategy. Population intake also spikes in early generations as individuals successfully acquire prey items from the fully stocked prey landscape (Fig. 2B). Subsequently, the resource landscape is depleted similar to scenario 1 within 10 generations (Fig. 2C; panel *gen: 1, gen: 10*). At this stage, it becomes more likely for a kleptoparasite to encounter a handler than for a searching forager to find a prey item, and the frequency of kleptoparasites and of stealing attempts as a share of the activity budget increases rapidly (Fig. 2A). Stealing attempts become the dominant activity within 30 generations, and this reflects the proportion of individuals with an inherited kleptoparasitic strategy; a stable ~70% of the population (Fig. 2A). However, this also indicates that most kleptoparasites are unsuccessful at finding handlers, as successful stealing attempts convert kleptoparasites to handlers. With few searching foragers, fewer prey items are extracted from the landscape, which recovers beyond its initial prey abundance within 50 generations (Fig. 2C; panel *gen: 50*).

On relatively saturated resource landscapes, searching foragers can move essentially randomly and yet stand a strong chance of findng prey items. Their main movement priority is thus avoiding non-handlers, which have a strong probability of being kleptoparasites, given their relative frequency in the population. As kleptoparasites, the numerically dominant strategy, seek to move towards handlers, their primary resource, they too are not strongly influenced by prey item abundances. Thus the correlations between forager abundance and cell productivity, and forager and prey abundance remain weak or zero across generations (Fig. 2D, 2E). While both searching and kleptoparasitic foragers evolve similar movement rules in relation to non-handlers (avoidance) and prey items (preference), the evolved movement response to handlers shows a

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rapid divergence. This divergence helps explain how kleptoparasites increase from a negligible fraction of scenario 2 populations to being the most common strategy (Fig. 3A). Kleptoparasites very rapidly (within 3 generations) evolve a strong preference for moving towards handlers, which are their primary resource (Fig. 3B, 3D). While all kleptoparasites prefer to move towards handlers, the strength of the preference shows multiple, distinct values or 'morphs', which are remarkably persistent across generations (Fig. 3B). On the other hand, searching foragers evolve no such preference, and have a much wider range of both positive and negative preferences for handlers (Fig. 3C, 3D). The strategy-dependent divergence of movement rules can be explained by strong correlational selection on kleptoparasites to move towards their primary resource, handlers.

4.3   Scenario 3: Condition-Dependent Competition Strategies

In scenario 3, the population's activity budget is very different from scenario 2 (Fig. 4A). By generation 30, all individuals have a propensity to steal from handlers, i.e., all individuals are opportunistic kleptoparasites (Fig. 4A; *orange line*). However, unlike scenario 2, the frequency of stealing attempts does not strongly track the frequency of opportunistic kleptoparasites, staying at or below 25%, approximately the same as the frequency of searching for prey items. However, handling prey is the most common activity ($\sim$45%) as in scenario 1, with a stable equilibrium within 30 generations (Fig. 4A; $r_{max} = 0.01$). Consequently, population intake stabilises (after an initial spike, as in scenarios 1 and 2) within ten generations to a level similar to scenario 1 (Fig. 4B). Unlike scenario 2, where the proliferation of kleptoparasites results in a reduction in handling and intake, no such reduction occurs in scenario 3. As in scenarios 1 and 2, the depletion of prey items results in the degradation of the resource landscape within ten generations (Fig. 4C; panels *gen: 1, gen: 10*). The reduced depletion following the evolution and persistence of kleptoparasitism leads to a resource landscape recovery intermediate between scenarios 1 and 2 within 50 generations (Fig. 4C; panel *gen: 50*). As individuals move and choose foraging strategies conditionally, they 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. Here too, in a departure from IFD expectations, the correlations between forager abundance and cell productivity, and forager and prey abundance, remain weak or zero across generations

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(Fig. 4D, 4E).

4.4 Evolution, the Ideal Free Distribution, and Alternative Movement Cues

In scenario 1, the proportion of cells from which it is possible to move to a neighbouring cell with more items is initially very high ($\sim$75%; $r_{max} = 0.01$) (Fig. 5A1 – panel *gen: 1*, Fig. 5A2 – green line). This proportion rapidly declines to $\sim$25% within 25 generations, as foragers approach a sort of IFD by depleting most cells on the landscape until they are devoid of prey items (Fig. 1C – panel *gen: 50*, Fig. 5A1 – panels *gen: 10, gen: 50*, Fig. 5A2 – green line). As a consequence, the majority of the landscape is a 'clueless plateau' (Perkins, 1992); on most cells, foragers cannot make directed movement decisions based on item abundances alone because all neighbouring items abundances are identical (see black areas in Fig. 5A1). In this context, foragers evolve to use an alternative cue, the presence of agents handling a prey item, with > 75% of individuals showing a preference for handlers within 100 generations (Fig. 5A2 – blue line). Forager preference for handlers (which do not represent a direct resource in scenario 1), may be explained as the sensing of a long-term cue of cell productivity. Since handlers are immobilised on the cell where they find a prey item, cells with handlers are *(1)* certain to have a non-zero rate of prey item generation, and *(2)* likely to border cells which can generate prey items, due to the patterning of the landscape.

Scenario 2 landscapes follow a similar pattern to scenario 1 in the first 10 generations ($r_{max} = 0.01$; Fig. 5B1 – panel *gen: 1, gen: 10*, Fig. 5B2 – black line). However, within 50 generations, the reduction in prey item extraction allows most cells to regenerate prey items, with differences among cells according to their productivity r (Fig. 2C). Thus it is possible to move to a neighbouring cell with more items from > 75% of the landscape, indicating a population very far from the IFD (Fig. 5B1 – panel *gen: 50*, 5B2). However, since the majority of foragers are kleptoparasites, which seek out handlers (Fig. 5B2 – red and blue lines), this recovery of the 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 correlational selection on kleptoparasites (see subsection above). Scenario 3 is similar to scenario 2, except that only about half the landscape allows movement to a neighbouring cell with more prey items (Fig. 5C1, 5C2). Here, the rapid evolution of a handler preference in movement

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decisions cannot be assigned a clear cause, since handlers are both a potential direct resource as well as indirect cues to the location of productive cells.

4.5 Landscape Productivity and Evolutionary Outcomes

The landscape's r_{max} has a marked effect on population activity budgets and total intake. The frequency of foraging reduces with r_{max} in scenarios 1 and 3; this is caused by more frequent acquisition of prey items (as regrowth keeps pace with depletion), which results in a greater frequency of handling rather than foraging. In scenario 2 however, the frequency of handling is relatively unaffected by increasing r_{max} (Fig. 6A). The difference between scenarios 2 and 3 has to do with the change in the frequency of kleptoparasitism (Fig. 6B). In scenario 2, kleptoparasitism forms $> 75\%$ of all activities at very low r_{max}, and is much more common than in scenario 3 populations at the same regrowth rate. However, at relatively high r_{max} (0.03), the fixed kleptoparasitic strategy goes extinct. At these regrowth rates, the scenario 2 population matches the scenario 1 population, with foragers rapidly converted to handlers. In scenario 3, kleptoparasitism persists at low frequencies even at the highest regrowth rates (Fig. 6B); thus some foragers lose time in extracting items which are then stolen from them. Consequently, while populations in all three scenarios achieve very similar intakes at low r_{max}, at intermediate regrowth rates (0.01 – 0.025), conditionally kleptoparasitic populations outperform populations using fixed strategies. Only at high regrowth rates, when fixed strategy populations (scenario 2) effectively convert to purely forager populations (scenario 1), do they achieve a higher intake than scenario 3 populations (Fig. 6C).

5 Discussion

Our spatially-explicit, evolutionary IBM implements the ecology and evolution of movement and foraging decisions, as well as resource dynamics, in biologically plausible ways, and reaches important conclusions about the distribution of animals in relation to their resources under different scenarios of competition. First, we show that when moving with a limited perception range (the Moore neighbourhood) and competing only by exploitation, individuals evolve movement rules for both direct and indirect resource cues (prey

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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. Second, we show that 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 strongly correlated with movement rules than favour moving towards handling foragers, which are the primary resource. In this sense, obligate kleptoparasites may be thought of as forming a quasi-predatory trophic level, with any handling foragers as their prey. Finally, we show that when foraging strategy is allowed to be conditional on local cues, all individuals are opportunistic kleptoparasites. In both the fixed and conditional strategy scenarios, however, foragers are unable to match their resource landscape, as would be predicted by IFD models.

5.1   Comparison with Previous Models

Our model stands in stark contrast with, and offers a plausible alternative to, existing models of individual foraging and movement decisions by allowing the decision-making mechanisms to evolve. The majority of literature in the field, which despite sometimes considering variation among individuals, typically only considers ecological scenarios within a single generation (see a review in Stillman and Goss-Custard, 2010). Previous mechanistic models of individual movement and competition decisions employed evolutionary algorithms for purposes of optimization only (Getz et al., 2015, 2016), whereas our model attempts to give a faithful representation of evolution by natural selection as a dynamical process. These divergent objectives are mirrored in the following design choices. First, instead of allowing the fittest 50% of the population to reproduce, we determined the number of offspring to be proportional to individual fitness (our 'weighted lottery'; but see a similar implementation in Tania et al., 2012). Second, the weight loci are subject to mutations independently, rather than subjecting all loci of an individual to simultaneous mutation. Finally, we abstained from using an artificial mutation regime such as 'simulated annealing', which (intentionally) leads to a reduction in the magnitude of mutations to the decision making weights over generations. Mutations were instead drawn from a Cauchy distribution centred on the current weight value.

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5.2 The Evolutionary Ecology of Movement Rules

Modelling the resource landscape as comprised of depletable prey items has significant ecological and evolutionary consequences not predicted by simpler models, even those focused on foraging birds (Stillman and Goss-Custard, 2010). The possibility of all discrete prey being depleted from a cell can leave many cells empty, forming 'clueless regions', i.e., areas within which movement informed by a gradient of resource cues is impossible (Perkins, 1992). In our scenario 1, this leads to a kind of local IFD — no move in a clueless region can improve resource intake — and to the conclusion that at IFD, all individuals in a population must move randomly, if at all (Cressman and Křivan, 2006).

In a clueless region, the presence of successful foragers is likely to indicate a suitable foraging spot, while the location of unsuccessful individuals signals the opposite. This selects for the evolution of movement rules that integrate individuals' assessment of the condition of intraspecific competitors — an important aspect of using 'social information' (see Dall et al., 2005, Danchin et al., 2004) — and aggregating on cells with handlers. When population density is high, and resources are spatially auto-correlated, individuals can evolve polymorphisms in movement rules such that only a fraction of the population tracks resource cues, while a larger proportion is relatively insensitive to resource cues, and follows the resource-tracking 'informed leaders' (Guttal and Couzin, 2010). In our model however, the relatively low density of foragers, the inability to share discrete prey items, and the breakdown of spatial autocorrelation in prey abundance due to foraging means that such a polymorphism does not evolve; all individuals must sense and track resources, while eventually also evolving to aggregate with handlers.

Forager aggregation is counter-intuitive, and especially so on resource-scarce landscapes where competition for food is expected to be more intense; it has usually been explained by invoking external costs, such as predation risks, which can be spread over grouping individuals (Folmer et al., 2012, Krause and Ruxton, 2002). Yet we find that information on the location of productive areas of the resource landscape alone may be a sufficient benefit to promote the evolution of social information use, and consequently aggregation. Thus, in contrast with expectations, resource-scarce landscapes are likely to have larger groups of foragers than would be expected under the IFD and the matching rule (Fretwell and Lucas, 1970, Parker, 1978); this potentially explains why our scenario 1 populations undermatch their landscape.

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In our scenarios 2 and 3, social information use is even more critical and strongly selected for by fixed or conditional kleptoparasitism. This coupling of movement and behavioural strategy is expected from the 'correlational selection hypothesis', which holds that suites of behaviours might be correlated into a syndrome when certain combinations of traits are favoured by selection (Sih et al., 2004, Wolf and Weissing, 2010). This correlational selection leads to a much more rapid fixation of handler preference among *(1)* scenario 2's fixed kleptoparasites, and *(2)* all foragers in scenario 3, which can opportunistically steal from handlers. In scenario 2, the emergence and persistence of kleptoparasitism at low r_{max} reduces resource depletion, prey-items are regenerated, and clueless regions are reduced. Ironically, the abundance of item cues is not functionally useful to most foragers; kleptoparasites find themselves in a 'desert of plenty' as their only resource is handlers, which are uncommon relative to prey items.

5.3   The Evolutionary Ecology of Competitive Strategies

Competition is a key process in determining animal space use across scales (Fretwell and Lucas, 1970, van der Meer and Ens, 1997), and is often suggested as a driver of phenotypic, behavioural, and foraging polymorphisms (Baldauf et al., 2014). In our scenario 2, the modelling of kleptoparasitic interference as a fixed strategy leads to the dimorphism between obligate searching foragers and kleptoparasites. This strategic constraint on scenario 2 individuals prevents the population from converging on a single behavioural and movement phenotype (but see below), as kleptoparasites are dependent on searching foragers for intake, and can almost always invade a pure searching forager population. The proportion of kleptoparasites to searching foragers in scenario 2 is quite tightly controlled by the density-dependent success of either strategy.

However, two spatio-temporal phenomena are absent from our model that are predicted in a conceptually similar, but very differently implemented chemotactic model of producer-scrounger foraging (Keller-Segel (KS) models Tania et al., 2012). Specifically, spatially explicit KS models predict that a wide range of parameterisations should lead to *(1)* limit cycles of kleptoparasites and foragers over generations, and *(2)* spatial limit cycles, or 'waves of pursuit', of searching foragers by kleptoparasites over the landscape (Tania et al., 2012). An important reason for this is our implementation of global natal dispersal, which ensures that strategies are well-mixed in each generation, rather than increasing densities of offspring (of either

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strategy) around the most successful ancestors ('differential reproduction'). Differential reproduction would allow instabilities related to spatial structuring, whereby increasing kleptoparasite density in an area would eventually lead to lower per-capita intake among kleptoparasites relative to foragers, and consequently an increase in the forager-to-kleptoparasite ratio.

Scenario 3, which allows individuals to opportunistically steal prey items, resolves the strategic constraint of scenario 2. Here, the frequency of stealing attempts better reflects the encounter rate of handlers, rather than the frequency of opportunistic stealing propensity in the population (which is nearly always 100%). Our implementation of strategic choice as conditional on local cues, rather than probabilistic or learned (see Tania et al., 2012) allows scenario 3 individuals' behaviour to be fine-tuned to immediate, local conditions; they lose much less time in futile stealing attempts than scenario 2 foragers, and thus achieve better intakes. Consequently, scenario 3 individuals rapidly converge upon a single, optimal strategy, which is to steal when handlers are available, and to search for prey otherwise. In this scenario, global natal dispersal is likely redundant; all foragers can (nearly optimally) choose their strategy in each turn, and there is no spatial segregation between the strategies.

5.4 Competitive Strategies and Landscape Productivity

Landscape productivity determines the probability of a searching forager finding prey and becoming a handler, but population density determines the probability of a kleptoparasite finding a handler. The balance of productivity and density controls whether obligate kleptoparasitism is a viable strategy (scenario 2), leading to the counterintuitive pattern of lower kleptoparasitism on higher productivity landscapes at the same population density. On more productive landscapes ($r_{max} \geq 0.02$), exploitation competition is reduced, and the probability of a forager-prey item encounter is much higher than the probability of a kleptoparasite-handler encounter. Consequently, fixed-strategy kleptoparasites rarely match the per-capita intakes of foragers, and rapidly go extinct. Thus high r_{max} instances of scenario 2 consistently produce populations that are functionally identical to scenario 1 populations, with no kleptoparasitism. Our implementation of a fixed population size contributes to our scenario 2 results, and a model with flexible population sizes that does not convert individuals' relative fitness into discrete individuals would allow kleptoparasites to persist at low levels. Con-

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ditional strategy populations (scenario 3) are free from constraints on behavioural strategy, and can extract and handle prey items directly; they thus outperform fixed-strategy populations, and have similar intakes as forager populations on low productivity landscapes. However, at high r_{max}, opportunistic kleptoparasites in scenario 3 have a greater per-capita intake rate than pure foragers, as kleptoparasitic prey acquisition deprives a (foraging) handler of its prey. Since scenario 3 kleptoparasitic behaviour is conditional, it persists even in populations on high productivity landscapes.

6 Acknowledgments

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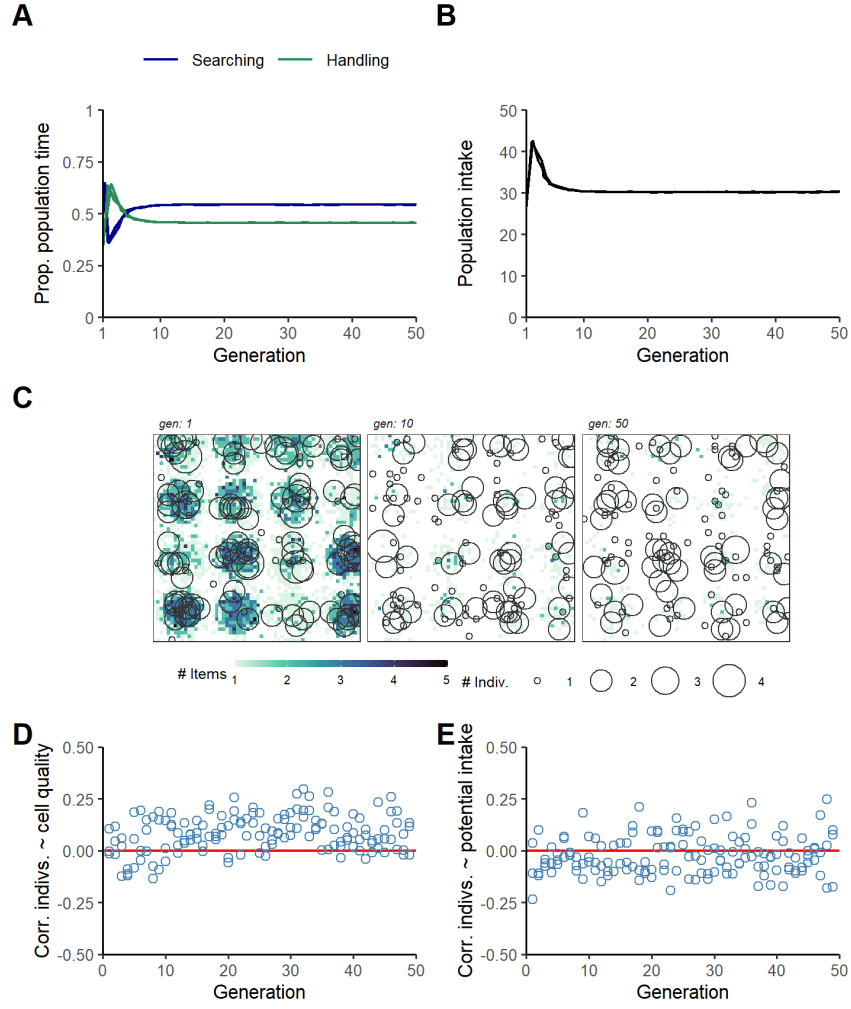
7 Figure legends

Figure 1: **Eco-evolutionary implications of pure exploitation competition (Scenario 1).** Within 20 generations of evolution, the population reaches an equilibrium in **(A)** the relative proportion of time spent on searching prey and handling prey, and in **(B)** the total intake of the population. **(C)** The sustained extraction of prey-items results in a rapid depletion of the resource landscape within 10 generations. The number of individuals on occupied cells is shown as black circles (size = number of individuals). In a departure from IFD predictions, at equilibrium, cell occupancy (number of foragers per cell) is only weakly correlated with cell productivity r **(D)**, while it is even negatively correlated with the number of food items in the cell **(E)**. Panels **A, B, D** and **E** show three replicates, while panel **C** shows a single replicate; all panels are for $r_{max} = 0.01$.
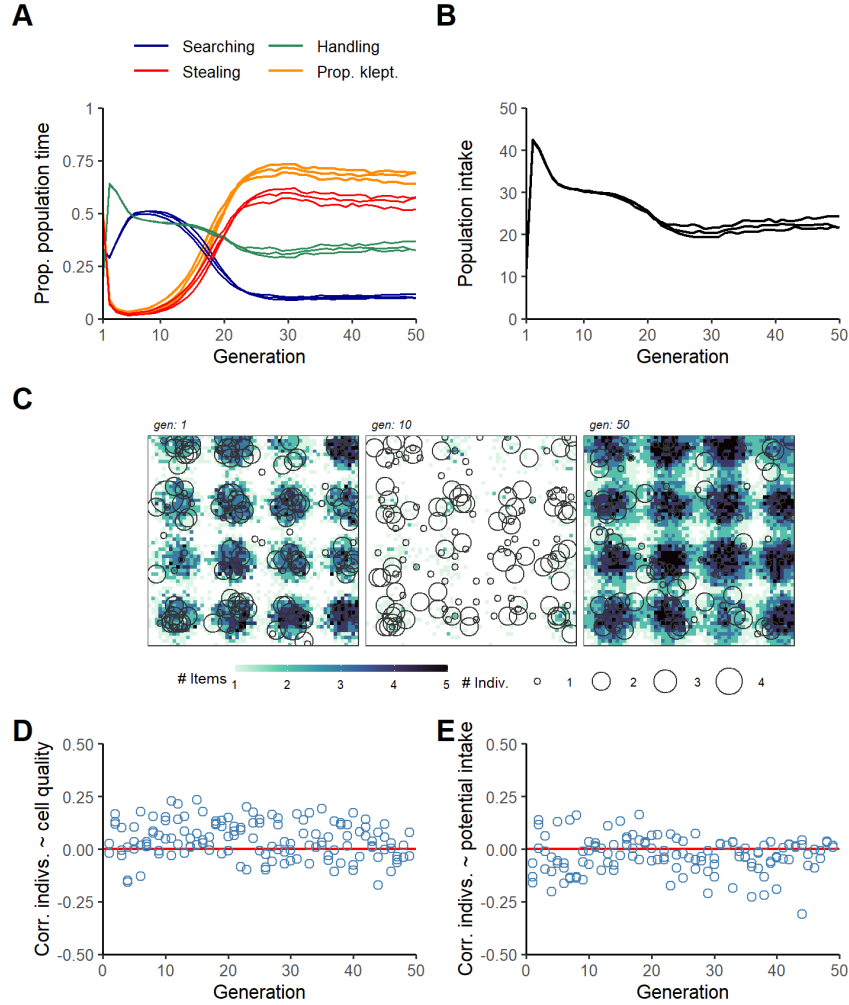
Figure 2: **Eco-evolutionary implications of exploitation combined with a fixed foraging strategy (Scenario 2).** In Scenario 2, the population reaches an equilibrium in **(A)** the relative proportion of time spent on searching prey and handling prey, and in **(B)** the total intake of the population. Stealing activities (red line; panel A) are less common than kleptoparasitic individuals (orange line; panel A), as successful kleptoparasites become handlers (green line; panel A). **(C)** With a reduction in foraging and handling due to increased stealing after generation 30 (panel A), prey-item depletion is reduced, and the resource landscape recovers by generation 50. The number of individuals on occupied cells is shown as black circles (size = number of individuals). At equilibrium, cell occupancy (number of foragers per cell) is only weakly correlated with cell productivity r **(D)**, and weakly negatively correlated with the number of food items in the cell, in contrast with IFD predictions **(E)**. Panels **A, B, D** and **E** show three replicates, while panel **C** shows a single replicate; all panels are for $r_{max} = 0.01$.
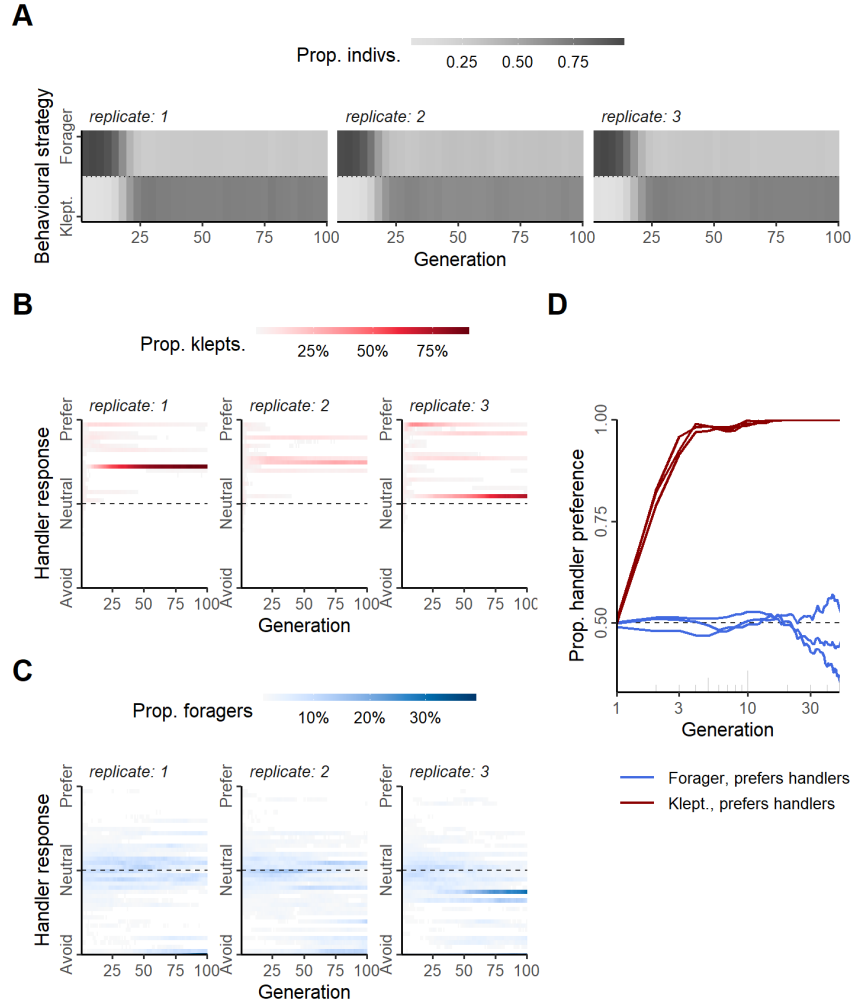
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Figure 3: **Rapid divergence of movement rules between fixed foraging strategies due to correlational selection (Scenario 2).** (A) Kleptoparasitism rapidly becomes the more frequent strategy in Model 2 populations, with no differences across replicates. (B) However, replicates differ strongly in the frequencies of evolved movement strategies among the two behavioural strategies. While nearly all kleptoparasites evolve to move towards handlers, their direct resource, the strength of their handler preference is polymorphic, with 2 or 3 morphs in most replicates. (C) Foragers are also polymorphic in their handler responses, but these morphs are the results of drift, rather than selection. (D) Overall, within 5 generations (shown on a log scale), all kleptoparasitic individuals ($\sim$75% of the population at equilibrium; see Fig. 3A) have an evolved preference for moving towards handlers. Meanwhile, forager individuals are agnostic to handlers, and are equally split between handler preference and avoidance. All panels show three replicates at $r_{max} = 0.01$.
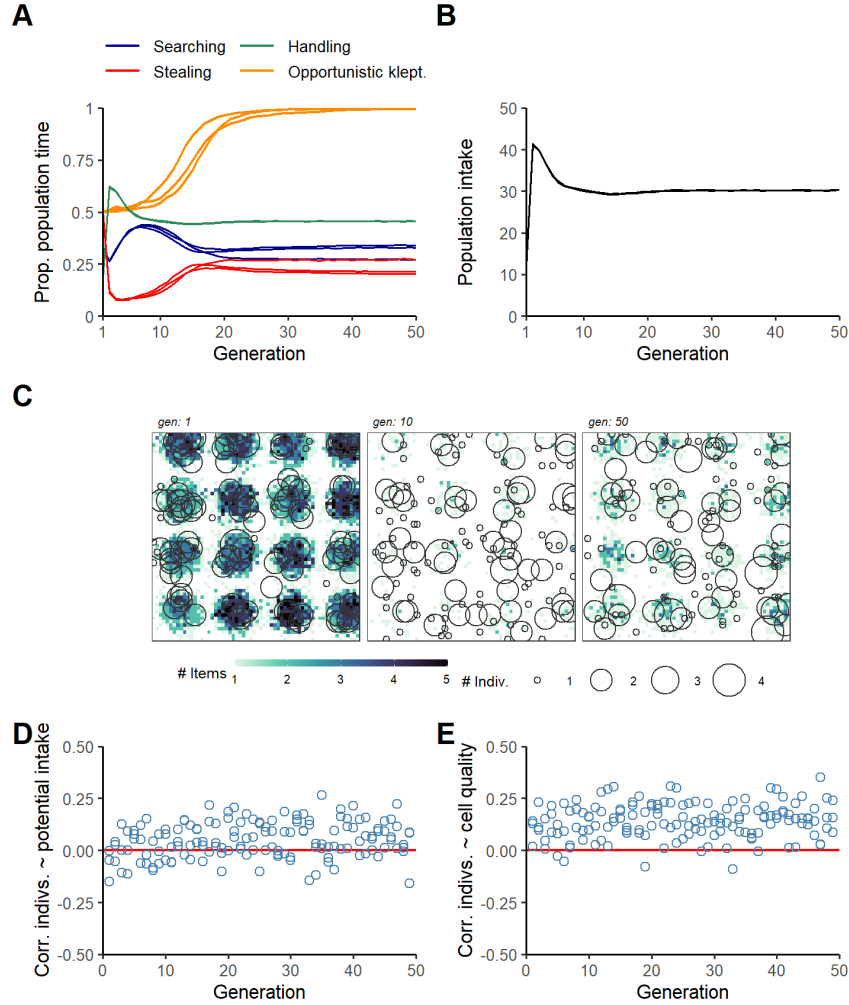
Figure 4: **Eco-evolutionary implications of exploitation combined with a conditional foraging strategy (Scenario 3).** Scenario 3 populations reach an equilibrium in **(A)** the relative proportion of time spent on searching prey and handling prey, and in **(B)** the total intake of the population within 30 generations of evolution. While an opportunistic kleptoparasitic strategy (orange line; panel A) becomes rapidly fixed in the population, the actual frequency of stealing remains relatively much lower (red line; panel A). **(C)** The initially rapid depletion of the resource landscape within 10 generations is halted as kleptoparasitism reduces foraging activities, and the resource landscape regenerates prey-items by generation 50. The number of individuals on occupied cells is shown as black circles (size = number of individuals). **(D)** Contrary to IFD expectations, the correlation between the number of individuals on a cell, and its productivity r_{max}, and **(E)** the correlation between individual counts and the probability of finding a prey-item are both weak across generations. Panels **A, B, D** and **E** show three replicates, while panel **C** shows a single replicate; all panels are for $r_{max} = 0.01$.
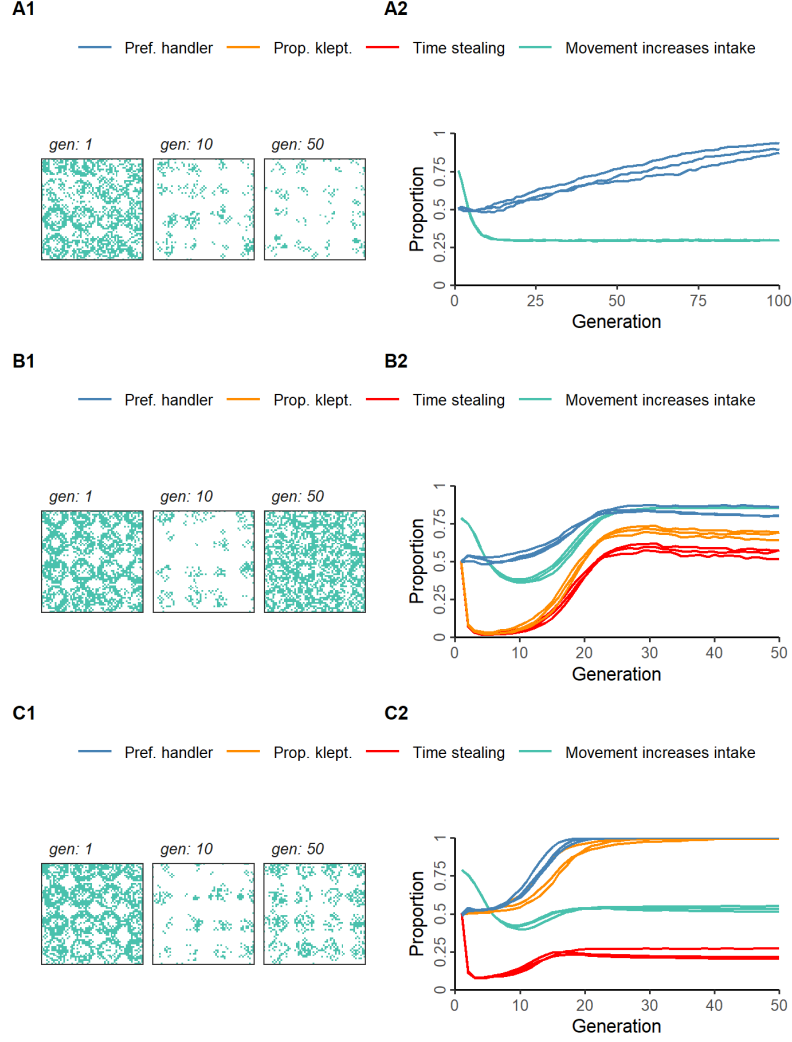
Figure 5: **Evolution, the IFD, and alternative movement cues.** The movement of foragers and their consumption of prey items leads to large areas of the resource landscape where moving to a neighbouring cell does not increase potential intake in terms of prey items (**A1, B1, C1** – panels *gen:1, gen:10,* **A2, B2, C2** – green line). This homogenisation to zero items leads to the creation of 'clueless regions', i.e., neighbouring cells with no difference in item counts, and thus no direct resource gradients (**A1, B1, C1** – white areas). Foragers in scenario 1 slowly evolve a preference for handlers, which indicate cells with a non-zero probability of generating prey items (**A2** – blue line). The evolution and persistence of a kleptoparasitic response (orange lines) in scenarios 2 (**B2**) and 3 (**C2**) and stealing events (red lines) reduces item depletion, allowing the spatial structure of the landscape to re-emerge. In both scenarios, there are large areas of the landscape where individuals can improve their intake of prey items by moving to a neighbouring cell, contrary to a population that has achieved an ideal free distribution (**B1, C1** – panel *gen: 50*). All panels show replicates at $r_{max} = 0.01$; landscape panels show only a single replicate.
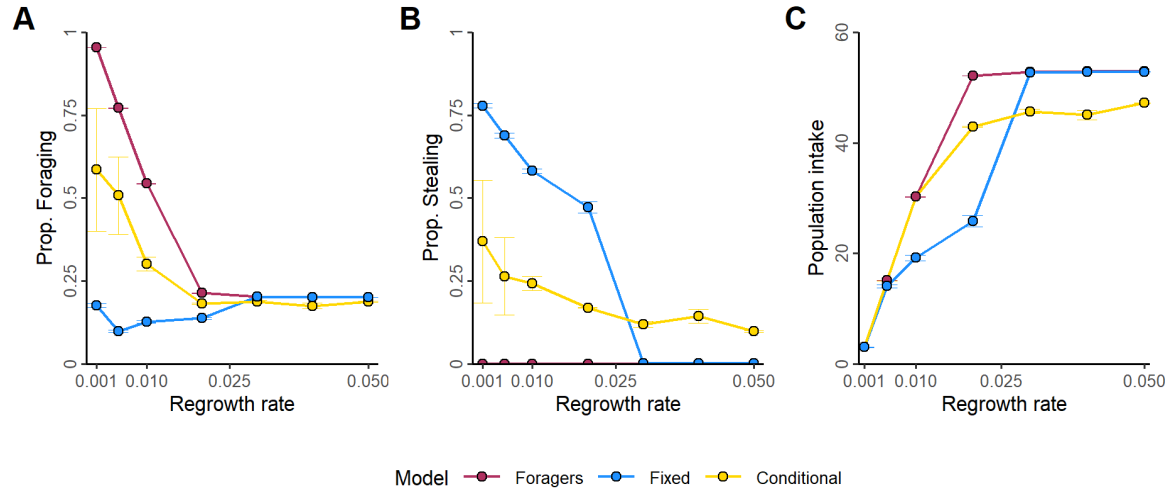
Figure 6: Landscape productivity strongly affects model outcomes. **(A)** The frequency foraging reduces with increasing r_{max} in models 1 and 3, but remains relatively stable in model 2. In all three models, this is partly due to an increase in handling caused by increased resoure availability, and **(B)** partly due to reduced kleptoparasitism in models 2 and 3. In model 2, kleptoparasitism goes extinct at higher r_{max}, and such model 2 populations are functionally identical with model 1 populations. **(C)** At low r_{max}, populations in all three models achieve similar intakes. At intermediate r_{max} however, popualtions with a conditional kleptoparasitic strategy outperform populations with fixed strategies. At high r_{max}, conditional kleptoparasitism populations (model 3) achieve lower intakes than populations in models 1 and 2, which are then functionally identical. Shaded regions around solid lines show the standard deviation of each value; these are not visible when the standard deviaiton is very small.