The joint evolution of movement and competition strategies

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Abstract

Competition is a key process in spatial ecology, driving movement decisions, spatial distributions and interactions. Yet, classical models often neglect the intricate interactions between individuals that can range from facilitation to competition over limited resources and kleptoparasitic encounters.

Here, we present a mechanistic, spatially-explicit model of intraspecific competition with the evolution of foraging competition and movement strategies. We examine *(1)* the evolution of movement under exploitation competition; the joint evolution of movement and genetically determined competition strategies (either foraging for resources or stealing resource items from conspecifics); and *(3)* behaviorally flexible competition strategies conditioned on local cues.

Different combinations of linked foraging and movement strategies evolve over the three scenarios. Exploitation competition produces broad 'clueless regions', where individuals use the presence of conspecifics as a proxy for resources. Interference in the form of kleptoparasitism leads to conspecific avoidance, maintaining landscape heterogeneity. Populations with fixed competition strategies generally lag foraging-only and conditional competition strategies' foraging efficiency.

1 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; Vahl et al., 2005*a*,*b*, 2007; Rutten et al., 2010*a*). 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; Schlägel et al., 2020). The fine-scale mechanisms and evolutionary consequences of competition are difficult to study in free-living animals, yet their knowledge is central to evolutionary ecology. It is nearly impossible to study competition and its coevolution with movement strategies at evolutionary time-scales in most animals, due to a lack of long-term data (Clutton-Brock and Sheldon, 2010) — this necessitates the use of models.

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

importance of interference competition, considering it unimportant, or even modelling a benefit of grouping (e.g. Amano et al., 2006). 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). While models such as Beauchamp (2008) and Tania et al. (2012) allow for individuals to either search for food or scrounge off exploited patches, they simplify the mechanisms by which this decision is made (see also Garay et al., 2020, for a game theoretic treatment). Few foraging ecology models — either IFD or producer-scrounger — allow for realistic movement strategies, often assuming 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, 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, *sensu* 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; Beauchamp, 2008). In addition to short-term, ecological effects, competition should also have evolutionary consequences for individual *movement strategies*, as it does for so many other aspects of behaviour (Baldauf et al., 2014), setting up feedback loops between ecology and evolution. 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; Tregenza, 1995; Amano et al., 2006). 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 styles (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 movement strategies. As foraging and movement decisions are taken by individuals, we study the joint evolution of both types of decision-making by means of a simulation model. Such models are well suited to modelling the evolution of complex behaviours (Guttal and Couzin, 2010; Kuijper et al., 2012; Getz et al., 2015, 2016; Long and Weissing, 2020; Netz et al., 2020, for conceptual underpinnings see Huston et al. (1988); DeAngelis and Diaz (2019)). 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 ecological and evolutionary timescales. 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 scenario, we examine only exploitation competition. In the second scenario, we introduce kleptoparasitic interference as an inherited strategy, fixed through an individual's life. 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 of increasing complexity whose most basic components — the environment's 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 the behaviour of waders (*Charadrii*). Waders 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) — but few, if any, models consider the interplay of ecology and evolution when studying wader movement and competition. 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, an ecological (or 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 1,000 generations of a population of 10,000 individuals; thus there are about 26 times more grid cells than individuals.

2.1 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 in landscape productivity by having the distribution of r across the grid take the form of 1,024 resource peaks, placed at regular distances of 16 grid cells from the peaks around them; r declines 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 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 items per 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). 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 $1 - q^P$. Individuals on a cell forage in a randomised sequence, and the probability of finding a prey item ($1 - q^P$) is updated as individuals find prey, reducing P. Foragers that are assigned a prey item in timestep t begin handling it, and are considered to be handlers from the end of the timestep, i.e., for the movement and foraging decisions of other individuals. Foragers that are not assigned 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, discrete steps of fixed size. These steps are the outcome of short-term individual movement decisions, which are made using evolved movement strategies. Movement decisions are modelled as the individual selection of a destination cell, after assessing potential destinations based on available cues (akin to the concept of step selection or resource selection Fortin et al., 2005; Manly et al., 2007). At the end of each timestep t, individuals scan the nine cells of their Moore neighbourhood for three environmental cues, *(1)* an indication of 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 N (referred to as 'non-handlers'). Based on these cues, a 'suitability score' S is assigned to each cell as $S = s_P P + s_H H + s_N N$. 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_N, are genetically encoded and and transmitted from parents to their offspring. 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.

Scenario 1: Exploitative Competition The first scenario simulates only exploitative competition; individuals (henceforth called 'foragers') move about on the landscape and probabilistically find and consume prey items. A forager can be either in a 'searching' state or in a 'handling' state, as we assume that 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). 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 the suitability scores (s_P, s_H and s_N).

Scenario 2: Fixed Interference Competition The second scenario builds on Scenario 1, but in addition to foragers there is a second category of individuals called 'kleptoparasites'. Kleptoparasites do not search for food, but rather for handlers from which they can steal prey. 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). However, if multiple kleptoparasites target the same handler, only one of them, randomly selected, is considered successful — thus kleptoparasites also compete exploitatively among themselves. Individuals that have been stolen from 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 a forager. 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. In scenario 2, there are two fixed competition strategies that are inherited from parents to offspring, and each of these strategies can evolve a (separate) movement strategy.

Scenario 3: Conditional Interference Competition In scenario 3, each individual can either act as a forager, searching for food, or as a kleptoparasite, dependent 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, our model considers a population of fixed size (10,000 individuals) with discrete, non-overlapping generations. Individuals are haploid and reproduction is asexual. Each individual has 7 gene loci that encode the decision making weights; only the weights in control of 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. Hence the alleles at these loci correspond to real numbers that are transmitted parent individuals to their offspring.

We assume that the expected number of offspring per individual is proportional to the individual's total lifetime intake of resources (hence resource intake is used as a proxy for fitness). 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 (see prior implementation in Tania et al., 2012; Netz et al., 2020). In all 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 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.

2.4 Simulation Output and Analysis

Population Activities and Intake 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 total population intake — the number of items consumed in each generation — as a measure of population productivity.

Resource Landscape and Individual Distribution Snapshots 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 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 Input 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 occupied patches should be proportional with patch productivity (Fretwell and Lucas, 1970; Parker, 1978; Houston, 2008). In real world systems, patch productivity is challenging to measure, but not so in simulation models, where it is among the model's building blocks. We calculated the correlation coefficient between the number of individuals (excluding handlers) and the cell-specific productivity r, and plotted it over generations for each replicate.

Informativeness of Resource Landscapes 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 sense differences in prey items, i.e., a cell with either more of fewer items. When it is impossible to sense such differences, movement informed by relative prey item abundances is difficult, and achieving the IFD becomes a challenge.

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

vidual 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.

Model Code, Analysis Code, and Data Availability The simulation model code can be found on Github (https://github.com/pratikunterwegs/Kleptomove) and archived on Zenodo (https://zenodo.org/record/4905476). Simulation data used in this study are available on the Dryad/IRODS/Zenodo repository **REPOSITORY LINK HERE**. Code for data analysis and preparing the figures in the main text and Supplementary Material is available on Github (https://github.com/pratikunterwegs/kleptomove-ms) and archived on Zenodo (https://doi.org/10.5281/z

3 Results

3.1 Scenario 1: No Kleptoparasitism

When only foragers are present in the population, individuals deplete prey items faster than they can be replenished, and the overall number of prey items is drastically reduced within only a few generations (Fig. 1A). The population's activity budget is split between searching and handling (Fig. 1B). The proportion of time spent handling and the population intake are both initially low, but then peak within ten generations (Fig. 1C). This is because individuals can easily acquire prey items from the fully stocked landscape in the first few generations. 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. 1C). Though in early generations, foragers are attracted to resource peaks and tend to accumulate on resource-rich locations (Fig. 1A), the correlation between the number of foragers on a cell and the productivity of that cell is only slightly positive (Fig. 1D). This is in contrast with the perfect correspondence between resource input rate and forager density (the 'input matching rule'), which is a defining property of the IFD (Parker, 1978; Houston, 2008). Contrary to standard IFD assumptions, foragers cannot directly "sense" the local cell productivity r; instead they can only use the (small) number

of prey items available in a cell as a cue for local productivity ("cell quality").

3.2 Scenario 2: Co-existence of Foragers and Kleptoparasites

When both foraging and kleptoparasitism is allowed, the spatial distribution of consumers and prey items at equilibrium are very different from a forager-only population. 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 explained by the presence of kleptoparasites (Fig. 2B), which reduce the prey intake rate of the population, and accordingly lead to a higher prey abundance. In early generations, kleptoparasites are very rare, and the activity budget, the population intake, and the distribution of consumers over the landscape show the same patterns as in Fig. 1. Population intake also spikes in early generations as individuals successfully acquire prey items from the fully stocked prey landscape (Fig. 2C). 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 from generation 30 onwards, as kleptoparasitism becomes the dominant strategy (a stable $\sim$70% of the population; see Fig. 2B), searching for handlers from whom to steal becomes the dominant 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, fewer 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 consumer abundance and cell productivity remains weak or zero across generations (Fig. 2D). This may be explained by the dynamics of kleptoparasitism: foragers fleeing a kleptoparasitic attack are displaced far from their original location, and kleptoparasites must track these foragers if they are to acquire resources. As kleptoparasites, the numerically dominant strategy, seek to move towards handlers (rather than prey), they are not strongly influenced by prey item abundances.

The increase of kleptoparasitism from a negligible fraction to the dominant strategy (Fig. 3A) is associated with the 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 Figure S5), 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 Figure S4), because the presence of handlers is an indirect indicator of productive cells. However, with kleptoparasites common in the population, searching foragers both avoid and prefer handlers in about equal proportions (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 dominant 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 polymorphism (Fig. 3C). Typically, there are no predominant movement strategies. Instead, a wide range of coexisting handler attraction/repulsion values emerges. In other words, some foragers are strongly attracted by handlers, others are strongly repelled by handlers, and yet others are neutral to the presence of handlers.

3.3 Scenario 3: Condition-dependent Kleptoparasitism

When individuals are allowed to choose their competition strategy (foraging or kleptoparasitism) 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 explained by the observation that by generation 30, all individuals have a propensity to steal from handlers, i.e., when handlers are present in the vicinity, consumers will choose to target handlers for prey items, rather than forage for prey themselves ("opportunistic kleptoparasitism"; Fig. 4B; *orange line*). However, unlike scenario 2, individu-

als search for prey more often and steal less (at or below 25%; compare with Fig. 2B), leading to a sustained high population intake rate and the depletion of the resource landscape. 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. 4C). 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. 4A). 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. Thus, while not as strong as predicted by IFD theory, the correlations between consumer abundance and cell productivity are weakly positive (Fig. 4D).

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

Orienting movement towards resources (Nathan et al., 2008, ; *where to move*) can be a challenge in a system with low densities of discrete prey items, because the local prey *density* may provide very limited information about local *productivity*. In fact, major parts of the resource landscape may be a 'clueless plateau' (Perkins, 1992); on most cells, 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 from which it is possible to move to a neighbouring cell with more items is initially very high (Fig. 5A1). This proportion rapidly declines to $\sim$25% within 10 generations, as foragers deplete most cells on the landscape until they are devoid of prey items, and the majority of the landscape is a clueless plateau. 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 (which do not represent 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, 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 autocorrelation (spatial patterning) of the landscape.

Scenario 2 landscapes follow a similar pattern to scenario 1 in the first 10 generations (r_{max} = 0.01; 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 productivity r (see also Fig. 2A). Thus it is possible to move to a neighbouring cell with more items from $> 75\%$ of the landscape (Fig. 5A2 – panel *gen: 50*, 5B2). However, since the majority of foragers are kleptoparasites, which seek out handlers, 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. 5A3, 5B3). Here, the rapid evolution of a handler preference in movement 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.

3.5 Effect of Landscape Productivity on Evolutionary Outcomes

The prey-item regrowth rate that characterises the peaks of the resource landscape (r_{max}) is a measure of the productivity of the resource landscape overall. Having thus far focused on scenarios with r_{max} = 0.01 (corresponding to a peak production of 4 food times per consumer lifetime), we find that, not unexpectedly, the value of r_{max} has a marked effect on evolved population activity budgets, total intake, and even evolved strategies. 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. This is because at high r_{max}, the probability of a forager finding prey is much greater than the probability of a kleptoparasite finding a handler, in both initial (< 10) and later generations (> 50). Consequently, kleptoparasites are responsible for only a very small fraction of the total population intake, have relatively much lower fitness, and do not proliferate. Thus at these regrowth rates, a scenario 2 population is nearly identical to a scenario 1 population; while some kleptoparasites may be seen in later generations, these are more likely due to mutation in the forager strategy, rather than longstanding lineages of kleptoparasites.

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 achieve a higher intake than 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).

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, and offers a new perspective 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 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. 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 with the evolution of movement strategies that favour moving towards handlers, which are the primary resource of the kleptoparasites. In this sense, obligate kleptoparasites may be thought of as forming a higher trophic level, with any handling consumers as their prey. Thirdly, we show that when foraging strategy is allowed to be conditional on local cues, *(1)* the population's 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.

TO BE RE-DONE: In both the fixed and conditional strategy scenarios, however, foragers are unable to match their resource landscape, as would be predicted by IFD models.

4.1 Modelling the Joint Evolution of Movement and Foraging Strategies

Our model stands in stark contrast with existing models of individual foraging and movement decisions, in which movement strategies are imposed to mimic either ideal or non-ideal foragers (Vickery et al., 1991; Cressman and Křivan, 2006; Amano et al., 2006; Beauchamp, 2008; Stillman and Goss-Custard, 2010), We, however, allow selection to determine how individuals should weigh local environmental cues for movement decisions (resource selection Manly et al., 2007, ; *but see* Getz et al. 2015). Modelling prey items on the resource landscape as discrete and exclusive (in the sense of a private good), contrary to most IFD models (Tregenza, 1995; Amano et al., 2006) also allows for a more plausible, fine-scale consideration of exploitation competition, which is often neglected. Similarly, breaking with the convention of 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). 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). Our model explicitly considers the evolutionary process, and our implementation of the evolutionary process is also novel. Previous mechanistic models of individual movement and competition decisions have used evolutionary algorithms to 'optimise' individuals' behaviour (Beauchamp, 2008; Getz et al., 2015, 2016). We have opted for a less teleological approach: first, instead of allow-

ing the fittest 50% of the population to replicate, we determined the number of offspring to be proportional to individual fitness (our 'weighted lottery'; see a similar idea 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.

4.2 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 consumers is likely to indicate a suitable foraging spot (local enhancement; see Giraldeau and Beauchamp, 1999; Beauchamp, 2008). The presence of unsuccessful individuals, meanwhile, signals potential costs — due to exploitation or interference competition, or even in the absence of other individuals, the time cost of searching for prey on an unproductive cell. This selects for the evolution of movement strategies that integrate individuals' assessment of the condition of intraspecific competitors — an important aspect of using 'social information' (see Danchin et al., 2004; Dall et al., 2005) — and thus aggregating on cells with handlers. When population density is high, and resources are spatially auto-correlated, individuals can evolve polymorphisms in movement strategies 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.

Foragers are expected, from IFD theory, to aggregate on the most productive patches; this is an emergent outcome of individuals balancing competition costs with higher intake. In our scenarios, cell productivity cannot be known, and individuals evolve movement strategies such that between two cells with identical prey densities, but different handler counts, they would move into the cell with more handlers. Such aggregation, especially on resource-scarce landscapes where competition for food is expected to be more intense, is counter-intuitive; it has usually been explained by invoking external costs, such as predation risks, which can be spread over grouping individuals (Krause and Ruxton, 2002; Folmer et al., 2012). We suggest 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 by IFD theory (Fretwell and Lucas, 1970; Parker, 1978); this potentially explains why our scenario 1 populations undermatch their landscape.

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 when certain combinations of traits are favoured by selection (the 'correlational selection hypothesis'; see Sih et al., 2004; Wolf and Weissing, 2010).

4.3 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.

In scenario 3, 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.

4.4 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. Conditional strategy populations (scenario 3) are free from constraints on behavioural strategy, and can extract and handle prey items directly; their intakes are thus higher than those of fixed-strategy populations, and similar to 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.

5 Acknowledgments

The authors thank Hanno Hildenbrandt for contributing extensively to the coding of the simulation model *Kleptomove*; Matteo Pederboni for contributing to the model's development; and members of the Modelling Adaptive Response Mechanisms Group, and of the Theoretical Biology department at the University of Groningen for helpful discussions on the manuscript. F.J.W. and C.F.G.N. acknowledge funding from the European Research Council (ERC Advanced Grant No. 789240). This work was supported by an Adaptive Life Programme grant awarded to F.J.W. made possible by the Groningen Institute for Evolutionary Life Sciences (GELIFES).

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6 Figure legends

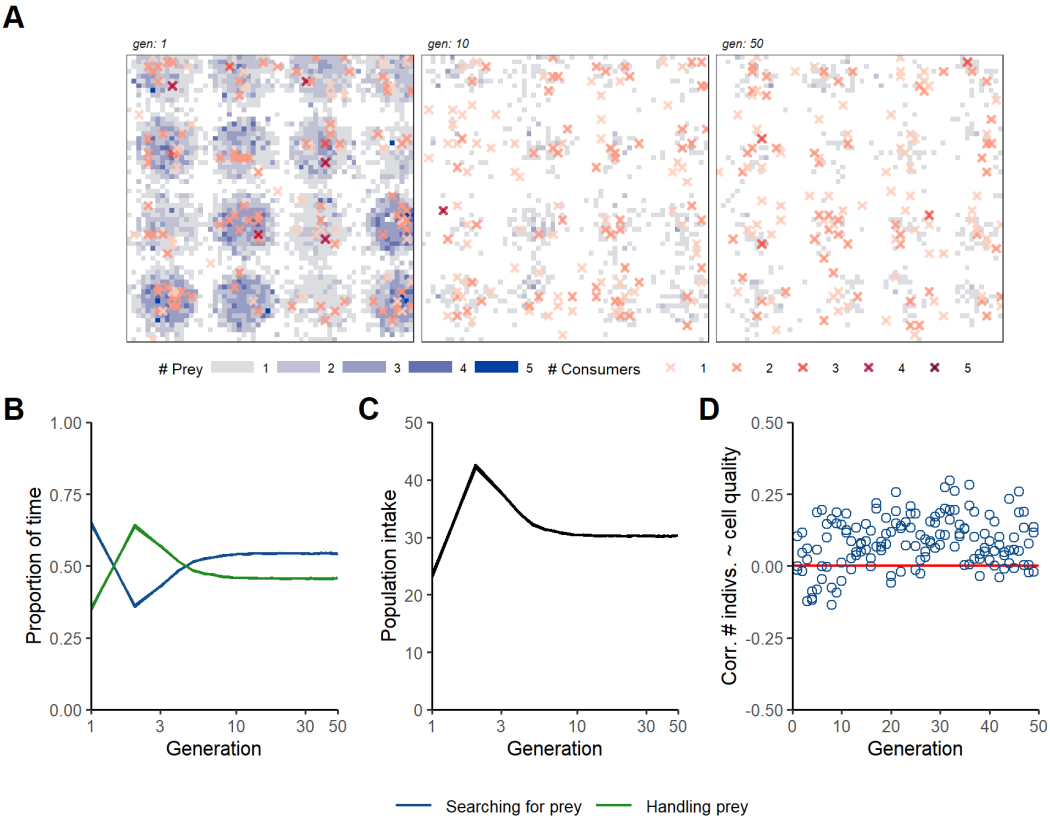

Figure 1: Eco-evolutionary implications of pure exploitation competition (scenario 1). (A) When a population is comprised solely of foragers seeking prey on a resource landscape, the initially well-stocked resource landscape is swiftly depleted within 10 generations (out of 1,000 simulated). This sparsity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

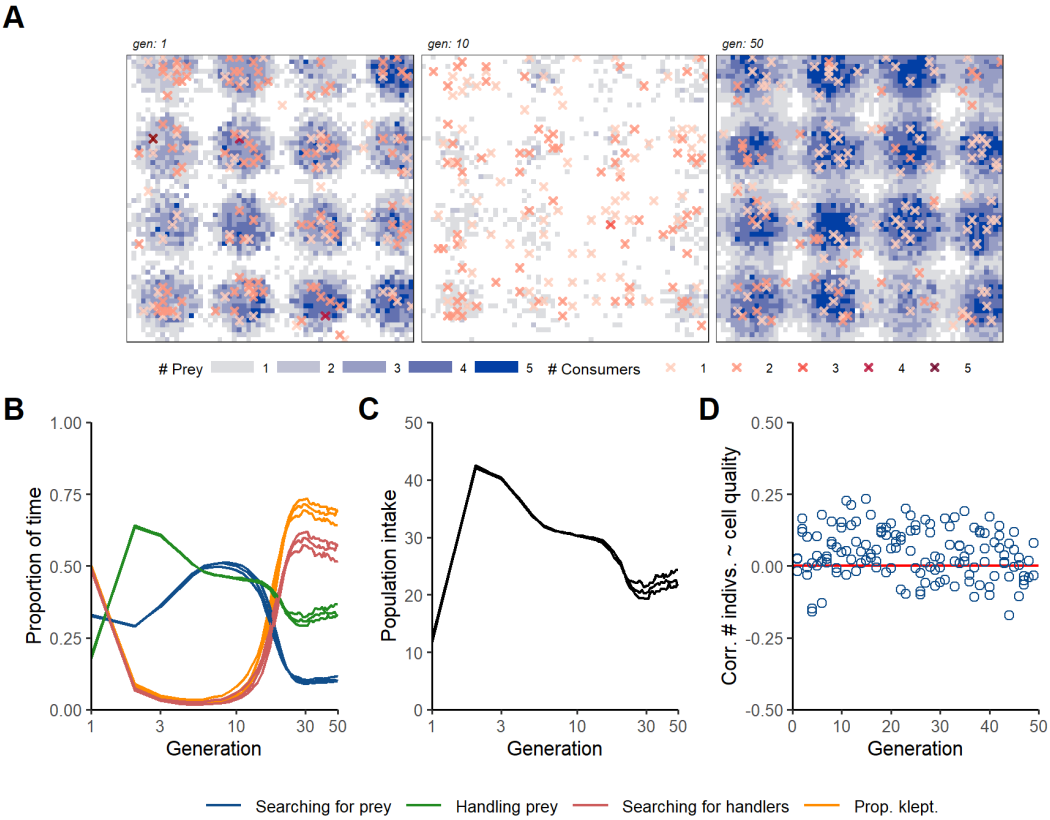

Figure 2: Eco-evolutionary implications of the coexistence of foragers and kleptoparasites (scenario 2). In populations with both foragers and kleptoparasites, **(A)** the initially well-stocked resource landscape is drastically depleted by generation 10; however, prey densities recover strongly by generation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

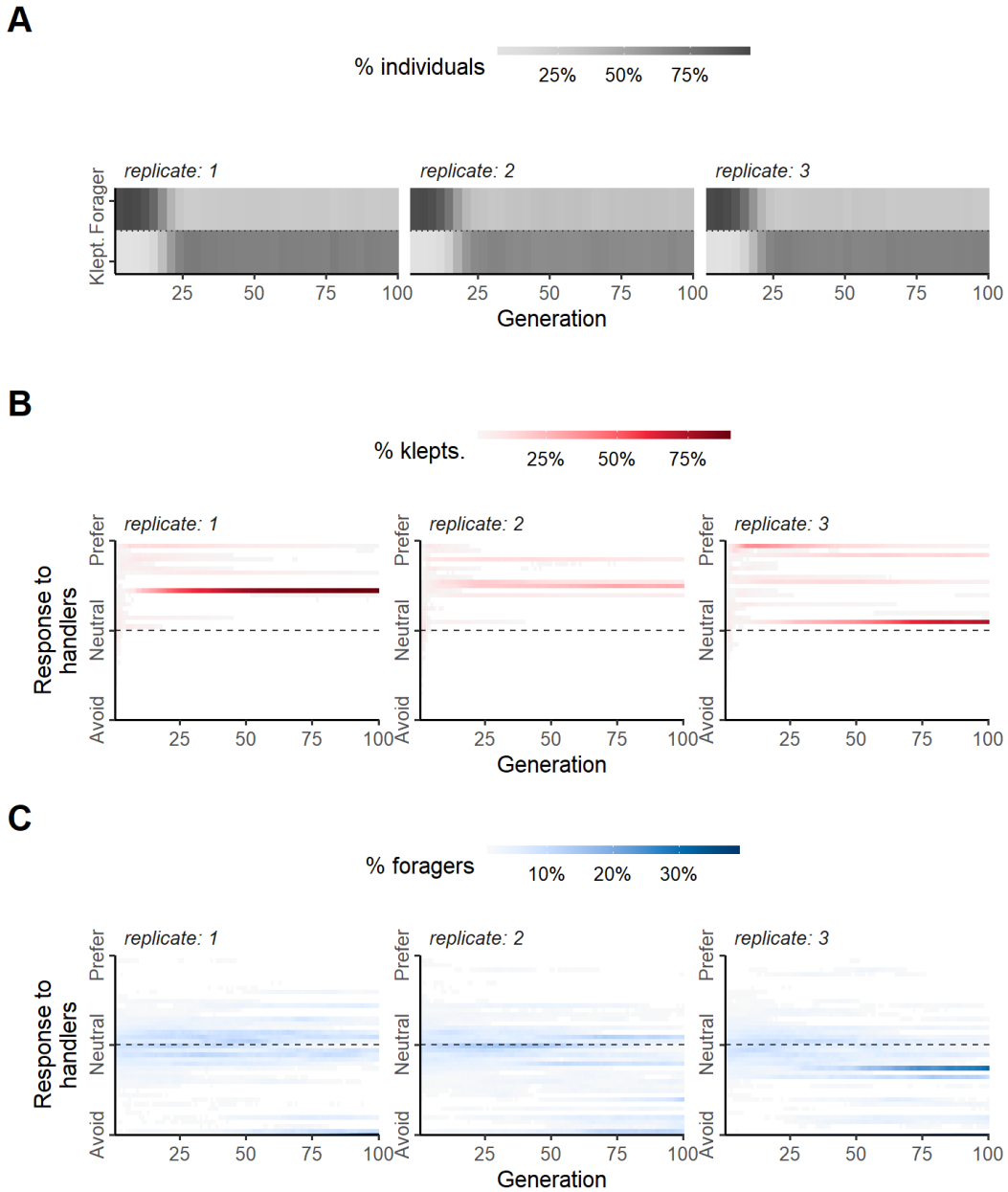

Figure 3: Divergence of movement strategies between foragers and kleptoparasites (scenario 2). (A) Kleptoparasitism rapidly becomes the more frequent strategy in scenario 2 populations for the parameters considered, with no differences across replicates. However, replicates differ considerably in the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

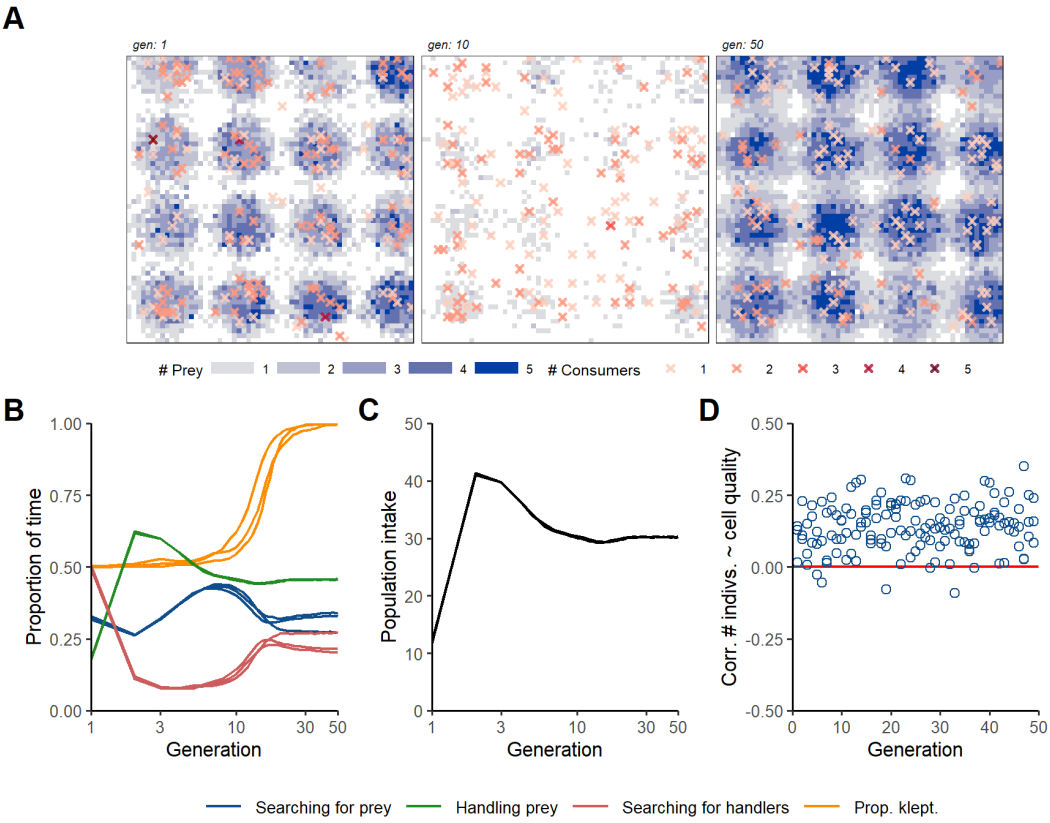

Figure 4: Eco-evolutionary implications of conditional foraging strategies (scenario 3). (A) The initially well-stocked resource landscape is rapidly depleted within 10 generations, yet within 50 generations, prey abundances recover on many cells, though not to the extent of scenario 2. The local density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

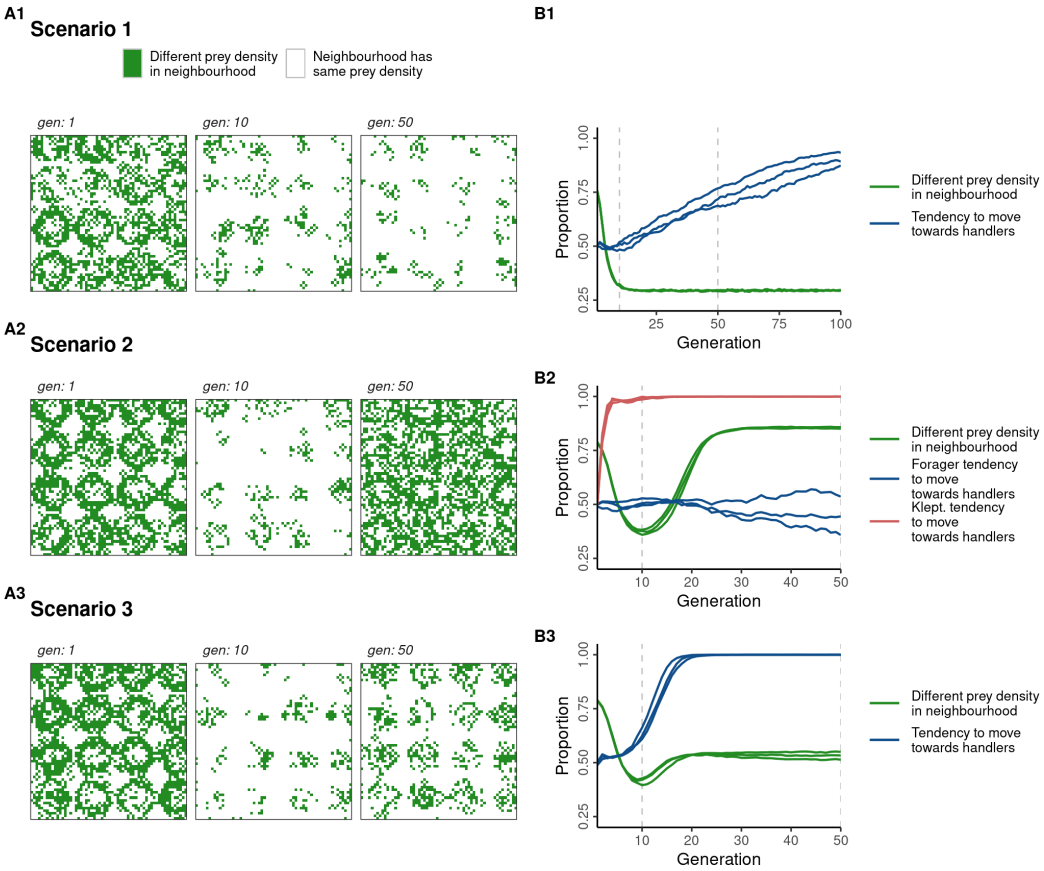

Figure 5: Uninformative prey densities and the evolution of alternative movement cues. (A1, A2, A3) On cells coloured green, local prey densities are informative for movement, as the central and neighbouring cells have different prey densities. While differences in local prey densities provide informative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

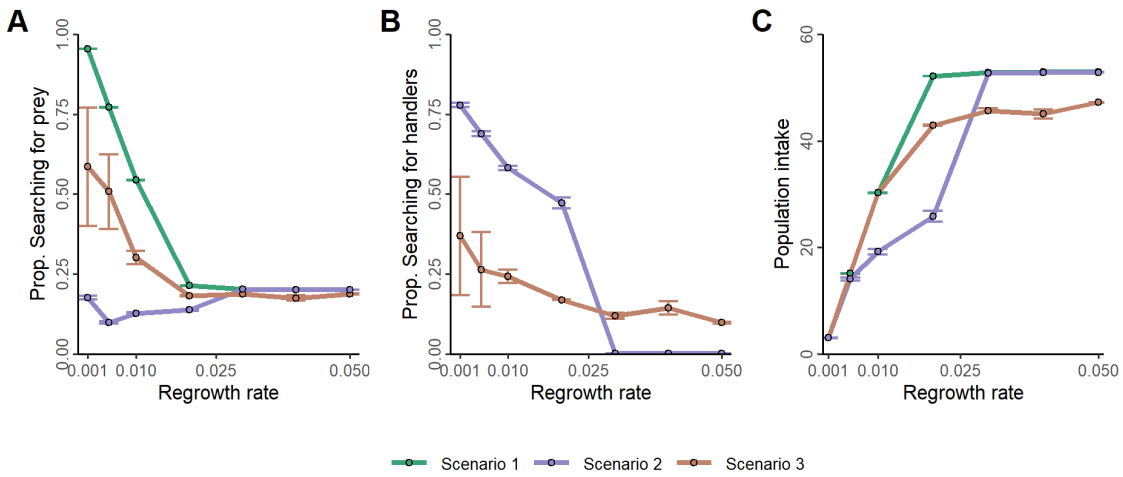

Figure 6: Landscape productivity strongly affects scenario outcomes. (A) The proportion of time spent searching for food decreases with increasing r_{max} in scenarios 1 and 3 but remains relatively stable within scenarios. This is partly due to a higher proportion of time spent handling at higher prey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