The joint evolution of movement and competition strategies

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Abstract

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

Introduction

Foraging competition is a ubiquitous feature of animal ecology (Krebs and Davies, 1978), and individuals can compete for food indirectly by depleting a common resource ('exploitation'), or through direct interactions that reduce resource intake ('interference'; Birch, 1957). Kleptoparasitism ('stealing' resources from another individual), is a special case of interference competition, widespread among animals (Iyengar, 2008). Since competition has a spatial context, animals should account for the locations of intraspecific foraging competitors when deciding where to move (Nathan et al., 2008). Experimental work shows that indeed, competition, as well as the pre-emptive avoidance of competitive interactions, affects animal movement decisions (Goss-Custard, 1980; Vahl et al., 2005a; Rutten et al., 2010b; Laskowski and Bell, 2013, see also Rutten et al. 2010a; Bijleveld et al. 2012). This is expected to have downstream effects on forager distributions across resource patches (e.g. Fretwell and Lucas, 1970), as well as species distributions (e.g. Duckworth and Badyaev, 2007, see Schlägel et al. 2020 for background). Animal movement decisions are thus likely to be adaptive responses to 'landscapes of competition', with competitive strategies themselves being evolved responses to animal distributions. Studying this joint evolution is key to understanding the spatial distribution of animals, but this is nearly impossible at large spatio-temporal scales — making models necessary.

Individual-to-population models of animal space-use, including the ideal free distribution (IFD; Fretwell and Lucas, 1970), information-sharing models (Giraldeau and Beauchamp, 1999; Folmer et al., 2012), and producer-scrounger models (Barnard and Sibly, 1981; Vickery et al., 1991; Beauchamp, 2008) often treat foraging competition in highly simplified ways. Most IFD models, for instance, consider resource depletion unimportant or negligible (continuous input models, see Tregenza, 1995; van der Meer and Ens, 1997), or make simplifying assumptions about interference competition, even modelling an *ad hoc* benefit of grouping (e.g. Amano et al., 2006). Producer-scrounger models primarily examine the benefits of choosing either a producer or scrounger strategy given local conditions, such as the number of conspecifics (Vickery et al., 1991), or the order of arrival on a patch (Beauchamp, 2008). These models simplify the mechanisms by which competitive decisions are made, often ignoring spatial structure (see also Holmgren, 1995; Garay et al., 2020; Spencer and Broom, 2018).

However, competition occurs in a spatial context, which can determine both *which* competitive interactions (epxloitation or interference) can occur, as well as their payoff (Beauchamp, 2008), making both the presence of resources and potential competitors important movement cues. How animals are assumed to integrate the payoffs of competition strategies into their movement decisions has important consequences for expected population distributions (van der Meer and Ens, 1997; Hamilton, 2002; Beauchamp, 2008). Many models assume ideal movement and competition according to fixed rules (Vickery et al., 1991; Holmgren, 1995; Amano et al., 2006), but populations likely contain significant individual variation in movement and competition characteristics, such that individuals make different decisions given the same cues (Laskowski and Bell, 2013). Rather than taking a purely ecological approach and assuming such differences (e.g. White et al., 2018), modelling the evolution of movement rules in a competitive landscape can reveal whether individual variation emerges in plausible ecological scenarios (as in Getz et al., 2015). Finally, the functional importance of environmental cues to movement and competition decisions in evolutionary models should ideally be joint outcomes of selection, allowing, for example, different competition strategies to be associated with different movement rules (Getz et al., 2015).

Here, we present a fine-scale, spatially-explicit, mechanistic model of foraging competition, with population distributions shaped by the *joint evolution* of competition and movement strategies. In our model, individuals move on a resource landscape with discrete, depletable prey which must be 'handled' before consumption (Ruxton et al., 1992). Foragers make movement decisions using an inherited (and evolvable) strategy which integrates local cues, such as the local resource and competitor densities. Individuals also choose between two foraging strategies: searching for prey (foraging) or stealing prey from conspecifics (kleptoparasitism); the mechanism underlying this foraging choice is also inherited. Over three scenarios, we first examine exploitation competition alone (scenario 1), then introduce kleptoparasitic interference as a fixed, inherited strategy (scenario 2), and finally allow kleptoparasitism to be conditioned on local environmental cues (scenario 3). Our model reveals how individual movement and competition strategies jointly evolve, and allows us to take ecological snapshots of the distribution of consumers and their resources over evolutionary time. These snapshots allow us to test whether consumer-resource distributions resulting from the co-evolution of compe-

tition and movement strategies correspond to standard IFD predictions. We investigate three primary questions: *(1)* Under what conditions does kleptoparasitism evolve and persist? *(2)* Does conditional kleptoparasitism evolve under broader conditions than a polymorphism of fixed strategies? *(3)* Does the spatial distribution of competitors and resources correspnd to IFD expectations?

The Model

We implemented an individual-based evolutionary simulation model based on wading birds (e.g. oystercatchers, *Haematopus* spp.), which are extensively studied in the context of foraging competition, both empirically (e.g. Vahl et al., 2005*a*,*b*, 2007; Rutten et al., 2010*a*,*b*), and using IBMs (reviewed in Stillman and Goss-Custard, 2010). We simulated a population with a fixed size (N = 10,000), moving on a landscape of 512^2 grid cells (approx. 1 individual per 26 cells), with wrapped boundaries; individuals passing beyond the bounds at one end re-appear on the opposite side. The model has two time scales, first, an ecological time scale of T timesteps comprising one generation (default = 400), during which individuals move, make foraging decisions, and handle prey-items they find or steal. Individuals are immobile while handling food items, creating the conditions for kleptoparasitism (Brockmann and Barnard, 1979; Ruxton et al., 1992). On the second, evolutionary time scale of 1,000 generations, individuals reproduce, transmitting their movement and foraging strategies to their offspring, whose number is proportional to individual intake at the ecological time scale (Hofbauer and Sigmund, 2003).

Resource Landscape

Resource landscape cells form 1,024 regularly spaced clusters of high-productivity areas ('resource peaks'; see Fig. 1C; panel *gen: 1*, showing a subset of 60^2 cells); each peak is approximately 16 cells away from neighbouring peaks. We considered our discrete resources, called 'prey-items' to represent mussels, a common prey of many waders. Each cell has a constant probability of generating one new prey-item per timestep, the cell-specific growth rate r, which declines from the centre of each peak (called r_{max}) to its periphery (see Fig. 1C). Thus the cen-

tral cell generates prey-items five times more frequently than peripheral cell: at r_{max} = 0.01, central cells generate one item per 100 timesteps (four items/generation), while the peripheral cells generate one item only every 500 timesteps (< one item/generation). All landscape cells have a uniform carrying capacity K of 5 prey-items; while a cell is at carrying capacity its r is 0.

Foragers perceive a cue indicating the number of prey-items P in a cell, but fail to detect each item with a probability q, and 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 find a prey-item must handle it for a fixed handling time T_H (default = 5 timesteps), before consuming it (Ruxton et al., 1992). Natural examples include the time required for an oystercatcher to break through a mussel shell, or a raptor to subdue prey; overall, the handling action is obvious, and the prey is not fully under the control of the finder (Brockmann and Barnard, 1979). Foragers that do not find a prey-item are considered idle, and are counted as 'non-handlers'. Similarly, handlers that finish processing their prey in timestep t return to the non-handler state, foraging only in timestep $t + 1$.

Movement and Competition Strategies

Movement Strategies   We model movement as comprised of small, discrete steps of fixed size, which are the outcome of individual movement decisions made using evolved movement strategies. Across scenarios, individuals make movement decisions by selecting a destination cell, after assessing potential destinations based on available cues (similar to resource selection; Manly et al., 2007), an approach used previously by Getz et al. (2015, 2016) and White et al. (2018). In timestep t, individuals scan the nine cells of their Moore neighbourhood (including their current location) for three environmental cues: the number of prey-items P, the density of handlers H, and the density of non-handlers N. Individuals rank potential destinations (including the current cell) by their suitability S, where $S = s_P P + s_H H + s_N N$, and move to the most suitable cell in timestep $t + 1$. The weighing factors for each cue, s_P, s_H, and s_N, are genetically encoded and transmitted between generations. All individuals move simultaneously, and then implement their foraging or kleptoparasitic behaviour to acquire prey.

6

However, handlers do not make any movements until they have fully handled and consumed their prey.

Scenario 1: Exploitative Competition In scenario 1, individuals (called foragers) move and probabilistically find, handle, and consume prey-items, competing only exploitatively. Foragers can be either in a 'searching' or a 'handling' state, and the only evolvable properties are the cue weighing factors which determine cell suitability scores (s_P, s_H and s_N).

Scenario 2: Fixed Interference Competition In scenario 2, the competition strategy is genetically determined and transmitted from parents to offspring: exploitative competition (by foragers), or kleptoparasitic interference (by kleptoparasites). Kleptoparasites cannot extract prey-items directly from the landscape, and only steal from handlers (see Holmgren, 1995). Kleptoparasites are modelled as always being successful in stealing from handlers, and such successful surprise attacks are commonly observed among birds (Brockmann and Barnard, 1979). However, if multiple kleptoparasites target the same handler, only one (randomly selected) is considered successful — thus kleptoparasites compete exploitatively among themselves. Handlers robbed of prey subsequently 'flee' up to 5 cells away from their location. Having acquired prey, kleptoparasites become handlers, 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. Unsuccessful kleptoparasites are considered idle, and are counted as non-handlers.

Scenario 3: Conditional Interference Competition In scenario 3, each individual can either act as a forager, or as a kleptoparasite, depending on its assessment of local circumstances. Additionally, individuals process cell-specific environmental cues in timestep t to determine their strategy in the next timestep as

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\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 heritable between generations. Apart from the ability to switch between foraging and kleptoparasitism, the com-

7

154 petition dynamics are the same as in scenario 2.

Reproduction and Inheritance

156 Our population of fixed size (N = 10,000) has discrete, non-overlapping generations, with hap-
157 loid, asexual reproduction. Each individual has 7 gene loci encoding the (numeric) decision
158 making weights; only the weights controlling individual movement (s_P, s_H, s_N) are active in
159 scenarios 1 and 2. In scenario 3, the weights for competition decisions (w_P, w_H, w_N, w_0) are
160 also active, and are transmitted from parents to offspring.

161 Each individual's number of offspring is proportional to the individual's total lifetime intake
162 of resources; hence, resource intake is used as a proxy for fitness (Hofbauer and Sigmund,
163 2003). A weighted lottery (with weights proportional to lifetime resource intake) selects a
164 parent for each offspring in the subsequent generation (prior implementation in Tania et al.,
165 2012; Netz et al., 2020). Across scenarios, the movement decision-making weights are subject
166 to rare, independent mutations ($p_{mutation}$ = 0.001). The mutational step size (either positive or
167 negative) is drawn from a Cauchy distribution with a scale of 0.01 centred on zero, allowing
168 for a small number of very large mutations while most mutations are small. In scenario 2, we
169 allow a forager to infrequently mutate into a kleptoparasite (or *vice versa*; $p_{mutation}$ = 0.001). In
170 scenario 3, the foraging weights also mutate as described above. We initialised each offspring
171 at random locations on the landscape, leading individuals to experience conditions potentially
172 very different from those of their parent.

Simulation Output and Analysis

174 We ran all three scenarios at a default r_{max} of 0.01, which we present in the RESULTS, and also
175 across a range of r_{max} values between 0.001 and 0.05 (see Fig. 6 and Supplementary Material
176 Figs. 1.1 – 1.3).

Population Activities and Intake   Across scenarios, in each generation, we counted the num-
178 ber of times foragers were searching for prey, kleptoparasites were searching for handlers, and
179 the number of timesteps that individuals of either strategy were handling a prey-item. We refer
180 to the ratio of these values as the population's 'activity budget'. We examined how the popula-

tion activity budget developed over evolutionary time, and whether a stable equilibrium was reached. Furthermore, we counted the population's mean per-capita intake per generation as a measure of population productivity.

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

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

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

9

Results

Scenario 1: No Kleptoparasitism

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

Scenario 2: Co-existence of Foragers and Kleptoparasites

In scenario 2, with fixed foraging and kleptoparasitism allowed, the spatial distribution of prey-items at equilibrium is very different from scenario 1. Consumers graze down resource peaks until few prey-items remain on the landscape; however, within 50 generations the resource landscape recovers with prey abundances higher than in the earliest generations (Fig. 2A). This is because of the emergence of kleptoparasites (Fig. 2B): in early generations, kleptoparasites are rare, and the activity budget, the mean per-capita intake, and the distribution of consumers over the landscape, are similar to scenario 1. As resources are depleted and kleptoparasite-handler ecounters become more common than forager-prey encounters, kleptoparasitism becomes the majority strategy (a stable $\sim 70\%$ of the population; see Fig. 2B), and searching for handlers to rob becomes the commonest activity. However, the high frequency of this activity and the low frequency of handling, indicate that few kleptoparasites are successful at robbing handlers. With few foragers, few prey-items are extracted from the landscape, which recovers beyond its initial prey abundance within 50 generations (Fig. 2A). As fewer prey-items are extracted overall, mean per-capita intake also declines from an initial peak (Fig. 2C). Despite the strong spatial structure of the resource landscape within 50 generations, the correlation between consumers (of either strategy) and cell productivity remains weak or zero

10

across generations (Fig. 2D).

The increase of kleptoparasites from a negligible fraction to the majority strategy (Fig. 3A) is associated with an evolutionary divergence of movement strategies between foragers and kleptoparasites. While all individuals (both foragers and kleptoparasites) evolve to prefer high prey density and avoid high non-handler density (see Supplementary Material Fig. 2.2), the two types of competition strategy differ substantially in their response to handlers (Fig. 3B, 3C). Kleptoparasites very rapidly (within 3 generations) evolve a strong preference for moving towards handlers, which are their primary resource (Fig. 3B). In the absence of kleptoparasites, foragers would evolve a preference for moving towards handlers (see Supplementary Material Fig. 2.1), but, with kleptoparasites common in the population, searching foragers avoid and prefer handlers in about equal proportions (Fig. 3C). While all kleptoparasites evolve to prefer moving towards handlers, the strength of the attraction to handlers shows multiple distinct values ('morphs'), which are remarkably persistent across generations (Fig. 3B). In replicate 3, for example, the commonest movement strategy is only weakly attracted to handlers, but this strategy coexists with various strategies that are all strongly attracted to handlers (Fig. 3B). The movement strategies of foragers show an even higher degree of polymorphism (Fig. 3C): no movement strategy dominates, some foragers strongly prefer handlers, others strongly avoid them, and yet others are neutral to handlers.

Scenario 3: Condition-dependent Kleptoparasitism

In scenario 3, with conditional competition strategies based on local environmental cues, consumer-resource distributions are substantially different from the two previous scenarios. Initially, as in scenario 1, individuals deplete the resource landscape of prey-items within ten generations (Fig. 4A). By generation 50, the resource landscape recovers some of the spatial structure of early generations, but prey-item abundances do not match the recovery seen in scenario 2. This too is because, by generation 30, all individuals choose to target any handlers in the vicinity for prey-items, rather than forage for prey themselves ("opportunistic kleptoparasitism"; Fig. 4B; *orange line*). However, unlike scenario 2, individuals search for prey more often and steal less (at or below 25%; compare Fig. 2B), preventing a full recovery of the resource landscape. Consequently, mean per-capita intake stabilises (after an initial spike, as in scenarios 1 and 2)

11

within ten generations to a level similar to scenario 1 (Fig. 4C). Using conditional foraging strategies, individuals are able to switch between resource types (prey and handlers) depending on which is more profitable (Emlen, 1966), and appear to track resources. Thus, while not as strong as predicted by IFD theory, the correlations between consumer abundance and cell productivity are weakly positive (Fig. 4D).

Movement Rules on Depleted Landscapes

Orienting movement can be a challenge when local prey *density* may provide very limited information about local *productivity*. In our model, prey-depletion leads parts of the resource landscape to become 'clueless regions' (Perkins, 1992), where foragers cannot make directed movements based on prey-item abundances alone, as all neighbouring item 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 cells with an intermediate r, which have more prey than peripheral cells of resource peaks, but fewer prey than the central cells. This proportion rapidly declines to a much lower value within 10 generations in all three scenarios.

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

Scenario 2 landscapes develop similarly to scenario 1 in early generations (Fig. 5A2). However, within 50 generations, most cells bear items as extraction is reduced, with differences among cells according to their r (see also Fig. 2A). Thus > 75% of cells have a different number of items from neighbouring cells (Fig. 5A2 – panel *gen: 50*, 5B2). Unlike scenario 1, the rapid increase in handler preference is driven by kleptoparasites becoming the majority strategy (see

12

above). Scenario 3 is similar to scenario 2, except that only about half of all cells have a different number of prey-items from neighbouring cells (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.

Effect of Landscape Productivity

The prey-item regrowth rate of central cells of resource peaks (r_{max}) is a proxy for the productivity of the resource landscape overall. Predictably, the value of r_{max} has a marked effect on evolved population activity budgets, mean per-capita intake, and even evolved strategies. The frequency of foraging reduces with r_{max} in scenarios 1 and 3, and handling increases, as prey-items become more abundant. In scenario 2 however, the frequency of handling is relatively unaffected by increasing r_{max} (Fig. 6A).

The frequency of kleptoparasitism differs between scenarios 2 and 3 (Fig. 6B). In scenario 2, kleptoparasitism forms $> 75\%$ of all activities at 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}, forager-prey encounters are more common than kleptoparasite-handler encounters, in both early (< 10) and later generations (> 50). Consequently, kleptoparasites have relatively much lower fitness than foragers, and do not proliferate. Thus at high r_{max}, a scenario 2 population is nearly identical to a scenario 1 population; while some kleptoparasites may be seen in later generations, these occur most likely due to ephemeral mutations in the forager strategy.

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 mean per-capita intakes at low r_{max}, at intermediate regrowth rates (0.01, 0.02), conditionally kleptoparasitic populations achieve a higher mean per-capita intake than populations using fixed strategies. Only at high r_{max}, when fixed strategy populations effectively convert to purely forager populations, do they achieve a higher intake than conditional strategy populations (Fig. 6C).

Discussion

Our spatially-explicit individual-based model implements the ecology and evolution of movement and competition decisions, as well as resource dynamics, in biologically plausible ways, offering a new perspective on individual-to-population distribution models. Individuals competing exploitatively by depleting discrete prey-items cause large areas to become devoid of direct resource cues, causing a mismatch between individual distributions and landscape productivity, and promoting the evolution of movement strategies integrating both direct (prey-items) and indirect resource cues (handlers). Fixed kleptoparasitic interference rapidly establishes itself on landscapes where stealing is more time-efficient than searching for prey. The emergence of kleptoparasitism is accompanied by the evolution of movement strategies that favour moving towards handlers, which are the primary resource of kleptoparasites. When competition strategy can be chosen conditional on local cues, the population's mean per-capita intake is significantly higher than that of a population with fixed strategies, and unlike fixed strategy populations, kleptoparasitism does not go extinct on high-productivity landscapes. However, across scenarios, individuals broadly do not match the productivity of the resource landscape, contrary to the predictions of IFD based models, which predict input matching for some (Parker and Sutherland, 1986; Holmgren, 1995; Hamilton, 2002), or all competitive types Korona (1989).

Existing models of competition and movement impose fixed movement rules on individuals to mimic either ideal or non-ideal individuals (Vickery et al., 1991; Cressman and Křivan, 2006; Amano et al., 2006; Beauchamp, 2008; Stillman and Goss-Custard, 2010; White et al., 2018). When included, individual competitive strategies represent differences in competitive ability (e.g. Parker and Sutherland, 1986; Holmgren, 1995; Hamilton, 2002), or a probabilistic switch between producing and scrounging (Beauchamp, 2008). In contrast, our model allows individuals' movement (and competition) decisions to be adaptive responses to local environmental cues. Similar to Getz et al. (2015, 2016) and White et al. (2018), our individuals choose from among the available movement options after weighing the local environmental cues, similar to resource selection functions (Manly et al., 2007; White et al., 2018). Local environmental cues in our model are constantly changing, as we model discrete, depletable prey-items, con-

14

trasting with many IFD models (Tregenza, 1995; Amano et al., 2006). This allows for a more plausible, fine-scale consideration of exploitation competition, which is often neglected, and allows the cues sensed by individuals to strongly structure the distribution of competitors (see below). Adaptive responses must have an explicit evolutionary context, and consider multiple generations of the population. We follow Beauchamp (2008) and Getz et al. (2015) in allowing the decision making weights for movement, and variation thereof, to be the outcomes of natural selection. However, instead of using 'evolutionary algorithms' (Beauchamp, 2008; Getz et al., 2015, 2016), we consider a more plausible evolutionary process — the number of offspring is proportional to individual fitness (Hofbauer and Sigmund, 2003), the genetic loci mutate independently, and mutation size does not decrease over generations ('simulated annealing' Beauchamp 2008; Getz et al. 2015), while large-effect mutations can occur throughout the simulation. Similarly, rather than determining competition strategy probabilistically or ideally (Vickery et al., 1991; Beauchamp, 2008; Tania et al., 2012), our individuals' competition decisions are also shaped by selection (in scenarios 2 and 3).

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

We find substantial individual variation in the strength of movement weights within popu-

15

lations, as expected from heterogeneous landscapes (see Supplementary Material Fig. 2.1 – 2.3; see Wolf and Weissing 2010 for background). The persistence of multiple 'movement morphs' across generations indicates that they are alternative movement strategies of equal fitness (see Getz et al., 2015). Indeed, polymorphism in movement rules may help reduce competition as individuals make subtly different movement and competition decisions when presented with the same cues (Laskowski and Bell, 2013, see also Wolf and Weissing 2012). Scenario 2 also shows significant within-strategy individual variation in movement weights, which might help ameliorate within-strategy exploitation competition, or help foragers avoid kleptoparasites (Wolf and Weissing, 2012; Laskowski and Bell, 2013). Interestingly, scenario 3 has the least individual variation in movement rules, potentially because plasticity in competition strategy dampens such diversification (Pfennig et al., 2010), but also possibly because the ability to switch between prey types reduces the intensity of competition. Here, non-handler avoidance shows the most morphs, but it is unclear whether this variation is linked to the frequency with which individuals use either foraging strategy — potentially leading to subtle, emergent behavioural differences that are conditioned on the local environment (Wolf and Weissing, 2010, 2012).

IFD models predict that individual movement should result in consumer distributions tracking the profitability of resource patches (Fretwell and Lucas, 1970; Parker, 1978), with dominant competitive types (including kleptoparasites) monopolising the best patches (Parker and Sutherland, 1986; Holmgren, 1995; Hamilton, 2002, but see Korona 1989). In scenarios 2 and 3, kleptoparasitic individuals unsurprisingly and rapidly evolve to track handlers (a direct resource), while avoiding non-handlers (potential competitors). However, these evolved rules do not lead kleptoparasites to occupy the best cells as predicted (Parker and Sutherland, 1986; Holmgren, 1995; Hamilton, 2002). Across our scenarios (including scenario 1), individual density is only weakly correlated with cell productivity. In scenario 2, this departure from predictions is driven by the contrasting movement rules of foragers, which evolve to *avoid* handlers as well as non-handlers, both of which might be kleptoparasites (cryptic interference; seen in interference-sensitive waders Folmer et al. 2010; Bijleveld et al. 2012; see Supplementary Material). Thus, foragers likely avoid resource peaks, which are more likely to have handlers (due to the higher probability of forager-prey encounters Parker and Sutherland, 1986; Holmgren,

1995; Hamilton, 2002). Fixed kleptoparasites cannot extract prey themselves, and must move off resource peaks to track and rob handlers (similar to Parker and Sutherland, 1986), breaking the link between individual density and productivity. This shows the pitfalls of simplistically linking current ecological conditions with population distributions without considering competitive strategies or evolutionary history.

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

17

Data and Code Availability

Simulation model code is on Github: github.com/pratikunterwegs/Kleptomove and Zenodo: zenodo.org/record/4905476.

Simulation data are available from DataverseNL as a draft: https://dataverse.nl/privateurl.xhtml?token=1467 2c30-486b-a059-1e37be815b7c; persistent link after publication: doi.org/10.34894/JFSC41.

Data analysis code is on Github: github.com/pratikunterwegs/kleptomove-ms and on Zenodo: doi.org/10.5281/zenodo.4904497.

Acknowledgments

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20

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1 Figure legends

A
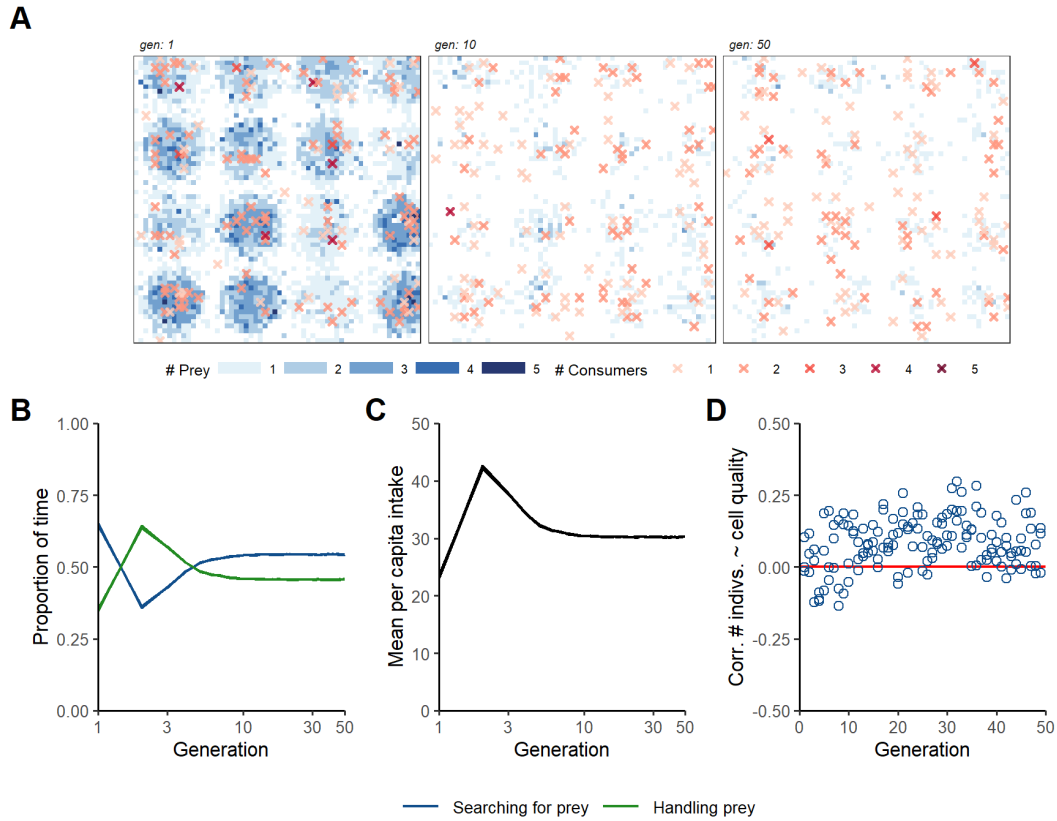
Figure 1: Eco-evolutionary implications of pure exploitation competition (scenario 1). (A) When a population is comprised solely of foragers seeking prey on a resource landscape, the initially well-stocked resource landscape is swiftly depleted within 10 generations (out of 1,000 simulated). This sparsity in prey-item abundance is maintained throughout the remaining generations of the simulation. Individuals, whose local density is shown by coloured crosses, are scattered over the landscape. These dynamics are explained by the fact that **(B)** within 20 generations of evolution, the population reaches an equilibrium in the relative proportion of time spent on searching prey and handling prey, and in **(C)** the total intake of the population. **(D)** In a departure from the intake matching rule of IFD theory, cell occupancy (number of foragers per cell) is only weakly correlated with cell productivity r. Panel **A** shows a single replicate, while panels **B, C** and **D** show three replicate simulations (lines overlap almost perfectly); all panels are for $r_{max} = 0.01$. NB: Both **B, C** show a log-scaled X axis to more clearly show dynamics in early generations.
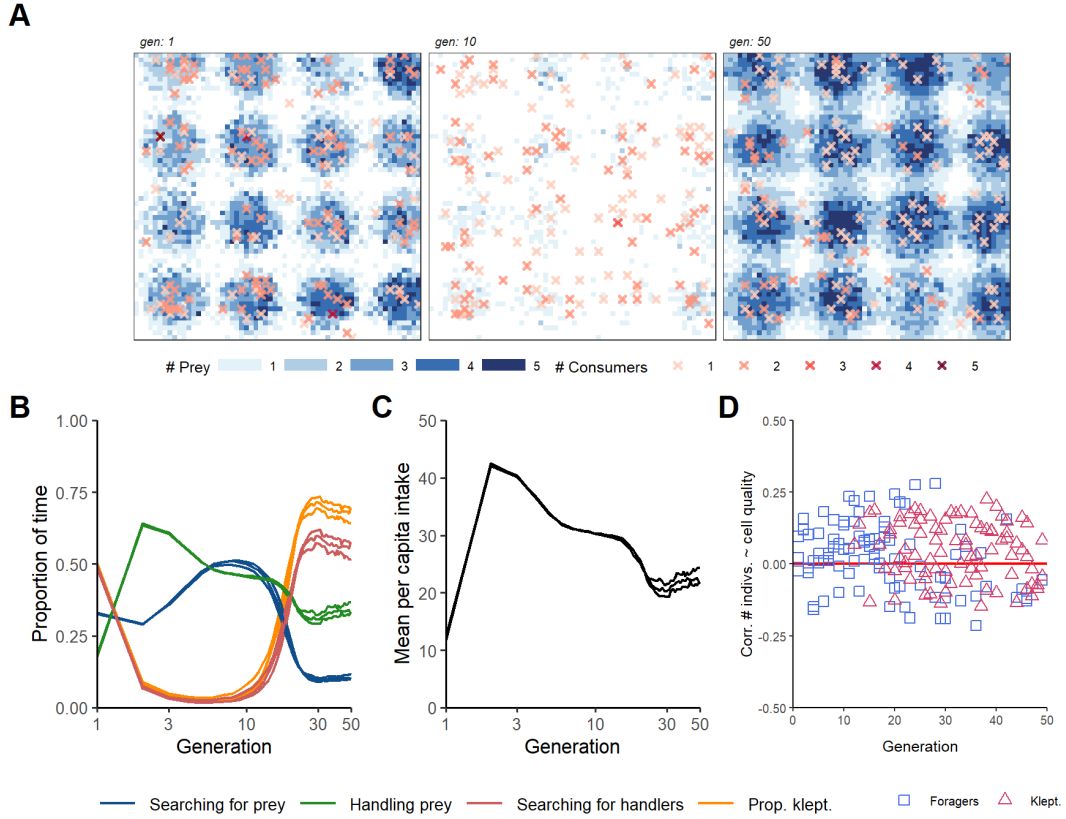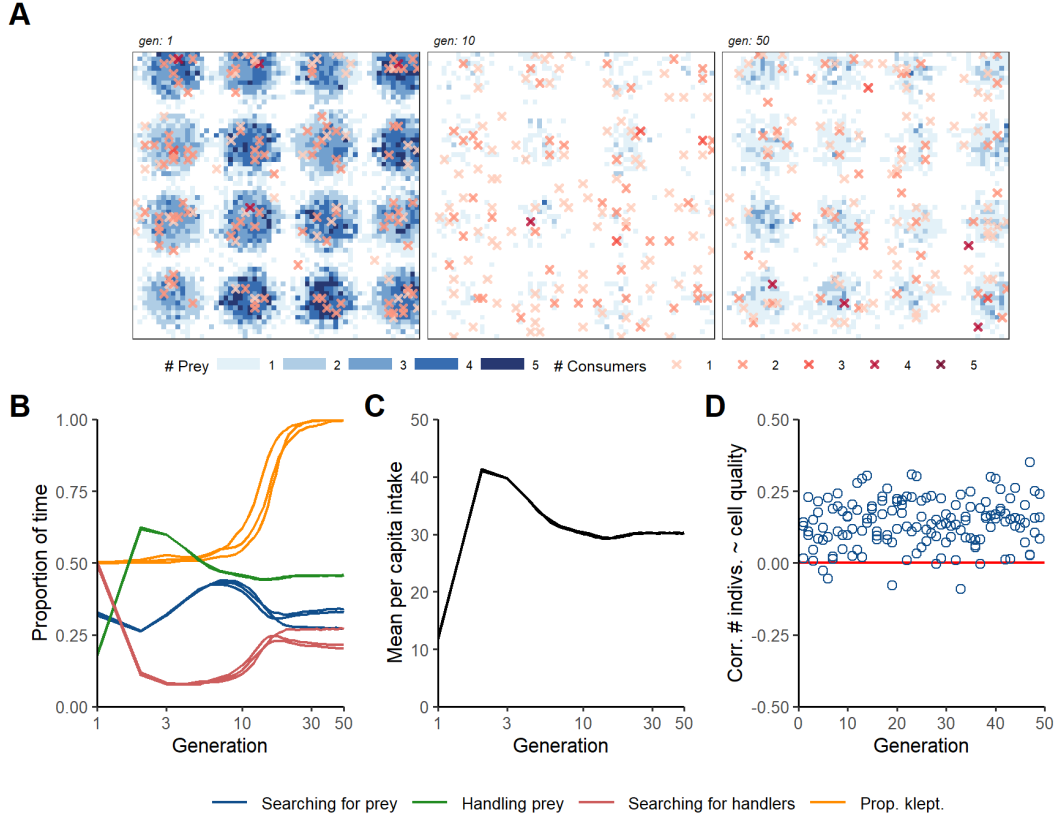
Figure 2: Eco-evolutionary implications of the coexistence of foragers and kleptoparasites (scenario 2). In populations with both foragers and kleptoparasites, **(A)** the initially well-stocked resource landscape is drastically depleted by generation 10; however, prey densities recover strongly by generation 50, even beyond the densities in generation 1. The local density of individuals on occupied cells is shown as coloured crosses. **(B)** An equilibrium between the strategies is reached within 30 generations, with the relative frequency of kleptoparasites (orange line) first dropping to very low levels but later recovering to reach a high level ($\sim 70\%$) in all three replicates. The activity budget parallels the relative frequency of kleptoparasites, and at equilibrium, about 10% of the individuals are foragers searching for prey, 50% are kleptoparasites searching for handlers, and 40% are handlers (either foragers or kleptoparasites). **(C)** In early generations, when kleptoparasites are rare, the population intake rate exhibits the same pattern as in Fig. 1B, dropping to a lower level with the emergence of kleptoparasites. This is accompanied by an increase in the proportion of time spent on stealing attempts (red line – **B**), and a corresponding decrease in prey seeking (by searching foragers; blue line – **B**), and handling (green line – **C**). **(D)** Cell occupancy (local density of foragers per cell) is only weakly correlated with cell productivity r, dropping to zero at equilibrium. Panel **A** shows a single replicate, while **B, C** and **D** show three replicates; all panels are for $r_{max} = 0.01$.
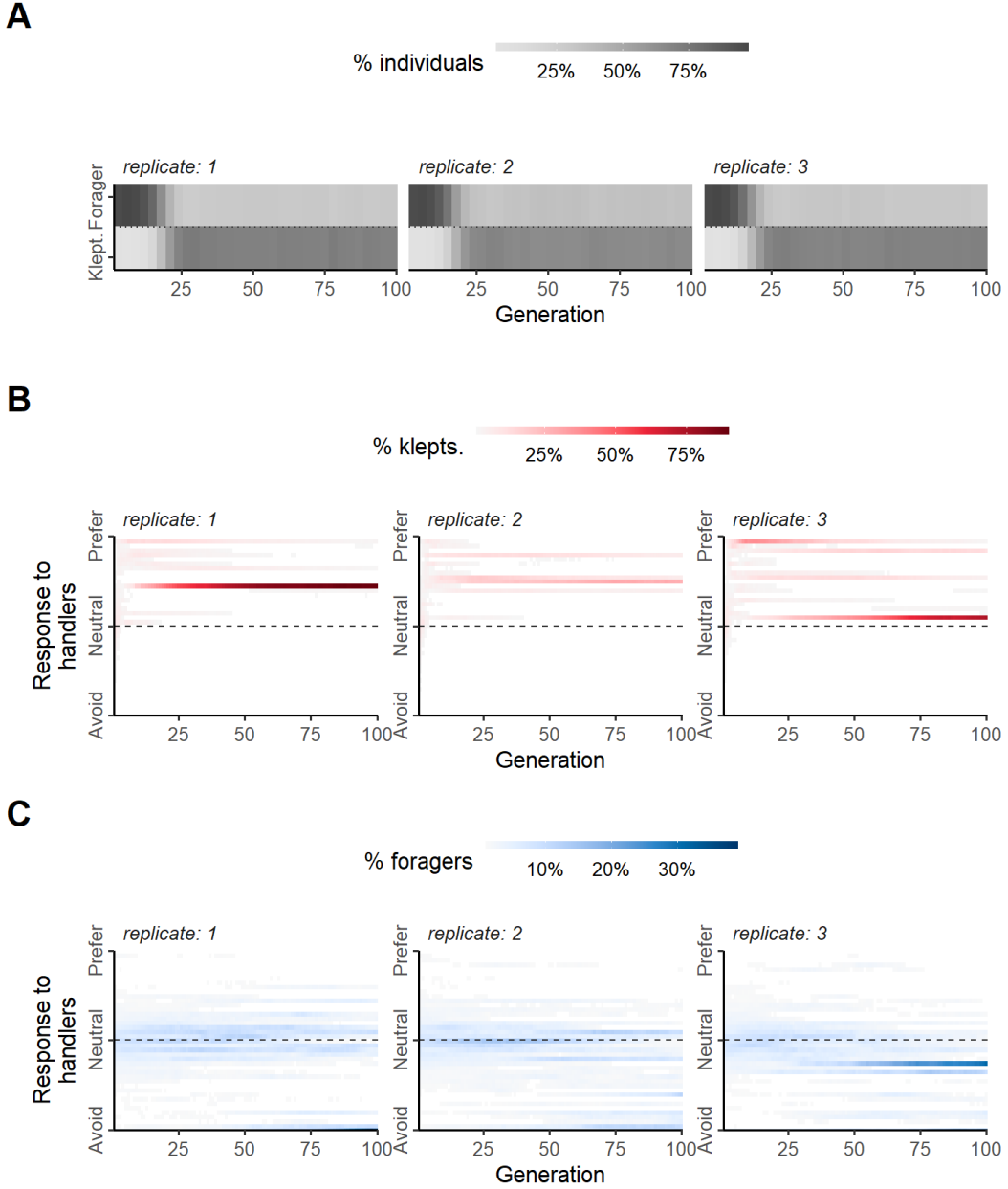
Figure 3: Divergence of movement strategies between foragers and kleptoparasites (scenario 2). **(A)** Kleptoparasitism rapidly becomes the more frequent strategy in scenario 2 populations for the parameters considered, with no differences across replicates. However, replicates differ considerably in 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 $r_{max} = 0.01$.
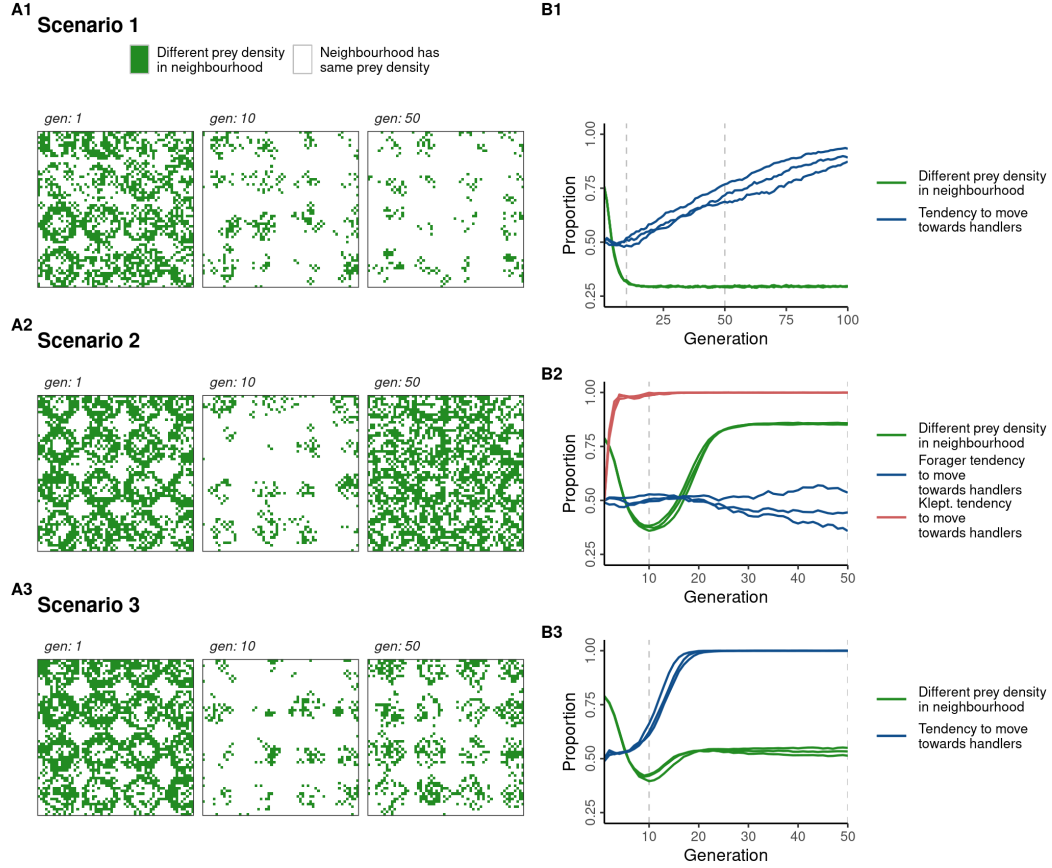
Figure 5: Uninformative prey densities and the evolution of alternative movement cues. **(A1, A2, A3)** On cells coloured green, local prey densities are informative for movement, as the central and neighbouring cells have different prey densities. While differences in local prey densities provide informative 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.
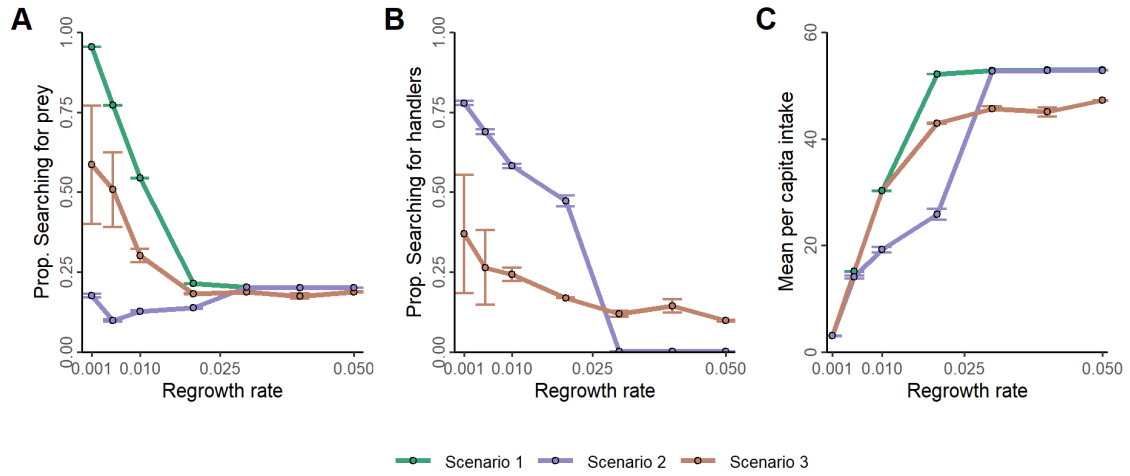
Figure 6: Landscape productivity strongly affects scenario outcomes. (A) The proportion of time spent searching for food decreases with increasing r_{max} in scenarios 1 and 3 but remains relatively stable within scenarios. This is partly due to a higher proportion of time spent handling at higher prey 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.