

The joint evolution of movement and competition strategies

Pratik R. Gupte^{1,*†}

Christoph F. G. Netz^{1,†}

Franz J. Weissing^{1,*}

1. Groningen Institute for Evolutionary Life Sciences, University of Groningen, Groningen 9747 AG, The Netherlands.

* Corresponding authors; e-mail: p.r.gupte@rug.nl or f.j.weissing@rug.nl

† Co-first authors.

Abstract

Competition is a key process in animal spatial ecology, and can drive movement decisions and thus, spatial distributions. In turn, movement decisions and local conditions can strongly affect the competitive strategy — exploitation or interference — of animals. Yet competition is often treated in highly simplified ways in classical models of animal space-use, and dissociated from its natural spatial context. Both movement and competition strategies are frequently modelled with arbitrary assumptions of how individual decision-making integrates available environmental cues, when these should be joint outcomes of evolutionary processes. Here, we present the first mechanistic, spatially-explicit, individual-based model of intraspecific competition with the evolution of foraging competition and movement strategies. Over the three scenarios of our model, we examine the joint evolution of movement with (1) exploitation competition, (2) exploitation or interference as fixed strategies, and (3) competition strategy conditioned on local cues. Thus, we allow different competition strategies to be associated with different movement styles, and to examine the evolution of individual movement rules, and consequences for the spatial structure of the resource landscape. We show that on our highly dynamic model landscapes, populations evolve multiple combinations of foraging and movement strategies, yet do not fit an ideal free distribution, which is a constantly moving target. Resource consumption leads to multiple, broad, ‘clueless regions’ where individuals have few cues to movement; thus consumer movement can lead to landscapes favouring interference strategies. While fixed competition strategies lag foraging-only and conditional competition strategies’ performance, abundant resources allow fixed strategies to outperform conditional kleptoparasites.

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*b,a*, 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. For instance, it is difficult to establish whether interference, and especially kleptoparasitism, represents a foraging specialisation shown by part of the population, or whether it is an opportunistic strategy conditioned on local cues. Furthermore, it is nearly impossible to study the causes and consequences of competition — such as its coevolution with movement strategies, or the effect on resource landscapes — at evolutionary time-scales in most animals, due to a lack of long-term data (Clutton-Brock and Sheldon, 2010).

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 continuous value (a

growth rate), such that no patches can be entirely devoid of resources (see a review in Tregenza, 1995). 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 rules, 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 rules*, 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 rules (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 rules (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 rules 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 the first mechanistic, individual-based model of intraspecific competition in a spatially explicit context, where competition is shaped by the 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 individual-based evolutionary simulation models (see for a conceptual basis Huston et al., 1988; DeAngelis and Diaz, 2019), which 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). This allows us to both focus more closely on the interplay of exploitation and interference competition, and to examine the feedback between movement and foraging behaviour at evolutionary scales. 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 rules, 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 four primary ques-

tions: (1) Do movement decisions, evolved in the context of exploitation competition, and based on localised cues of resource abundance and competitor presence, lead to an ideal free distribution? (2) Under what conditions does kleptoparasitic interference evolve and persist in a population? (3) What is the association between competition and movement strategies?

2 The Model

We implement an individual-based evolutionary simulation model with three scenarios 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., 2005b,a, 2007; Rutten et al., 2010b,a), 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 25 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 $1 - (q^P)$. As foraging events occur simultaneously, it is possible for more foragers to be considered successful in finding prey than there are discrete items in that cell. This simple case of exploitation competition is resolved by assigning P prey among some N successful searchers at random. Foragers that are assigned a prey item in timestep t begin handling it, and are considered to be handlers 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 rules. 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 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 move about on the landscape and probabilistically find and consume prey items. Between finding and consuming a prey item, individuals must ‘handle’ each prey for a fixed handling time T_H (set at 5 timesteps by default). The handling time dynamic is well known from many systems; for instance, it could be the time required for an oystercatcher to break through a mussel shell, or the time between catching and subduing prey for raptors, with the handling action obvious to nearby individuals, and the prey not fully under the control of the finder (Brockmann and Barnard, 1979). We refer to such individuals as ‘handlers’ for convenience. Handlers are assumed to be fully absorbed in their processing of prey, and do not make any movements until they have fully handled and consumed their prey.

Scenario 2: Fixed Interference Competition The second scenario builds on Scenario 1, with the addition that individuals inherit a fixed strategy to either forage or to steal prey items

193 from handlers. Agents that steal are termed kleptoparasites. Kleptoparasites are always suc-
 194 cessful in stealing from a handler; this may be thought of as the benefit of the element of sur-
 195 prise, a common observation among birds (Brockmann and Barnard, 1979). Individuals that
 196 have been stolen from subsequently ‘flee’ and are moved to a random cell within a Chebyshev
 197 distance of 5. Having acquired prey, a kleptoparasite converts into a handler, but need only
 198 handle prey for $T_H - t_h$ timesteps, where t_h is the time that the prey has already been handled
 199 by its previous owner; thus kleptoparasites save time on handling compared to a forager. Un-
 200 successful kleptoparasites are considered idle, and are also counted as non-handlers. Handlers
 201 that finish processing their prey in timestep t return to the non-handler state and are assessed
 202 as such by other individuals when determining their movements.

203 **Scenario 3: Conditional Interference Competition** In scenario 3, each individual can either
 204 act as a forager, searching for food, or as a kleptoparasite, dependent on its local circumstances.
 205 Individuals process the cell-specific environmental cues P , H , and N to determine their strat-
 206 egy in the next timestep as

$$207 \quad \text{strategy} = \begin{cases} \text{forager,} & \text{if } w_P P + w_H H + w_N N \geq w_0 \\ \text{kleptoparasite,} & \text{otherwise} \end{cases} \quad (1)$$

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

211 2.3 Reproduction and Inheritance

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

mitted parent individuals to their offspring. Population size was fixed, and each generation of individuals is considered to be replaced by its 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 scenario 1, the foraging-decision weights are not relevant, while in scenario 2, the mutation in foraging strategy is modelled as a discrete shift from a searching to a stealing strategy (or vice-versa) with a probability of 0.001. In scenario 3, the foraging weights mutate in the same way as the movement weights, described above. We initialised each offspring at a random location on the landscape; this 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 the forager or kleptoparasite strategy was used in each generation of our simulations, as well as the number of times no strategy could be used because individuals were handling a food item. We refer to the ratio of time spent foraging, stealing, and handling as the population's 'activity budget'. We examined how the population activity budget developed over evolutionary time, and whether a stable ecological equilibrium was reached. Furthermore, we counted the total population intake — the number of items consumed in each generation — as a measure of population productivity.

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

dividuals using either a (3) searching strategy or (4) kleptoparasitic strategy, on each grid cell. We used only a subset of the total landscape (60^2 of 512^2 cells) for further analyses to speed up computation.

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

Resource Landscape Gradients Another measure of whether foragers have achieved the IFD on their resource landscape is whether individuals can improve their intake by moving to another location; in our model, this would be to a neighbouring cell. We calculated the cell-specific item gradient for each landscape snapshot, as the difference in item counts between each cell and its neighbouring cells. We then calculated the proportion of grid cells from which it was possible to move to a neighbouring cell with more prey items, with the expectation that higher values would indicate that achieving the IFD is intrinsically difficult.

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

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 in the Supplementary Material is available on Github (<https://github.com/pratikunterwegs/kleptomove-ms>) and archived on Zenodo (<https://doi.org/10.5281/zenodo.4904497>).

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 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), yet, 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 'habitat matching rule' underlying the IFD Parker (1978), which predicts a near perfect correspondence. 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"). With little variation in this cue initially, and even less variation once prey items are extracted, the foragers move essentially randomly on the landscape.

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 may be explained by the frequency of kleptoparasites, which at first decreases precipitously, but then rises dramatically until kleptoparasites at about 70%, are the more common of the two strategies (Fig. 2B). 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 the frequency of kleptoparasites increases rapidly (Fig. 2B). From generation 30 onwards, as kleptoparasitism becomes the dominant strategy, stealing becomes the dominant activity, and this reflects the proportion of individuals with an inherited kleptoparasitic strategy; a stable $\sim 70\%$ of the population (Fig. 2B). However, the high frequency of futile stealing attempts also indicates that many kleptoparasites are 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. Furthermore, on relatively saturated resource landscapes, searching foragers can move essentially randomly with respect to prey-items, and yet stand a strong chance of finding prey. As kleptoparasites, the numerically dominant strategy, seek to move towards handlers, their primary resource, they too 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 a divergence of the movement rules 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, 3D). In the absence of kleptoparasites, foragers would evolve a preference for moving towards handlers (see Supplementary Figure S4), presumably because handlers are 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, 3D). While all kleptoparasites evolve to prefer moving towards handlers, the strength of the preference shows multiple, distinct values or 'morphs', which are remarkably persistent across generations (Fig. 3B). Many more such 'morphs' are seen among foragers (Fig. 3C).

3.3 Scenario 3: Condition-Dependent Competition Strategies

When individuals are allowed to choose their competition strategy based on local environmental cues, the distribution of individuals and prey items is substantially different from the foragers-only case (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 may be explained by the observation that by generation 30, all individuals have a propensity to steal from handlers (Fig. 4B; *orange line*). However, unlike scenario 2, individuals 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. 4B). 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; B1: scenario 1, B2: scenario 2, B3: scenario 3). In scenario 1, the proportion of cells from which it is possible to move to a neighbouring cell with more items is initially very high ($\sim 75\%$; $r_{max} = 0.01$; Fig. 5A1). 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’ (Perkins, 1992). 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 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, indicating a population very far from the IFD (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 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. At these regrowth rates, the scenario 2 population matches the scenario 1 population, with foragers rapidly converted to handlers.

In scenario 3, kleptoparasitism persists at low frequencies even at the highest regrowth rates (Fig. 6B); thus some foragers lose time in extracting items which are then stolen from them. Consequently, while populations in all three scenarios achieve very similar intakes at low r_{max} , at intermediate regrowth rates (0.01 – 0.025), conditionally kleptoparasitic populations out-

perform 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, evolutionary IBM implements the ecology and evolution of movement and foraging decisions, as well as resource dynamics, in biologically plausible ways, and reaches important conclusions about the distribution of animals in relation to their resources under different scenarios of competition. First, we show that when moving with a limited perception range (the Moore neighbourhood) and competing only by exploitation, individuals evolve movement rules for both direct and indirect resource cues (prey items and handlers, respectively). Regardless, on a resource landscape with discrete prey items, large areas may become devoid of any movement cues, leading to a mismatch between individual distribution, prey item distribution, and landscape productivity. Second, we show that when interference competition in the form of kleptoparasitism is allowed as a fixed strategy, it rapidly establishes itself on landscapes where stealing is more time-efficient than searching for prey. This rapid increase in kleptoparasitism as a strategy is strongly correlated with movement rules than favour moving towards handling foragers, which are the primary resource. In this sense, obligate kleptoparasites may be thought of as forming a quasi-predatory trophic level, with any handling foragers as their prey. Finally, we show that when foraging strategy is allowed to be conditional on local cues, all individuals are opportunistic kleptoparasites. In both the fixed and conditional strategy scenarios, however, foragers are unable to match their resource landscape, as would be predicted by IFD models.

4.1 Comparison with Previous Models

Our model stands in stark contrast with, and offers a plausible alternative to, existing models of individual foraging and movement decisions. The primary difference is in allowing movement and foraging rules to evolve. Unlike models in which movement rules 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 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 gives evolution a first-class treatment, 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 allowing 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 Krivan, 2006).

In a clueless region, the presence of successful foragers is likely to indicate a suitable foraging spot, while the location of unsuccessful individuals signals the opposite (local enhancement; see Giraldeau and Beauchamp, 1999; Beauchamp, 2008). This selects for the evolution of movement rules that integrate individuals' assessment of the condition of intraspecific competitors — an important aspect of using 'social information' (see 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 rules such that only a fraction of the population tracks resource cues, while a larger proportion is relatively insensitive to resource cues, and follows the resource-tracking 'informed leaders' (Guttal and Couzin, 2010). In our model however, the relatively low density of foragers, the inability to share discrete prey items, and the breakdown of spatial autocorrelation in prey abundance due to foraging, means that such a polymorphism does not evolve; all individuals must sense and track resources, while eventually also evolving to aggregate with handlers.

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

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). This correlational selection leads to a much more rapid fixation of handler preference among (1) scenario 2's fixed kleptoparasites, and (2) all foragers in scenario 3, which can opportunistically steal from handlers.

In scenario 2, the emergence and persistence of kleptoparasitism at low r_{max} reduces resource depletion, prey-items are regenerated, and clueless regions are reduced. Ironically, the abundance of item cues is not functionally useful to most foragers; kleptoparasites find themselves in a ‘desert of plenty’ as their only resource is handlers, which are uncommon relative to prey items.

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.

However, two spatio-temporal phenomena are absent from our model that are predicted in a conceptually similar, but very differently implemented chemotactic model of producer-scrounger foraging (Keller-Segel (KS) models Tania et al., 2012). Specifically, spatially explicit KS models predict that a wide range of parameterisations should lead to (1) limit cycles of kleptoparasites and foragers over generations, and (2) spatial limit cycles, or ‘waves of pursuit’, of searching foragers by kleptoparasites over the landscape (Tania et al., 2012). An important reason for this is our implementation of global natal dispersal, which ensures that strategies are well-mixed in each generation, rather than increasing densities of offspring (of either strategy) around the most successful ancestors (‘differential reproduction’). Differential reproduction would allow instabilities related to spatial structuring, whereby increasing kleptoparasite density in an area would eventually lead to lower per-capita intake among kleptoparasites relative to foragers, and consequently an increase in the forager-to-kleptoparasite ratio.

Scenario 3, which allows individuals to opportunistically steal prey items, resolves the strate-

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

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; they thus outperform fixed-strategy populations, and have similar intakes as forager populations on low productivity landscapes. However, at high r_{max} , opportunistic kleptoparasites in scenario 3 have a greater per-capita intake rate than pure foragers, as kleptoparasitic prey acquisition deprives a (foraging) handler of its prey.

Since scenario 3 kleptoparasitic behaviour is conditional, it persists even in populations on high productivity landscapes.

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 research has been carried out in the Theoretical Research in Evolutionary Life Sciences (TRES) group at the Groningen Institute for Evolutionary Life Sciences (GELIFES), according to the requirements of the Graduate School of Science and Engineering (Faculty of Science and Engineering, University of Groningen; Groningen, The Netherlands). This research was supported by an Adaptive Life Programme grant awarded to F.J.W. made possible by the Board of the University of Groningen, the Faculty of Science and Engineering and the Groningen Institute for Evolutionary Life Sciences (GELIFES).

References

- Amano, T., K. Ushiyama, S. Moriguchi, G. Fujita, and H. Higuchi. 2006. Decision-Making in Group Foragers with Incomplete Information: Test of Individual-Based Model in Geese. *Ecological Monographs* 76:601–616.
- Baldauf, S. A., L. Engqvist, and F. J. Weissing. 2014. Diversifying evolution of competitiveness. *Nature Communications* 5:5233.
- Barnard, C. J., and R. M. Sibly. 1981. Producers and scroungers: A general model and its application to captive flocks of house sparrows. *Animal behaviour* 29:543–550.
- Beauchamp, G. 2008. A spatial model of producing and scrounging. *Animal Behaviour* 76:1935–1942.
- Bijleveld, A. I., E. O. Folmer, and T. Piersma. 2012. Experimental evidence for cryptic interference among socially foraging shorebirds. *Behavioral Ecology* 23:806–814.
- Birch, L. C. 1957. The Meanings of Competition. *The American Naturalist* 91:5–18.
- Brockmann, H., and C. Barnard. 1979. Kleptoparasitism in birds. *Animal Behaviour* 27:487–514.

- Case, T. J., and M. E. Gilpin. 1974. Interference Competition and Niche Theory. *Proceedings of the National Academy of Sciences* 71:3073–3077.
- Clutton-Brock, T., and B. C. Sheldon. 2010. Individuals and populations: The role of long-term, individual-based studies of animals in ecology and evolutionary biology. *Trends in Ecology & Evolution* 25:562–573.
- Cressman, R., and V. Křivan. 2006. Migration Dynamics for the Ideal Free Distribution. *The American Naturalist* 168:384–397.
- Dall, S. R. X., L.-A. Giraldeau, O. Olsson, J. M. McNamara, and D. W. Stephens. 2005. Information and its use by animals in evolutionary ecology. *Trends in Ecology & Evolution* 20:187–193.
- Danchin, É., L.-A. Giraldeau, T. J. Valone, and R. H. Wagner. 2004. Public Information: From Nosy Neighbors to Cultural Evolution. *Science* 305:487–491.
- de Jager, M., J. van de Koppel, E. J. Weerman, and F. J. Weissing. 2020. Patterning in Mussel Beds Explained by the Interplay of Multi-Level Selection and Spatial Self-Organization. *Frontiers in Ecology and Evolution* 8.
- de Jager, M., F. J. Weissing, P. M. J. Herman, B. A. Nolet, and J. van de Koppel. 2011. Lévy Walks Evolve Through Interaction Between Movement and Environmental Complexity. *Science* 332:1551–1553.
- DeAngelis, D. L., and S. G. Diaz. 2019. Decision-Making in Agent-Based Modeling: A Current Review and Future Prospectus. *Frontiers in Ecology and Evolution* 6.
- Duckworth, R. A., and A. V. Badyaev. 2007. Coupling of dispersal and aggression facilitates the rapid range expansion of a passerine bird. *Proceedings of the National Academy of Sciences of the United States of America* 104:15017–22.
- Folmer, E. O., H. Olff, and T. Piersma. 2012. The spatial distribution of flocking foragers: Disentangling the effects of food availability, interference and conspecific attraction by means of spatial autoregressive modeling. *Oikos* 121:551–561.
- Fortin, D., H. L. Beyer, M. S. Boyce, D. W. Smith, T. Duchesne, and J. S. Mao. 2005. Wolves Influence Elk Movements: Behavior Shapes a Trophic Cascade in Yellowstone National Park. *Ecology* 86:1320–1330.
- Fretwell, S. D., and H. L. Lucas. 1970. On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheoretica* 19:16–36.
- Garay, J., R. Cressman, F. Xu, M. Broom, V. Csiszár, and T. F. Móri. 2020. When optimal foragers meet in a game theoretical conflict: A model of kleptoparasitism. *Journal of Theoretical Biology* 502:110306.
- Getz, W. M., R. Salter, A. J. Lyons, and N. Sippl-Swezey. 2015. Panmictic and Clonal Evolution on a Single Patchy Resource Produces Polymorphic Foraging Guilds. *PLOS ONE* 10:e0133732–e0133732.
- Getz, W. M., R. Salter, D. P. Seidel, and P. van Hooft. 2016. Sympatric speciation in structureless environments. *BMC Evolutionary Biology* 16:50–50.

- 629 Giraldeau, L.-A., and G. Beauchamp. 1999. Food exploitation: Searching for the optimal joining
630 policy. *Trends in Ecology & Evolution* 14:102–106.
- 631 Goss-Custard, J. D. 1980. Competition for food and interference among waders. *Ardea* 55:31–
632 53.
- 633 Guttal, V., and I. D. Couzin. 2010. Social interactions, information use, and the evolution of
634 collective migration. *Proceedings of the National Academy of Sciences* 107:16172.
- 635 Huston, M., D. DeAngelis, and W. Post. 1988. New Computer Models Unify Ecological The-
636 oryComputer simulations show that many ecological patterns can be explained by interac-
637 tions among individual organisms. *BioScience* 38:682–691.
- 638 Iyengar, E. V. 2008. Kleptoparasitic interactions throughout the animal kingdom and a re-
639 evaluation, based on participant mobility, of the conditions promoting the evolution of klep-
640 toparasitism. *Biological Journal of the Linnean Society* 93:745–762.
- 641 Keddy, P. A. 2001. Studying competition. Pages 1–59 *in* P. A. Keddy, ed. *Competition, Popula-*
642 *tion and Community Biology Series*. Springer Netherlands, Dordrecht.
- 643 Krause, J., and G. D. Ruxton. 2002. *Living in Groups*. Oxford University Press.
- 644 Krebs, J., and N. Davies. 1978. *Behavioural Ecology: An Evolutionary Approach* .
- 645 Kuijper, B., I. Pen, and F. J. Weissing. 2012. A guide to sexual selection theory. *Annual Review*
646 *of Ecology, Evolution, and Systematics* 43:287–311.
- 647 Long, X., and F. J. Weissing. 2020. Individual variation in parental care drives divergence of
648 sex roles. *bioRxiv* page 2020.10.18.344218.
- 649 Manly, B., L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2007. *Resource*
650 *Selection by Animals: Statistical Design and Analysis for Field Studies*. Springer Science &
651 *Business Media*.
- 652 Nathan, R., W. M. Getz, E. Revilla, M. Holyoak, R. Kadmon, D. Saltz, and P. E. Smouse. 2008.
653 A movement ecology paradigm for unifying organismal movement research. *Proceedings*
654 *of the National Academy of Sciences* 105:19052–19059.
- 655 Netz, C., H. Hildenbrandt, and F. J. Weissing. 2020. Complex eco-evolutionary dynam-
656 ics induced by the coevolution of predator-prey movement strategies. *bioRxiv* page
657 2020.12.14.422657.
- 658 Parker, G. 1978. Searching for mates.[In: *Behavioural ecology. An evolutionary approach*. JR
659 Krebs and NB Davies, eds] .
- 660 Perkins, D. N. 1992. Topography of Invention. Page 238 *in* *Inventive Minds: Creativity in*
661 *Technology*, vol. 10. Oxford University Press, New York, NY, USA.
- 662 Rutten, A. L., K. Oosterbeek, J. van der Meer, S. Verhulst, and B. J. Ens. 2010*a*. Experimental
663 evidence for interference competition in oystercatchers, *Haematopus ostralegus*. I. Captive
664 birds. *Behavioral Ecology* 21:1251–1260.

- 665 Rutten, A. L., K. Oosterbeek, S. Verhulst, N. J. Dingemanse, and B. J. Ens. 2010*b*. Experimental
666 evidence for interference competition in oystercatchers, *Haematopus ostralegus*. II. Free-
667 living birds. *Behavioral Ecology* 21:1261–1270.
- 668 Schlägel, U. E., V. Grimm, N. Blaum, P. Colangeli, M. Dammhahn, J. A. Eccard, S. L. Haus-
669 mann, A. Herde, H. Hofer, J. Joshi, S. Kramer-Schadt, M. Litwin, S. D. Lozada-Gobilard,
670 M. E. H. Müller, T. Müller, R. Nathan, J. S. Petermann, K. Pirhofer-Walzl, V. Radchuk, M. C.
671 Rillig, M. Roeleke, M. Schäfer, C. Scherer, G. Schiro, C. Scholz, L. Teckentrup, R. Tiedemann,
672 W. Ullmann, C. C. Voigt, G. Weithoff, and F. Jeltsch. 2020. Movement-mediated community
673 assembly and coexistence. *Biological Reviews* .
- 674 Sih, A., A. Bell, and J. C. Johnson. 2004. Behavioral syndromes: An ecological and evolutionary
675 overview. *Trends in Ecology & Evolution* 19:372–378.
- 676 Stillman, R. A., and J. D. Goss-Custard. 2010. Individual-based ecology of coastal birds. *Bio-*
677 *logical Reviews* 85:413–434.
- 678 Tania, N., B. Vanderlei, J. P. Heath, and L. Edelstein-Keshet. 2012. Role of social interactions in
679 dynamic patterns of resource patches and forager aggregation. *Proceedings of the National*
680 *Academy of Sciences* 109:11228–11233.
- 681 Tregenza, T. 1995. Building on the Ideal Free Distribution. Pages 253–307 *in* *Advances in*
682 *Ecological Research*, vol. 26. Elsevier.
- 683 Vahl, W. K., T. Lok, J. van der Meer, T. Piersma, and F. J. Weissing. 2005*a*. Spatial clumping of
684 food and social dominance affect interference competition among ruddy turnstones. *Behav-*
685 *ioral Ecology* 16:834–844.
- 686 Vahl, W. K., J. Van Der Meer, K. Meijer, T. Piersma, and F. J. Weissing. 2007. Interference
687 competition, the spatial distribution of food and free-living foragers. *Animal Behaviour*
688 74:1493–1503.
- 689 Vahl, W. K., J. van der Meer, F. J. Weissing, D. van Dulleman, and T. Piersma. 2005*b*. The
690 mechanisms of interference competition: Two experiments on foraging waders. *Behavioral*
691 *Ecology* 16:845–855.
- 692 van der Meer, J., and B. J. Ens. 1997. Models of Interference and Their Consequences for the
693 Spatial Distribution of Ideal and Free Predators. *The Journal of Animal Ecology* 66:846.
- 694 Vickery, W. L., L.-A. Giraldeau, J. J. Templeton, D. L. Kramer, and C. A. Chapman. 1991. Pro-
695 ducers, Scroungers, and Group Foraging. *The American Naturalist* 137:847–863.
- 696 Wolf, M., and F. J. Weissing. 2010. An explanatory framework for adaptive personality differ-
697 ences. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365:3959–3968.

6 Figure legends

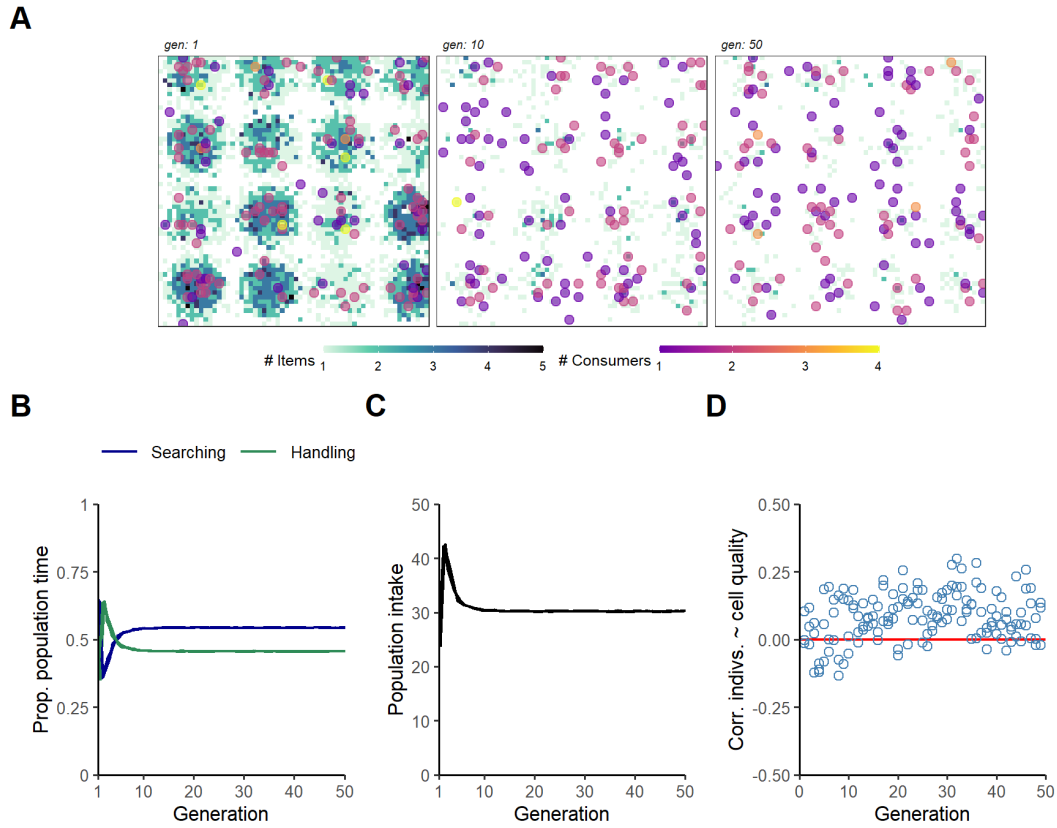


Figure 1: Eco-evolutionary implications of pure exploitation competition (scenario 1). (A) The sustained extraction of prey-items results in a rapid depletion of the resource landscape within 10 generations. The number of individuals on occupied cells is shown as coloured circles. (B) Within 20 generations 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 IFD predictions, at equilibrium, 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; all panels are for $r_{max} = 0.01$.

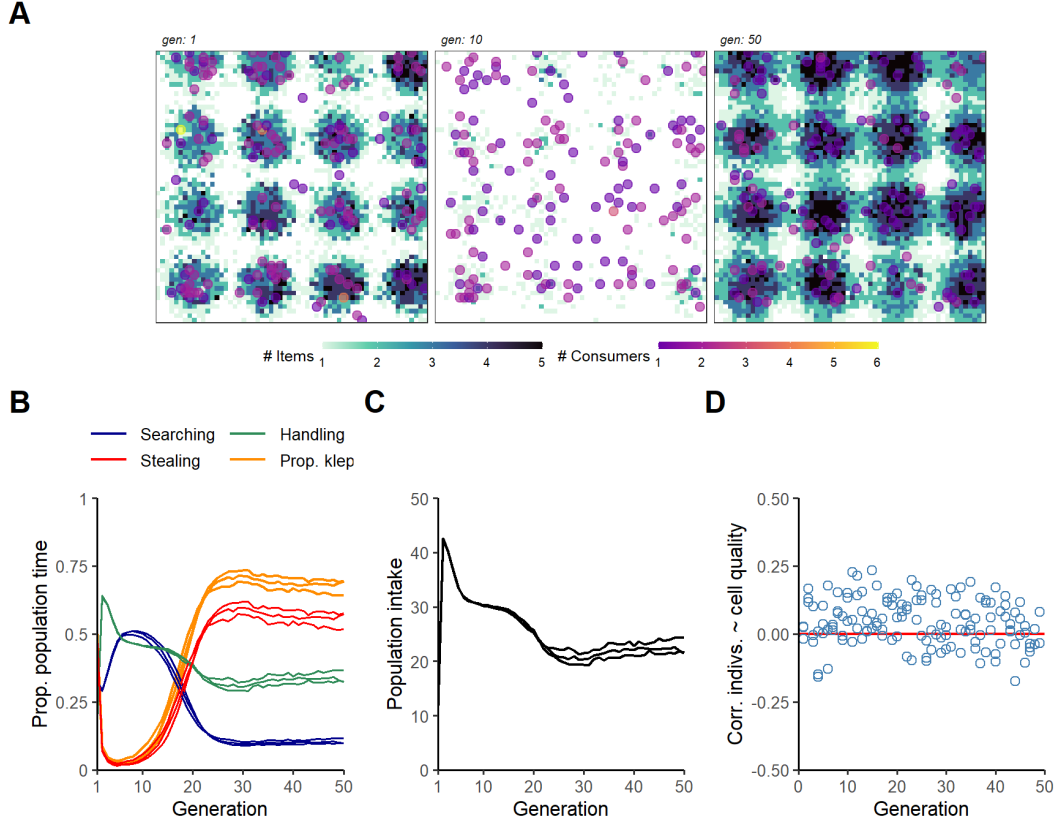


Figure 2: Eco-evolutionary implications of the coexistence of foragers and kleptoparasites (scenario 2). When both foragers and kleptoparasites are in the population, it takes about 30 generations before an equilibrium is reached. **(A)** With a reduction in foraging and handling due to increased stealing after generation 30, prey-item depletion is reduced, and the resource landscape recovers by generation 50. The number of individuals on occupied cells is shown as coloured circles. **(B)** The relative frequency of kleptoparasites (orange line) first drops to low levels but later recovers and reaches a high level ($\sim 60\%$) in all three replicates. The activity budget changes in parallel with the relative frequency of kleptoparasites. 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. With the increase of kleptoparasitism, it drops to a lower level. This is accompanied by an increase in the proportion of time spent on stealing attempts (red line), and a corresponding decrease in prey seeking (by searching foragers) and handling. **(D)** At equilibrium, cell occupancy (number of foragers per cell) is only weakly correlated with cell productivity r . Panel A shows a single replicate, while B, C and D show three replicates; all panels are for $r_{max} = 0.01$.

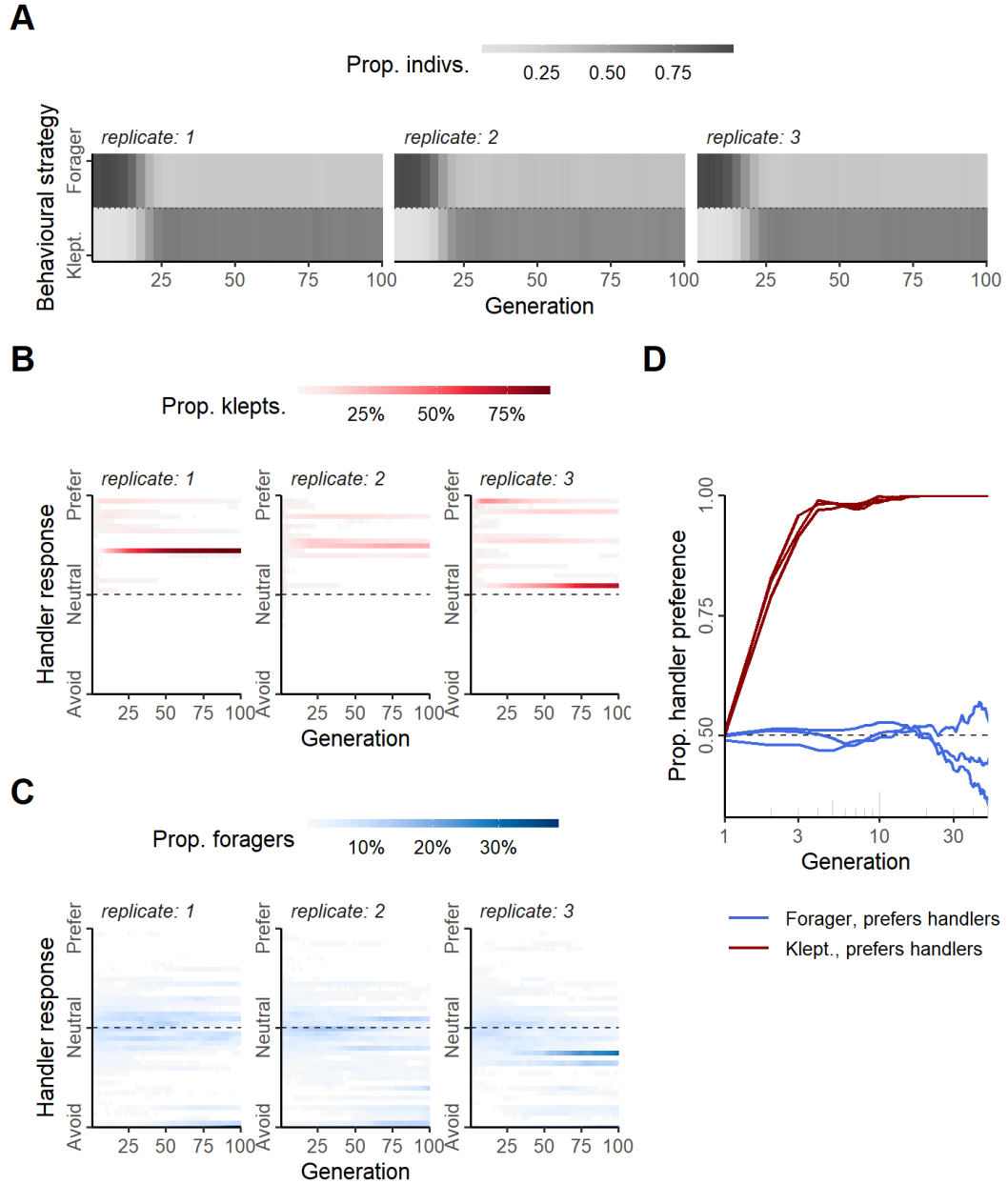


Figure 3: Divergence of movement rules between foragers and kleptoparasites (scenario 2). (A) Kleptoparasitism rapidly becomes the more frequent strategy in scenario 2 populations for the parameters considered, with no differences across replicates. However, replicates differ considerably in the evolved 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). (D) Overall, within 5 generations (shown on a log scale), all kleptoparasitic individuals have an evolved preference for moving towards handlers. Meanwhile, forager individuals are agnostic to handlers, and are equally split between handler preference and avoidance. All panels show three replicates at $r_{max} = 0.01$.

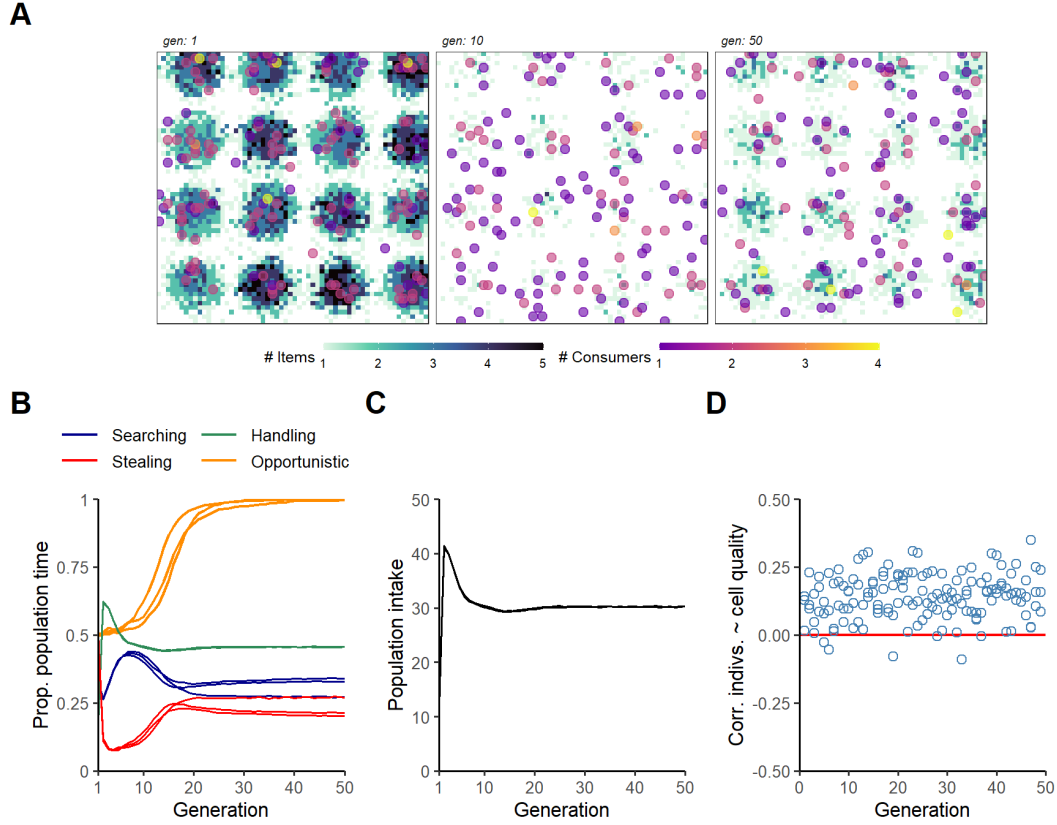


Figure 4: Eco-evolutionary implications of conditional foraging strategies (scenario 3). (A) The initially rapid depletion of the resource landscape within 10 generations is halted as kleptoparasitism reduces foraging activities, and the resource landscape regenerates prey-items by generation 50. The number of individuals on occupied cells is shown as coloured circles. (B) When conditional strategies can evolve, the proportion of individuals with a propensity to steal from handlers (“opportunistic kleptoparasitism”) increases in all replicates and reaches 1.0 by generation 30 (orange line). 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) Contrary to IFD expectations, the correlation between the number of individuals on a cell, and its productivity r_{max} . Panel A shows a single replicate, while B, C and D show three replicates; all panels are for $r_{max} = 0.01$.

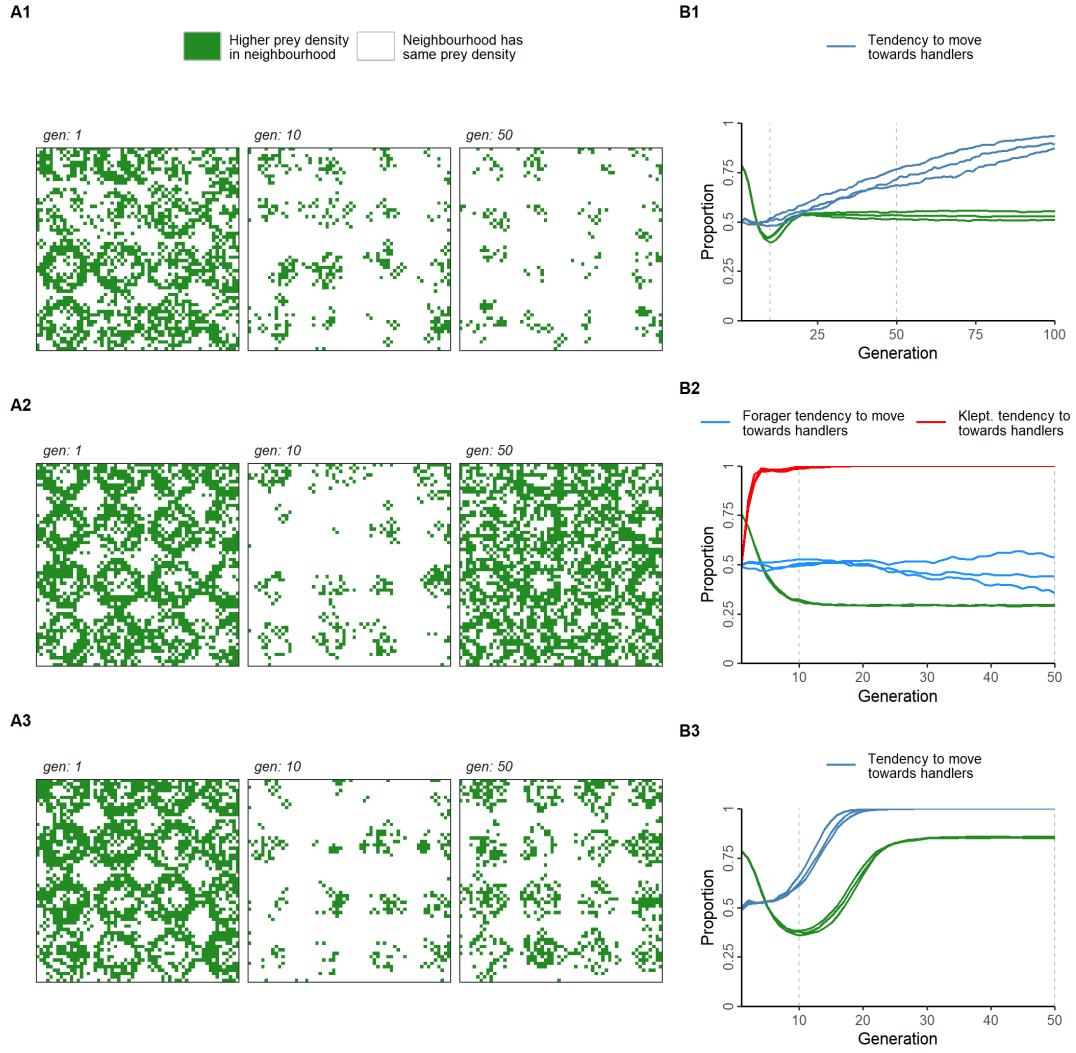


Figure 5: Uninformative prey densities and the evolution of alternative movement cues. The movement of foragers and their consumption of prey items leads to differences among scenarios in the proportion of the landscape where differences in prey-item densities can be detected, and which thus hold informative cues for movement (green areas in **A1**, **A2**, **A3**, green line in **B1**, **B2**, **B3**). Panels: **A1**, **B1** – scenario 1; **A2**, **B2** – scenario 2; **A3**, **B3** – scenario 3. In scenario 1, only about 25% of the landscape holds informative movement cues at equilibrium (**A1**, **B1**), while this proportion is higher in scenarios 2 (**A2**, **B2**) and 3 (**A3**, **B3**), due to reduced prey-item depletion. On such uninformative landscapes, foragers in scenario 1 slowly evolve a preference for handlers, which are an indirect indicator of local resource productivity (**B1** – blue line). In scenario 2, all kleptoparasites rapidly evolve a preference for handlers, which are their primary resource (**B2** – red line), while foragers do not evolve a distinct preference (**B2** – blue line). In scenario 3, all consumers evolve to move towards handlers, as they are both a direct resource and an indirect cue to local productivity (**B3**). All panels show replicates at $r_{max} = 0.01$; landscape panels show only a single replicate.

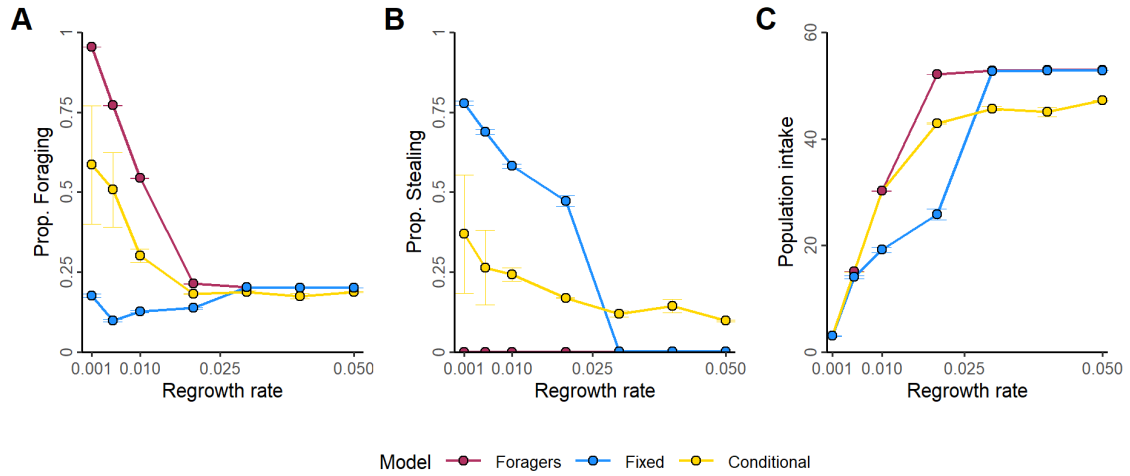


Figure 6: Landscape productivity strongly affects model outcomes. (A) The frequency foraging reduces with increasing r_{max} in models 1 and 3, but remains relatively stable in model 2. In all three models, this is partly due to an increase in handling caused by increased resource availability, and (B) partly due to reduced kleptoparasitism in models 2 and 3. In model 2, kleptoparasitism goes extinct at higher r_{max} , and such model 2 populations are functionally identical with model 1 populations. (C) At low r_{max} , populations in all three models achieve similar intakes. At intermediate r_{max} however, populations with a conditional kleptoparasitic strategy outperform populations with fixed strategies. At high r_{max} , conditional kleptoparasitism populations (model 3) achieve lower intakes than populations in models 1 and 2, which are then functionally identical. Shaded regions around solid lines show the standard deviation of each value; these are not visible when the standard deviation is very small.