

Animal Movement in the Presence of Competition: Insights from Individual Based Modelling

Pratik R. Gupte^{1,*}

Christoph F. G. Netz^{1,*}

Franz J. Weissing¹

1. University of Groningen, Groningen 9747AG, The Netherlands.

* Corresponding authors; e-mail: p.r.gupte@rug.nl OR pratikgupte16@gmail.com; c.f.g.netz@rug.nl

Manuscript elements: EXAMPLE: Figure 1, figure 2, table 1, online appendices A and B (including figure A1 and figure A2). Figure 2 is to print in color.

Keywords: Examples, model, template, guidelines.

Manuscript type: Article.

Prepared using the suggested L^AT_EX template for *Am. Nat.*

1 Abstract

Understanding the causes and consequences of animal movement is key to mechanistically linking individual behaviour with population-level patterns. Classical models of individual-to-population foraging distributions do not account for the complex and changeable resource landscapes animals must navigate. Neither are the rich behavioural repertoires addressed that animals may exhibit in a foraging context, and their evolution is almost entirely ignored. We take a spatially explicit, individual-based simulation approach to model the evolution of individual movement and foraging strategies, and its consequences for population distributions in three simple foraging scenarios of increasing behavioural complexity. We show that broad equilibrium conditions are reached within only a few generations. This equilibrium obscures ever-changing conditions including the constant redistribution of individuals as they harvest prey-items and steal from each other. Individual movement decisions evolve such that populations can track resource gradients even in the absence of direct cues of landscape quality. We show that kleptoparasitism as a foraging strategy is able to rapidly invade a population due to pre-adaptations in the movement mechanism. Phenomenological models of intake rate in relation to competitors and prey-items misrepresent the underlying behavioural mechanisms, and are thus an unreliable guide to evolutionary trajectories. However, these models show that kleptoparasitic foragers are an endogeneously evolved third trophic level whose intake depends on harvesting primary consumers and competition with other kleptoparasites. The behavioural complexity of multiple foraging strategies, a handling time for prey-items, as well as the difficulty of detecting resource gradients in the landscape, result in individuals undermatching their landscape. As a result, populations with low behavioural complexity can still deviate easily from the ideal free distribution.

2 Introduction

something movement ecology and lacking theory. something about animal distributions and why they are important — emergent/emerged field of movement ecology — theory on animal movement still short of the resolution of data now available — analytical models for individual distribution were developed to fit or inspired by very large scale/coarse sampling — do not take into account complex behavioural mechanisms, or individual differences

something about movement lacking evolutionary basis. why do animals evolve to move the way they do — animal movement is entirely about correlation between proximate cues and short-term outcomes — evolutionary thinking is lacking and mostly related to game theory (habitat selection games) — ignores the stochasticity of real individuals, also behavioural mechanisms, and individual differences (i suppose)

the individual based modelling approach. why individual based simulation modelling — increase in computational power — allows modelling the mechanisms underlying the behaviour of large numbers of individuals — can give rise to complex emergent phenomena (examples) — IBMs often different results from analytical models

what we have done. we chose a classic scenario that has the potential to span conceptual and spatial scales (individual foraging with different kinds of competition) — we implemented a plausible individual based model and compared the results to predictions from the literature — we find that — 1. behavioural mechanisms are very important for the observed ecological outcomes, but ecological equilibria are often reached, — 2. the ecology of moving with very reduced cues selects for the evolution of a second cue channel (moving towards handlers), which in turn makes the ecological phenomenon of kleptoparasitism possible, — 3. functional response of intake depends on the behavioural strategies of nearby competitors, and not only on their number, — 4. the aggregative response is better determined from a stable indicator of landscape

productivity due to non-independence of short term prey abundance but the IFD breaks down with Kleptoparasitism, — 5. kleptoparasitism has a similar landscape effect as predation (maybe supplement)

3 Methods: Simulation Model of Movement-Behaviour Co-Evolution

Our model is an individual-based evolutionary simulation whose most basic components — the environment size and shape, its gridded structure and each cell's capacity to hold multiple individuals, as well as the discrete conception of time within and between generations — is taken from Netz et al. *in prep.*. We conceptualised the model and the scenarios around the behaviour of waders (*Charadrii*, and especially oystercatchers *Haematopus sp.*), which are extensively studied in an optimal foraging context (e.g. Ens et al., 1990; Vahl et al., 2005*a,b,c*). We simulated a fixed population with a fixed size of 10,000 individuals 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. Individuals have a lifetime of T timesteps, with T set to 400 by default. After their lifetime, individuals reproduce and transmit their heritable traits proportional to their fitness over their lifetime. The model code (in C++) can be found as part of the Supplementary Material in the Zenodo repository at **Zenodo/other repository here**.

3.1 Three Foraging Strategy Scenarios

Our model considers three main scenarios of individual foraging strategies. The **first scenario** is a forager-only case, in which individuals move about on the landscape and probabilistically find and consume discrete prey items. Between finding and consuming a prey item, individuals must 'handle' the prey for a fixed handling time T_H which is constant across prey items. Prey handling time T_H is 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 a wader to break through a mussel shell, with the handling action obvious to nearby individuals, and the prey not fully

under the control of the finder. 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. The **second scenario** is a fixed-strategy case in which individuals inherit a fixed strategy, to either forage or to steal prey items from handlers, exclusively. Agents that steal are termed kleptoparasites. Kleptoparasites can steal from any handler, regardless of whether that handler acquired its prey by searching or theft. Kleptoparasites are always successful in stealing from the handler they target; this may be thought of as the benefit of the element of surprise, a common observation in nature. Having acquired prey, a kleptoparasite need only handle it for $T_H - t_h$ timesteps, where t_h is the time that the prey has already been handled by its previous handler. The targeted handler deprived of its prey is assumed to flee from the area, and does not make a further foraging decision. Thus kleptoparasites clearly save time on handling compared to a forager, and the time saved increases with the handling time T_H of the prey. The **third scenario** is a conditional-strategy case. Individuals process local environmental cues and pick either the forager or kleptoparasite strategy to use in the next timestep. Apart from the frequency of the choice, the actual foraging dynamics are the same as described in the fixed-strategy case.

3.2 *Movement and Foraging Decisions*

Individuals use cues available in timestep t to predict their best move for the next timestep $t + 1$, and the strategy associated with that move. The movement decision is based on three local environmental cues: (1) the number of discrete prey items G , (2) the number of individuals handling prey H (referred to as ‘handlers’), and (3) the number of individuals not handling prey P (referred to as ‘non-handlers’). Individuals are assumed to not be able to determine the intentions of others to either forage or steal, in scenarios 2 and 3. The notation is chosen in keeping with Netz et al. *in prep.*. These cues are available to individuals in all three model scenarios. Individuals occupy a single grid cell on the environment at a time, and assign a suitability score S incorporating G , H , and P per cell to the nine cells in their Moore neighbourhood (including

their current cell). Following Netz et al. *in prep.*, individuals calculate the cell-specific S as

$$S = m_g G + m_h H + m_p P \quad (1)$$

where the weighing factors for each cue m_g , m_h and m_p are genetically encoded and heritable between generations. Individuals rank their Moore neighbourhood by S in timestep t and move to the highest ranked cell in timestep $t + 1$. Individuals in scenario 3 process the cell-specific environmental cues G , H , and P to determine their next foraging strategy as

$$strategy = \begin{cases} producer, & \text{if } f_g G + f_h H + f_p P + f_b \geq 0 \\ scrounger, & \text{otherwise} \end{cases} \quad (2)$$

where the cue weights f_g , f_h and f_p , and the bias f_b are also genetically encoded and heritable between generations.

In both latter cases that allow for kleptoparasitism, individuals make their foraging strategy choice for the next timestep after they have passed through the ecological dynamics of their current location. This excludes individuals that have been stolen from are an important exception; these fleeing individuals are moved to a random cell within a Chebyshev distance of 5, and do not make a foraging decision there. Thus kleptoparasitism not only gains individuals prey items while depriving the targeted individual, it also displaces a potential competitor. All individuals move simultaneously, and attempt to implement the foraging strategy chosen for their new location (see below).

3.3 Prey Environment and Ecological Dynamics

Since our model was initially conceived to represent foraging waders, we developed a resource landscape based on mussels (family *Mytilidae*) that are commonly found in inter-tidal systems. Mussels beds share some important characteristics with other discrete prey items. Firstly, mussels are immobile relative to their consumers, and their abundances are largely driven by extrinsic environmental gradients and very small-scale interactions (de Jager et al., 2020, 2011). Secondly,

in common with many ecological systems (Levin, 1992), mussels are not uniformly distributed across the inter-tidal mudflats, and are instead strongly spatially patterned into clusters ('beds') (de Jager et al., 2020, 2011). Thirdly, while prey or their signs in an area are often visible to consumers, consumers are not always certain of obtaining one of these prey.

We captured these essential aspects of prey dynamics when implementing the resource landscape on which our individuals move. We modelled relative prey immobility and extrinsically driven abundance by assigning each grid cell of the resource landscape a constant probability of generating a new prey item per timestep, which we refer to as the cell growth rate r . We modelled clustering in the abundance of prey by having the distribution of r across the grid cells take the form of 1,024 uniformly distributed resource peaks with r declining from the centre of each peak to its periphery (Figure X). Effectively, the cell at the centre of each patch generates a prey item five times more frequently than the cells at the edges. We ran the simulation across a range of r_{max} values (0.001 – 0.25), which we considered a sufficiently broad range. Cells in our landscape were modelled as having a carrying capacity K of 5 prey items, and while a cell is at carrying capacity its r is 0. We modelled near-perfect intermediate-range perception but uncertain short-range acquisition of prey by allowing individuals to perceive all prey items G in a cell, but giving individuals which choose a forager strategy only a probability of finding one of these prey. The probability of finding a prey item $p(success)$ is given as the probability of not finding any of G prey each with a detection probability of $p_i = 0.2$.

$$p(success) = 1 - (1 - p_i)^G \quad (3)$$

Since we model foraging events as occurring simultaneously, it is possible for more foragers to be considered successful in finding prey than there are discrete items in that cell. We resolve this simple case of exploitation competition by assigning G prey among some N successful finders at random. Foragers that are assigned a prey item in timestep t begin handling it, and are considered to be handlers for the purposes of timestep $t + 1$ (primarily movement and foraging decisions of other individuals). Foragers that are not assigned a prey item are considered idle

during timestep t , and are counted as non-handlers for $t + 1$.

Kleptoparasites in the fixed- or conditional-strategy case face a slightly different challenge. All kleptoparasites in a cell successfully steal from a handler, contingent on the number of handlers matching or exceeding the number of kleptoparasites in timestep t . When the number of kleptoparasites exceeds handlers, handlers are assigned among kleptoparasites at random. Successful kleptoparasites convert into handlers. Unsuccessful kleptoparasites are considered idle, and are also counted as non-handlers for timestep $t + 1$. A handler that finishes processing its prey in timestep t returns to the non-handler state and is assessed as such by other individuals when determining movements for $t + 1$.

Individuals move and forage on the resource landscape for T timesteps per generation, and T is set at 400 by default. Handlers are immobile while they process prey for T_H timesteps.

3.4 *Reproduction and the Evolution of Decision Making*

At the end of each generation, the population is replaced by its offspring, maintaining the fixed population size, and the decision-making weights which determine individual movement (m_g , m_h , m_p) and foraging strategy choice (f_g , f_h , f_p , f_b) are transmitted from parent individuals to offspring. The total lifetime intake of individuals is used as a proxy of fitness, and the population's total fitness is its total intake. The number of offspring of each parent is proportional to the parent's share of the population fitness, and this is implemented as a weighted lottery that selects a parent for each offspring. The decision-making weights are subject to independent random mutations with a probability of 0.001. The size of the mutation (either positive or negative) is drawn from a Cauchy distribution with a scale of 0.01 centred on the current value of the weight to be mutated. This allows for a small number of very large mutations while the majority of mutations are small. We recognised that spatial autocorrelation in the landscape coupled with limited natal dispersal can lead to spatial heterogeneity in evolved movement rules, as lineages adapt to local conditions (Wolf and Weissing, 2010). Furthermore, limited natal dispersal could lead to population-level movements due to differential reproduction that mirror shifts in resource

abundance, rather than individual movement rules. To ensure that global individual movement rules evolved, we initialised each offspring at a random location on the landscape, and also reset its total intake to zero.

3.5 *Simulation Output and Analysis*

3.5.1 *Ecological Equilibria*

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 handled completely and consumed in each generation — as a measure of population productivity.

3.5.2 *Evolution of Decision Making Weights*

To understand the evolutionary consequences of our simulation, we exported the the decision-making weights which determine individual movement and foraging strategy choice of each individual in every generation of the simulation. We examined how the frequency of these weights changed over the simulation, i.e., how the weights evolved. We visualised weights’ evolution after scaling them between -1 and +1 using a hyperbolic tangent function, and binning the scaled values into intervals of 0.1. We refer to these scaled and binned values as phenotypes for convenience. Weights at or near -1 would represent the maximum evolved avoidance of an environmental cue (in relation to a movement weight) or the greatest evolved negative effect of a cue on choosing the foraging strategy (in relation to a strategy choice weight). Similarly, weights at or near +1 represent the greatest evolved preference for or positive effect of a cue on the movement and strategy choice mechanism of an individual.

3.5.3 *Functional Response of Intake and Population Distribution*

In our simulation, individuals perceive and respond to the standing stock of prey items on a cell rather than its productivity, which they cannot sense directly. This standing stock is unpredictable due to consumption by other individuals, and the movement (and consumption) of individuals is also unpredictable. To understand the consequences of evolved movement rules, we must investigate how individual intake varies with the presence of items and other individuals. Determining the functional response of intake to competitors, and the distribution of predators relative to prey *sensu* Meer and Ens (1997) is a prevalent method in spatial ecology. Over the final ten generations of each simulation run, we summed the number of individuals and items on each cell, as well as the total intake on the cell. We were able to record the number of individuals following a forager and kleptoparasite strategy, as well as intake due to foraging or stealing, separately. This allowed us to determine the average per-capita, per-strategy intake on each cell, which we plotted against the number of competing individuals on the cell (Figure X). Additionally, we plotted the average number of individuals following each strategy against the number of prey items on the cell (Figure Y). In both cases, we used data only from the second half of each generation so as to capture the system in a state of ecological equilibrium.

While recognising that individuals move in response to their rapidly-changing prey landscape, it is useful to determine how individuals distribute along more slowly-changing productivity gradients; this is because these may often be easier to measure in the real world. The ideal free distribution (IFD) and the matching rule robustly predict that individuals should distribute themselves such that intake rates are equalised over patches of similar productivity. The large volume of pseudo-ecological data generated by our simulation allowed us to test whether intake rates were indeed equalised over the productivity gradient. Having previously calculated the average numbers of each strategy, and the average per-capita intake for each strategy on each cell, we plotted both against the productivity of the cell (Figure Z). Here too, we used data only from the second half of each generation to approximate ecological equilibrium.

3.5.4 Landscape Effects of Kleptoparasitism

optional: to be added

Data Availability. Simulation data used in this study are available on the Dryad/IRODS/Zenodo repository **REPOSITORY LINK HERE**; simulation code is available on Github and archived on Zenodo at **ZENODO LINK HERE**; data analysis and figure code is available on Github and archived on Zenodo at **ZENODO LINK HERE**.

4 Results: Simulation Model Outcomes

4.1 Emergence of an Ecological Equilibrium

All three simulation scenarios result in population level activity budget equilibria with stable proportions of foraging, kleptoparasitism, and handling (Figure 2). Populations reach this stable state within 100 generations, i.e., 10% of evolutionary time (but see below). Once a population reaches an activity budget equilibrium, it also reaches an intake equilibrium which is closely related to the proportion of handling (Figure 2).

In the foragers-only **scenario 1** case, the population is split among foraging and handling, and the ratio of handling to foraging reflects the probability of an individual finding a food item. In the fixed-strategy **scenario 2**, kleptoparasitism rapidly increases to a stable proportion of the population's activity budget within 100 generations. In the conditional-strategy **scenario 3** too, a stable proportion of kleptoparasitism is rapidly established. However, conditional-strategy populations largely handle prey, with kleptoparasitism and foraging relatively reduced (Figure 2). Differences among scenarios in the proportion of handling translate to differences in total population intake. With the highest proportion of handling, scenario 1 has the highest per-generation population intake, while populations with fixed strategies (scenario 2) have a significantly lower intake than populations with conditional strategies (scenario 3).

4.2 Movement-Behaviour Co-Evolution

4.2.1 The Case of Exploitative Competition

In scenario 1, movement and behavioural rules evolve to maximise intake in the presence of exploitation competition only, since individuals cannot steal. Individuals evolve to move towards food items regardless of the simulation specific regrowth rate. Individuals also evolve a movement preference for handling individuals at low and intermediate growth rates ($r_{max} < 0.1$); at high growth rates individuals evolve to be agnostic towards handlers. Similarly, individuals are agnostic towards non-handling individuals at high growth rates, but evolve an avoidance at low – intermediate growth rates.

4.2.2 The Case of Kleptoparasitism

Scenario 2. In both scenarios 2 and 3, movement rules evolve to account for the additional pressure of interference competition in the form of kleptoparasitism. In both scenarios and in common with scenario 1, individuals evolve to move towards food items across all r_{max} . In the fixed-strategy scenario 2, individuals evolve to move towards handlers at low to intermediate growth rates, but with an increasing proportion of individuals agnostic to handling individuals at higher growth rates. Similarly, fixed-strategy individuals avoid non-handlers at lower growth rates, and are agnostic to non-handlers at higher growth rates. At lower growth rates, the majority of fixed-strategy individuals are kleptoparasites, and this proportion decreases in favour of the forager strategy with increasing r_{max} until all individuals are foragers.

Scenario 3. In the conditional-strategy scenario 3, individuals retain a preference for moving towards handlers across growth rates, unlike scenarios 1 and 2. Conditional-strategy individuals also evolve a preference for moving towards non-handlers at high growth rates, while at low and intermediate growth rates they evolve to avoid non-handlers. The behavioural strategy of scenario 3 individuals is allowed to be conditional on local environmental cues, but unlike

movement rules, few clear strategy choice rules evolve. The only consistent signal is that of choosing a stealing strategy in the presence of handlers, with all scenario 3 individuals preferring to steal when possible, across r_{max} .

4.3 *Functional Response of Intake*

The foragers-only case presents a useful starting point: forager intake is invariant with individual (forager) density, and only declines at very high or low densities (Fig. 4.a,d). Similarly, the functional response of both foragers and kleptoparasite strategies in the fixed-strategy and conditional-strategy case is hump-shaped, with an apparently ‘optimal’ competitor density at which individual intake rates are maximised (Fig. 4.b,c). Furthermore, the kleptoparasitic strategy’s per-capita intake is always greater than that of the forager strategy (Fig. 4.b,c). However on separating potential competitors by strategy, we find that the individual intake of both strategies increases with increasing forager density (Fig. 4.e,f), but decreases with increasing kleptoparasite density (Fig. 4.g,h). These consistently opposite responses to foragers and kleptoparasites explain why the overall functional response to all competitors appears hump-shaped. With growing forager densities, exploitative, scramble competition for prey items is increased, but foragers also accumulate on high-productivity cells, increasing average per-capita intake overall. When kleptoparasites accumulate, however, interference competition results in both lower extraction (as only foragers extract prey) as well as lower intake, as the same item is repeatedly passed between individuals in stealing interactions. Thus we show that taking the type of competition, and behavioural variation among individuals more generally into account is crucial to correctly understand the consequences of multiple competing individuals foraging on the same patch (or in the same group/in proximity to each other).

4.4 *Aggregative Response and Population Distribution*

Predicting the distribution of a population on a heterogeneous landscape is among the key goals of spatial ecology. While the ideal undertaking of such an endeavour involves fine-scale measurement of prey availability and predator densities, it is often much more realistic to find the aggregative response of individuals to a relatively static indicator of landscape quality. Our simulation data allowed us compare and contrast these approaches, and we examined the aggregative response of individuals in relation to both the number of discrete food items, as well as the underlying landscape productivity.

4.4.1 *Aggregative Response of Predators to Prey*

The aggregative response of predators to prey item density is strongly non-linear, and depends on the behavioural strategy as well as the regrowth rate. In scenario 1, at the reference r_{max} of 0.1, predator density shows a humped response to predator density. This arises from individual preference for cells with more prey items, and the consumption of prey by predators; prey are unlikely to accumulate on cells which are occupied by many predators. In scenario 2 at $r_{max} = 0.1$, forager density is invariant with prey density except at very high prey densities, where predators are reduced. This latter is once again due to the feedback of predators on prey. However, kleptoparasite density increases nonlinearly with prey density, with many more kleptoparasites present at high prey densities than foragers. The ratio of kleptoparasites to foragers at high prey densities is significantly higher at low r_{max} , in part due to the relatively greater prevalence of kleptoparasitism overall when landscape productivity is low. In scenario 3 for $r_{max} = 0.1$, forager and kleptoparasite densities respond similarly to prey density, with a roughly 2:1 ratio of foragers to kleptoparasites.

4.5 *Population Distribution in Relation to Productivity*

We find that in the foragers-only case, individuals follow the matching rule in relation to grid-cell productivity, with more foragers on higher productivity cells (Fig. 5.a). Individuals distribute such that their intake is equalised on cells with productivity above a threshold, while it is zero on cells below this threshold. In this sense, the population appears to reach an ideal free distribution, as individuals can only increase their productivity by moving to cells above the threshold productivity, but not by moving any further up the productivity gradient. In the fixed-strategy case, the aggregative response of foragers and kleptoparasites differs; forager counts peak on lower productivity cells and declines with further increases in productivity. Kleptoparasite counts initially increase with cell productivity and then stabilise (Fig. 5.b). In the conditional-strategy case, both foragers and kleptoparasite counts peak on intermediate productivity cells and then begin to decline (Fig. 5.c). In the spatial context of our simulation, this translates to three distinct patterns with (1) individuals clustered on productivity peaks in scenario 1, (2) kleptoparasites dominating productivity peaks with fewer foragers in scenario 2, and (3) individuals using a forager strategy more frequently than a kleptoparasitic strategy on productivity peaks in scenario 3. We further find that there are appreciable differences between average and median counts of individuals of each strategy on cells, with the mean typically higher than the median.

4.6 *Landscape Effects of Kleptoparasitism*

Work in progress: – add also landscape metrics etc

5 Discussion

5.1 *Relative Performance of Fixed and Conditional Strategies*

fixed strategies do nearly as well as conditional strategies at low growth rates — conditional strategies pull ahead when resources are plentiful

5.2 *Evolution of Kleptoparasitism Requires Movement Pre-Adaptation*

The scrounging kleptoparasitic strategy evolves and is established in populations in some tens of generations, and emerges relatively quickly in the evolutionary history of populations (see Figure 2) This rapid emergence and invasion is made possible by the pre-adaptation of individuals to use the kleptoparasitic strategy successfully. **Scenarios 2** and **3** prior to the emergence and establishment of kleptoparasitism are identical to **scenario 1**, and all individuals are producers. Producers evolve to move towards both items and handlers at most regrowth rates (Figure X), since these are cues to the immediate benefit, and the regrowth rate of a cell, respectively. For the kleptoparasitic strategy, the mapping of cues is reversed but the direction of preference remains the same. To kleptoparasites, the number of handlers indicates the immediate resource abundance, while the number of items indicates the probability of resource generation, i.e., individuals converting into handlers. This coincidental alignment of movement decisions with either behavioural strategy is essential to the persistence of kleptoparasitism.

The initial evolution of kleptoparasitism is then only conditional on the mutation of any one of the strategy weights to a sufficiently negative value such that the individual attempts to steal rather than search for prey. At very high regrowth ($r_{max} = 0.25$), the landscape is saturated with prey-items, and individuals can ignore the presence of handlers and evolve to move only in response to prey-items ('socially naive producers'). Under such circumstances in **scenario 2**, though strategy weight mutations lead to some few individuals using a fixed kleptoparasitic strategy, they do not move optimally for their strategy. Thus kleptoparasitism as a fixed-strategy repeatedly evolves and goes extinct in high-productivity environments, as these individuals find themselves in a 'desert of plenty'. Under the same conditions in **scenario 3** however, a mixed foraging strategy allows individuals to be producers when appropriate, and yet steal a march on pure-producers when kleptoparasitism is possible.

5.3 *Functional Response Must Consider Competitor Behaviour*

functional response of intake competition that does not consider individual strategies would lead to wrong conclusions — facilitative effects may be entirely due to chance

5.4 *Clueless Plateaus Cause IFD Deviations*

individual consumption forms ‘clueless plateaus’ — individuals cannot find high productivity cells without cues — this leads to undermatching

5.5 *Animal Behaviour Can Shape Landscapes*

Something about klepts allowing landscape regrowth — similar to predation — landscape of fear etc etc

6 Conclusion

7 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.

Literature Cited

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.
- Ens, B. J., P. Esselink, and L. Zwarts. 1990. Kleptoparasitism as a problem of prey choice: A study on mudflat-feeding curlews, *Numenius arquata*. *Animal Behaviour* 39:219–230.
- Levin, S. A. 1992. The Problem of Pattern and Scale in Ecology: The Robert H. MacArthur Award Lecture. *Ecology* 73:1943–1967.
- Meer, J. V. D., and B. J. Ens. 1997. Models of Interference and Their Consequences for the Spatial Distribution of Ideal and Free Predators. *The Journal of Animal Ecology* 66:846.
- Vahl, W. K., T. Lok, J. van der Meer, T. Piersma, and F. J. Weissing. 2005a. Spatial clumping of food and social dominance affect interference competition among ruddy turnstones. *Behavioral Ecology* 16:834–844.
- Vahl, W. K., J. van der Meer, F. J. Weissing, D. van Dulleman, and T. Piersma. 2005b. The mechanisms of interference competition: Two experiments on foraging waders. *Behavioral Ecology* 16:845–855.
- . 2005c. The mechanisms of interference competition: Two experiments on foraging waders. *Behavioral Ecology* 16:845–855.
- Wolf, M., and F. J. Weissing. 2010. An explanatory framework for adaptive personality differences. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365:3959–3968.

8 Appendix A: Supplementary Figures

8.1 *Fox–dog encounters through the ages*

401

9 Appendix B: Additional Methods

402

9.1 *Measuring the height of fox jumps without a meterstick*

10 Tables

11 Figure legends

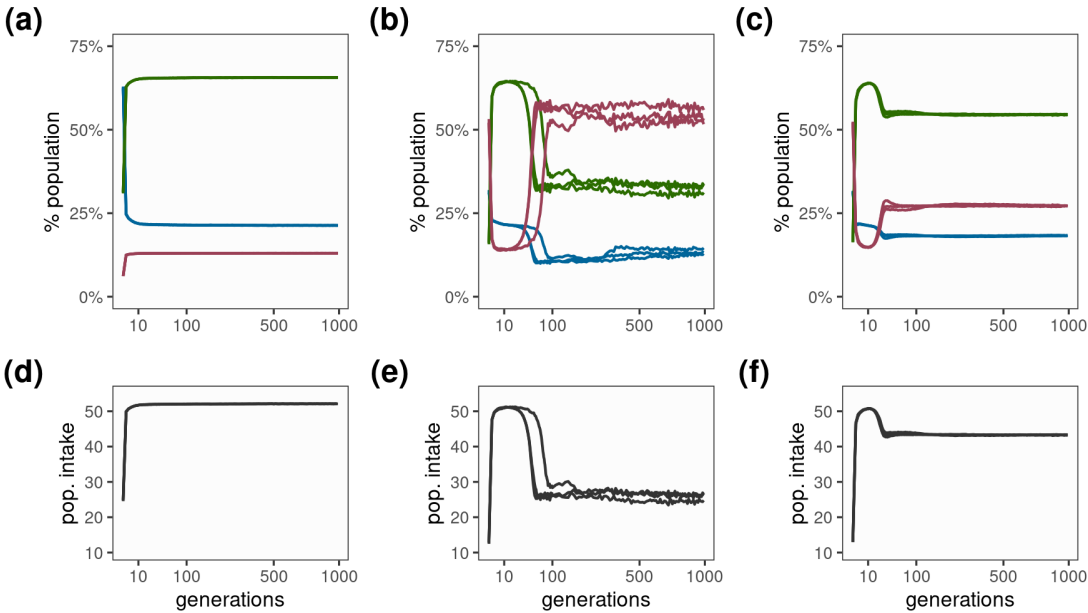


Figure 1:

11.1 Online figure legends

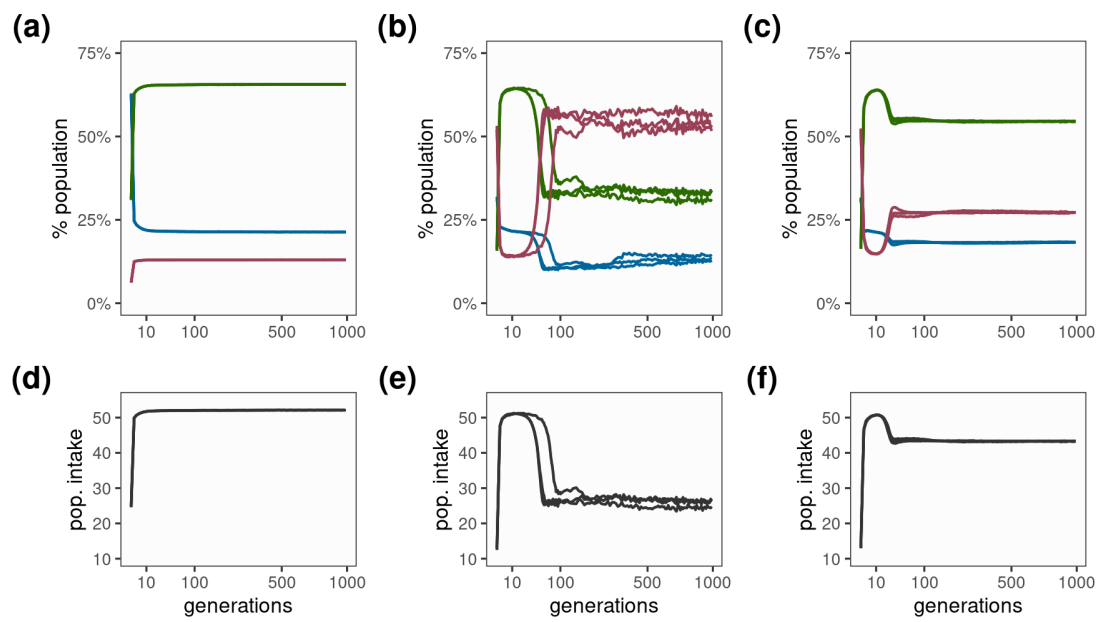


Figure 2: