

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

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1 Abstract

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3 2 Introduction

4 Intraspecific competition is a constant feature of animal ecology, and an important driver of population dy-
5 namics and the spatial distribution of organisms (Krebs and Davies, 1978). Competition can be broadly
6 classified into two main types, ‘exploitation’ and ‘interference’. In exploitation competition, individuals
7 compete indirectly by depleting a common resource, while in interference competition, individuals compete
8 directly by interacting with each other (Birch, 1957; Case and Gilpin, 1974; Keddy, 2001). A special case
9 of interference competition which is widespread among animal taxa is ‘kleptoparasitism’, in which an indi-
10 vidual steals a resource from its owner (Iyengar, 2008). Experiments with foraging birds have shown that
11 competition, including kleptoparasitism, can affect the spatial distribution of individuals across resource
12 patches (Goss-Custard, 1980; Rutten et al., 2010b; Vahl et al., 2005a, 2007, 2005b). The avoidance of
13 competitive interactions can also affect the distribution and behaviour of animals foraging in groups (Rutten
14 et al., 2010a; ?). At larger scales, competition among different behavioural types in a species can strongly in-
15 fluence species distributions and animal movement decisions (e.g. Duckworth and Badyaev, 2007; Schlägel
16 et al., 2020).

17 Competition is difficult to study in free living animals, yet knowledge of the fine-scale mechanisms and
18 evolutionary consequences of competition is central to basic evolutionary ecology. For instance, it is sur-
19 mised that interference is more important than exploitation under natural conditions (see Case and Gilpin,
20 1974), but it is difficult to establish whether interference, and especially kleptoparasitism, represents a for-
21 aging specialisation shown by part of the population, or whether it is an opportunistic strategy conditioned
22 on local cues, that can be used by all individuals. Furthermore, it is nearly impossible to study the causes and
23 consequences of competition — such as its coevolution with movement strategies, or the effect on resource
24 landscapes — at evolutionary time-scales in most animals, due to a lack of long-term data (Clutton-Brock
25 and Sheldon, 2010). Our poor understanding of competition poses a problem, since it is key to models such

as the Ideal Free Distribution (IFD), which is a cornerstone of evolutionary ecology (Fretwell and Lucas, 1970). The IFD posits that individuals should distribute on a heterogeneous resource landscape such that their intake rate is identical at all occupied locations, after accounting for competition. As suggested by the name, the IFD assumes that competing individuals are omniscient ("ideal"), and move instantaneously, without costs, to any location on the landscape ("free"). While these evidently unrealistic assumptions have their own ramifications (Amano et al., 2006; Cressman and Křivan, 2006; Matsumura et al., 2010; Tregenza, 1995), IFD models also neglect important mechanisms underlying competition. For instance, IFD models ignore resource depletion (Cressman and Křivan, 2006; Fretwell and Lucas, 1970; ?), or treat interference as an almost inevitable part of the foraging process (reviewed in Tregenza, 1995; ?, ; see also Cressman and Křivan 2006; Garay et al. 2020). On the contrary, the abundance of resources and their depletion is of obvious importance to individuals' movement decisions. Similarly, interference competition is a complex individual behaviour which is closely related to movement decisions, and even minor differences in its treatment in models can have important ecological and evolutionary consequences (?).

Here, we present a mechanistic model of intraspecific competition in a spatially explicit context, as the outcome of evolved behavioural and movement strategies. This allows us to both focus more closely on the interplay of exploitation and interference competition, and to examine the feedbacks between movement and foraging behaviour at evolutionary scales. As foraging and movement decisions are taken by individuals, we study the joint evolution of both types of decision by means of individual-based evolutionary simulation models (IBMs; DeAngelis and Diaz, 2019; Huston et al., 1988), which are well suited to modelling the evolution of complex behaviours (Getz et al., 2015, 2016,?; Guttal and Couzin, 2010; Netz et al., 2020). We implement a spatially explicit IBM approach to competition and animal movement decisions, using one model with three scenarios of increasing complexity. In our model, individuals move on a spatially fine-grained resource landscape with discrete, depleteable food items. They make movement decisions using an inherited (and evolvable) strategy which integrates local cues such as the local resource and competitor densities. After each move, individuals choose between two foraging strategies: whether to search for a food item or steal from another individual; the mechanism underlying this foraging choice is also inherited. We consider lifetime resource consumption as a proxy for fitness, such that more successful individuals

produce more offspring, and thus are more efficient in transmitting their movement and foraging strategies to future generations (subject to small mutations). In the first scenario, we examine how exploitation competition influences the evolution individual movement rules, population level resource intake, and the spatial structure of the resource landscape. In the second scenario, we introduce kleptoparasitic interference as an inherited strategy, fixed through an individual’s life, and investigate how individual movement and behaviour decisions coevolve. In the third scenario, we model kleptoparasitism more realistically, as a behavioural strategy conditioned on local environmental and social cues, compare the population-level and landscape-scale outcomes between scenarios 2 and 3 to show the influence of modelling choices.

QUESTIONS HERE.

3 The Model

We implement three individual-based evolutionary simulation models whose most basic components — the environment size and shape, its gridded structure and each cell’s capacity to hold multiple individuals, as well as the discrete conception of time within and between generations — are inspired by Netz et al. (2020). We conceptualised the models around the behaviour of waders (*Charadrii*, and especially oystercatchers *Haematopus sp.*), which are extensively studied in the context of foraging competition (e.g. Rutten et al., 2010a,b; Vahl et al., 2007, 2005b; ?; ?). 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 Resource

Inspiration from Mussel Beds Since our model was conceived to represent foraging waders, we developed a resource landscape based on mussels (family *Mytilidae*) that are commonly found in inter-tidal

systems. Mussels (and prey generally) are often less mobile than their consumers, their abundances in the absence of predators are largely driven by external environmental gradients, and they may be frequently found in clusters (de Jager et al., 2020, 2011).

Prey Abundance 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-specific 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 (called r_{max}) to its periphery (Fig. 1). 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 all three models across a range of r_{max} values (0.001 – 0.25). 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.

Prey Acquisition by Predators Individuals can perceive all prey items G in a cell, but have only a probability of finding a prey item $p(success)$. The $p(success)$ is the probability of not finding any of F prey, each with a detection probability of $p_i = 0.2$.

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

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 F 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 $t + 1$, i.e., movement and foraging decisions of other individuals). Foragers that are not assigned a prey item are considered idle during timestep t , and are counted as non-handlers for $t + 1$.

Kleptoparasites 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 $t + 1$.

Handlers that finish processing their prey in timestep t return to the non-handler state and are assessed as such by other individuals when determining movements for $t + 1$.

3.2 Competition and Movement Strategies

Scenario 1: Exploitative Competition The first model simulates only exploitative competition; 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.

subsection Scenarios 2 and 3: Kleptoparasitic Interference Competition

The second model builds on Model 1, with the addition that individuals inherit a fixed strategy to either forage or to steal prey items from handlers, exclusively. Agents that steal are termed kleptoparasites. 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 among birds Brockmann and Barnard (1979). 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 owner; thus kleptoparasites clearly save time on handling compared to a forager. The targeted handler deprived of its prey is assumed to flee from the area, and does not make a further foraging decision. Model 3 is similar to model 2, except that individuals process local environmental cues and pick either the forager or kleptoparasite strategy to use in the next timestep. Apart from the frequency of the choice, the actual foraging dynamics are the same as described in the fixed-strategy case.

Movement Strategies In all models, individuals use cues available in timestep t to predict their best move for the next timestep $t + 1$. The movement decision is based on three local environmental cues: (1) the number of discrete prey items F , (2) the number of individuals handling prey H (referred to as ‘handlers’), and (3) the number of individuals not handling prey K (referred to as ‘non-handlers’). Individuals occupy a single grid cell on the environment at a time, and assign a suitability score S per cell to the nine cells in their Moore neighbourhood as

$$S = m_f F + m_h H + m_k K \quad (2)$$

where the weighing factors for each cue m_f , m_h and m_k 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 model 1 only forage for prey, while individuals in model 2 either forage or steal based on their inherited strategy. However, individuals in model 3 process the cell-specific environmental cues F , H , and K to determine their next foraging strategy as

$$\text{strategy} = \begin{cases} \text{forager,} & \text{if } w_f F + w_h H + w_k K + w_b \geq 0 \\ \text{kleptoparasite,} & \text{otherwise} \end{cases} \quad (3)$$

where the cue weights f_g , f_h and f_p , and the bias f_b are also genetically encoded and heritable between generations. 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. All individuals move simultaneously, and then implement their foraging or kleptoparasitic behaviour to acquire prey. Individuals move and forage on the resource landscape for T timesteps per generation, and T is set at 400 by default. Handlers are immobile while they process prey for T_H timesteps.

Competition Strategies TEXT HERE

3.3 Reproduction and Inheritance

At the end of each generation, the population is replaced by its offspring, maintaining a fixed population size. The decision-making weights which determine individual movement (m_f , m_h , m_k) and foraging strategy choice (w_f , w_h , w_k , w_b) are transmitted from parent individuals to offspring. The total lifetime intake of

individuals is used as a proxy of fitness. The number of offspring of each parent is thus proportional to the parent's share of the population intake, and this is implemented as a weighted lottery that selects a parent for each offspring. 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.

3.4 Simulation Output and Analysis

Population Activities and Individual Decisions 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. 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.

Changes in the Resource Landscape Anticipating that the prevalence of different foraging strategies would affect the spatial structure of the prey-item landscape, we examined changes in the prey-item abundances of landscape grid cells. We exported a snapshot of the the number of items per grid-cell at the mid-point of each generation ($t = 200$), for each simulation run, and we visually examined how landscape patterns changed over generations. We then addressed a specific question: how would the ability of in-

dividuals to navigate their landscape change with the reduced depletion expected with kleptoparasitism? Individuals can only choose an optimal move when they can sense profitability differences (such as the number of prey-items) among the various destinations. We quantified the cell-specific item gradient for each landscape snapshot, and determined the difference in items between each cell and its neighbours (the item gradient). We calculated the proportion of the landscape that formed a ‘clueless plateau’, i.e., where the item gradient was zero (*sensu* ?).

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

4.1 Model Outcomes

All three models result in population level activity budget equilibria with stable proportions of foraging, kleptoparasitism, and handling (see Fig. 2A, 3A, 4A). Populations reach this stable state within 100 generations, i.e., 10% of evolutionary time. Once a population reaches an activity budget equilibrium, it also reaches an intake equilibrium which is closely related to the proportion of handling (Figure 2B, 3B, 4B).

Model 1: Exploitative Competition In Model 1, the population’s activities is split among foraging and handling (Fig. 2A; $r_{max} = 0.01$). The proportion of handling in the activity budget, and the population intake are both initially low, but then peak within ten generations (Fig. 2B). This is because individuals can easily acquire prey items from the fully stocked landscape in the first few generations, as movement strategies improve via evolution. As individuals deplete prey items faster than they can be replenished, the overall number of prey items is reduced (Fig. 2C). Population handling activity declines to a stable value $\sim 45\%$ within 50 generations, leading to a similar stabilisation in population intake (Fig. 2A, 2B). The number of

individuals per occupied cell, i.e. the level of aggregation, declines between generations one and fifty (Fig. 2C).

Model 2: Interference as a Fixed Strategy In Model 2, the population activity budget comprises of foraging, handling, and stealing (Fig. 3A; $r_{max} = 0.01$). Population handling and intake shows an initial spike similar to Model 1 as individuals successfully acquire prey items from the fully stocked prey landscape, but then declines to a stable value within 50 generations (Fig. 2A, 2B). The proportion of individuals with an inherited kleptoparasitic strategy, initially 50%, declines rapidly to nearly none within the first couple of generations. However, after this initial crash, kleptoparasitic individuals rise in frequency to a stable $\sim 70\%$ of the population (Fig. 3A). This is reflected in the activity budget, in which stealing rises from nearly zero to form $> 50\%$ of all activities; this is associated with a stabilisation of the proportion of handling at $> 25\%$ (Fig. 3A). This lower proportion of handling results in lower population intake (Fig. 3B), and a strong *increase* in the number of prey items on the landscape (Fig. 3C). The number of individuals per occupied cell does not change significantly between generations one and fifty (Fig. 3C).

Model 3: Interference as a Conditional Strategy In Model 3, the activity budget is quite different from either Models 1 or 2. Handling is the most common activity ($\sim 45\%$) as in Model 1, with the remaining activities split evenly between foraging and stealing, and a stable equilibrium within 50 generations (Fig. 4A; $r_{max} = 0.01$). However, unlike Model 2, the frequency of stealing does not strongly track the frequency of individuals which would show a kleptoparasitic response to handlers (i.e., nearly all individuals within 50 generations; Fig. 4A). Population intake stabilises within ten generations to a level similar to Model 1 (Fig. 4B). The reduced depletion following the evolution and persistence of kleptoparasitism leads to landscape change intermediate between Models 1 and 2 within 50 generations; the number of individuals per cell is also reduced (Fig. 4C).

4.2 The Effect of Landscape Productivity

The landscape's r_{max} has a marked effect on population activity budgets and total intake. The frequency of foraging reduces with r_{max} in Models 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 Model 2 however, the frequency of handling is relatively unaffected by increasing r_{max} (Fig. 5A). The difference between Models 2 and 3 has to do with the change in the frequency of kleptoparasitism (Fig. 5B). In Model 2, kleptoparasitism forms $> 75\%$ of all activities at very low r_{max} , and is much more common than in Model 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 Model 2 population matches the Model 1 population, with foragers rapidly converted to handlers. In Model 3, kleptoparasitism persists at low frequencies even at the highest regrowth rates (Fig. 5B); thus some foragers lose time in extracting items which are then stolen from them. Consequently, while populations in all three models achieve very similar intakes at low r_{max} , at intermediate regrowth rates (0.01 – 0.025), conditionally kleptoparasitic populations outperform populations using fixed strategies. Only at high regrowth rates, when fixed strategy populations (Model 2) effectively convert to purely forager populations (Model 1), do they achieve a higher intake than Model 3 populations (Fig. 5C).

4.3 The Evolutionary and Ecological Consequences of kleptoparasitism

The evolution and persistence of kleptoparasitism reduces prey-item depletion compared to the foragers-only case, and allows many localised gradients of prey-item abundance to re-emerge (Figs. 2C, 3C, 4C). In Model 1, depletion reaches a stable value, and the proportion of the landscape with no item cues ('clueless plateaus') follows it to a stable level of 75% by generation 10 ($r_{max} = 0.01$; Fig. 6A, 6D). Consequently, forager individuals slowly evolve to move towards handlers (blue line; Fig. 6A), as the presence of a handler marks a cell as having a non-zero probability of generating a prey item. In model 2, clueless plateaus comprise $\geq 50\%$ of the landscape by generation 10, but then rapidly subside to $\leq 25\%$ by generation 20, following rapid reductions in resource landscape depletion (Fig. 6B, 6E). As most individuals are kleptoparasites (orange line; Fig. 6B), and moving towards handlers is the only viable kleptoparasite movement strategy, the population as a whole evolves to move towards handlers (blue line; Fig. 6B). In Model 3, depletion stabilises at a value intermediate between Models 1 and 2, and, clueless plateaus stabilise at $\sim 50\%$ of the landscape (Fig. 6C, 6F). Model 3 individuals are faced with both a lesser abundance of prey-items than in

model 2, as well as being able to steal from any handlers they encounter; as a consequences, all individuals evolve a preference for moving towards handlers (blue line; Fig. 6C), which represent both a direct resource as well as an indication of prey item abundance.

When kleptoparasitism is a fixed, inherited strategy (model 2), kleptoparasitic individuals face a particularly strong selection pressure to move towards handlers, as these are their only food source (Fig. 7A). As kleptoparasites form an increasing proportion of the population, they also form an increasing proportion of individuals with a preference for moving towards handlers (Fig. 7B). In contrast, foragers are largely neutral to handlers, and as they decrease in frequency, they form a decreasing proportion of individuals with a preference for handlers (Fig. 7A, 7B).

5 Discussion

short summary of results?

5.1 Polymorphism as the Outcome of Constraints

Competition is a key process in determining animal space use across scales Fretwell and Lucas (1970); ?, and is often suggested as a driver of phenotypic, behavioural, and foraging polymorphisms (CITE). In our Model 1 with only exploitative competition, only a single movement morph evolves. Previous models of the evolution of movement rules suggest that multiple movement morphs can evolve in a consumer-resource context (Getz et al., 2015, Netz et al. in prep.). In our model 1, there instead seems to be a globally optimal movement strategy associated with foraging that shows no frequency-dependence, and thus polymorphisms do not emerge.

In our Model 2, the modelling of kleptoparasitic interference as a fixed strategy leads to the dimorphism between obligate foragers and kleptoparasites. This constraint is resolved in Model 3, and individuals evolve to be kleptoparasitic in the presence of handlers, and turn to foraging otherwise. The strategy constraint on Model 2 individuals prevents the population from converging on a single behavioural and movement phenotype, as kleptoparasites are dependent on foragers for intake.

Fixed-strategy populations evolve a further polymorphism in movement behaviour, with kleptoparasites moving towards handlers, and foragers neutral to handlers. This coupling of movement and behavioural strategy is expected from the ‘correlational selection hypothesis’, which holds that suites of behaviours might be correlated into a syndrome when certain combinations of traits are favoured by selection (Sih et al. 2004b: Q. Rev. Biol. 79: 241–277.). Obligate kleptoparasites functionally occupy a higher trophic level whose primary resource is handling foragers, rather than prey items, and thus gregarious kleptoparasites are very quickly the only kleptoparasites to survive. Once the handler-preference is fixed in kleptoparasitic lineages, it becomes the more frequent handler response in the population (over avoidance) as kleptoparasites increase in frequency.

The proportion of kleptoparasites to foragers in Model 2 is quite tightly controlled by the density-dependent success of either strategy. The population requires a certain number of foragers, without which kleptoparasites would have no intake, while at low densities, kleptoparasites rapidly outcompete foragers and increase in number. However, limit cycles of kleptoparasites and foragers do not emerge. One important cause for this is global natal dispersal, which ensures a well-mixed population 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.

5.2 Plasticity, Polymorphisms, and Productivity

Model 3, which allows individuals to opportunistically steal prey items, resolves the strategic constraint of Model 2. When the inherited decision making weight is conditionally coupled with expressed behaviour, the frequency of stealing attempts better reflects the encounter rate of handlers, rather than the frequency of stealing propensity in the population. Model 3 individuals’ behaviour is thus more adapted to immediate, local conditions; they lose less time in futile stealing attempts, and thus achieve better intakes. Consequently, individuals rapidly converge upon a single, optimal strategy, which is to steal when handlers are available, and to forage otherwise.

Conditional strategy populations thus outperform fixed-strategy populations, and have similar intakes as forager populations, on low productivity landscapes. 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 Model 2 consistently produce populations that are functionally identical to Model 1 populations, with no kleptoparasitism. However, at high r_{max} , opportunistic kleptoparasites in Model 3 have a greater per-capita intake rate than pure foragers, as kleptoparasitic prey acquisition deprives a (foraging) handler of its prey. This allows kleptoparasitic interference to persist, while also resulting in slightly lower total population intake than the pure forager populations of Model 1 and high r_{max} Model 2.

5.3 Competition and Landscape Effects

Competition strongly influences landscape structure, which has cascading ecological and evolutionary effects. In Model 1, foragers face exploitation competition alone, and rapidly deplete prey items, which results in a large, stable proportion of the landscape forming clueless plateaus, with few movement cues (?). Consequently, individuals slowly converge upon a movement strategy that makes use of public information in the form of handling individuals, which indicate a profitable prey-item generation probability. In Model 2, the emergence and persistence of kleptoparasitism at low r_{max} reduces resource depletion, prey-items are regenerated, and the proportion of clueless plateaus is reduced. Ironically, the abundance of item cues is not functionally useful to most individuals; kleptoparasites find themselves in a ‘desert of plenty’ as their only resource is handlers, which are uncommon relative to prey items. Model 3 populations evolve kleptoparasitism, which similarly depresses prey-item depletion, and reduces the proportion of clueless plateaus. However, due to their conditional strategies, these individuals make use of the full range of cues for movement and behaviour decisions.

5.4 Conclusion

Work in progress.

324 Ssomething about klepts allowing landscape regrowth — similar to predation — landscape of fear etc
325 etc

326 **6 Conclusion**

327 **7 Acknowledgments**

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332 **References**

- 333 Amano, T., K. Ushiyama, S. Moriguchi, G. Fujita, and H. Higuchi. 2006. Decision-Making in Group
334 Foragers with Incomplete Information: Test of Individual-Based Model in Geese. *Ecological Monographs*
335 76:601–616.
- 336 Birch, L. C. 1957. The Meanings of Competition. *The American Naturalist* 91:5–18.
- 337 Brockmann, H., and C. Barnard. 1979. Kleptoparasitism in birds. *Animal Behaviour* 27:487–514.
- 338 Case, T. J., and M. E. Gilpin. 1974. Interference Competition and Niche Theory. *Proceedings of the National*
339 *Academy of Sciences* 71:3073–3077.
- 340 Clutton-Brock, T., and B. C. Sheldon. 2010. Individuals and populations: The role of long-term, individual-
341 based studies of animals in ecology and evolutionary biology. *Trends in Ecology & Evolution* 25:562–
342 573.
- 343 Cressman, R., and V. Krivan. 2006. Migration Dynamics for the Ideal Free Distribution. *The American*
344 *Naturalist* 168:384–397.

- 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.
- 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.
- Goss-Custard, J. D. 1980. Competition for food and interference among waders. *Ardea* 55:31–53.
- Guttal, V., and I. D. Couzin. 2010. Social interactions, information use, and the evolution of collective migration. *Proceedings of the National Academy of Sciences* 107:16172.
- Huston, M., D. DeAngelis, and W. Post. 1988. New Computer Models Unify Ecological Theory Computer simulations show that many ecological patterns can be explained by interactions among individual organisms. *BioScience* 38:682–691.

- Iyengar, E. V. 2008. Kleptoparasitic interactions throughout the animal kingdom and a re-evaluation, based on participant mobility, of the conditions promoting the evolution of kleptoparasitism. *Biological Journal of the Linnean Society* 93:745–762.
- Keddy, P. A. 2001. Studying competition. Pages 1–59 in P. A. Keddy, ed. *Competition, Population and Community Biology Series*. Springer Netherlands, Dordrecht.
- Krebs, J., and N. Davies. 1978. *Behavioural Ecology: An Evolutionary Approach*.
- Matsumura, S., R. Arlinghaus, and U. Dieckmann. 2010. Foraging on spatially distributed resources with sub-optimal movement, imperfect information, and travelling costs: Departures from the ideal free distribution. *Oikos* 119:1469–1483.
- Netz, C., H. Hildenbrandt, and F. J. Weissing. 2020. Complex eco-evolutionary dynamics induced by the coevolution of predator-prey movement strategies. *bioRxiv* page 2020.12.14.422657.
- Rutten, A. L., K. Oosterbeek, J. van der Meer, S. Verhulst, and B. J. Ens. 2010a. Experimental evidence for interference competition in oystercatchers, *Haematopus ostralegus*. I. Captive birds. *Behavioral Ecology* 21:1251–1260.
- Rutten, A. L., K. Oosterbeek, S. Verhulst, N. J. Dingemanse, and B. J. Ens. 2010b. Experimental evidence for interference competition in oystercatchers, *Haematopus ostralegus*. II. Free-living birds. *Behavioral Ecology* 21:1261–1270.
- Schlägel, U. E., V. Grimm, N. Blaum, P. Colangeli, M. Dammhahn, J. A. Eccard, S. L. Hausmann, A. Herde, H. Hofer, J. Joshi, S. Kramer-Schadt, M. Litwin, S. D. Lozada-Gobilard, M. E. H. Müller, T. Müller, R. Nathan, J. S. Petermann, K. Pirhofer-Walzl, V. Radchuk, M. C. Rillig, M. Roeleke, M. Schäfer, C. Scherer, G. Schiro, C. Scholz, L. Teckentrup, R. Tiedemann, W. Ullmann, C. C. Voigt, G. Weithoff, and F. Jeltsch. 2020. Movement-mediated community assembly and coexistence. *Biological Reviews*.
- Tregenza, T. 1995. Building on the Ideal Free Distribution. Pages 253–307 in *Advances in Ecological Research*, vol. 26. Elsevier.

- 393 Vahl, W. K., T. Lok, J. van der Meer, T. Piersma, and F. J. Weissing. 2005*a*. Spatial clumping of food and
394 social dominance affect interference competition among ruddy turnstones. *Behavioral Ecology* 16:834–
395 844.
- 396 Vahl, W. K., J. Van Der Meer, K. Meijer, T. Piersma, and F. J. Weissing. 2007. Interference competition, the
397 spatial distribution of food and free-living foragers. *Animal Behaviour* 74:1493–1503.
- 398 Vahl, W. K., J. van der Meer, F. J. Weissing, D. van Dullemen, and T. Piersma. 2005*b*. The mechanisms of
399 interference competition: Two experiments on foraging waders. *Behavioral Ecology* 16:845–855.
- 400 Wolf, M., and F. J. Weissing. 2010. An explanatory framework for adaptive personality differences. *Philo-*
401 *sophical Transactions of the Royal Society B: Biological Sciences* 365:3959–3968.

402 **8 Appendix A: Supplementary Figures**

403 **8.1 Fox–dog encounters through the ages**

404 **9 Appendix B: Additional Methods**

405 **9.1 Measuring the height of fox jumps without a meterstick**

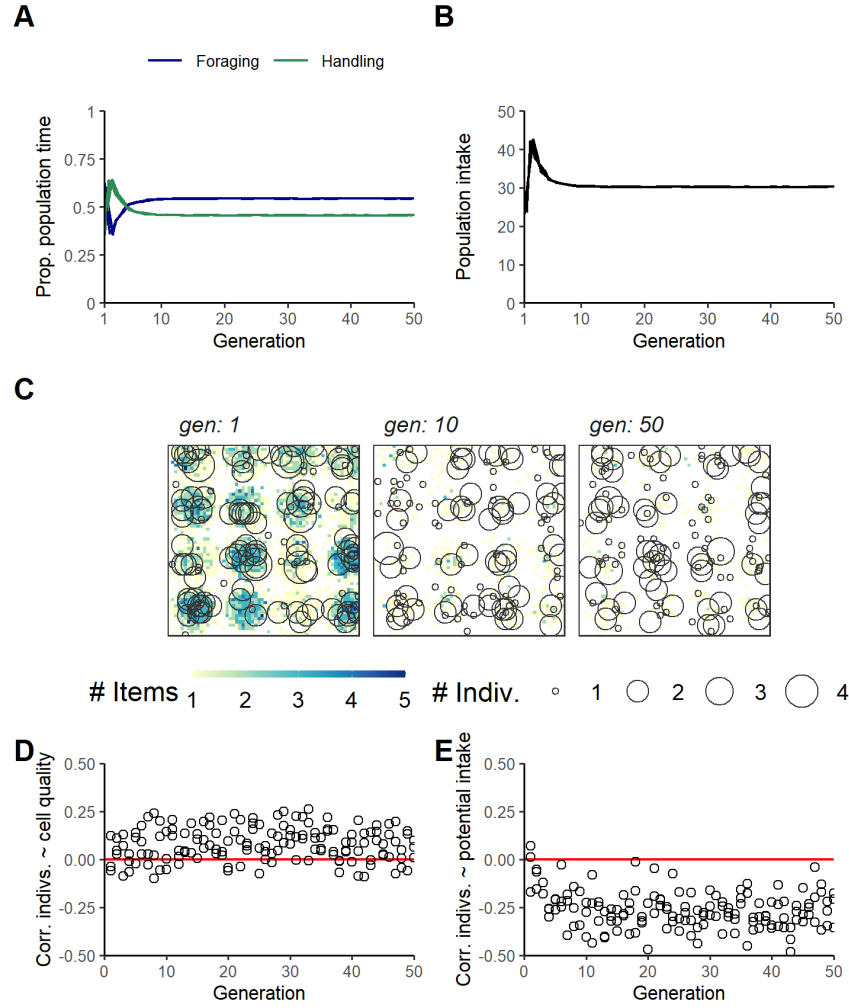


Figure 1: Model 1 populations with only exploitation competition rapidly reach an **(A)** activity budget and **(B)** total intake equilibrium. The initial spike in handling and population intake is due to initially high foraging success on a fully stocked resource landscape. **(C)** The sustained extraction of prey-items results in a rapid depletion of the resource landscape within 10 generations. The number of individuals on occupied cells is shown as black circles (size = number of individuals). **(D)** The correlation between the number of individuals on a cell, and its productivity r_{max} , remains low across generations, while the **(E)** correlation between individual counts and the probability of finding a prey-item (which relates to the item count) rapidly reaches a negative value, between -0.5 and -0.25. Panels **A**, **B**, **D** and **E** show three replicates, while panel **C** shows a single replicate; all panels are for $r_{max} = 0.01$.

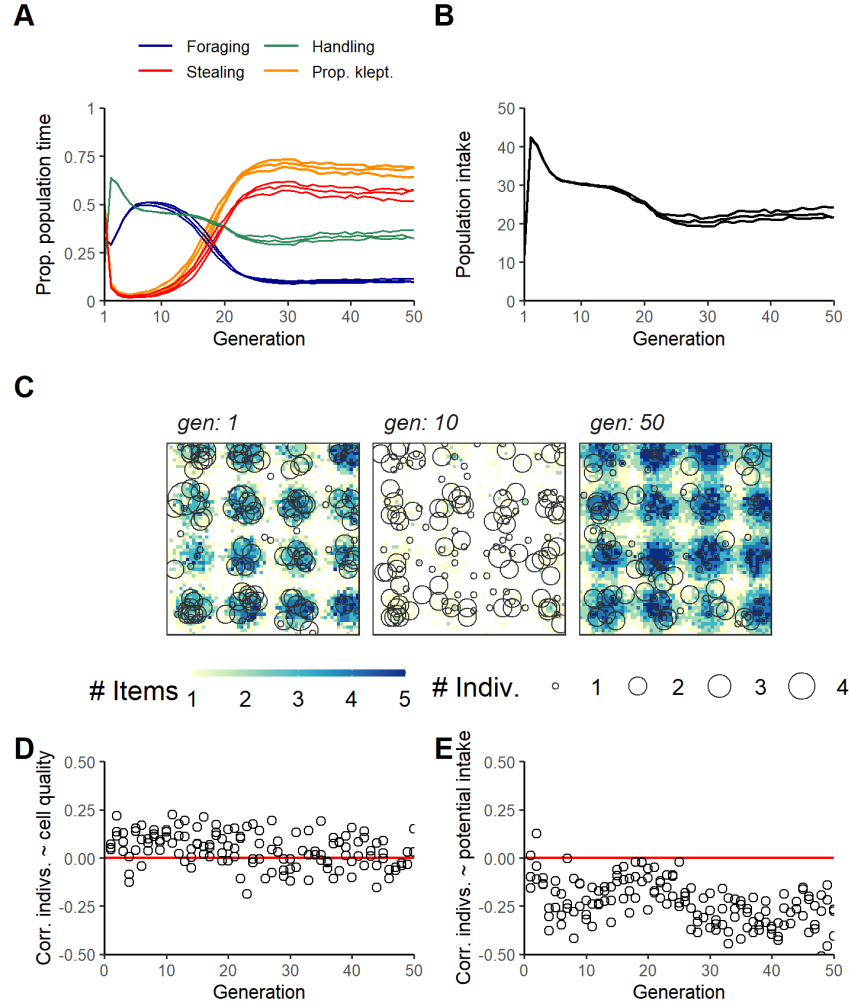


Figure 2: Model 2 populations with both exploitation competition, and kleptoparasitism as a fixed, inherited strategy reach an (A) activity budget and (B) total intake equilibrium rapidly. The initial handling and intake spike is due to very successful handling on undepleted resource landscapes. The frequency of stealing activities (red line; panel A) is less than the proportion of kleptoparasitic individuals (orange line; panel A), as successful kleptoparasites are counted as handlers. (C) With a reduction in foraging and handling due to increased stealing after generation 30 (panel A), prey-item depletion is reduced, and the resource landscape recovers by generation 50. The number of individuals on occupied cells is shown as black circles (size = number of individuals). (D) The correlation between the number of individuals on a cell, and its productivity r_{max} , remains low across generations, while the (E) correlation between individual counts and the probability of finding a prey-item (which relates to the item count) rapidly reaches a negative value, between -0.5 and -0.25. Panels A, B, D and E show three replicates, while panel C shows a single replicate; all panels are for $r_{max} = 0.01$.

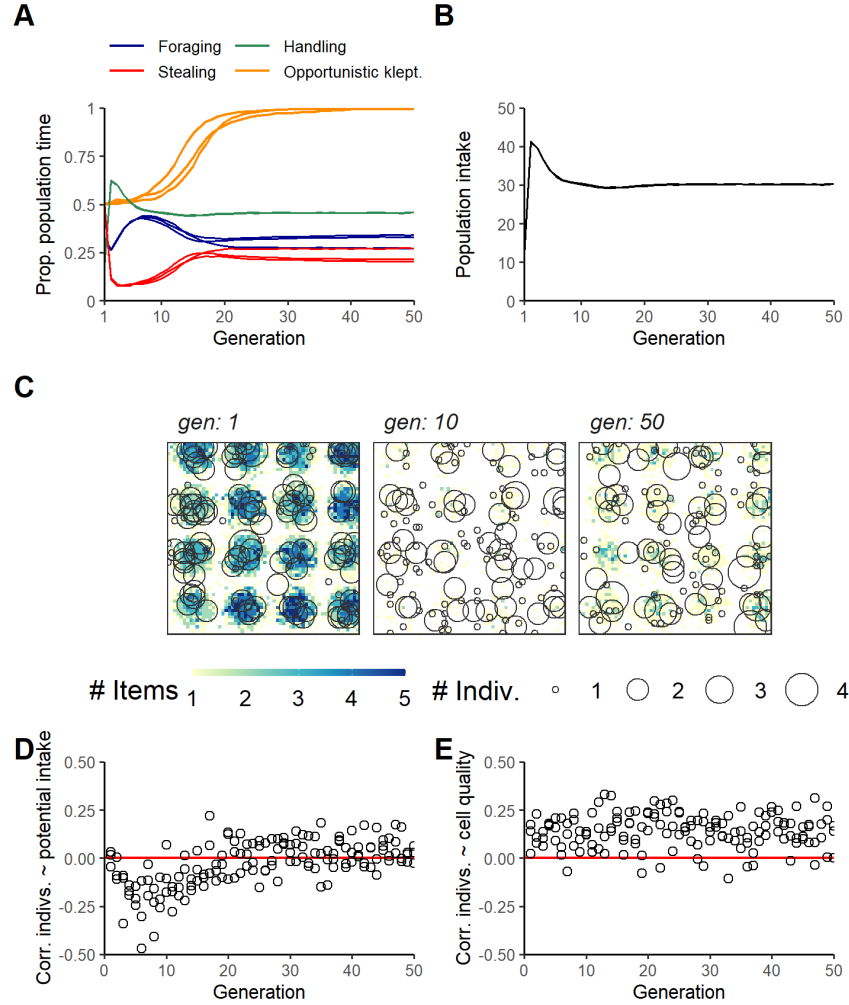


Figure 3: Model 3 populations with both exploitation competition, and kleptoparasitism as strategy conditional on local cues, reach an (A) activity budget and (B) total intake equilibrium rapidly. The initial handling and intake spike is due to very successful handling on undepleted resource landscapes. A kleptoparasitic response to handlers (orange line; panel A) becomes rapidly fixed in the population, but the frequency of stealing remains relatively much lower (red line; panel A). (C) The initially rapid depletion of the resource landscape within 10 generations is halted as kleptoparasitism reduces foraging activities, and the resource landscape regenerates prey-items by generation 50. The number of individuals on occupied cells is shown as black circles (size = number of individuals). (D) The correlation between the number of individuals on a cell, and its productivity r_{max} , and (E) the correlation between individual counts and the probability of finding a prey-item are both quite weak across generations. Panels A, B, D and E show three replicates, while panel C shows a single replicate; all panels are for $r_{max} = 0.01$.

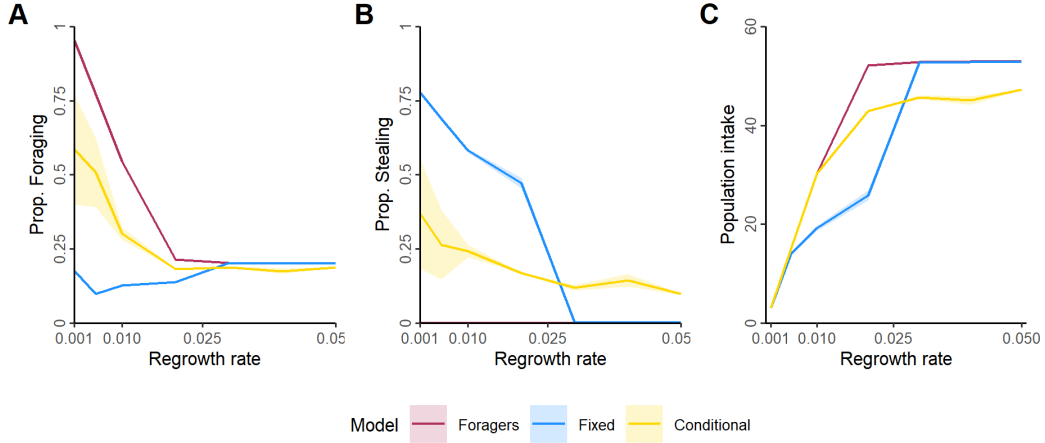


Figure 4: Landscape productivity strongly affects model outcomes. **(A)** The frequency foraging reduces with increasing r_{max} in models 1 and 3, but remains relatively stable in model 2. In all three models, this is partly due to an increase in handling caused by increased resource availability, and **(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.

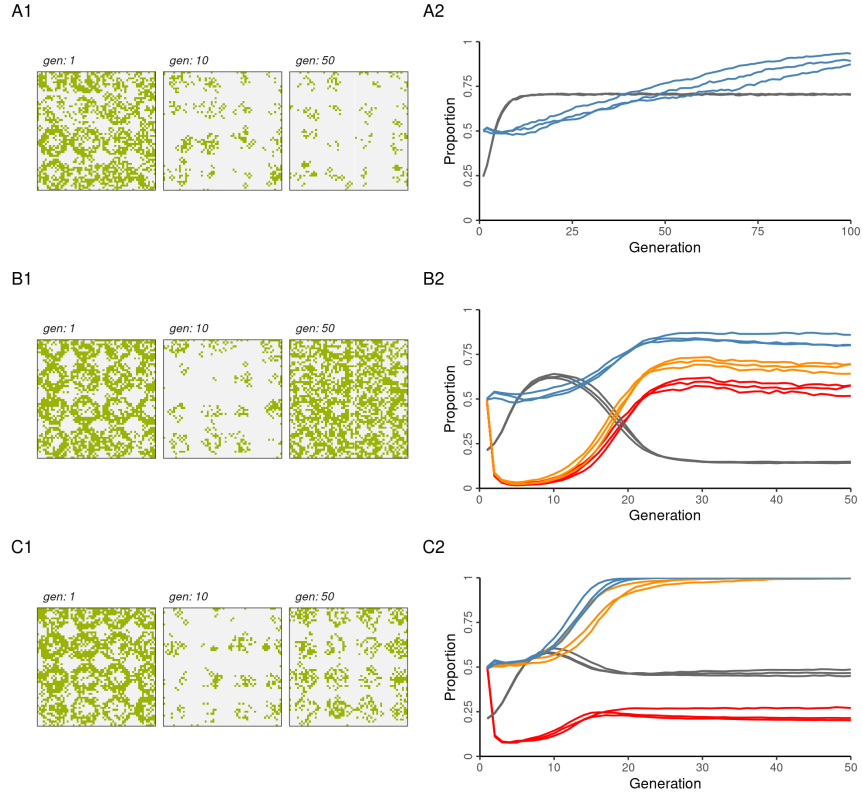


Figure 5: The sustained depletion of prey-items leads to the homogenisation of large parts of the resource landscape within 10 generations. This homogenisation to zero items leads to the creation of ‘clueless regions’, i.e., neighbouring cells with no difference in item counts, and thus no direct resource gradients (grey areas in **A1**, **B1**, **C1**; green areas show cells which differ from neighbours in item counts). Black lines in (**A2**, **B2**, **C2**) show the proportion of the landscape that is ‘clueless’. The evolution and persistence of a kleptoparasitic response (orange lines) and stealing events (red lines) reduces item depletion. (**A1**, **A2**) Strong depletion of the resource landscape in Model 1 leads to large areas with no item gradient. When the majority of the landscape is ‘clueless’, moving towards handlers, which are an indirect indicator of resources, becomes a common strategy (blue line). (**B1**, **B2**) The emergence and persistence of fixed kleptoparasitism in Model 2 leads to a reduction in the area of clueless plateaus within 40 generations. (**C1**, **C2**) In Model 3, the conditional kleptoparasitic strategy leads to depletion intermediate between Models 1 and 2, and a similarly intermediate proportion of clueless plateaus on the landscape. All panels show replicates at $r_{max} = 0.01$; landscape panels show only a single replicate.

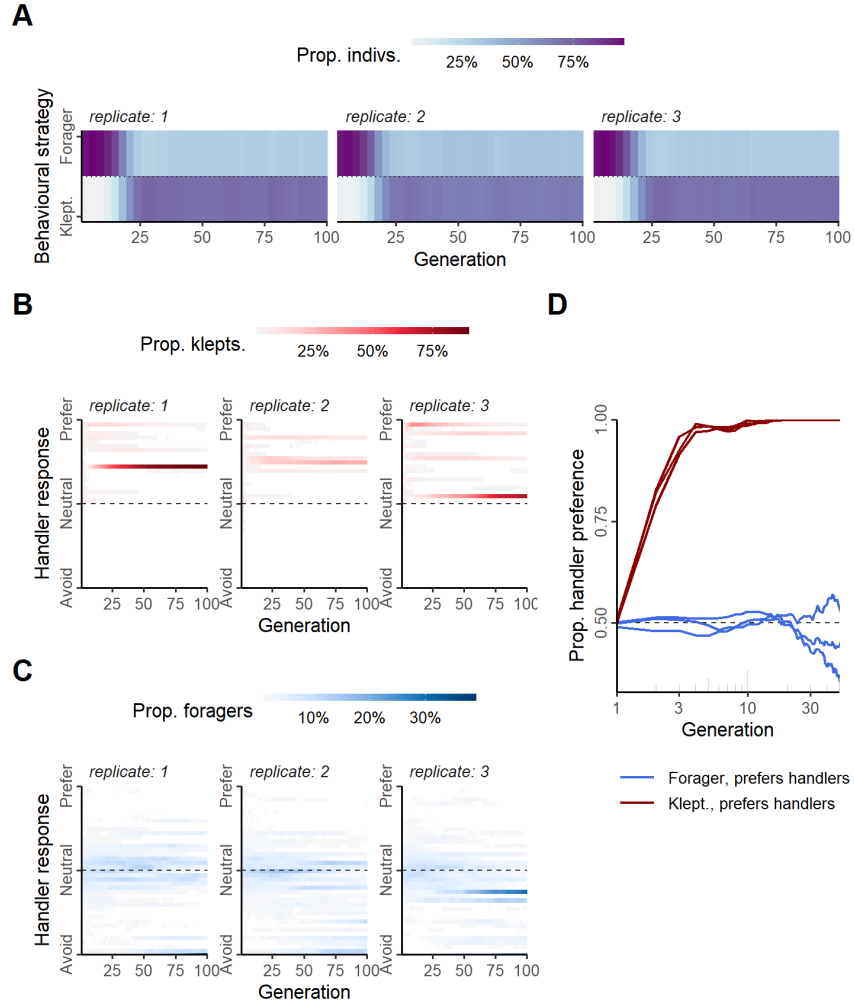


Figure 6: Movement rules rapidly diverge between fixed behavioural strategies in Model 2. **(A)** Kleptoparasitism rapidly becomes the more frequent strategy in Model 2 populations, with no differences across replicates. **(B)** However, replicates differ strongly in the frequencies of evolved movement strategies among the two behavioural strategies. While nearly all kleptoparasites evolve to move towards handlers, their direct resource, the strength of their handler preference is polymorphic, with 2 – 3 morphs in most replicates. **(C)** Foragers are also polymorphic in their handler responses, but these morphs are the results of drift, rather than selection. **(D)** Overall, within 5 generations (shown on a log scale), all kleptoparasitic individuals ($\sim 75\%$ of the population at equilibrium; see Fig. 3A) have an evolved preference for moving towards handlers. Meanwhile, forager individuals are agnostic to handlers, and are equally split between handler preference and avoidance. All panels show three replicates at $r_{max} = 0.01$.