To be decided: Competition — movement — evolution

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1 Abstract

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2 Introduction

Competition is a constant feature of animal ecology, and can be an important driver of population dynamics and animal distributions (Krebs 1972; Stephens et al. 2007). 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 et al. 2008; e.g. Furness 1987; Carbone et al. 1997; other examples here). Experiments with foraging birds have shown that competition, including kleptoparasitism, can affect the spatial distribution of individuals across resource patches (Goss-Custard 1980 Ardea; Vahl et al. 2005a, 2005b, 2007; Rutten et al. 2010a). The avoidance of competitive interactions too can affect the distribution and behaviour of animals foraging in groups (Bijleveld et al. 2012; Rutten et al. 2010b). At larger scales, competition among different behavioural types in a species (e.g. Duckworth and Badyaev 2007), or between species (e.g. Petren and Case 1997; Duckworth and Badyaev 2007), can strongly influence species distributions and animal movement decisions (Ovaskainen et al. 2015 MEE; Schlaegel et al. 2020).

Competition is difficult to study in free living animals, yet knowledge of the fine-scale mechanisms and evolutionary consequences of competition is central to basic evolutionary ecology. For instance, it is surmised that interference is more important than exploitation under natural conditions (Case and Gilpin 1974, or citations from their first para), but 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,

that can be used by all individuals. 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). Our poor understanding of competition poses a problem, since it is key to models such as the ideal free distribution concept, which is a cornerstone of evolutionary ecology (Fretwell and Lucas, 1970). The IFD and its developments model competition in quite rudimentary ways (Amano et al., 2006; Cressman and Křivan, 2006; Folmer et al., 2012; Fretwell and Lucas, 1970; Garay et al., 2020, 2015; Garay and Móri, 2010; Matsumura et al., 2010; Meer and Ens, 1997; Tregenza, 1995); IFD-based models ignore resource depletion (Cressman and Křivan, 2006; Fretwell and Lucas, 1970; Meer and Ens, 1997), assume unrealistic movement rules (Cressman and Křivan, 2006; Cressman et al., 2014; Garay et al., 2020), or treat interference as an almost inevitable part of the foraging process (reviewed in Meer and Ens, 1997; Tregenza, 1995, ; see also Cressman and Křivan 2006; Garay et al. 2020). On the contrary, interference competition is a complex individual behaviour which is closely related to movement decisions, and its treatment in models is likely to have important ecological and evolutionary consequences (Meer and Ens, 1997).

Modelling competition in a spatially-explicit context, as the outcome of evolved individual movement and behavioural rules, would allow us to (1) better examine the feedbacks between movement and foraging behaviour, and to (2) study the influence of different modelling choices. Individual-based simulation modelling (IBM) is an increasingly powerful technique that allows us to more realistically model competition among foraging individuals, as well as their interactions with the environment (DeAngelis, 2018; DeAngelis and Mooij, 2005; Grimm et al., 2017; Huston et al., 1988; Railsback et al., 2020). IBMs take a bottom-up view to encode many thousands of unique individuals with decision making mechanisms, and allow these individuals to interact with their environment, and each other (DeAngelis and Diaz, 2019; Huston et al., 1988). Conceptual and computational advances in IBMs (DeAngelis, 2018; DeAngelis and Mooij, 2005) allow us to make general, testable predictions for population-level phenomena (e.g. animal space

use, or life-history strategies; see Folmer et al., 2012; Schaefer et al., 2018; Spiegel et al., 2017), and they are well suited to modelling the evolution of complex behaviours (Getz et al., 2015, 2016; Guttal and Couzin, 2010; Netz et al., 2020).

Here, we implement a spatially explicit IBM approach to competition and animal movement decisions, with three different models. In the first model, 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 model, 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 model, 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 models 2 and 3 to show the influence of modelling choices. From these models, we show that 1. Foraging with only exploitation competition is the most productive strategy from a population standpoint, but can be invaded by both fixed and conditional kleptoparasites as kleptoparasitism is the more productive *individual* strategy; 2. The evolution of movement towards successful foragers is an outcome of depleted resource-landscape lacking cues for optimal movement, and is itself a prerequisite for the persistence of obligate kleptoparasitism; 3. The emergence of kleptoparasitism reduces resource-landscape depletion, and restores cues for optimal movement.

3 Methods

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. Ens et al., 1990; Rutten et al., 2010*a*,*b*; Vahl et al., 2005*a*,

2007, 2005*b*). 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 Model 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.

3.2 Models 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.

3.3 Movement and Behavioural Strategy

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

$$S = m_f F + m_h H + m_k K \tag{1}$$

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

$$\text{strategy} = \begin{cases} \text{forager}, & \text{if } w_f F + w_h H + w_k K + w_b \geq 0 \\ \text{kleptoparasite}, & \text{otherwise} \end{cases} \tag{2}$$

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

3.4 Prey Environment and Ecological Dynamics

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 $p_i = 0.2$.

$$p(success) = 1 - (1 - p_i)^G \tag{3}$$

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 $t+1$.

3.5 Reproduction and the Evolution of Decision Making

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 intialised each offspring at a random location on the landscape, and also reset its total intake to zero.

3.6 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 individuals 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* Perkins 1992).

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 ∼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); Meer and Ens (1997), 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 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 (Perkins, 1992). 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.

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

6 Conclusion

7 Acknowledgments

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8 Appendix A: Supplementary Figures

8.1 Fox–dog encounters through the ages

9 Appendix B: Additional Methods

9.1 Measuring the height of fox jumps without a meterstick

10 Tables

11 Figure legends

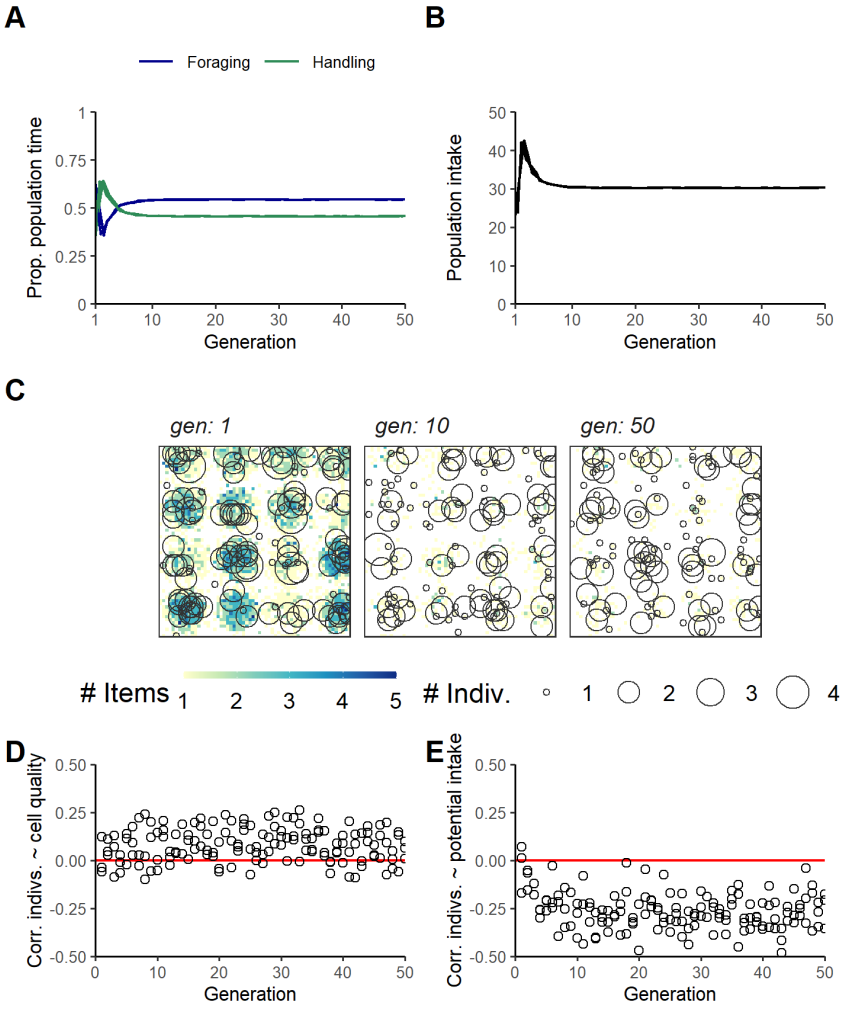

Figure 1: Model 1 populations with only exploitation competition rapidly reach an **(A)** activity budget and **(B)** total intake equlibrium. The initial spike in handling and population intake is due to initially high foraging success on a fully stocked resource landscape. **(C)** The sustained extraction 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.

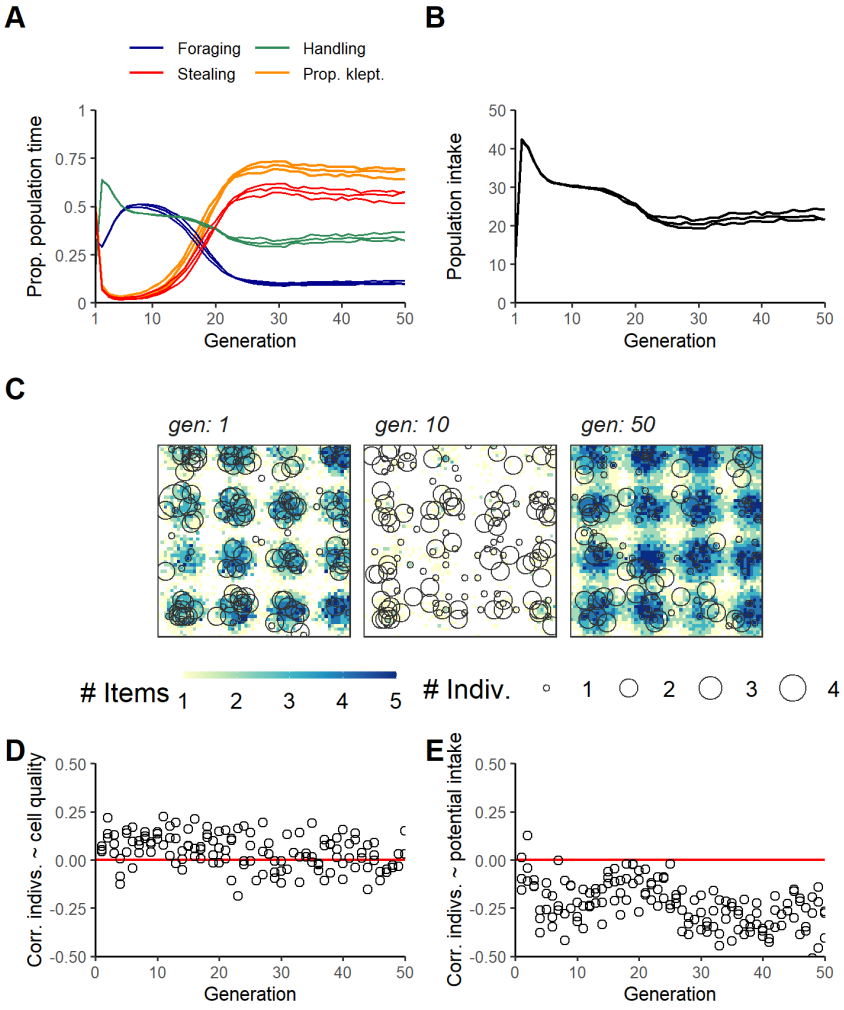

Figure 2: Model 2 populations with both exploitation competition, and kleptoparasitism as a fixed, inherited strategy reach an **(A)** activity budget and **(B)** total intake equlibrium rapidly. The initial handling and intake spike is due to very successful handling on undepleted resource landscapes. 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.

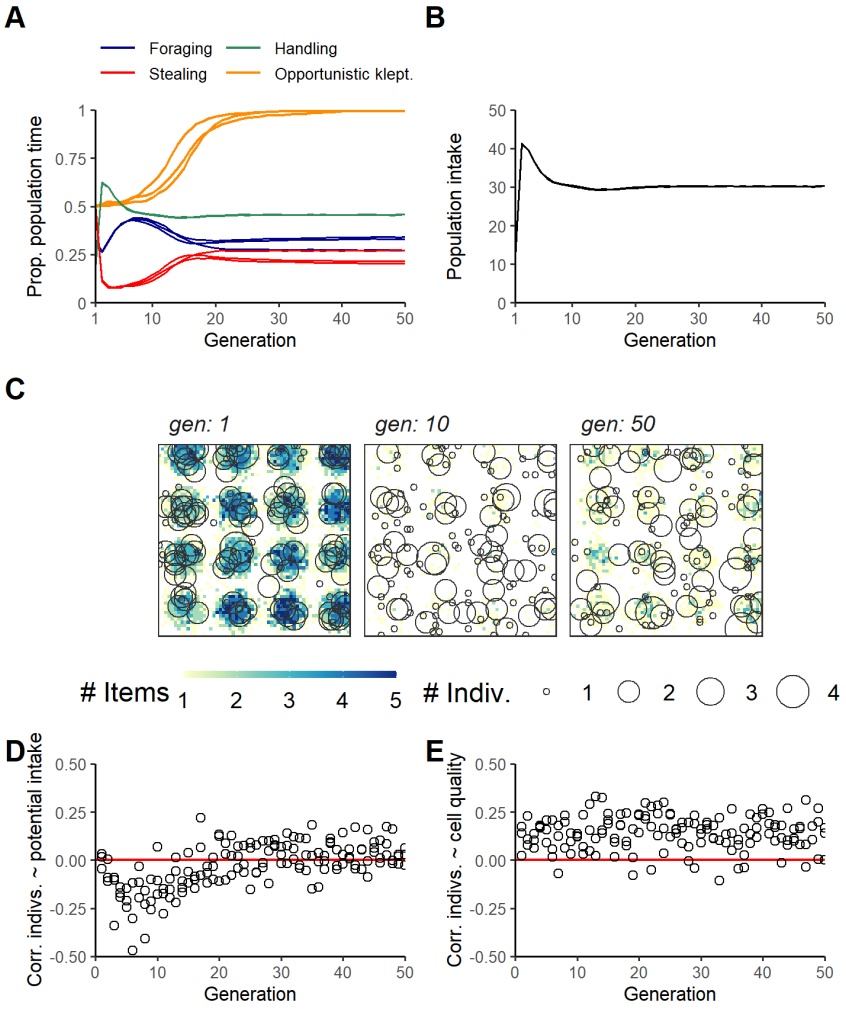

Figure 3: Model 3 populations with both exploitation competition, and kleptoparasitism as strategy conditional on local cues, reach an **(A)** activity budget and **(B)** total intake equlibrium rapidly. The initial handling and intake spike is due to very successful handling on undepleted resource landscapes. 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.

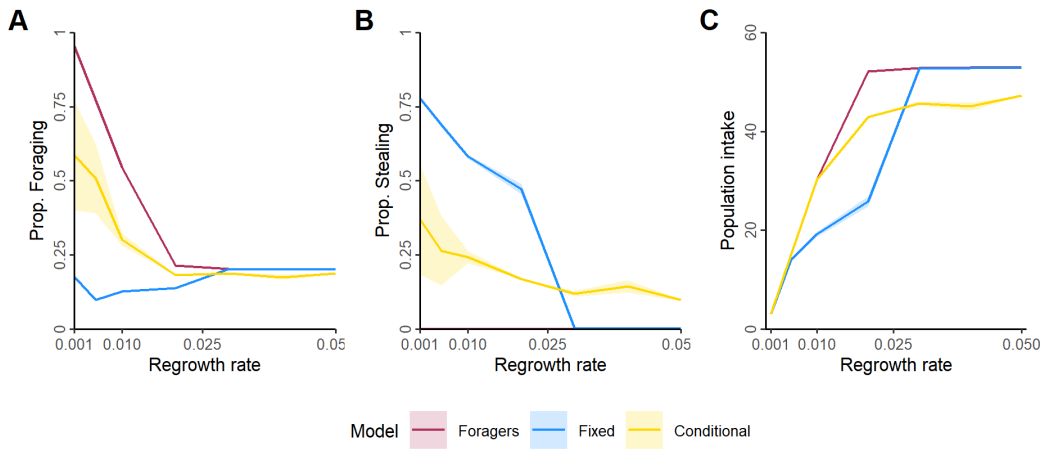

Figure 4: Landscape productivity strongly affects model outcomes. **(A)** The frequency foraging reduces with increasing r_{max} in models 1 and 3, but remains relatively stable in model 2. In all three models, this is partly due to an increase in handling caused by increased resoure availability, and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

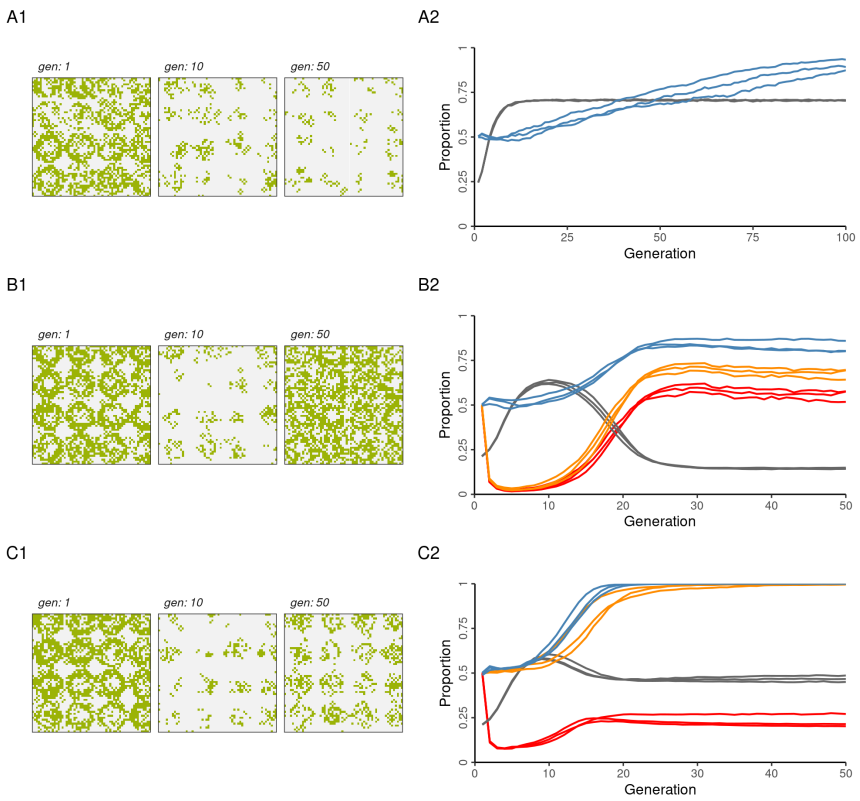

Figure 5: The sustained depletion of prey-items leads to the homogenisation of large parts of the resource landscape within 10 generations. This homogenisation to zero items leads to the creation of 'clueless regions', i.e., neighbouring cells with no difference in item counts, and thus no direct resource 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.

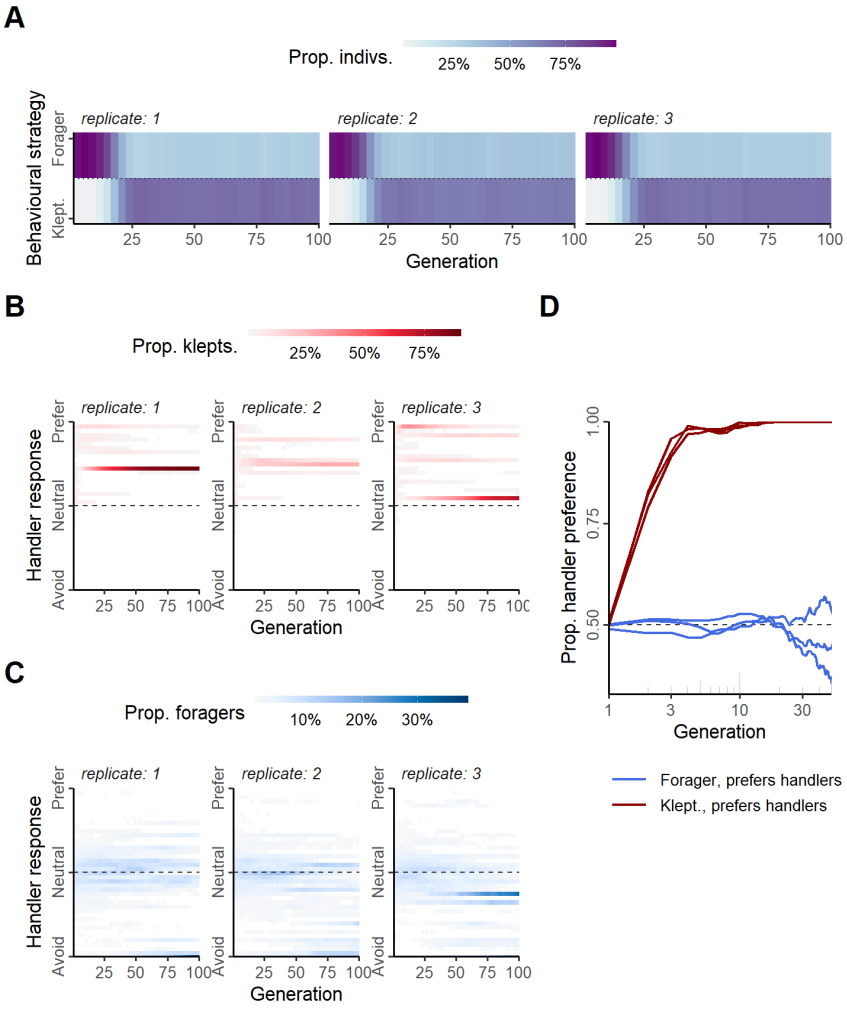

Figure 6: Movement rules rapidly diverge between fixed behavioural strategies in Model 2. **(A)** Kleptoparasitism rapidly becomes the more frequent strategy in Model 2 populations, with no differences across replicates. **(B)** However, replicates differ strongly in the frequencies of evolved movement 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 (~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.