The Evolutionary Ecology of Individual Foraging Decisions

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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

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   *Flexibility in Foraging Strategies*

Our model considers three main scenarios of flexibility in individual foraging strategies. The **first scenario** is an inflexible producer-only case, in which individuals move about on the landscape and probabilistically find and consume discrete prey food items. Between finding and consuming a food 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 which adds some flexibility. Individuals at the start of their lifetime each choose between two foraging strategies, which are then fixed through life. The strategy choice is based on local environmental cues, and is covered in "Movement and Foraging Decisions". The two strategies are to produce, i.e., to probabilistically find, handle, and consume discrete prey (as in the producer-only case), or to scrounge as a kleptoparasite, i.e., to steal a found prey item from the individual handling it. We refer to such scroungers as 'kleptoparasites' from here onwards. 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 movement decision. Thus kleptoparasites clearly save time on handling compared to a producer, and the time saved increases with the handling time T_H of the prey. The **third scenario** is a flexible-strategy case, and individuals are allowed to be plastic in their foraging strategies, and choose between producing and scrounging strategies in each timestep. Apart from the frequency of the choice, the actual foraging dynamics are the same as described in the fixed-strategy case. Individuals move about on the environment, and each foraging strategy choice is based on local environmental cues (see "Movement and Foraging Decisions").

3.2 *Movement and Foraging Decisions*

Individuals essentially use cues available in timestep t to predict their best move for the next timestep $t + 1$, and the strategy associated with that move (when this is allowed). The movement decision is based on three local environmental cues: (1) the number of discrete prey items G,

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(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'). 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

$$S = m_g G + m_h H + m_p P + m_b \tag{1}$$

where the weighing factors for each cue m_g, m_h and m_p, and the bias m_b 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 the producers-only case make no foraging decisions and find food items probabilistically (see "Prey Environment and Ecological Dynamics"). In the fixed-strategy case, individuals pick a lifelong foraging strategy in their first timestep (t_0), while in the flexible-strategy case, individuals pick a strategy in each timestep t to be deployed in $t + 1$. Individuals in these latter two cases process the cell-specific environmental cues G, H, and P to determine their foraging strategy F for life (fixed strategy), or in the grid cell into which they have chosen to move in $t + 1$ (flexible strategy). F is determined as

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

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

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 agents 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

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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, since prey can show small-scale anti-predator avoidance responses.

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 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. Thus for a simulation-specific baseline r_{base} = 0.03, the central cell of a resource peak would have an r_{centre} = 0.03, and generate 3 items every 100 timesteps, compared with r_{edge} = 0.006, or 0.6 items generated in 100 timesteps. We ran the simulation with r_{base} values of 0.001, 0.01, 0.03, and 0.05, which we considered a sufficiently broad range. Cells in our landscape were modelled as being able to hold a maximum of K prey

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items, with the default $K = 5$. 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 producer 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

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

where p_i is the detection probability of each of G items, which is uniformly set to 0.2 by default for all items.

Since we model foraging events as occurring simultaneously, it is possible for more producers 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. Producers 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). It is important to note that a producer that has converted into a handler in timestep t is not an available target for kleptoparasites until timestep $t + 1$. Producers 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 flexible-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, and similar to producer-handlers are unavailable as targets to other kleptoparasites until the next timestep. 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 agents 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. Handling a food item requires a maximum of T_H timesteps, during which the handler is immobile.

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, m_b) and foraging strategy choice (f_g, f_h, f_p, f_b) are transmitted from parent individuals to offspring. 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 total lifetime intake of individuals is used as a proxy of fitness, and the population's total fitness is its total intake. 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. Furthermore, limited natal dispersal could lead to population-level movements due to differential reproduction that mirror shifts in resource abundance, rather than individual movement. 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.

3.5 Simulation Output and Analysis

3.5.1 Decision Making Weights

To understand the evolutionary consequences of our simulation, we exported the the decision-making weights which determine individual movement (m_g, m_h, m_p, m_b) and foraging strategy

choice (f_g, f_h, f_p, f_b) 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 evovled preference for or positive effect of a cue on the movement and strategy choice mechanism of an individual.

3.5.2 *Functional and Aggregative Response*

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. Adopting this method, we sought to fit the widely used Beddington model of functional and aggregative response to pseudo-ecological data generated by our simulation. 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 agents 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

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generation so as to capture the system in a state of ecological equilibrium.

3.5.3 Distribution Along Productivity Gradients

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 pseduo-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-captia 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.

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 Evolutionary Equilibrium

Work in progress: Dynamic equilibrium emerges within 1000 generations — equilibria are identical across replicates — kleptoparasites emerge in most replicates when allowed — kleptoparasites establish as a stable and significant proportion of individuals, or individual strategies.

4.2 Movement-Behaviour Co-Evolution

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.

4.2.1 The Case of Kleptoparasitism

In 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.

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

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when possible, across r_{max}.

4.3   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 X) 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_{base} = 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.

4.4   Functional Response of Intake

Understanding the consequences of aggregating with other individuals is key to explaining why animals form groups. We examined the functional response of individual intake of each behavioural strategy on a cell to the number of individuals on that cell. 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 agents 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).

4.5   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 mea-

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surement 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.

4.5.1   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 signficantly higher at low r_{max}, in part due to the relatively greater prevalence of kleptoparasitism overall. 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.

4.5.2   Population Distribution in Relation to Productivity

We find that in the foragers-only case, individuals follows the matching rule in relation to grid-cell productivity, with more foragers on higher productivity cells (Fig. 5.a). 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

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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 *Kleptoparasitism and Predation Have Similar Landscape Effects*

Work in progress: Kleptoparasite intake depends only on the number of individuals — kleptoparasite intake is highest when cells have few kleptoparasites and many producers — kleptoparasite emergence is associated with a reduction in item depletion — add also landscape metrics etc

5 Discussion

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

11.1   Online figure legends