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E-Article

The Joint Evolution of Animal Movement and Competition Strategies

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ABSTRACT: Competition typically takes place in a spatial context, but eco-evolutionary models rarely address the joint evolution of movement and competition strategies. Here we investigate a spatially explicit forager-kleptoparasite model where consumers can either forage on a heterogeneous resource landscape or steal resource items from conspecifics (kleptoparasitism). We consider three scenarios: (1) foragers without kleptoparasites, (2) consumers specializing as foragers or as kleptoparasites, and (3) consumers that can switch between foraging and kleptoparasitism depending on local conditions. We model movement strategies as individual-specific combinations of preferences for environmental cues, similar to step-selection coefficients. Using mechanistic, individual-based simulations, we study the joint evolution of movement and competition strategies, and we investigate the implications for the distribution of consumers over this landscape. Movement and competition strategies evolve rapidly and consistently across scenarios, with marked differences among scenarios, leading to differences in resource exploitation patterns. In scenario 1, foragers evolve considerable individual variation in movement strategies, while in scenario 2, movement strategies show a swift divergence between foragers and kleptoparasites. In scenario 3, where individuals' competition strategies are conditional on local cues, movement strategies facilitate kleptoparasitism, and individual consistency in competition strategy also emerges. Even in the absence of kleptoparasitism (scenario 1), the distribution of consumers deviates considerably from predictions of ideal free distribution models because of the intrinsic difficulty of moving effectively on a depleted resource landscape with few reliable cues. Our study emphasizes the advantages of a mechanistic approach when studying competition in a spatial context and suggests how evolutionary modeling can be integrated with current work in animal movement ecology.

Keywords: movement ecology, intraspecific competition, individual differences, ideal free distribution, kleptoparasitism, individual-based modeling.

Introduction

Intraspecific competition is an important driver of population dynamics, and the spatial distribution of organisms (Krebs and Davies 1978) and has 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 that is widespread among animal taxa is kleptoparasitism, in which an individual steals a resource from its owner (Iyengar 2008). Since competition has an obvious spatial context, animals should account for the locations of competitors when deciding where to move (Nathan et al. 2008). This is expected to have downstream effects on animal distributions across spatial scales (from resource patches [Fretwell and Lucas 1970] to species distributions [Duckworth and Badyaev 2007; Schlägel et al. 2020]). Animal movement strategies are thus likely to be adaptive responses to landscapes of competition, with competitive strategies themselves being evolved responses to animal distributions. Empirical studies of this joint evolution are nearly impossible at large spatiotemporal scales. This makes models linking individual movement and competition strategies with population distributions necessary.

Contemporary individual-to-population models of animal space use (reviewed in DeAngelis and Diaz 2019) and competition, however, are only sufficient to represent very simple movement and prey choice decisions. For example, these models, including ideal free distribution (IFD) models (Fretwell and Lucas 1970), information-sharing models (Giraldeau and Beauchamp 1999; Folmer et al. 2012), and producer-scrounger models (Barnard and Sibly 1981; Vickery et al. 1991; Beauchamp 2008), often treat foraging competition in highly simplified ways. Most IFD models consider resource depletion unimportant or

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negligible (continuous input models; see Tregenza 1995; van der Meer and Ens 1997), make simplifying assumptions about interference competition, or even model an ad hoc benefit of grouping (e.g., Amano et al. 2006). Meanwhile, producer-scrounger models primarily examine the benefits of choosing either a producer strategy or a scrounger strategy given local conditions, such as conspecific density (Vickery et al. 1991) or the order of arrival on a patch (Beauchamp 2008). Overall, these models simplify the mechanisms by which competition decisions are made and downplay spatial structure (see also Holmgren 1995; Spencer and Broom 2018; Garay et al. 2020).

In contrast, spatial structure is key to foraging (competition) decisions (Beauchamp 2008). How animals are assumed to integrate the costs (and potential benefits) of competition into their movement decisions has important consequences for theoretical expectations of population distributions (van der Meer and Ens 1997; Hamilton 2002; Beauchamp 2008). In addition to short-term ecological effects, competition also likely has evolutionary consequences for individual movement strategies, setting up feedback loops between ecology and evolution. Modeling competition and movement decisions jointly is thus a major challenge. Some models take an entirely ecological view, assuming that individuals move or compete ideally or according to fixed strategies (Vickery et al. 1991; Holmgren 1995; Tregenza 1995; Amano et al. 2006; but see Hamilton 2002). Models that include evolutionary dynamics in movement (de Jager et al. 2011, 2020) and foraging competition strategies (Beauchamp 2008; Tania et al. 2012) are more plausible, but they too make arbitrary assumptions about the functional importance of environmental cues to individual decisions.

Mechanistic, individual-based models are well suited to capturing the complexities of spatial structure, animal decision-making, and evolutionary dynamics (Guttal and Couzin 2010; Kuijper et al. 2012; Getz et al. 2015, 2016; White et al. 2018; Long and Weissing 2020; Gupte et al. 2022; Netz et al. 2022*a*; for conceptual underpinnings see, Huston et al. 1988; Mueller et al. 2011; DeAngelis and Diaz 2019). Individual-based models can incorporate the often-significant variation in movement and competition preferences found in populations, allowing individuals to make different decisions given similar cues (Laskowski and Bell 2013; Bierbach et al. 2017). Individual-based models also force researchers to be explicit about their modeling assumptions, such as how exactly competition affects fitness. Similarly, rather than taking a purely ecological approach and assuming individual differences (e.g., in movement rules; White et al. 2018), allowing movement strategies to evolve in a competitive landscape can reveal whether individual variation emerges in plausible ecological scenarios (as in Getz et al. 2015). This allows the functional importance of environmental cues for movement (see, e.g., Scherer et al. 2020) and competition decisions in evolutionary models to be joint outcomes of selection and lets different competition strategies be associated with different movement strategies (Getz et al. 2015).

Here, we present a spatially explicit, mechanistic, individual-based model of intraspecific foraging competition, where movement and competition strategies jointly evolve on a resource landscape with discrete, depletable food items that need to be processed ("handled") before consumption. In our model, foragers make movement decisions using inherited, evolvable preferences for local ecological cues, such as resource and competitor densities; the combination of preferences for each cue forms individuals' movement strategies (similar to relative step selection; Fortin et al. 2005; Avgar et al. 2016). We consider three scenarios. In the first scenario, we examine only exploitation competition. In the second scenario, we introduce kleptoparasitic interference as an inherited strategy, fixed through an individual's life. In the third scenario, we model kleptoparasitism as a behavioral strategy conditioned on local environmental and social cues; the mechanism underlying this foraging choice is also inherited.

Our model allows us to examine the evolution of individual movement strategies, population-level resource intake, and the spatial structure of the resource landscape. The model enables us to take ecological snapshots of consumer-resource dynamics (animal distributions, resource depletion, and competition) proceeding at evolutionary timescales. We investigate (1) which movement strategies evolve in our three competition scenarios, (2) whether movement strategies differ within and between competition strategies in our scenarios, and (3) how resource densities and the association between forager and resource densities differ between scenarios.

The Model

Individual-based models have to explicitly specify numerous assumptions (e.g., spatial structure, individual interactions, event timescales), but this helps expose assumptions that are often hidden below the surface in analytical models. We kept our model assumptions as simple and generic as possible, striving for general conceptual insights. To be concrete, the model reflects the foraging behavior of shorebirds, such as oystercatchers (*Haematopus* spp.), which are extensively studied in the context of foraging competition, both empirically (e.g., Vahl et al. 2005*a*, 2005*b*, 2007; Rutten et al. 2010*a*, 2010*b*) and using individual-based models (reviewed in Stillman and Goss-Custard 2010). Our environment is a fine grid of cells, and each grid cell can hold multiple individuals.

Resources are discrete, as is our conception of time within and between generations. Our population, with a fixed number of individuals ($N = 10{,}000$), moves on a landscape of 512×512 grid cells (approximately one individual per 26 cells), with wrapped boundaries (i.e., a torus); individuals passing beyond the bounds at one end reappear on the opposite side. The model has two timescales. The first is an ecological timescale of T time steps comprising one generation (default $T = 400$) during which individuals move, make foraging decisions, and handle prey items they find or steal. Individuals are immobile while handling food items, creating the conditions for kleptoparasitism (Brockmann and Barnard 1979; Ruxton et al. 1992). At the end of each generation, individuals reproduce, transmitting their movement and foraging strategies to their offspring, whose number is proportional to individual intake at the ecological timescale. Our model has 1,000 generations, and this comprises the timescale at which evolution occurs.

Resource Landscape

Prey Abundance. We considered our discrete resources, called prey items, to represent mussels, a common prey of many shorebirds, whose abundances are largely driven by external gradients. We assigned each cell a constant probability of generating a new prey item per time step, which we refer to as the cell-specific growth rate r. We modeled clustering in landscape productivity by having the distribution of r across the grid take the form of 1,024 resource peaks, placed at regular distances of 16 grid cells from the peaks around them. The distance between peaks corresponds to the average lifetime diffusion distance of a randomly moving individual; thus, individuals shift between resource peaks regularly and can experience the whole range of environmental variation throughout their lifetime. The growth rate r declines from the center of each peak ($r_{\max}$) to its periphery (see fig. 1*A*); the central cell generates prey items five times more frequently than a peripheral cell. At $r_{\max} = 0.01$, central cells generate one item per 100 time steps (four items per generation), while the peripheral cells generate one item only every 500 time steps (<1 item per generation). All landscape cells have a uniform carrying capacity K of five prey items. While a cell is at carrying capacity, its r is 0. Cells are initialized with prey items proportional to their r (see fig. 1*A*).

Prey Acquisition by Foragers. Foragers perceive a cue indicating the number of prey items P in a cell but fail to detect each item with a probability q and are thus successful in finding a prey item with probability $1 - q^P$. Individuals on a cell forage in a randomized sequence, and the probability of finding a prey item is updated if other individuals find prey, reducing P. Foragers that find a prey item must handle it for a fixed handling time, T_{H} (default = 5 time steps), before consuming it (Ruxton et al. 1992). Natural examples include the time required for an oystercatcher to break through a mussel shell or a raptor to subdue prey; overall, the handling action is obvious, and the prey is not fully under the control of the finder (Brockmann and Barnard 1979). Foragers that do not find a prey item are considered idle in that time step and are counted as nonhandlers. Similarly, handlers that finish processing their prey in time step t can forage again only in time step $t + 1$ (i.e., they are idle in the time step t).

Movement Strategies

All individuals move simultaneously at the end of each time step and then implement their foraging or kleptoparasitic behavior to acquire prey. Handlers do not make any movements until they have fully handled and consumed their prey. We model movement as composed of small, discrete steps between adjacent cells. Across scenarios, individuals make movement decisions using evolved cue preferences. Individuals select a destination cell after assessing potential destinations according to available cues, similar to approaches used previously (Getz et al. 2015, 2016; White et al. 2018; Scherer et al. 2020; Netz et al. 2022*a*).

To move, individuals scan the nine cells of their Moore neighborhood for three environmental cues: (1) an indication of the number P of discrete prey items, (2) the number H of individuals handling prey (handlers), and (3) the number N of individuals not handling prey (nonhandlers). Individuals rank the potential destinations (including their current cell) by their suitability $S = s_{\mathrm{P}}P + s_{\mathrm{H}}H + s_{\mathrm{N}}N$ and move to the most suitable cell in time step $t + 1$. The individual weighting factors for each cue, s_{P}, s_{H}, and s_{N} (numeric values that can be positive or negative), are evolvable traits that are submitted from parents to their offspring, subject to rare mutations. Since individuals are constrained to perceiving and moving short distances, they may not always sense their best long-term move.

It is the combination of cue preferences, and especially their value relative to each other, that determines individual movement decisions (similar to relative selection coefficients; Fortin et al. 2005; Avgar et al. 2016; White et al. 2018). For example, an extreme value of s_{P} relative to the other weighting factors would mean that an individual's movement decisions are primarily guided by differences in the local density of prey items. We call an individual's combination of inherited weighting factors its movement strategy (see, e.g., fig. 1*E*).

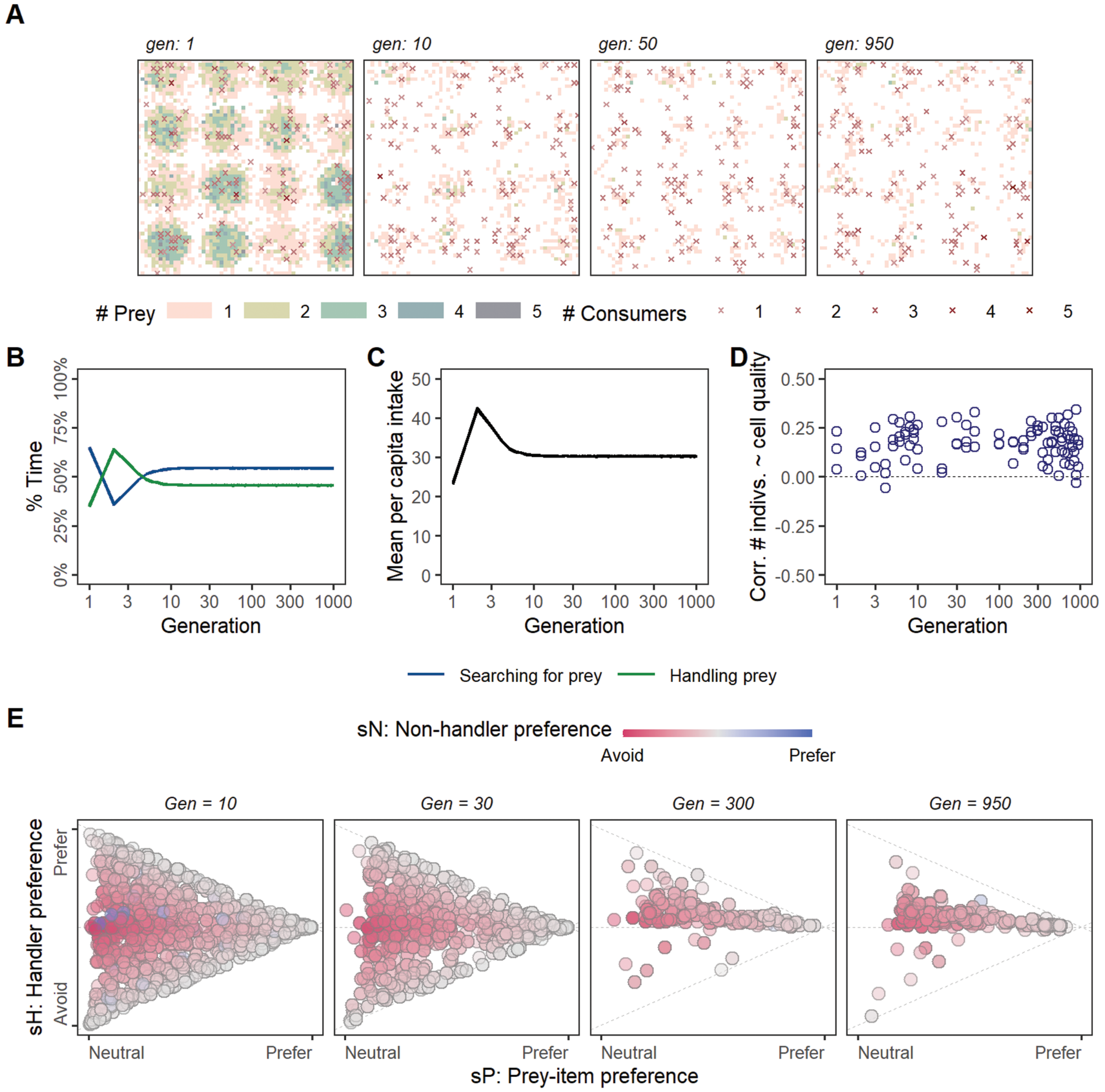

Figure 1: Eco-evolutionary implications of pure exploitation competition in scenario 1. *A*, A population comprised solely of foragers seeking prey on a resource landscape swiftly depletes initially abundant prey items within 10 generations (of 1,000 simulated). Foragers maintain this prey item scarcity throughout the remaining generations of the simulation, despite regular resource regeneration (see generation 950). *B*, *C*, Within 20 generations of evolution, the population reaches an equilibrium in the relative proportion of time spent searching for prey and handling prey (*B*) and in mean per capita intake (*C*). *D*, The number of foragers per cell is only weakly correlated with cell productivity *r*, contrary to the input-matching rule of ideal free distribution theory. *E*, Individuals evolve preferences for handlers and prey and avoid nonhandlers. Given the signs of the preferences, a wide range of movement strategies coexist over hundreds of generations. Individuals may focus on moving up gradients of prey items ($s_P \approx 1.0$; prefer), moving toward successful foragers (handlers), or moving away from unsuccessful foragers that are potential competitors ($s_N \approx$ red). *A* and *E* show a single replicate, and *B*–*D* show three replicate simulations with log-scaled *x*-axes (lines overlap almost perfectly). All panels are for $r_{max} = 0.01$; *E* shows 2,500 individuals.

Competition Strategies

Scenario 1: Exploitative Competition. In scenario 1, we simulate only exploitative competition; individuals (henceforth called "foragers") move about on the landscape and probabilistically find, handle, and consume prey items. Foragers can be in either a searching state or a handling state (Holmgren 1995).

Scenario 2: Foraging or Kleptoparasitism as Fixed Strategies. In scenario 2, the competition strategy is genetically determined and transmitted from parents to offspring: exploitative competition (by foragers) or kleptoparasitic interference (by kleptoparasites). Kleptoparasites thus cannot extract prey items directly from the landscape and only steal from handlers (see Holmgren 1995). With probability K, kleptoparasites are successful in stealing from handlers. Throughout, we chose $K = 1$, as successful surprise attacks are commonly observed among birds (Brockmann and Barnard 1979). For smaller values of K, the prevalence of kleptoparasitism decreases up to the point where it becomes unviable, but the effect of K was gradual rather than leading to qualitatively different outcomes. When multiple kleptoparasites target the same handler, only one (randomly selected) is considered successful; thus, kleptoparasites compete exploitatively among themselves. Kleptoparasites displace the handler that they robbed of prey up to five cells away from their location. Having acquired prey, kleptoparasites become handlers but need only handle prey for $T_\mathrm{H} - t_\mathrm{h}$ time steps, where t_h is the time that the prey has already been handled by its previous owner. Once a kleptoparasite becomes a handler, it can also be targeted by other kleptoparasites. Unsuccessful kleptoparasites are considered idle and are counted as nonhandlers. Movement strategies evolve independently of the competition strategy, as in scenario 1; however, the optimal movement strategy for foragers need not be the same as that for kleptoparasites.

Scenario 3: Conditional Interference Competition. In scenario 3, each individual can act either as a forager or as a kleptoparasite, depending on its assessment of local conditions. Similar to how movement decisions are made according to local cues, individuals process cell-specific environmental cues in time step t to determine their competition strategy in the next time step as

$$\text{strategy} = \begin{cases} \text{forager} & \text{if } w_\mathrm{P}P + w_\mathrm{H}H + w_\mathrm{N}N \geq w_0, \\ \text{kleptoparasite} & \text{otherwise}, \end{cases} \tag{1}$$

where the weighting factors w_P, w_H, and w_N of the cues and the threshold value w_0 are evolvable parameters that are transmitted from parents to their offspring (subject to rare mutations). The combination of the four weighting factors forms each individual's competition strategy. Individuals' competition strategies may lead to specialization as foragers or kleptoparasites (as in scenario 2) or to plastic behavior conditioned on local cues. The competition dynamics are the same as in scenario 2.

Reproduction and Inheritance

Our model considers a population of fixed size (10,000 individuals) with discrete, nonoverlapping generations. For simplicity, we assume that individuals are haploid and reproduction is asexual. In scenarios 1 and 2, individuals inherit and transmit only the weighting factors (s_P, s_H, s_N) determining their movement decisions. In scenario 3, individuals also inherit and transmit the weighting factors (w_P, w_H, w_N, w_0) determining their competition decisions. Each individual's expected number of offspring is proportional to the individual's total lifetime intake of resources; hence, resource intake is used as a proxy for fitness. A weighted lottery (with weights proportional to lifetime resource intake) selects a parent for each offspring in the subsequent generation (see, e.g., Tania et al. 2012; Netz et al. 2022*a*). Each offspring is placed at a random location on the landscape, leading individuals to experience conditions that are potentially different from those of their parents. Across scenarios, the weighting factors for movement and competition are subject to rare, independent mutations that occur with probability $\mu = 0.001$ per weighting factor. The mutational step size (either positive or negative) is drawn from a Cauchy distribution with scale parameter 0.01 that is centered on zero, allowing for the rare occurrence of large mutations, while most mutations are small. In scenario 2, foragers may infrequently mutate into a kleptoparasite, or vice versa; both events happen with probability $\mu = 0.001$.

Simulation Output and Analysis

We ran all three scenarios at a default r_max of 0.01, which we present in "Results," and also across a range of r_max values between 0.001 and 0.05 (see figs. 6, S7–S9). We initialized all weighting factors with values drawn independently from a Cauchy distribution with scale parameter 0.01 centered on zero. Although the initial amount of variation in weighting factors was very small (see, e.g., fig. 1*E*), the simulations started with a considerable range of movement strategies. Starting with high-variation conditions is not unrealistic (Wolf and Weissing 2012), and it speeds up evolutionary simulations, as evolution is less mutation limited in the early phases. To confirm that our results do not merely reflect initialization conditions, we also ran simulations starting in a monomorphic state (see "Effect of

Initialisation of Cue Preferences” in the supplemental PDF). We found that the initialization does not significantly affect the evolutionary outcome, so we present only the default implementation here. Below, we visualize the movement strategies by dividing the weighting factors s_i by the sum ($|s_P| + |s_H| + |s_N|$) of their absolute values. After this normalization (which does not affect the movement behavior), the individual movement strategies are represented by points in a three-dimensional trait space of relative preferences that is bounded by -1.0 (strongly avoid) and 1.0 (strongly prefer). This visualization indicated that the evolutionary outcome of replicate simulations is remarkably consistent. We therefore show only three replicates here. More data can be generated and analyzed using the code linked below.

Population Activities and Intake. Across scenarios, in each generation, we counted the number of times foragers were searching for prey, the number of times kleptoparasites were searching for handlers, and the number of time steps that individuals of either strategy were handling a prey item. We refer to the ratio of these values as the population’s activity budget. We examined how the population activity budget developed over evolutionary time and whether a stable equilibrium was reached. Furthermore, we counted the population’s mean per capita intake per generation as a measure of population productivity.

Spatial Distribution of Individuals. A basic prediction of the IFD model and the related input-matching rule is that the number of individuals on occupied patches should be proportional to patch productivity (Fretwell and Lucas 1970; Parker 1978; Houston 2008). Patch productivity is challenging to measure in real-world systems, but it is among our model’s building blocks. We examined the correlation between the number of individuals and the cell-specific productivity r to see whether, and to what extent, the spatial distribution of individuals aligned with productivity.

Results

Scenario 1: No Kleptoparasitism

In scenario 1, foragers deplete prey items faster than they are replenished, drastically reducing the overall number of prey within 50 generations (fig. 1*A*). The population activity budget is split between searching and handling (fig. 1*B*); while handling and the mean per capita intake are both initially low, they peak within 10 generations (fig. 1*C*), as individuals easily acquire prey items from the fully stocked landscape in the first few generations. With dwindling prey items, fewer searching foragers find prey, handling as a share of the activity budget declines to a stable ~45% within 50 generations, and mean per capita intake also stabilizes (fig. 1*C*). Across generations, the correlation between the number of foragers and cell productivity is only moderately positive (fig. 1*D*). This is in contrast with IFD theory that predicts a perfect correspondence between local forager density and local productivity (Parker 1978; Houston 2008). Obviously, a perfect correlation between the number of foragers and cell productivity is not to be expected in a stochastic model like ours, but one might expect a stronger correlation between forager density and productivity than in cases of random movement. However, as shown in figure S1, this is not the case. We think that the relatively low correlation between forager density and productivity is related to the fact that foragers cannot directly sense the local cell productivity r; instead, they can use only the (small) number of prey items available in a cell as a cue for local productivity. Evolved movement strategies overall exhibit a preference for handlers and prey and avoid nonhandlers ($s_P > 0$, $s_H > 0$, $s_N < 0$; fig. 1*E*). Given these conditions, a wide range of movement strategies coexist; some individuals focus mainly on prey density ($s_P \approx 1$, $s_H \approx 0$, $s_N \approx 0$), others move primarily toward successful foragers (handlers), while still others primarily move away from unsuccessful foragers ($s_N \approx -1$), which are potential competitors.

Scenario 2: Coexistence of Foragers and Kleptoparasites

In scenario 2, with fixed foraging and kleptoparasitism allowed, the spatial distribution of prey items at equilibrium is very different from scenario 1. Initially, consumers graze down resource peaks until few prey items remain on the landscape; however, within 50 generations the resource landscape recovers, with prey abundances higher than in the earliest generations (fig. 2*A*). This is because of the emergence of kleptoparasites (fig. 2*B*): in early generations, kleptoparasites are rare, and the activity budget, the mean per capita intake, and the distribution of consumers over the landscape are similar to scenario 1. As resources are depleted and kleptoparasite-handler encounters become more common than forager-prey encounters, kleptoparasitism becomes the majority strategy (a stable ~70% of the population; see fig. 2*B*), and searching for handlers to rob becomes the commonest activity. However, the high frequency of this activity and the low frequency of handling indicate that few kleptoparasites are successful at robbing handlers.

With few foragers, few prey items are extracted from the landscape, which recovers beyond its initial prey abundance within 50 generations (fig. 2*A*). As fewer prey items are extracted overall, mean per capita intake also declines from an initial peak (fig. 2*C*). The reemergence of strong

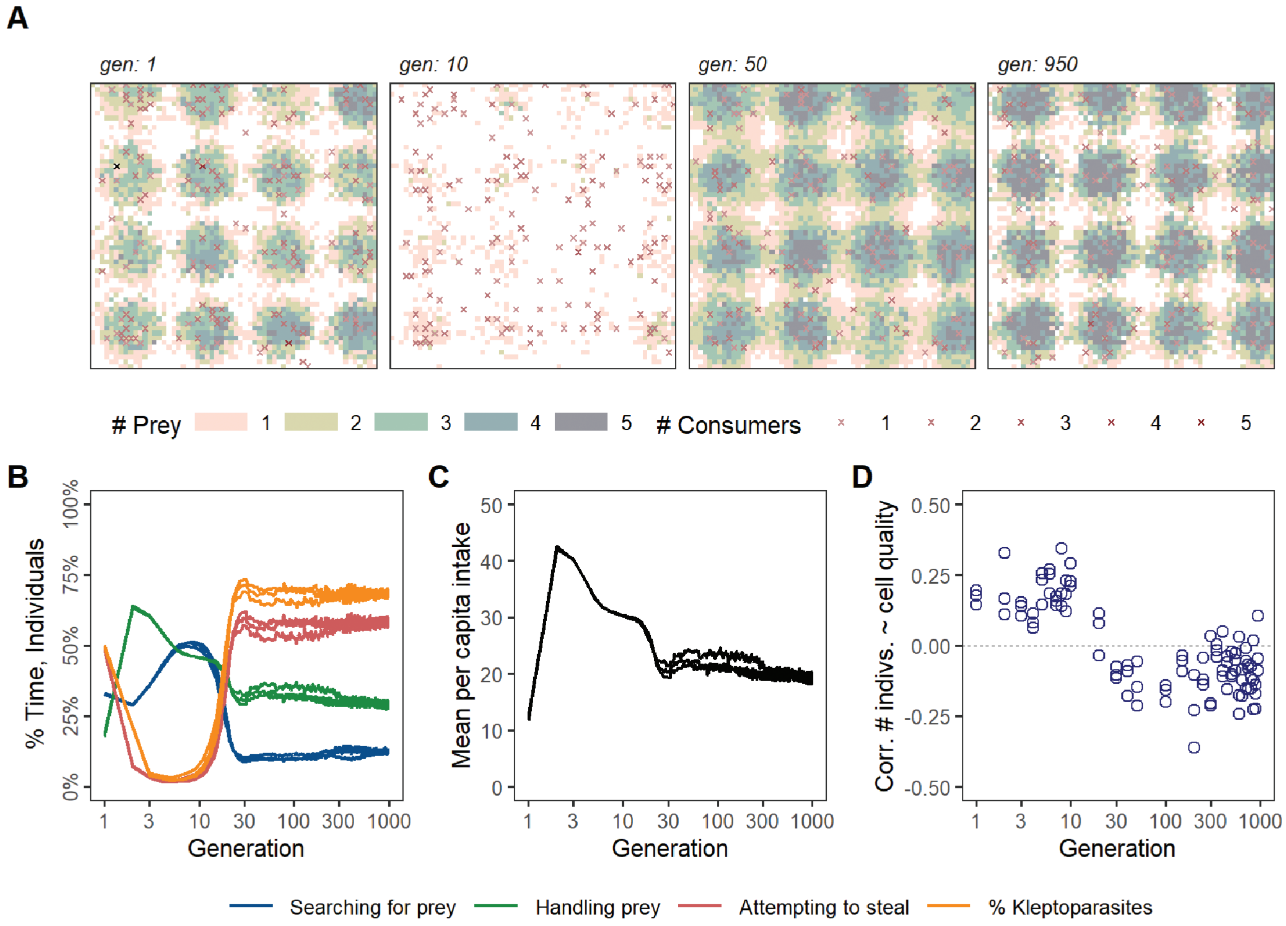

Figure 2: Eco-evolutionary implications of the coexistence of foragers and kleptoparasites following fixed competition strategies in scenario 2. *A*, Populations with both foragers and kleptoparasites drastically deplete the initially well-stocked resource landscape by generation 10; however, prey densities recover strongly by generation 50, even beyond the densities in generation 1. *B*, A surprisingly stable equilibrium between the forager strategy and the kleptoparasite strategy is reached within 30 generations, with the relative frequency of kleptoparasites (orange line) first dropping to very low levels but later recovering to reach a high level (~70%) in all three replicates. Consequently, at equilibrium, only about 10% of individuals are foragers searching for prey, 50% are kleptoparasites attempting to steal from handlers, and 40% are handlers processing prey items (either foragers or kleptoparasites). *C*, When kleptoparasites are rare, the population intake rate exhibits the same pattern as in scenario 1, dropping to a lower level with the emergence of kleptoparasites. Naturally, there is an increase in the proportion of time spent on stealing attempts (red line in *B*) and a corresponding decrease in prey seeking (by searching foragers; blue line in *B*) and handling (green line in *B*). *D*, The correlation of consumers with cell productivity is initially only weakly positive, but after kleptoparasites become more prevalent (generation 30), the correlation of consumer abundance with cell productivity r is actually moderately negative. *A* shows a single replicate, while *B*–*D* show three replicates with log-scaled x-axes. All panels are for $r_{\max} = 0.01$.

spatial structure of the resource landscape within 50 generations should easily allow individuals to move to areas with more resources and thus match the productivity of the landscape, but this does not happen. Instead, the correlation between individuals and cell productivity—initially weak—actually becomes negative once kleptoparasites become prevalent (generation ≈ 30; fig. 2*D*). This may be explained by the prevalence of kleptoparasitism near resource peaks: since handlers flee from a site after being stolen from and kleptoparasitism occurs more frequently on resource peaks, individuals overall get displaced away from resource peaks. As shown in figure 3, the movement strategies of foragers and kleptoparasites rapidly diverge (see also figs. S3, S5). While both foragers and kleptoparasites evolve a near-neutral but positive preference for prey and avoidance of nonhandlers, their response to handlers is very different. Kleptoparasites very rapidly evolve a strong preference for moving toward handlers, which are their primary resource (fig. 3). In the absence of kleptoparasites, foragers would also evolve a similar preference (fig. 1*E*),

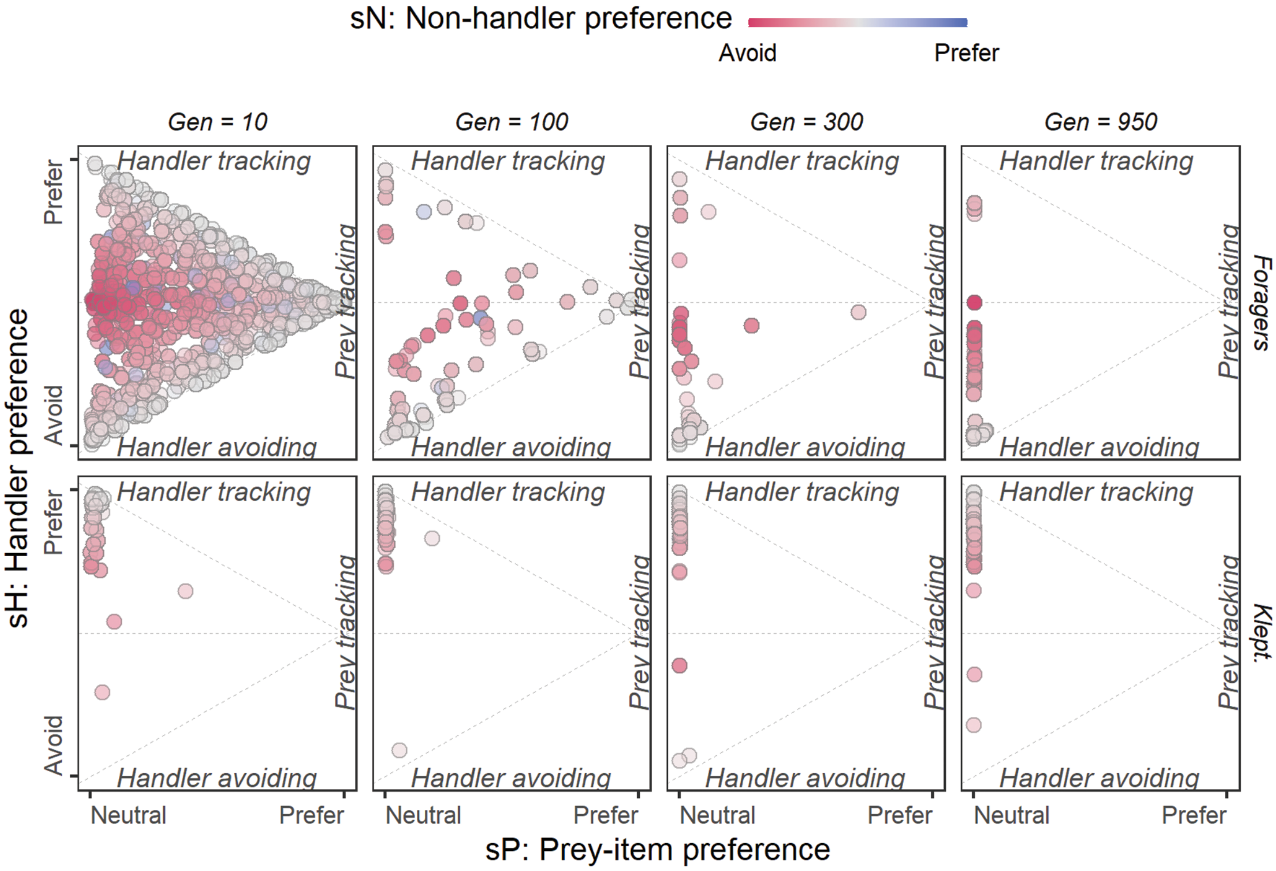

Figure 3: Rapid divergence of movement strategies between foragers and kleptoparasites in scenario 2. Kleptoparasites rapidly diverge (within 10 generations) from foragers in their movement strategy, clustering around $s_H = 1.0$, a handler-tracking strategy. This strategy is stably maintained throughout the simulation (generations 100, 300, 950). Foragers retain substantial diversity in movement strategies for many generations (see generation 100), but unlike in scenario 1, they tend to be repelled (relative $s_H < 0$) by handlers. Over time, foragers adopt a strategy that helps them avoid all other individuals (generations 300, 950). A few individuals sporadically adopt a movement strategy associated with the opposite competition strategy (e.g., foragers with relative $s_H > 0$); this is most likely due to mutations in the competition strategy rather than to a new movement morph within either foragers or kleptoparasites. At the evolutionary equilibrium then, social information (either s_H or s_N) is the strongest component of all of the movement strategies. All panels show 2,500 individuals (25% of total) from the same simulation replicate ($r_{max} = 0.01$), and earlier generations are ancestors of later generations.

but with kleptoparasites common in the population, foragers converge on a handler-avoiding strategy (fig. 3). This completes the explanation for why consumers do not match landscape productivity: foragers evolve strategies to avoid high-productivity areas (which are more likely to have many handlers), while kleptoparasites evolve strategies to find handlers (which need not be on high-productivity cells).

Scenario 3: Condition-Dependent Kleptoparasitism

When individuals are allowed to choose their competition strategy (foraging or kleptoparasitism) according to local environmental cues, the distribution of prey items is substantially different from the two previous scenarios (fig. 4*A*). Initially, individuals deplete the resource landscape of prey items within 10 generations. By generation 50, the resource landscape recovers some of the spatial structure of early generations, but prey item abundances do not match the recovery seen in scenario 2. This is because unlike scenario 2, individuals search for prey more often and steal less (at or below 25%; compare figs. 4*B* and 2*B*), preventing a full recovery of the resource landscape. Consequently, mean per capita intake stabilizes (after an initial spike, as in scenarios 1 and 2) within 10 generations to a level similar to scenario 1 (fig. 4*C*). The correlation between consumer abundance and cell productivity is perhaps a bit more positive than in scenario 1 (fig. 1*D*)

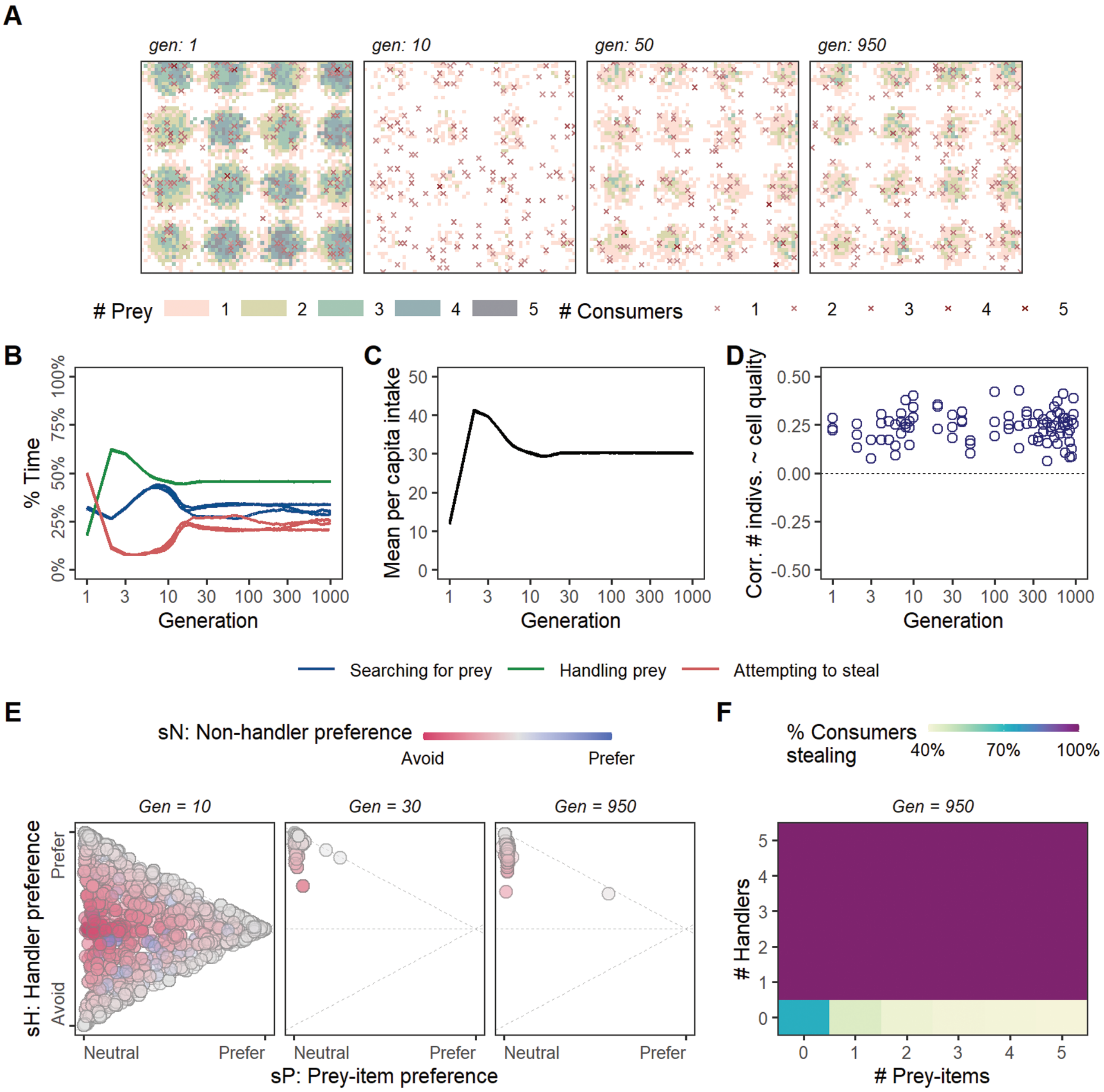

Figure 4: Eco-evolutionary implications of conditional foraging strategies in scenario 3. *A*, The initially well-stocked resource landscape is rapidly depleted within 10 generations, yet within 50 generations prey abundances recover on many cells, although not to the extent of scenario 2. The local density of individuals on occupied cells is shown as colored Xs. *B*, By generation 30, the proportions of time spent searching (blue line), handling (green line), and stealing (red line) prey reach an equilibrium that differs somewhat across replicates. *C*, The total intake of the population reaches the same equilibrium value in all three replicates. *D*, The correlation between the local density of individuals on a cell and its productivity r is stronger than in scenario 2. *E*, From an initially high diversity of movement strategies, there is a rapid convergence (within 30 generations) of all individuals to strongly prefer moving toward successful foragers or handlers, nearly to the exclusion of all other movement cues. This handler-tracking strategy is maintained once established (generations 30, 950). *F*, Population competition strategies are more varied. While most individuals will choose to forage as prey density increases, about 40% of individuals attempt to steal even when prey is abundant and handlers are scarce. All individuals will steal when handlers are available. *A* and *E* show a single replicate, *B*–*D* show three replicates, and *F* shows the mean across replicates. All panels are for $r_{\max} = 0.01$.

but not larger than in the case of random movement (fig. S1).

Using conditional foraging strategies, individuals are able to switch between resource types (prey and handlers) depending on which is more profitable (Emlen 1966; opportunistic kleptoparasitism; fig. 4*F*; see fig. S6). All individuals would choose to steal when handlers are present, even when prey items are more common. Indeed, about 40% of individuals would choose to steal even when prey are abundant and there are no handlers at all. Whether individuals choose to forage or steal in the absence of both handlers and prey determines the variation observed between replicates (see activity budgets in fig. 4*B*) but does not impact the population-level intake rates. Over longer evolutionary timescales the replicates' activity budgets converge. About 70% of individuals have an intrinsic bias toward kleptoparasitism (i.e., they would by default attempt to steal when there are no cues to inform their decision; fig. 4*F*; $P = 0$, $H = 0$).

Movement Strategies on Depleted Landscapes

Orienting movement toward resources (Nathan et al. 2008; where to move) can be a challenge in a system with low densities of discrete prey items. Resources are difficult to find, and landscape productivity is difficult to assess. In our model, prey depletion leads parts of the resource landscape to become "clueless regions" (Perkins 1992), where foragers cannot make directed movements according to prey item abundances, as all neighboring item abundances are identical (see white areas in fig. 5*A*). At the beginning of all three scenarios, about 75% of landscape cells have a different number of prey items from the cells around them; these are primarily cells with an intermediate *r*, which have more prey than peripheral cells of resource peaks but fewer prey than the central cells. This proportion rapidly declines to a much lower value within 10 generations in all three scenarios.

The "cluelessness" of the landscapes develops differently across scenarios on evolutionary timescales (fig. 5*B*). In scenario 1, the proportion of cells with a different number of items in the neighborhood rapidly declines to ~25% within 10 generations, as foragers deplete most prey items, making most of the landscape a clueless region. Interestingly, the evolved movement strategy itself (which includes an attraction to food items) may have contributed to rapid resource depletion and, hence, the cluelessness of the landscape. In the absence of prey cues, foragers evolve to move toward handlers, with >75% of individuals showing a preference for handlers within 100 generations (fig. 5*B*1). Forager preference for handlers may be explained as the sensing of a long-term cue of local productivity. Since handlers are immobilized on the cell where they find a prey item, handler density is an indirect indicator of cell *r* and, because of spatial autocorrelation, also of the *r* of bordering cells.

Scenario 2 landscapes develop similarly to scenario 1 in early generations (fig. 5*A*2). However, within 50 generations, most cells again contain items, as extraction is reduced by the rise of kleptoparasitism, with differences among cells according to their *r* (see also fig. 2*A*). Thus, >75% of cells have a different number of items from neighboring cells (fig. 5*A*2 [see generation 950], 5*B*2). Unlike scenario 1, the rapid increase in handler preference is driven by kleptoparasites becoming the majority strategy (see above). Scenario 3 is similar to scenario 2 except that only about half of all cells have a different number of prey items from neighboring cells (fig. 5*A*3, 5*B*3). Here, the rapid evolution of a handler preference in movement decisions cannot be assigned a clear cause, since handlers are both a potential direct resource and indirect cues to the location of productive cells.

Effect of Landscape Productivity

The prey item regrowth rate that characterizes the peaks of the resource landscape ($r_{\max}$) is a measure of the productivity of the resource landscape overall. Having thus far focused on scenarios with $r_{\max} = 0.01$ (corresponding to a peak production of four food items per consumer lifetime), we find that, not unexpectedly, the value of $r_{\max}$ has a marked effect on evolved population activity budgets, mean per capita intake, and even evolved strategies. The frequency of foraging reduces with $r_{\max}$ in scenarios 1 and 3; this is caused by more frequent acquisition of prey items (as regrowth keeps pace with depletion), which results in a greater frequency of handling rather than foraging.

In scenario 2, however, the frequency of handling is relatively unaffected by increasing $r_{\max}$ (fig. 6*A*). The difference between scenarios 2 and 3 has to do with the change in the frequency of kleptoparasitism (fig. 6*B*). In scenario 2, kleptoparasitism forms >75% of all activities at low $r_{\max}$ and is much more common than in scenario 3 populations at the same regrowth rate. However, at relatively high $r_{\max}$ (0.03), the fixed kleptoparasitic strategy goes extinct. This is because at high $r_{\max}$, forager-prey encounters are more common than kleptoparasite-handler encounters, in both early generations (<10) and later generations (>50). Consequently, kleptoparasites have relatively much lower fitness than foragers and do not proliferate. Thus, at high $r_{\max}$, a scenario 2 population is nearly identical to a scenario 1 population; while some kleptoparasites may be seen in later generations, these occur most likely as a result of ephemeral mutations in the forager strategy.

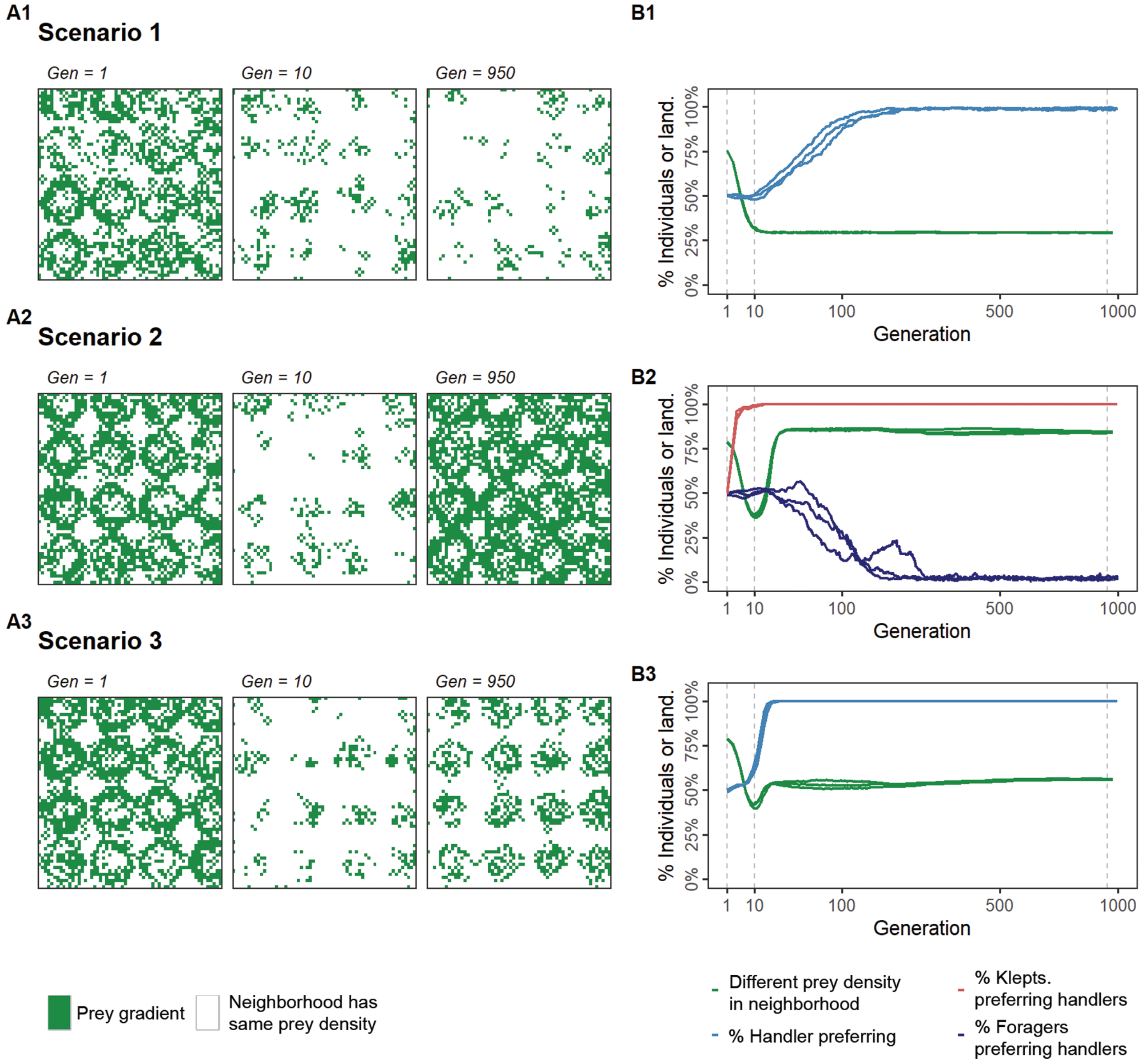

Figure 5: Uninformative prey densities and the evolution of social information as an alternative movement cue. *A*1–*A*3, On green cells, local prey densities are informative for movement, as the central and neighboring cells have different prey densities. While differences in local prey densities provide informative cues for adaptive movement in early generations, this is much less true once the resource landscape is depleted of prey items (depending on the scenario). *B*1–*B*3, Proportion of cells where differences in local prey densities provide informative movement cues (green line) and proportion of individuals preferring to move toward handlers (blue line), whose presence may be used as an alternative cue for movement toward higher-productivity areas of the landscape. In *B*2, representing scenario 2, this proportion is shown separately for foragers (blue line) and kleptoparasites (red line). While *A*1–*A*3 show a single representative replicate for $r_{\max} = 0.01$, *B*1–*B*3 show three replicates. All *x*-axes are scaled to show early generations more clearly.

In scenario 3, kleptoparasitism persists at low frequencies even at the highest regrowth rates (fig. 6*B*); thus, some foragers lose time in extracting items that are then stolen from them. Consequently, while populations in all three scenarios achieve very similar mean per capita intakes at low $r_{\max}$, at intermediate regrowth rates (0.01, 0.02), conditionally kleptoparasitic populations achieve a higher mean per capita intake than populations using fixed strategies. Only at high $r_{\max}$, when fixed-strategy populations effectively convert to pure forager populations, do they

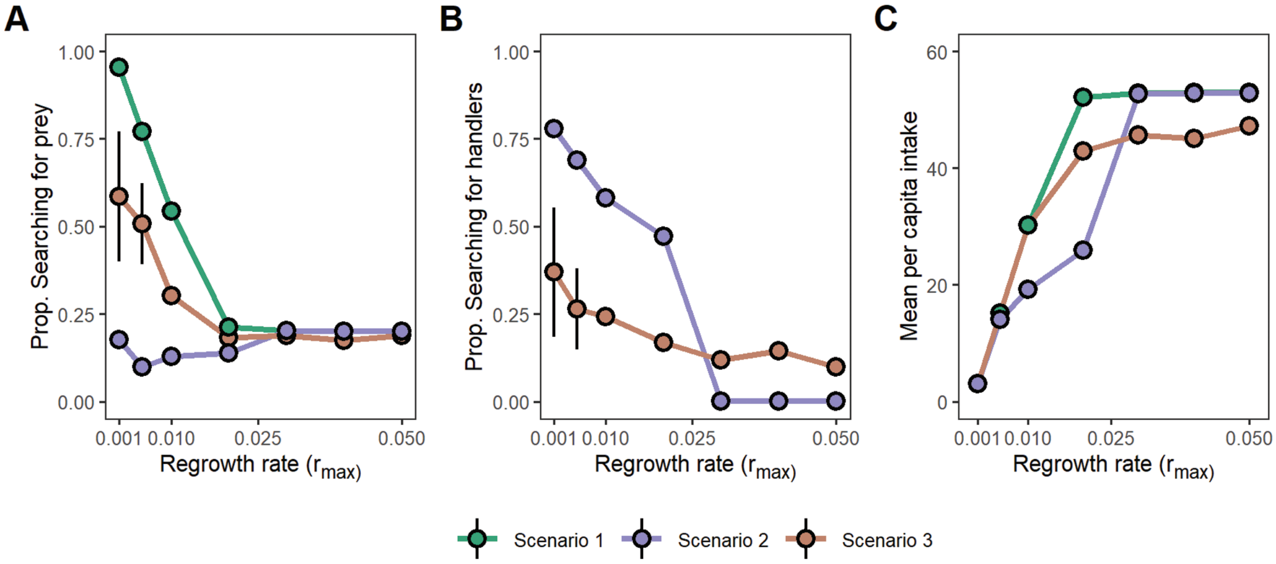

Figure 6: Landscape productivity strongly affects scenario outcomes. *A*, The proportion of time spent searching for food decreases with increasing $r_{\max}$ in scenarios 1 and 3 but remains relatively stable within scenarios. This is partly due to a higher proportion of time spent handling at higher prey densities. *B*, The proportion of time spent searching for handlers (to steal prey from them) also decreases with increasing $r_{\max}$. In scenario 2, kleptoparasites go extinct for $r_{\max}$ values above 0.025. *C*, At low productivity, the average intake is similar in all three scenarios. For higher $r_{\max}$ values, the average intake rate is lowest in scenario 2, until $r_{\max}$ is larger than 0.025 and kleptoparasites go extinct (leading to the same kind of population as in scenario 1). At high $r_{\max}$, the average intake rate in populations with conditional kleptoparasites (scenario 3) is substantially lower than in populations without kleptoparasitism. All panels show conditions at generation 1,000; error ranges show standard deviation around values; some error ranges are too small to be visible.

achieve a higher intake than conditional strategy populations (fig. 6*C*).

Discussion

Our spatially explicit individual-based model implements the ecology and evolution of movement and foraging decisions, as well as resource dynamics, in biologically plausible ways and offers a new perspective on the distribution of animals in relation to their resources under different scenarios of competition. First, individuals moving with a limited perception range and competing only by exploitation evolve movement strategies for both direct and indirect resource cues (prey items and handlers, respectively). Regardless, on a resource landscape with discrete prey items, large areas may become devoid of any movement cues, leading to a mismatch between individual distribution, prey item distribution, and landscape productivity. Second, interference competition in the form of kleptoparasitism rapidly establishes itself on landscapes where stealing is more time efficient than searching for prey, even when such interference is a fixed strategy and kleptoparasites cannot forage for prey. This rapid increase in kleptoparasitism as a strategy is accompanied by the divergent evolution of movement strategies that favor moving toward handlers, which are the primary resource of the kleptoparasites. In this sense, obligate kleptoparasites may be thought of as forming a higher trophic level, with handlers as their prey, and the ecological consequences of the rapidly evolving avoidance behavior of conspecifics are similar to those of the ecology of fear (Brown et al. 1999; Zanette and Clinchy 2019), except that here the relevant interactions occur within the same species. Third, when the foraging strategy is allowed to be conditional on local cues, (1) the population's mean per capita intake can be significantly higher than that of a population with fixed strategies, provided that kleptoparasitism occurs in both, and (2) unlike fixed-strategy populations, kleptoparasitism as a strategy does not go extinct on high-productivity landscapes.

Comparison with Existing Models

Existing models of competition and movement impose fixed movement rules on individuals to mimic either ideal individuals or nonideal individuals (Vickery et al. 1991; Amano et al. 2006; Cressman and Křivan 2006; Beauchamp 2008; Stillman and Goss-Custard 2010; White et al. 2018). When individual competitive strategies are included in models, they represent differences in competitive ability (e.g., Parker and Sutherland 1986; Holmgren 1995; Hamilton 2002; Netz et al. 2022*b*), or a probabilistic switch between producing and scrounging (Beauchamp 2008). In contrast, our model allows individuals' movement (and competition) decisions to be adaptive responses to local environmental cues. Similar to the individuals in Getz et al. (2015, 2016) and White et al. (2018), our individuals choose from among the available movement options after weighing the local environmental cues, similar to step-selection functions (Fortin et al. 2005; Avgar et al. 2016; White et al. 2018). Local environmental cues are constantly changing, as we model discrete, depletable prey items, contrasting with many IFD models (Tregenza 1995; Amano et al. 2006). This allows for a more plausible, fine-scale consideration of exploitation competition, which is often neglected, and allows the cues sensed by individuals to strongly structure the distribution of competitors (see below).

Adaptive responses must have an explicit evolutionary context and consider multiple generations of the population. We follow Beauchamp (2008) and Getz et al. (2015) in allowing the cue preferences that decide movement, and variation therein, to be the outcomes of natural selection. However, instead of using evolutionary algorithms (Beauchamp 2008; Getz et al. 2015, 2016) to optimize individual movement rules through techniques such as simulated annealing (i.e., changing the mutation rates or mutation effect sizes as a local optimum is approached) or automatically discarding the lower 50% of the population, we tried to faithfully represent an evolutionary process as it occurs in natural populations.

Evolution of Movement Strategies Using Social Information

In scenario 1, depletion of discrete prey can leave many areas empty of prey items: in such areas, movement informed by a resource gradient is impossible, and individuals move more or less at random (Perkins 1992). This lack of direct resource cues for locally optimal movement might be among the mechanisms by which unsuitable matrix habitats modify animal movement on heterogeneous landscapes (Kuefler et al. 2010). When individuals do not sense resource gradients, the presence of more successful conspecifics may indicate a suitable foraging spot (local enhancement; Giraldeau and Beauchamp 1999; Beauchamp 2008; Cortés-Avizanda et al. 2014). The presence of unsuccessful individuals, meanwhile, may signal potential costs from exploitation or interference competition. This selects for movement strategies incorporating the presence and condition of competitors into individual movement decisions, or social movement strategies (see an example in Guttal and Couzin 2010; for social information, see Dall et al. 2005). Consequently, consumer aggregation—often explained by invoking external costs such as predation (Krause and Ruxton 2002; Folmer et al. 2012)—could also be the outcome of movement strategies that have evolved to trade competition costs for valuable social information on the underlying spatial structure (here, *r*) of uninformative landscapes (Folmer et al. 2010; Cortés-Avizanda et al. 2014).

Individual Variation in Movement Strategies

Our movement strategies, comprising preferences for local ecological cues, may lead individuals to move in ways that are potentially unique to each individual. These strategies may not maximize their intake over short timescales (a few time steps), but their coexistance implies equal intake rates over a lifetime. This makes them consistent with prevalent ideas about consistent individual differences in behavior, or "animal personalities" (Wolf and Weissing 2012; Laskowski and Bell 2013; Bierbach et al. 2017; Spiegel et al. 2017; Shaw 2020). In scenario 1, the persistence of multiple movement strategies across generations indicates that they have equivalent fitness (see Getz et al. 2015) and that there are multiple ways to navigate a heterogeneous environment (Wolf and Weissing 2010; Shaw 2020). Such differences may help reduce competition, as individuals make subtly different movement decisions when presented with the same cues (Laskowski and Bell 2013; see also Wolf and Weissing 2012). Interestingly, scenario 3 has the least individual variation in movement rules, presumably because plasticity in competition strategy reduces the need for such diversification (Botero et al. 2010; Pfennig et al. 2010).

Scenario 2 cautions that (1) individual variation may be evident only when accounting for the main driver of movement decisions (s_H or s_N; see fig. S8 for scenario 3 as well) and (2) spatial context determines whether individual differences in movement strategy lead to functional variation in movement outcomes. Subtle variation in relative prey density preferences (s_P) could be revealed if individuals were measured in isolation and could lead to differences in movement paths (given a continuous gradient in prey cues). However, in natural settings with substantial collective behavior, different social movement strategies (correlated with foraging competition strategy) would be the primary driver of movement. Overall, then, (*a*) measuring movement behavior in settings that correspond to animals' evolutionary contexts and (*b*) accounting for movement-competition strategy correlations are both key when studying how individual differences translate to functional consequences.

Competition Strategies and the Spatial Distributions of Foragers

IFD models predict that individual movement should result in consumer distributions tracking the profitability of resource patches (Fretwell and Lucas 1970; Parker 1978). In scenario 1, where the situation is not complicated by the occurrence of kleptoparasitism, we observed a positive correlation between local productivity and local forager density. Nevertheless, it would be premature to interpret such a correlation as evidence that the model predictions are in line with IFD theory. Instead, such a positive correlation is also predicted by random movement models (fig. S1), where the correlation just reflects the fact that because of prey handling, successful predators tend to stay a bit longer on productive sites. In scenarios 2 and 3, kleptoparasitic individuals unsurprisingly and rapidly evolve to track handlers (a direct resource) while avoiding nonhandlers (potential competitors). These evolved rules, however, do not lead kleptoparasites to occupy the best cells, as predicted by Parker and Sutherland (1986), Holmgren (1995), and Hamilton (2002). In scenario 3, just as in scenario 1 and as observed under random movement, local population density is weakly positively correlated with cell productivity. Scenario 2, in contrast, shows a negative correlation of population density with cell productivity. This is driven on the one hand by the handler avoidance of other foragers and on the other by the prevalence of kleptoparasitism on resource peaks. Handler presence may indicate a risk of kleptoparasitism and is therefore avoided by foragers. Also, since foragers quickly turn into handlers when entering the resource peaks, they may then become victims of kleptoparasitism, whereupon they are displaced away from their original position. Thus, foragers may spend a lot of time searching for prey items in resource-poor areas but avoid resource peaks hosting handlers and, when entering the peaks, are quickly displaced. Which of the two mechanisms predominates we cannot say with certainty, but the correlation between cell quality and individuals turns out negative as a consequence. We would suggest that these results exemplify the pitfalls of simplistically linking current ecological conditions with population distributions without considering the presence of the competitive interactions that occur within a population.

Constraints on Competition Strategies

Foraging strategies involving specialization on a resource type are expected to be constrained by the availability of that resource. Thus, kleptoparasitism, seen as a prey choice problem, should be constrained by the density of targets (Ens et al. 1990). In scenarios 2 and 3, more kleptoparasitism should be expected with increasing $r_{\max}$, as prey and, consequently, handlers are expected to be more abundant. Instead, kleptoparasitism declines with increasing $r_{\max}$, in line with Emlen (1966), who predicted that the commoner food type (prey) rather than the more efficiently exploited one (handlers) should be preferred. This prey choice problem, playing out at evolutionary scales, leads kleptoparasites in scenario 2 to go extinct when prey are very common at high $r_{\max}$. At stable population densities, the persistence of fixed kleptoparasitism depends on their intake relative to foragers. Modeling discrete prey items and individuals in a spatial context, then, leads to the finding that obligate kleptoparasitism is a viable strategy only when forager-prey encounters are less common than kleptoparasite-handler encounters. Reducing the relative profitability of kleptoparasitism in other ways—such as imposing a cost on kleptoparasitic attacks for the initiator or reducing the probability of success (currently, 1.0)—would also lead to a reduced incidence of kleptoparasitism and eventual extinction even on less productive landscapes. In scenario 3, about 40% of individuals choose to attempt to steal even when prey are available and handlers are not. This suggests a more realistic proportion of consistently kleptoparasitic individuals among populations with flexible foraging strategies. Many seabirds, which forage for prey when they are superabundant but also readily harass other birds for prey, are a good example (Brockmann and Barnard 1979). Finally, comparing across regrowth rates shows why possibly cryptic behavioral complexity should be considered in predictions of the long-term effect of environmental change on populations. While populations in both scenarios 1 and 2 appear identical at high $r_{\max}$, even a small decrease in environmental productivity could lead to an abrupt drop in per capita intake—and potentially strongly reduced growth or survival—for fixed-strategy populations because of unexpected, emergent kleptoparasitism.

Model Limitations

While we tried to make our model more “lifelike” in certain aspects, especially by allowing for individual variation, evolving movement strategies, and a heterogeneous and dynamic resource landscape, in other places we have made simplifying assumptions, both for computational reasons and to ease the understanding of an already fairly complex model environment. Here, we briefly highlight two of these assumptions. First, we kept the population size constant throughout our simulations. Including population dynamics in the model is straightforward (e.g., Netz et al. 2022*a*) and could have important implications. For example, our model predicts a strongly depleted resource landscape in scenario 1 (fig. 1*A*). If resource depletion led to population decline, the landscape might recover, potentially leading to quite different eco-evolutionary outcomes. In this first effort, we did not address population dynamics to avoid the introduction of additional parameters to be explored within the context of an already quite complicated model. Conceivably, population sizes could fluctuate in response to the prevalence of kleptoparasitism, particularly in scenario 2 where distinctive types can be observed, and this could lead to rich eco-evolutionary dynamics involving different behavioral types (Netz et al. 2022*a*). A lot more detail could be added to the assumptions underpinning how resource consumption influences mortality and reproduction, with potentially wide-reaching consequences for evolving movement strategies. If, for example, mortality of individuals occurred within generations (e.g., via starvation of unsuccessful foragers), the presence or absence of conspecifics could be a more reliable indicator of overall habitat quality.

Second, we assumed global offspring dispersal in all simulations presented in the text (although local dispersal is implemented in our simulation program). Considering primarily global dispersal, we produce a well-mixed system in which local adaptation or spatial dynamics do not occur. The spatial scale of resource peaks was chosen such that individuals can easily move between peaks. The success or failure of different movement and foraging strategies over multiple generations is therefore determined by the environments encountered across the entire landscape and not of local conditions, where specific strategies might be concentrated. Under local dispersal, movement strategies can cluster locally, and local adaptation and kin competition, as well as the spatial scale of resource peaks, may become important. However, in scenarios 1 and 3, simulations under local dispersal lead to the same activity budgets and evolved movement strategies as under global dispersal (figs. S13, S14). Only the correlation between forager density and cell productivity is higher, a straightforward consequence of differential reproductive success in relation to cell productivity. In scenario 2, local dispersal produces strong oscillations and spatial dynamics, where kleptoparasites and foragers form the two required components of a reaction-diffusion system (Kondo and Miura 2010; fig. S15).

Individual-Based Models in Animal Movement Ecology

Linking individual-based models with empirical data is difficult and is still rarely done (see works tailored to management: Stillman and Goss-Custard 2010; Diaz et al. 2021). Animal-tracking technology is still on the cusp of allowing us to track entire populations (though small ones) and classify their behavior at the fine temporal scales of animal decision-making (Nathan et al. 2022; see, e.g., Lieber et al. 2021; Sankey et al. 2021). Classifying dyadic and collective behavior from animal tracking is especially challenging (Sankey et al. 2021; Vissat et al. 2021); this makes the detection of rapid competitive interactions in large populations unlikely. Instead, experimental approaches may reveal movement strategies that reduce competitive interactions (Vahl et al. 2005*a*, 2005*b*; Rutten et al. 2010*b*; Bijleveld et al. 2012). However, consistent behavior in cue-poor captive environments may not always translate to consistency in natural settings with abundant resource cues (Carter et al. 2013), making it necessary to corroborate experimental findings with field studies.

Animal movement ecology takes an explicitly individual-based approach, centered around individual decisions (Nathan et al. 2008). This makes individual-based models a good choice when seeking general insights into the evolutionary ecology of animal movement strategies (see, e.g., Getz et al. 2015), whose ultimate causes are otherwise difficult to study empirically. Modeling mechanistic movement decisions has substantial consequences for ecological outcomes (e.g., Mueller et al. 2011; White et al. 2018; Scherer et al. 2020), yet few individual-based models in animal movement are mechanistic (see review in DeAngelis and Diaz 2019), and even fewer models include evolutionary dynamics (but see Getz et al. 2015, 2016; Gupte et al. 2022; Netz et al. 2022*a*). Yet explicitly modeling both ecological interactions and evolutionary dynamics, as we do here, can reveal surprising outcomes ranging from innovative predator-prey strategies (Netz et al. 2022*a*) to rapid disease-dominated eco-evolutionary cascades (Gupte et al. 2022) to sympatric speciation (Getz et al. 2016).

The use of resource- and step-selection functions in mechanistic modeling (see, e.g., White et al. 2018) gives empirical movement ecologists a familiar starting point in individual-based modeling. Simulating an animal's potential space use, conditional on environmental data (similar to our cues) and using selection coefficients estimated from tracking data (our cue preferences), is already accepted in movement ecology and follows our grid-based approach (Avgar et al. 2016, 2020; Signer et al. 2019; Fieberg et al. 2021). It is relatively easy to implement movement decisions in continuous space by sampling cues at discrete locations and (1) choosing among them or (2) translating them into a movement distance and turning angle. The second approach would require more complex functions with more coefficients (preferences), such as neural networks (Mueller et al. 2011), and this could make it difficult to interpret the evolved movement strategies. Models could implement survival and reproduction (the key ingredients of natural selection), as well as other demographic processes, and reproduction and inheritance can be incorporated in a more realistic manner.

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Statement of Authorship

P.R.G., C.N., and F.J.W. conceived of the study. P.R.G. and C.N. developed the simulation program and analyzed the model. P.R.G. performed data visualization and wrote the first draft of the manuscript, and C.N. and F.J.W. reviewed and edited the manuscript and performed subsequent revisions. F.J.W. supervised the project and acquired funding.

Data and Code Availability

Simulation model code (https://doi.org/10.5281/zenodo.5887618; Netz and Gupte 2022), simulation data (https://doi.org/10.5281/zenodo.7729566; Gupte et al. 2023*a*), and data analysis code and supplement (https://doi.org/10.5281/zenodo.7726052; Gupte et al. 2023*b*) are available on Zenodo.

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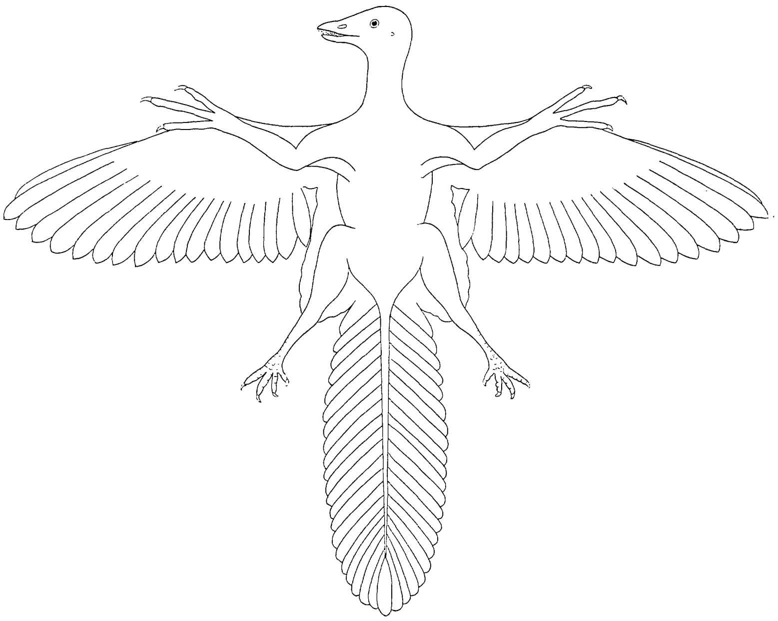

"Archæopteryx exhibits naturally a more primitive condition of structure than do modern birds, but even here the features are truly bird-like." From "Volant Adaptation in Vertebrates" by Richard S. Lull (*The American Naturalist*, 1906, 40:537–566).