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Foraging of wading birds on a patchy landscape: Simulating effects of social information, interference competition, and patch selection on prey intake and individual distribution

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ABSTRACT

Foragers on patchy landscapes must acquire sufficient resources despite uncertainty in the location and amount of the resources. Optimal Foraging Theory posits that foragers deal with this uncertainty by using strategies that optimize resource intake within foraging periods. For species such as wading birds, this optimization is closely linked to their survival and reproductive success. Understanding the influence of patch selection on individual resource intake and foraging distribution is therefore crucial. In this study, we simulated how resource distribution, interference competition, and social cues—such as aggregation behaviors—influence resource intake and foraging spatial distribution. We employed an individual-based model simulating wading bird foraging behaviors, with 900 individuals simultaneously foraging across a landscape with unknown resource distribution. Birds employed one of three patch-finding strategies: random, cue-searching, or hybrid, which uses both searching strategies. Each bird decided whether to remain in a patch based on a prey density threshold. We compared the daily resource intake and foraging distribution of birds across different modeled patch-finding strategies, resource distribution patterns, and the presence or absence of interference competition. Wading birds exhibiting aggregation behavior displayed increased intake rates when resources were concentrated and interference minimal. Aggregation behavior led to a closer match with the ideal free distribution when the prey density threshold was optimal. These findings provide theoretical support that aggregation behavior is effective in scenarios where resources are concentrated in a few patches, social cues are used by relatively few individuals, and interference competition is limited.

1. Introduction

Optimal foraging theory (OFT) is a widely used theory in behavioral ecology that assumes individuals make foraging decisions consistent with expected value across the landscape; that is, they prefer high value areas over low value ones. Foragers are assumed to optimize their own individual fitness, which can lead to optimization over a population (Stephens and Krebs, 1986). Attempts to corroborate this theory often involve observations of foragers in a setting with known spatial variation in resources, established either experimentally (e.g., mesocosms) or by monitoring real landscapes (Bell, 1990). Observed behaviors are evaluated for whether they agree with expectations, represented by the known resource distributions. Many studies have identified behaviors that appear to follow optimal foraging principles, for species that include arthropods, birds, fish, and mammals (Elner and Hughes, 1978; Krebs et al., 1977; Stephens and Krebs, 1986; Stephens, 2008). However, the connection of individual behaviors with population-level outcomes is often not made (Schoener, 1987). In some cases, individuals do not even appear to behave consistently with expectations (Bell, 1990). The ongoing challenge then for research into OFT is to identify the types of behaviors that could produce improved outcomes for populations.

A commonly examined behavior in OFT is patch selection, in which foragers decide where to forage in a landscape and for how long. The goal is to identify rules that dictate how a forager chooses which resource patches to use, from which it can be inferred if the forager is behaving optimally. One example is the Marginal Value Theorem

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(MVT), which assumes that foragers consider a tradeoff between the value of a given patch currently under use, and the opportunity costs of not using other patches (Charnov, 1976). MVT employs a concept of “giving up time”, which specifies that when current food intake in a patch drops below the average expected intake across the landscape, the forager will abandon that patch to search for a new, higher quality patch. MVT is a special case that usually assumes depletion of patch contents at the time scale of an individual occupying it. However, MVT can be adapted to situations where individuals forage on landscapes where resource density does not change significantly within a typical foraging period. In such cases, the foragers face a sequence of decisions: first deciding which areas of the landscape to sample, then sampling patches within that area and deciding whether to remain in or abandon any given selected patch.

As for many other species (Lima, 1984; Krebs et al., 1978; Naef-Daenzer, 2000; Naug and Arathi, 2007; Templeton and Giraldeau, 1996), sampling of patches is known to be typical for wading birds such as white ibises and egrets foraging in wetlands such as the Florida Everglades. Sampling is necessary because of the spatio-temporal variability of prey densities in patches resulting from changing water levels on a complex topography (Kushlan, 1979, 1981; DeAngelis et al., 2021). During the dry season, when the Everglades landscape can support large numbers of nesting wading birds, prey density (generally fish and crayfish) becomes concentrated as water levels fall (Beerens et al., 2015; Botson et al., 2016; Binkley et al., 2019; Essian et al., 2025). This can result in a changing spatial gradient of prey availability as water levels drop along an elevational gradient (Gatto and Trexler, 2019). Although the pattern of available prey patches changes during the nesting season of wading birds, prey density may stay relatively constant during a day in a given patch, as patch area may itself be slowly decreasing due to evaporation even as prey are being removed, maintaining prey density. Because of the spatial variation in prey densities, wading birds may search several patches before staying in one to forage over a long period (Kushlan, 1979; Gawlik, 2002). Prey intake rate is a critical factor for wading birds during the breeding season, as they must meet their own energetic requirements and those of their offspring. Due to this heavy demand, wading birds adapt behavioral strategies that optimize their ability to locate good patches (Gawlik and Crozier, 2007).

Another widely used concept in OFT is the ideal free distribution (IFD), which predicts at the population level that animals will distribute themselves optimally across patches, such that no individual can improve its intake rate by moving to another patch (Fretwell and Lucas, 1970; Holmgren, 1995; Sutherland, 1983; van der Meer and Ens, 1997). The expectation of the IFD is that the number of foragers using any given patch is directly proportional to the concentration of resources in that patch, compared to all others. It is usually assumed that a population needs perfect knowledge of the environment to reach an IFD. However, individuals generally have only limited information about the distribution of resource patches. To overcome this lack, in some species social cues are used; that is, individuals track the numbers of other foragers for the same resources on patches and use that information as an indicator of prey density.

Many wading bird species, such as egrets and ibises, are social foragers (Beacuchamp and Heeb, 2001; Smith 1995). Multiple studies indicate that social cues are important for individuals deciding where to forage (e.g., Green and Leberg, 2005; Gawlik and Crozier, 2007), which can compensate for imperfect knowledge of the environment (Toquenaga et al., 1995). Thus, wading birds may improve foraging success by integrating cue-following in their sampling strategy. The mechanism of social foraging is likely beneficial when patches are large, but short-lived (Buckley, 1997), as in the Everglades landscape, where prey-abundant patches can be large but may not last for more than a day or so. In this study, we investigate how social cues can contribute to species forming an IFD without a priori knowledge of the distribution of prey densities on the landscape. Cue-following in foraging is related to the concept of ‘producers and scroungers’, in which some foragers, termed producers, are better at finding resources and others, scroungers, follow producers to patches with high prey availability, saving searching time. But this can be at the expense of being led to patches with higher competition, (e.g., Beauchamp, 2008; Giraldeau and Dubois, 2008; Morand-Ferron et al., 2011; Vickery et al., 1991) where they suffer negative density-dependent effects on patches (Beauchamp and Ruxton, 2014). As in a game-theoretic model, the strategies are frequency-dependent, with fitness generally declining in proportion as users of a strategy in the population increase (Giraldeau and Caraco, 2000). The present study includes assumptions from these studies but focuses on optimization of patch selection strategy under the given conditions and shows that interactions between individuals affect the patterns that emerge, rather than explicitly following producer-scrounger theory.

To study patch-selecting situations of wading birds, Lee et al. (2022) explored analytical models that estimated resource intake when single individuals were actively selecting a patch. The authors assumed two different strategies that they called the ‘daily memory strategy’ and ‘prey density threshold strategy.’ In the daily memory strategy, birds visited several patches and then returned to the best patch among those they visited after they had visited a pre-determined number of patches. In the prey density threshold strategy, the birds continuously searched for and sampled patches until they found a patch above a pre-determined specific prey density threshold. That study showed that intake rate by wading birds could be affected by the behavioral strategies employed and the pattern of the resource distribution available to the birds. Patch selecting strategies were shown in the model to be more effective when the prey density distribution on patches included a high proportion of high prey densities. However, that study had limitations, as it did not consider interactions between and variability among many individuals searching simultaneously, or variation in the distances between patches, which could greatly alter travel times between patches. Additionally, Lee et al. (2022) did not consider details of prey intake at the patch level, such as a saturating functional response and interference competition. Also, they assumed a continuous distribution of patch prey densities across the landscape, rather than a finite number of discrete patches.

While Lee et al. (2022) produced information on how strategies of patch selection affected foraging success, in order to include both behavioral strategies and individual variability in modeling studies, it is necessary to use agent- or individual-based modeling (IBM hereafter), which can incorporate these factors. Yurek et al. (2024) conducted a wading bird foraging simulation using a spatially explicit model to investigate trade-offs between random searching and aggregation behavior, and between meeting daily minimum energetic intake requirements and minimizing foraging time, assuming that a reduction in foraging time also reduces predation risk during foraging activities. Their findings showed that aggregation increased the birds’ foraging efficiency. However, the possibility of interference competition among wading birds was not taken into account in the model. Interference competition has been defined as a decrease in the instantaneous feeding rate due to the presence of competitors (Stillman et al. 1997) and has been shown to be an important mechanism among foraging wader birds (Vahl et al. 2005). Table 1 summarizes the shared features and differences among the models used in the previous studies by Lee et al. (2022); Yurek et al. (2024), and the model tested in this study.

IBM is widely used to study foraging behavior (e.g., Dumont and Hill, 2004). As in other waterbird IBMs, as reviewed by Brown and Stillman (2021), IBM enables detailed spatial and behavioral properties to be incorporated that are not accounted for in analytical models, including the use of social cues and interference competition. Similar to Yurek et al. (2024), the present model specifies a finite number of patches with randomly assigned spatial locations and prey densities drawn from gamma distributions, analogous to the analytical model of Lee et al. (2022), and multiple wading birds are simulated foraging over the course of a day. Unlike the previous models, the model includes

Table 1
Comparison of wading bird foraging models from previous studies. The table compares the model from this study to two previous wading bird patch-selection models. Lee et al. (2022) provides an analytical model for the threshold strategy, which is used in Yurek et al. (2024) and in this study. Yurek's model is an individual-based model of the threshold strategy but has a different optimization approach and does not include interference competition.

	Analytical Model (Lee et al., 2022)	Yurek et al. (2024) Model	This study
Model type	Analytical equation	Individual-based model	Individual-based model
Model structural	Spatially implicit	Spatially explicit	Spatially explicit
Scale	Continuous gamma distribution, single forager	30 patches sampled from gamma distribution, 200 birds	500 patches sampled from gamma distribution, 900 birds
Interactions	None	Aggregation via visual cues	Aggregation via visual cues, interference competition
Optimization	Maximizing expected daily intake	Minimize foraging time to fulfill daily requirement	Maximizing expected daily intake
Patch selecting strategies	Daily memory, prey density threshold	Prey density threshold	Prey density threshold
Patch searching strategies	Random searching.	Hybrid-searching compared to random-only searching. Hybrid starts as random then switches to aggregation sampling with/ without replacement	Random searching, Cue-searching, Hybrid-searching
Functional response	Type1	Type1	Crowley-Martin
Resource distribution	Continuous gamma distribution	Discrete number of patches sampled from gamma distribution	Discrete number of patches sampled from gamma distribution
Purpose	Theoretical baseline for optimal patch selection	Understand the effect of aggregation behavioral in dynamic wetland systems	Investigate the impact of interactions and variance between individuals to their intake and foraging distribution

interference competition and variation in prey density threshold strategies among foraging individuals.

The present work had the following objectives. (1) Compare an earlier analytic model (Lee et al. 2022) with an IBM with the same basic assumptions on foraging. (2) Determine how interference competition among wading birds in prey patches affects their prey intakes. (3) Investigate the effect of aggregation behavior when individuals are foraging in an unknown environment, and include interference competition within patches. (4) Test the prediction that any strategy will do better when it is present in small proportions in the whole population. (5) Test the predictions that a cue-following strategy, with constraints due to local interference competition, might produce a spatial distribution over the spatial patches that approximates an IFD. In an appendix, an IBM similar to the analytic model is developed to see how well the analytic model approximates a typical finite patch model.

2. Methods

The Overview, Design concepts, and Details (ODD) framework for describing individual–based models (Grimm et al. 2020) is used to describe the model. Some language is repeated to aid adherence to ODD guidelines. Simulations and summary analyses were executed in NetLogo 6.2.2, Excel, and MATLAB version 2021b (Mathworks, Inc.). The simulations used to perform the study's objectives are addressed as five cases in the results.

2.1. Purpose and patterns

The model simulates a hypothetical nesting colony of 900 wading birds foraging across the patchy wetland of heterogeneously distributed prey availability during a single day. The model is designed to estimate the total daily intake (prey captures) of the wading birds when the birds have limited *a priori* information about the environment. Foraging success is evaluated by calculating daily energetic intake in the simulation. The model also produces results regarding the advantage of following social cues to forage in groups and produces spatial patterns that are compared with IDF.

2.2. Entities, state variables, and scales

The model includes two types of entities, individual wading birds and patches. The number of individual foraging wading birds could be set arbitrarily, but for concreteness a breeding colony of 900 foragers is used in all simulations. Wading birds are distinguished from each other by each having its own distinct state variables of foraging starting time in the morning, temporally changing locations on patches, cumulative daily prey consumed at each time step, and patch selection mode (random search or following social cues). The environment comprises 500 prey patches (small temporary waterbodies with prey) on a continuous 100×100 landscape. The patches have randomly assigned locations, and thus a Poisson spatial distribution. Although the spatial units are not explicitly defined, the environment might represent an area of some tens of square kilometers of wetland. Each patch has a prey density determined by random sampling from a gamma distribution (see Section 2.7.2 for details). The density of prey in a patch is assumed not to change during the course of a day (see discussion above or in Lee et al. 2022).

2.3. Process overview and scheduling

All simulations follow wading birds over a period of one day of foraging, or 600 min of possible foraging time and the basic time step is one minute. Modeling foraging on a single day is sufficiently representative of that over the whole nesting period. At any time, a wading bird is in one of four different possible states. The first state is waiting to start searching, and the second is sampling a patch to estimate prey density, which required a time of t_{min}. The third is traveling to a new patch after not finding sufficiently high prey density in the previous patch. After a wading bird has left a resource patch, it chooses one of the patches within its visual range, either randomly or through cue-following, and makes a straight movement to that patch. All birds have the same movement speed. The average travel time between patches is 20 min, but individual travel times vary since distances between patches vary. When birds are in the travel state, their intake rate is 0. The fourth state is the 'foraging state', in which the wading bird has found a patch with prey density above its threshold, and in which the wading bird stays for the remainder of the day. In some simulations, intraspecific competition is allowed to occur in patches, lowering prey intake rates. A wading bird accumulates prey in both the patches that it samples, and the patch in which it stays because it has the desired prey density, if it had found such a patch. The accumulated intake is recorded as total daily prey intake.

2.4. Design concepts

2.4.1. Basic principles

The basic theoretical principle is optimal foraging through sampling of prey patches. Wading birds make decisions on which patches to visit and how long to stay in patches visited based on finding a prey patch with prey density exceeding a pre-determined threshold, aimed at maximizing prey intake over a day. Movement to a new patch can be either random, based on cue-following, as in social foraging theory, or a hybrid of the two. The effects of such social foraging, along with interference competition on patches, are studied using simulations.

2.4.2. Emergence

There are two main emergent properties from the simulations. One is the distribution of prey intakes among wading birds over the course of one day. The second is the final spatial distribution of wading birds across the patches of different prey density.

2.4.3. Adaptation

One adaptation of the wading birds is the use of sampling of prey patches, which allows searching over a number of patches to find a prey density that provides the possibility of finding a patch with high prey availability during the day. A second adaptation is to use cue-following or a hybrid of random searching and cue-following.

2.4.4. Objectives

The objective of the wading birds is maximization of prey intake over the course of a day.

2.4.5. Learning

The only learning mechanism is through watching other wading birds to gain information about possible prey densities on patches.

2.4.6. Sensing and tradeoff

Wading birds perceive the patches within a limited visual cone with a 240-degree range. This prevents a cue-searching birds from returning to its previous patch. The birds also recognize the density of other wading birds on patches. They also sense and are affected by the density of wading birds on patches that they visit, that is, by conspecific interference competition.

2.4.7. Interaction

Wading birds interact by taking social cues and following other wading birds, as well as experiencing interference competition in prey patches.

2.4.8. Stochasticity

Movements between various patches by wading birds are selected probabilistically, with cue-following biasing the probability of a wading bird toward choosing particular patches with high wading bird numbers. The distributions of prey density thresholds among wading birds in simulations with 900 foragers are selected randomly from a Gaussian distribution about a mean.

2.4.9. Collectives

Mean prey intake is calculated for the total population of foragers or for subpopulations of randomly searching, cue-following, or hybrid foragers.

2.4.10. Predictions

The decision to remain in a current patch is based on the prediction that the high prey density is sufficient to achieve high prey intake. Contrariwise, low prey density triggers a decision to abandon the present patch to search for another. Basing patch selection decisions on cues from other birds assumes that high densities of birds on a patch predicts high prey densities. Note that expectations can deviate from what is realized since foragers have imperfect knowledge and resources vary across space.

2.4.11. Observations

The simulations keep track of the prey intake and spatial location of each wading bird on 15-minute intervals.

2.5. Initialization

2.5.1. Wading bird starting sites and strategies

At the beginning of the simulation of daily foraging, each of 900 wading birds starts in a randomly selected patch, assuming that it has no prior knowledge of patch prey densities. Wading birds in some simulations also have initially assigned patch-selecting strategies among three options: random-searching, cue-searching, and hybrid-searching.

2.5.2. Prey density thresholds

Individual variation in the prey density thresholds of the wading birds is included in some cases. Each bird has a slightly different prey density threshold chosen from a Gaussian distribution about a mean. Simulations are run for a series of possible threshold values from 0 to 90 prey/m^2.

2.6. Input data

Input data from outside literature includes the parameter values of the Bazykin-Crowley-Martin (BCM) functional response (see 2.7.3).

2.7. Submodels

2.7.1. Basic foraging behavior

When a wading bird arrives at a patch, it spends a fixed amount of time investigating the quality of the patch. After the fixed sampling time, if the prey intake rate from the patch is above the intake rate that the bird expects based on its predetermined prey threshold density, the wading bird stays on the patch for the rest of the day, Otherwise, it moves to another patch within a randomly selected 240-degree angle and within 10 spatial units of distance (10 % of the landscape grid). The prey intake rate of a patch is calculated from the functional response of Eq. (2) (see 2.7.3), and the intake is accumulated over a day. The unit of intake rate is catches of prey per minute. At the end of the simulation of a day, the total intake of the bird (total catch in a day) is recorded from the intake rates over the patches visited by the bird.

2.7.2. Patch quality model

Patch quality, in terms of prey density, is assigned from random sampling. We use the gamma distribution for prey density distribution over patches,

$$f(prey_{dens}) = \frac{\alpha^{\nu}}{\Gamma(\nu)} e^{-\alpha * prey_{dens}} (prey_{dens})^{\nu-1}. \tag{1}$$

We test two prey distributions (Fig. 1): first, where the prey concentration distribution is monotonically decreasing, so that there are a relatively larger number of high prey densities ($\nu = 1$, α=0.1), and second, where prey distribution is unimodal, so that there is a more even distribution of prey ($\nu = 5$, α=0.5) and a relatively smaller number of high prey density patches.

2.7.3. Feeding and interference competition

Feeding of the birds within patches is described as follows. Prey intake of the wading birds on a patch is calculated using a functional response model based on field observations of wading bird foraging rate as a function of both prey and wading bird density (Collazo et al. 2010). We use the BCM functional response since this model showed the best fit with the field observations of Collazo et al. and allows us to test the effect of interference competition of foragers in a waterbody,

$$G = \frac{0.0003 * prey_{dens}}{(1 + 0.002 * prey_{dens})(1 + C * (bird_{dens} - 1))} * 60, \tag{2}$$

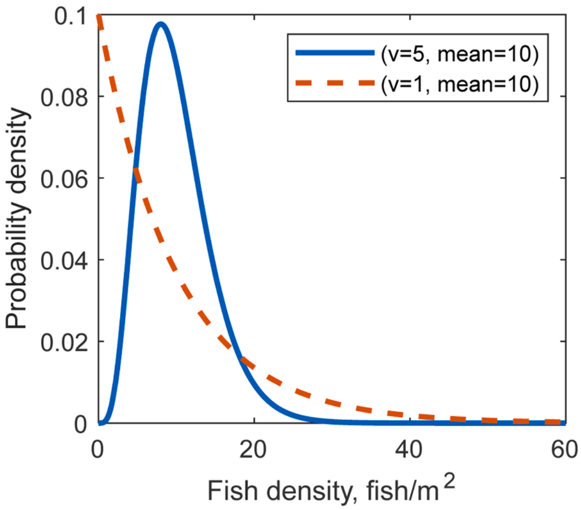


Fig. 1. Prey distribution on two different assumed landscapes. Solid line shows probability density of gamma distribution with $\nu = 5$ and α=0.5. This distribution has large numbers of patches that are close to mean quality while small numbers of patches are in each extreme. Dotted line shows a gamma distribution with $\nu = 1$ and α=0.1 which has a relatively larger number of high prey density patches compared with $\nu = 5$ and α=0.5. Both distributions have mean at 10 prey/m^2.

where G is an intake rate in catches per minute, and C is a parameter of interference competition. For simulation without competition, we assume $C = 0$, for simulations with competition, we assume $C = 0.03$.

2.7.4. *Aggregation behaviors in patch choice*

One variation of the model described in 2.7.1 considers tradeoffs regarding the use of social cues. By using social cues to select patches on which other birds are already foraging, a wading bird could increase its chance to find a better than average patch, as it is likely that prey density is high on the patch. However, following other wading birds could also potentially lead to increased interference competition among the birds (see Section 2.7.3), as competition increases with bird density. To test the effect of social cues, we apply behavioral patch selection strategies: cue-search and hybrid-search, where hybrid-search is a mixture of random and cue-following search. In hybrid-searching scenarios, wading birds use random searching during the first half of the foraging time and then switch to cue-search. Since a wading bird is assumed to have no prior knowledge of that patch quality, it bases its patch selection decision on an assumption that more birds in a patch indicates higher prey densities. However, this information could be inaccurate, and the searching bird could unintentionally follow other birds to suboptimal patches, which delays finding a sufficient patch, as pointed out in theory of social foraging (e.g., Vickery et al., 1991; Yurek et al., 2024). The prediction here, however, is that cue-following will produce higher prey intake than random searching.

2.7.5. *Comparison to the IFD using the Bhattacharyya distance*

We also compare the final wading bird distribution of each simulation with its theoretical IFD, where the latter is calculated as follows. As the IFD suggests, any new forager to an arena will choose the patch with the highest patch quality compared to other patches, where patch quality decreases as the ratio of forager density to patch quality increases (Fretwell and Lucas, 1970). This procedure is demonstrated in Fig. 12 of Doligez et al. (2008). We calculated the theoretical IFD by the procedure of starting with a given distribution of prey densities on the 500 patches with no wading birds present, and then sequentially adding 900 wading birds, one by one, to whichever patch had the highest prey intake rate at that point, where interference competition was included. The spatial distributions of wading birds at the end of the day in the simulations is compared with the theoretical IFD using the Bhattacharyya distance (BD, Bhattacharyya 1990; Eq. (3)) to estimate how closely they agree. The Bhattacharyya distance measures overlap of two probability distributions. The overlap is perfect if BD=0. BD is plotted against the threshold prey density for strategies that we term RANDOM and HYBRID search for patches,

$$BD = -ln\left(\sum_{i=1}^{500}\sqrt{IFD_i * SIM_i}\right) . \tag{3}$$

Here, IFD_i represents the proportion of birds on i^{th} patch in the theoretical IFD and SIM_i is the proportion of birds on i^{th} patch from the simulation results.

2.8. *Scenarios*

We performed five types of simulations (i.e., cases) assuming in each case wading bird prey density thresholds ranging from 0 to 90 prey per square meter to observe how total intake changed according to the thresholds.

3. Results

Case 1. Comparison of analytic and simplified simulation models and inclusion of variation of prey density thresholds

In the first set of simulations under Case 1, we compare the simulation model with the analytic model of Lee et al. (2022). The analytical model is modified to apply the functional response used in this model (Equation 2; Appendix 1). In the simulation 900 wading birds are followed simultaneously through the day, with all wading birds having the same prey density threshold and no interactions with other wading birds. Because the wading birds forage independently, this is effectively the same as in the analytic model, which simulates only a single foraging wading bird. Under these simplifying conditions, the IBM produces results similar to those of the analytical model of a single foraging wading bird (Fig. 2). For both prey density distributions, that is, for both gamma distribution parameters $\nu = 1$, and $\nu = 5$, the average daily prey intake of the wading birds in the IBM nearly overlaps the output of the analytic model expectations.

When $\nu = 1$, the analytic model predicts the highest intake (at the peak of the prey intake vs. prey density threshold curve) of 197.5 catches per day when the prey density threshold is set to 17 prey/m^2, which we

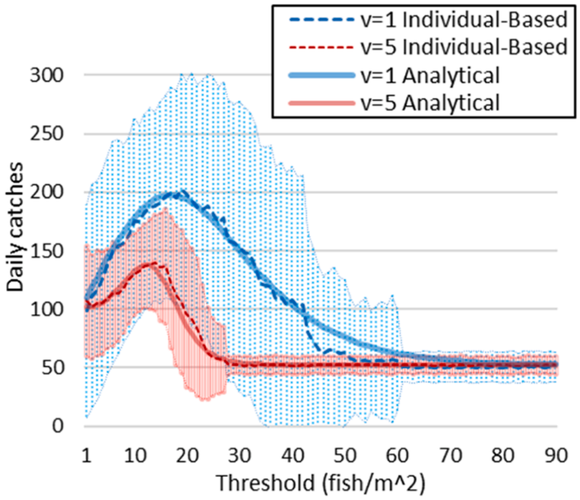


Fig. 2. Comparison between individual-based model and analytic model. The dotted lines are average daily intake from the individual-based model, while the solid lines are expected intakes from the analytic model. The colored areas show ranges based on standard deviation of 900 birds in each simulation.

call the ‘ideal threshold’ (Fig. 2). For a gamma distribution with $\nu = 5$, the highest intake rate is 137.8 catches per day with a threshold of 12 prey/m^2. In the IBM simulations, for gamma distribution parameter $\nu = 1$, the highest average daily intake is 202.2 catches per day at a threshold of 19 prey/m^2, while for $\nu = 5$ the highest average daily intake is 140.2 catches per day at a threshold of 14 prey/m^2 (Table 2).

The slight differences between the simulation and analytic models are attributed to variations between the theoretical continuous probability distribution of prey densities across the patches in the analytic model versus the discrete distribution of patches of prey densities in the IBM simulation. The standard deviation of individual daily intake is greater when $\nu = 1$ than when ν=5 in Fig. 2. A drop in standard deviation occurs when the prey density threshold surpasses the prey density in the patch with the highest prey density in the simulation (Fig. 2). The results show there is a higher maximum daily intake for $\nu = 1$ than for $\nu = 5$. Results for $\nu = 1$ also have a relatively higher ideal prey density threshold compared to $\nu = 5$.

In the second set of simulations in Case 1, a distribution of prey density thresholds among wading birds is added to the simulation model; that is, each wading bird has its own unique prey density threshold, chosen from a Gaussian distribution about a mean with a variance. When the standard deviation of the distribution of individual prey density thresholds is large, the intake curve is flatter than for the smaller standard deviation, resulting in a higher intake at high thresholds but a lower intake around the threshold that produces the highest prey intake without variation in thresholds (Fig. 3A for $\nu = 5$, Fig. 3B for $\nu = 1$). In summary, the IBM simulations of 900 identical wading birds on a set of 500 discrete patches are in good agreement with the earlier analytic model (Lee et al. 2022). However, when the wading birds are simulated with a distribution of prey density thresholds, the prey intake curve is flattened.

Table 2

Summary of simulations. This table summarizes the conditions and results for each simulation that appears in the figures. v, competition, and number of birds indicate the conditions of each simulation. The number of birds refers to the total number of individuals in the simulation for each searching strategy. The ideal threshold is the value at which the highest average intake occurred.

v	competition	[Random, Cue, Hybrid]			Appeared fig. #
		Number of birds	ideal threshold (prey/mˆ2)	highest average intake (catches/ day)	
1	no	[900 0, 0]	[19, -, -]	[202.2, -, -]	2, 3, 4
5	no	[900, 0, 0]	[14, -, -]	[140.2, -, -]	2, 3, 4
1	yes	[900, 0, 0]	[13, -, -]	[163.4, -, -]	4, 5, 9, 10
5	yes	[900, 0, 0]	[11, -, -]	[122.5, -, -]	4, 5, 9. 11
1	no	[450, 450, 0]	[19, 31, -]	[194.5, 283.7, -]	6
1	yes	[450, 450, 0]	[12, 17, -]	[160.5, 179.7, -]	6
5	no	[450, 450, 0]	[13, 18, -]	[138.8, 163.0, -]	6
5	yes	[450, 450, 0]	[11, 12, -]	[117.1, 117.3, -]	6
5	yes	[100, 800, 0]	[11, 11, -]	[131.3, 118.3, -]	7
5	yes	[800, 100, 0]	[11, 12, -]	[127.8, 137.1, -]	7
1	no	[300, 300, 300]	[17, 34, 29]	[221.0292.6, 242.1]	8
1	yes	[300, 300, 300]	[12, 19, 15]	[180.4, 212.5, 188.7]	8
5	no	[300, 300, 300]	[12, 17, 16]	[149.0 178.9, 155.2]	8
5	yes	[300, 300, 300]	[11, 12, 11]	[128.7, 130.7, 129.8]	8
1	yes	[0, 0, 900]	[-, -, 15]	[-, -, 184.5]	9, 10
5	yes	[0, 0, 900]	[-, -, 12]	[-, -, 128.1]	9, 11

v is a parameter from gamma distribution. $\nu = 5$ indicates evenly distributed resources and $\nu = 1$ indicated concentrated distribution of resources.

$C = 0.03$ for yes competition simulations and $C = 0$ for no competition simulations (Equation2).

Case 2. Inclusion of interference competition among individuals

Density-dependent interference competition among individuals foraging within prey patches, which is included by setting $C = 0.03$ in Eq. (2), decreases the peak of the prey biomass intake curve, indicating that individuals have lower potential intake when they are interfering with each other’s ability to obtain prey. Moreover, the peak of the prey intake curve is shifted to a lower threshold (Fig. 4A for $\nu = 5$, Fig. 4B for $\nu = 1$). The simulations show peak intake rates of 163.4 catches/day when prey intake threshold is 13 prey/m^2 ($\nu = 1$) and 122.5 catches/day when the threshold is 11 prey/m^2 ($\nu = 5$). Fig. 5 illustrates the effect of individual variability in the prey density threshold, along with interference competition among individuals in prey patches (Fig. 5A for $\nu = 5$, Fig. 5B for $\nu = 1$). Individual variation of prey threshold strategies shows similar changes in simulations both with and without interference competition. In summary, when there is competitive interference in the model, the prey intake peak is lower and shifts to a lower prey density threshold.

Case 3. Inclusion of social cues and interference competition

Social cues used by foraging wading birds are included, in which individuals have a higher than random probability of visiting prey patches in which a high number of wading birds are already present. Social cues cause noticeable changes in prey intake in a scenario in which 450 individuals employ random searching while 450 employ cue-searching. In the absence of interference competition within the patches, cue-searching individuals show a higher average intake than randomly searching individuals in scenarios with gamma distribution parameters of both $\nu = 1$ (Fig. 6D) and $\nu = 5$ (Fig. 6B). Random search exhibits its highest average daily intake of 195.5 catches per day at a peak prey density threshold of 19 prey/m^2 ($\nu = 1$) and its highest average daily intake of 138.8 catches per day at an ideal threshold of 13 prey/m^2 ($\nu = 5$), while cue-searching shows its highest average daily intake of 283.7 catches per day at an ideal

threshold value of 31 prey/m^2 ($\nu = 1$) and 161.2 catches per day at an ideal threshold of 16 prey/m^2 ($\nu = 5$). The optimal prey density threshold for the foragers is higher in cue-searching individuals than in randomly searching individuals in simulations without interference competition. However, when density-dependent interference competition within the patches is included, following social cues shows less effectiveness. When $\nu = 5$, cue-searching does not exhibit noticeably better performance than random search (Fig. 6A). Cue-searching shows the highest average daily intake of 117.3 catches per day at an ideal threshold of 12 prey/m^2, while random searching shows the highest average daily intake of 117.1 catches per day at an ideal threshold of 11 prey/m^2. Cue-searching shows better performance at $\nu = 1$ than at $\nu = 5$, but the difference is not as large as it is without interference competition (Fig. 6C). The highest average daily intake of random search is 160.4 at an ideal threshold of 14 prey/m^2, and the highest average daily intake of cue-searching is 179.7 catches per day at an ideal threshold of 17 prey/m^2 (Table 2). In summary, inclusion of cue-following substantially increases the prey intake of wading birds over that of random search in the absence of competition and shifts the peak towards a higher prey density threshold. In the presence of interference, cue following increases prey intake noticeably only for the ν= 1 density distribution.

Case 4. Different proportions of wading birds using random, cue-following, and hybrid strategies when the interference occurred

The relative rarity of a given foraging strategy among individuals also affects the performance of the strategy when the interference occurs (Fig. 7). Both the cue-following and hybrid strategies show better performance when the strategy is used by only a small proportion of individuals among the population. In a scenario with 100 randomly searching individuals and 800 cue-searching individuals ($\nu = 5$),

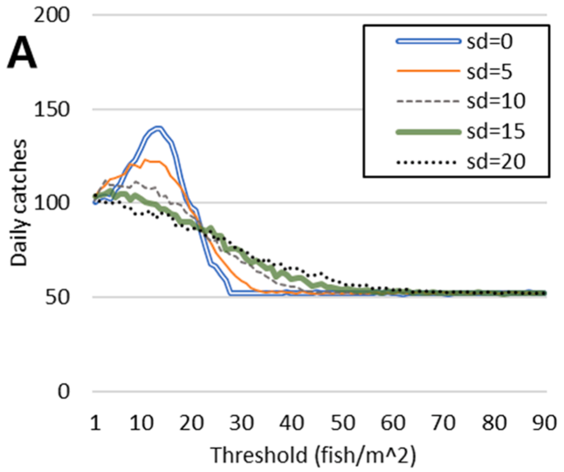


Fig. 3. Average daily intake as a function of prey density threshold densities and individual variation (sd) in thresholds. The x-axis shows the average threshold of the population, and the y-axis shows the average intake of the population. sd represents the standard deviation of threshold among the 900 individuals. (A) shows simulations for $v = 5$ and (B) shows simulations for $v = 1$.

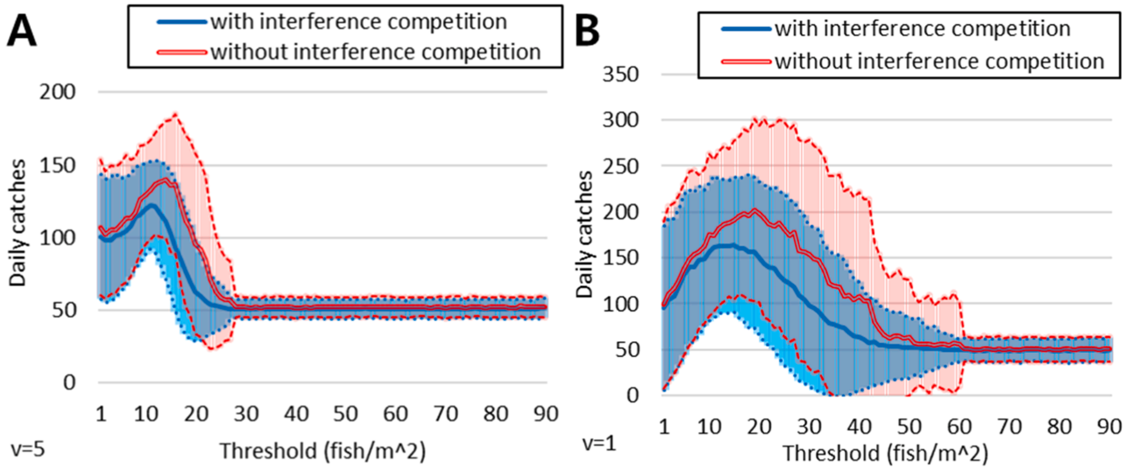


Fig. 4. Average daily intake of wading birds across different threshold prey density values with and without competition in patches. Red lines and colored areas show the average and the range of one standard deviation of the 900 individuals without interference competition and blue line and colored areas show the average and the range of one standard deviation of 900 individuals with interference competition. (A) shows simulations in which $v = 5$ and (B) shows simulation in which $v = 1$.

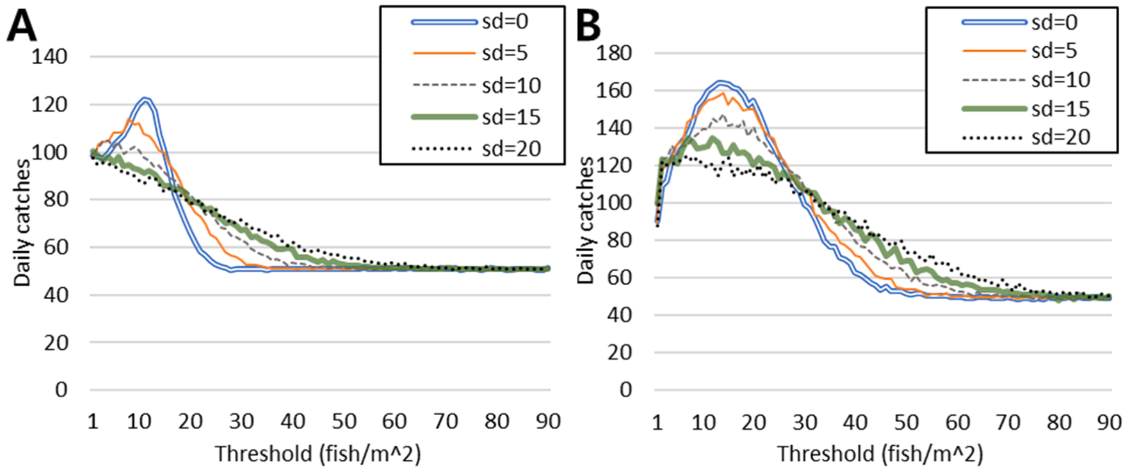
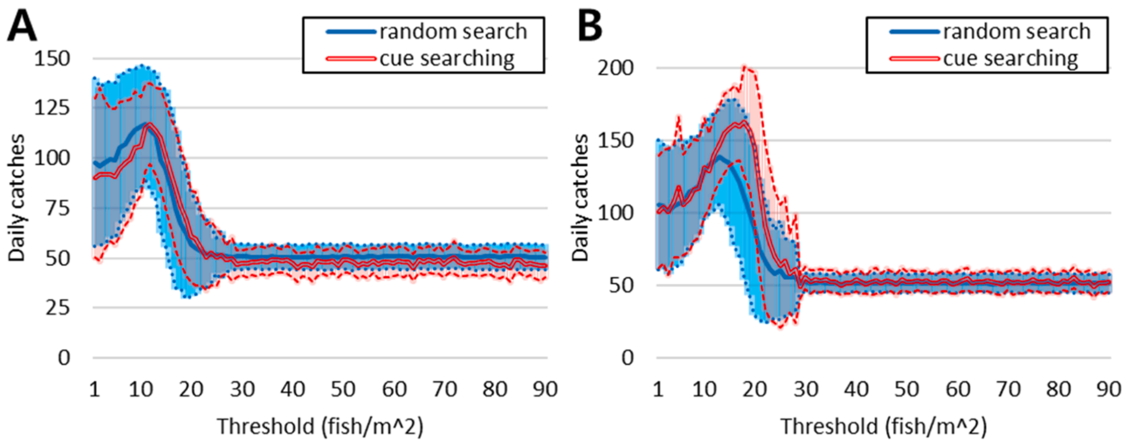
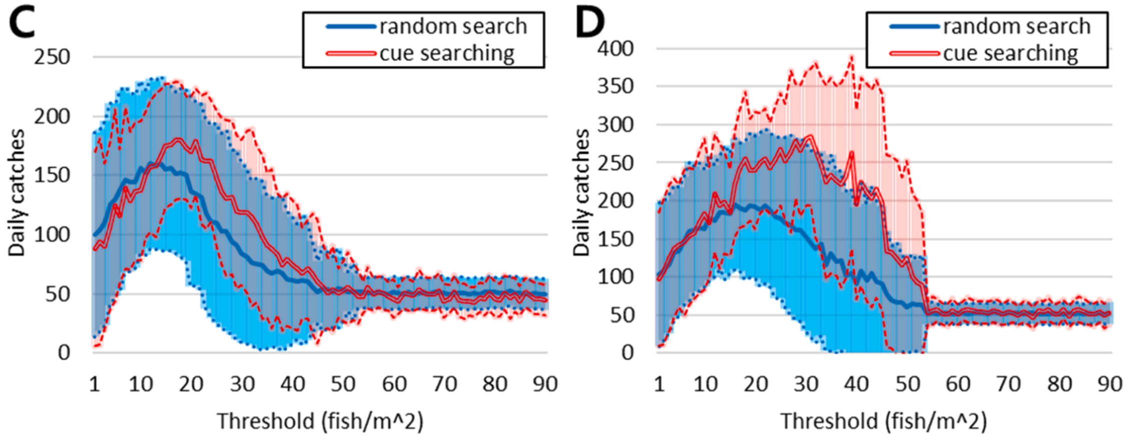


Fig. 5. Effect of individual variation with interference competition. sd is the standard deviation of individual thresholds, which represents the degree of individual variation. (A) shows the effect of individual variation when $v = 5$ and (B) shows the effect when $v = 1$.



v=5, with interference competition

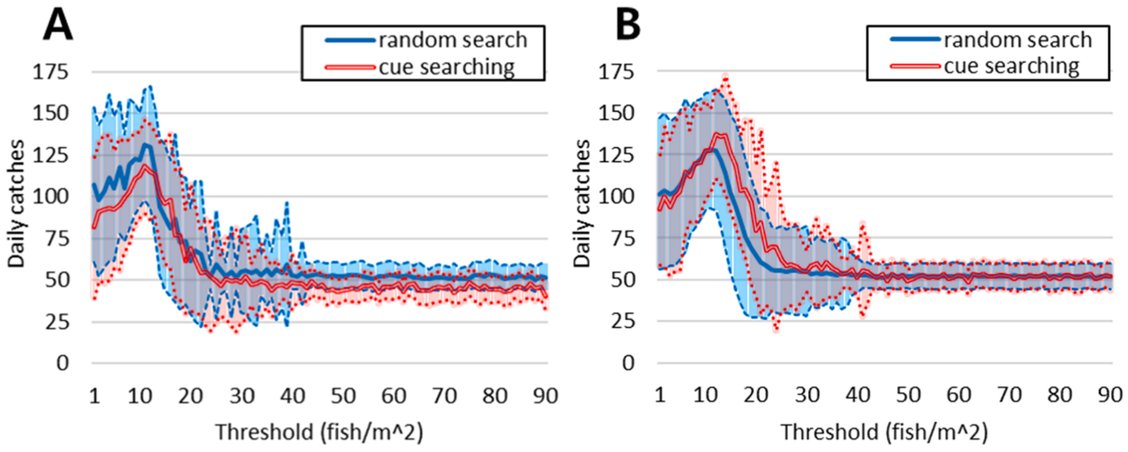
v=5, without interference competition



v=1, with interference competition

v=1, without interference competition

Fig. 6. Comparison of random searching and cue-searching where 450 random searching and 450 cue-searching individuals co-occur in the simulations. Each line shows average intake according to the prey density threshold and the colored areas show ranges of one standard deviation. The performance of cue-searching strategies increase when $v = 1$, that is, an environment where there are proportionally more high prey density patches, and when individuals are not interfering each other on patches. (A) shows when $v = 5$ and with interference competition, (B) shows when $v = 5$ and without interference competition, (C) shows when $v = 1$ and with interference competition, (D) shows when $v = 1$ and without interference competition.



v=5, with interference competition

v=5, with interference competition

Fig. 7. Comparison of randomly searching and cue-searching strategy when one strategy is rare. When cue-searching and random searching co-occur, the rare strategy shows better performance than the common strategy. (A) shows simulations with 100 randomly searching and 800 cue-searching individuals while (B) shows 800 randomly searching and 100 cue searching individuals.

randomly searching individuals exhibit the highest average daily intake of 131.2 catches per day at an ideal threshold of 11 prey/m^2, while cue-searching individuals obtain 118.3 catches per day at an ideal threshold of 11 prey/m^2 (Fig. 7A). In contrast, in the simulation with 800 randomly searching individuals and 100 cue-searching individuals, random searching results in a maximum average daily intake of 127.8 catches per day at an ideal threshold of 11 prey/m^2, while cue-searching results in 137.1 catches per day at an ideal threshold of 12 prey/m^2 (Fig. 7B) (Table 2).

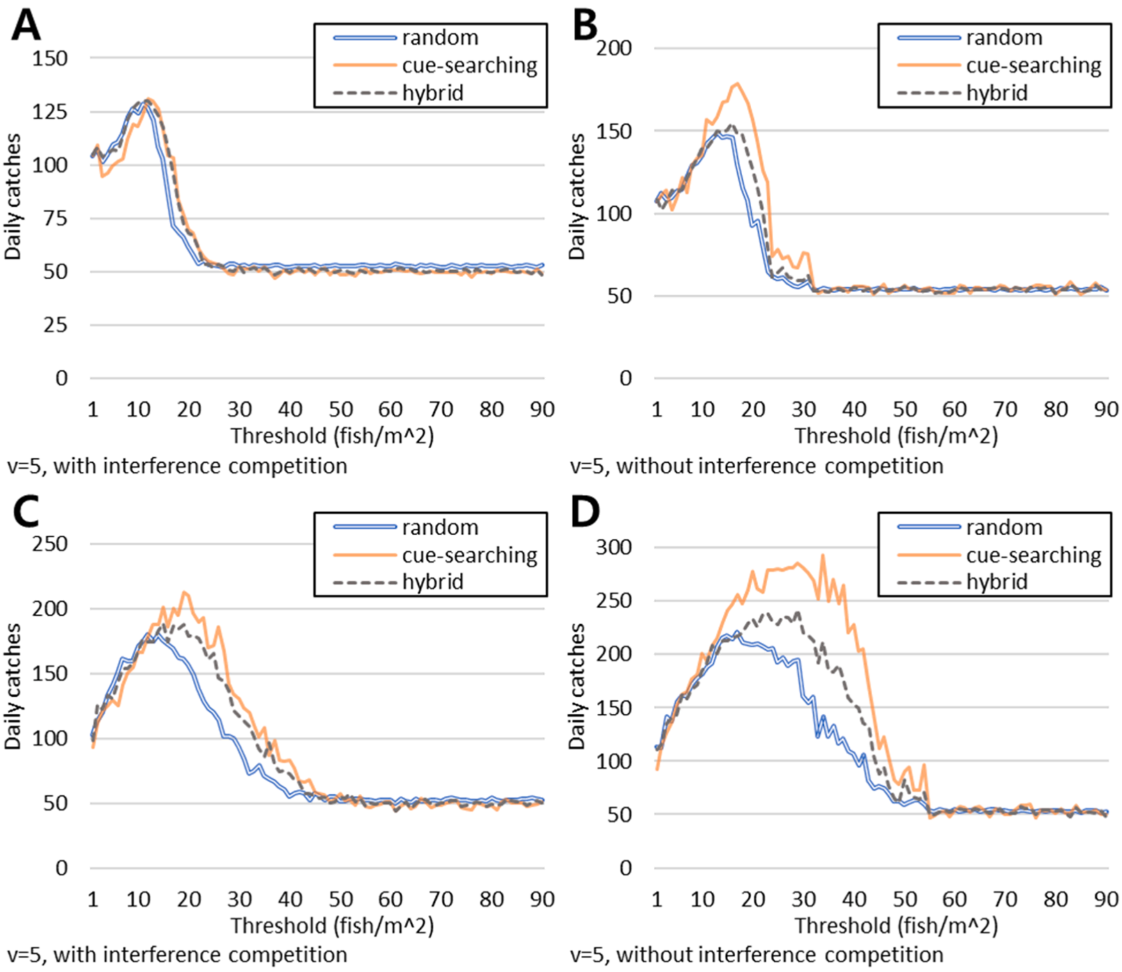
To compare all three strategies at once, we conduct simulations containing 300 individuals for each strategy: random-searching, cue-searching, and hybrid-searching. The results show similar trends with the comparison of the two strategies, random-searching, and cue-searching. Cue-searching exhibits better performance when the proportion of high prey densities is greater (i.e., for $\nu = 1$) and when individuals are not interfering with each other. Hybrid-searching demonstrates intermediate efficiency between cue-searching and random searching (Fig. 8). The cue-searching strategy is clearly better and random clearly worse when there is no interference competition among individuals in patches (Fig. 8B for $\nu = 5$ and Fig. 8D for $\nu = 1$). The same differences among strategies are also relatively strong when there is interference competition and $\nu = 1$ (Fig. 8C), but small when there is interference competition and $\nu = 5$ (Fig. 8A). In summary, when in small proportion in the population, either randomly sampling or cue-following could produce the higher prey intake when interference occurs. When there are 300 random, cue-following, and hybrid wading birds each, cue-following is superior both in the presence and absence of interference competition.

Case 5. Comparison of wading bird distribution in the simulation to the theoretical IFD

In comparing final (end-of-day) wading bird distribution with the theoretical IFD, for each of the cases, we use the prey density threshold strategy that shows the highest total daily prey intake in each scenario. We compare simulations with 900 randomly searching birds (termed RANDOM) with those of 900 hybrid-searching birds (termed HYBRID). We conduct simulations for both $\nu = 1$ and $\nu = 5$ environments.

The simulations with $\nu = 1$ (Fig. 9A) and $\nu = 5$ (Fig. 9B) show similar relationships between the Bhattacharyya distance (BD) and the prey density threshold, where the lowest BD corresponds to closest wading bird distribution to IFD. Additionally, we conducted the Kolmogorov-Smirnov test and calculated R^2 values, summarized in Appendix 3, Supplementary Information. In both environments, RANDOM and HYBRID show a similar BD when prey density threshold was low. Near the ideal threshold, where the highest daily intake and smallest BD occurs, HYBRID shows a smaller BD, indicating higher similarity to IFD than RANDOM. In contrast, when the threshold is high, RANDOM shows smaller BD than HYBRID.

The IFD, by its definition, means there should be a linear relationship



v=5, with interference competition

v=5, without interference competition

v=5, with interference competition

v=5, without interference competition

Fig. 8. Daily prey intakes when three strategies co-occur. The simulations have 300 individuals for each strategy. In general, cue-searching individuals show higher daily intake while randomly searching individuals show low daily intake. Random-searching individuals show peak daily intake at relatively lower prey density threshold than the peak of cue-searching individuals. Hybrid-searching shows an intermediate pattern between random-searching and cue-searching. (A) shows $\nu = 5$ with interference competition, (B) shows $\nu = 5$ without interference competition, (C) shows $\nu = 1$with interference competition, and (D) shows $\nu = 1$ without interference competition.

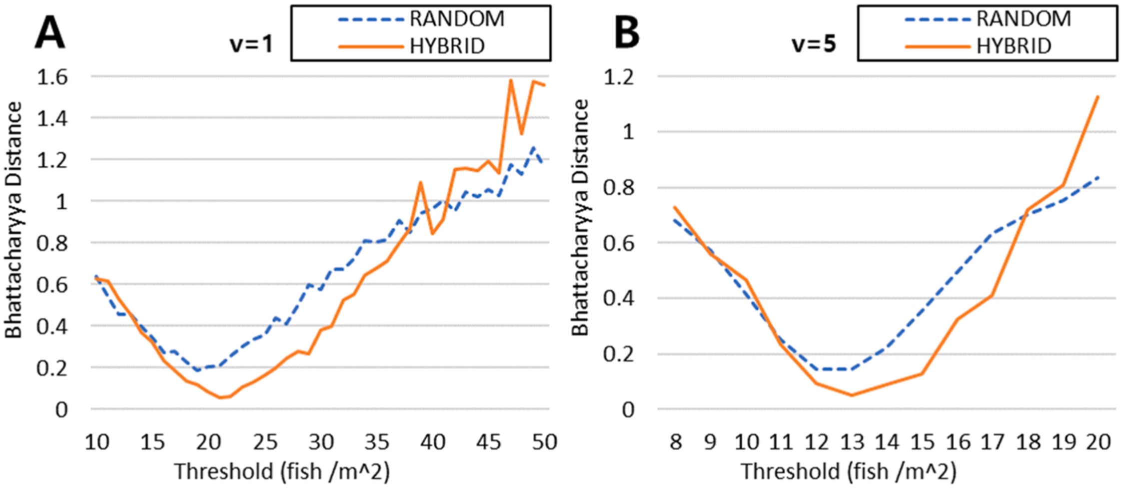


Fig. 9. Bhattacharyya distance (BD) of the final wading bird distribution compared to the IFD. Smaller BD indicates higher similarity. Hybrid-searching shows higher similarity to IFD than random-searching near the ideal threshold (confirmed with Kolmogorov-Smirnoff statistics not shown). When the prey density threshold is small, both strategies show a similar distribution, while when threshold is large, random-searching shows higher similarity than hybrid-searching. (A) shows BD when $\nu = 1$. Dotted lines show the result from simulation of 900 random-searching birds and solid lines show the result from simulation of 900 hybrid-searching birds. (B) shows BD when $\nu = 5$. Dotted lines show the results from simulation of 900 random-searching birds and solid lines show the result from simulation of 900 hybrid-searching birds.

between the number of foragers and the quality of patches (e. g., Sutherland 1983), in this case between wading bird numbers and the prey densities of the patches, as it assumes that the wading birds would distribute themselves across patches such that no wading bird could improve its prey intake by moving to another patch. We compare the RANDOM and HYBRID strategies with IFD for four cases of prey density thresholds with $\nu = 1$ and $\nu = 5$ (Figs. 10 and 11), with interference included in all cases. First, we check the BD of the ideal threshold, where the highest daily intake occurs. First, for $\nu = 1$, RANDOM shows the highest daily intake at a threshold of 13 prey/m^2, with BD=0.454 (Fig. 10A). HYBRID shows the highest intake at a threshold of 15 prey/m^2, with BD=0.325 (Fig. 10B). The smallest BD occurs at a higher

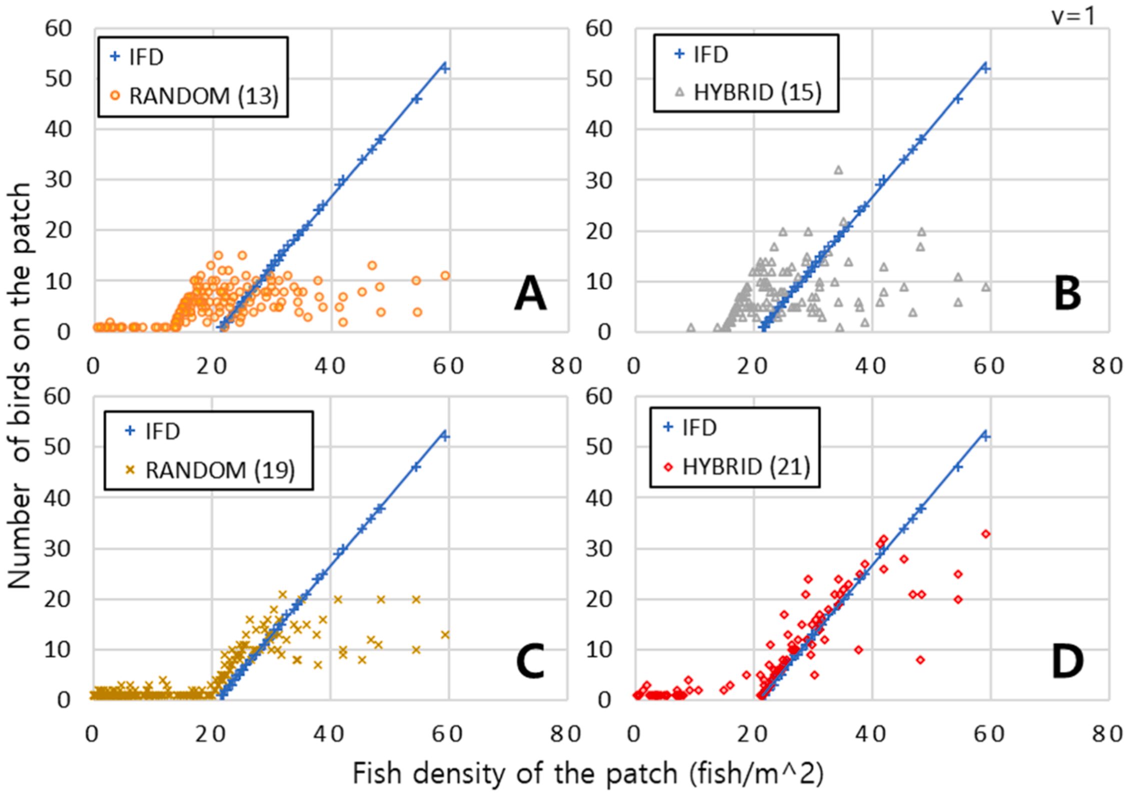


Fig. 10. Distribution of the wading birds with highest expected daily intake when $\nu = 1$. Blue crosses mark the plot of the IFD, and the blue line is the linear regression. (A) final distribution of the 900 random-searching birds when they have the highest daily intake (threshold=13 prey/m^2). (B) the final distribution of the 900 hybrid-searching birds when they have the highest daily intake (threshold=15 prey/m^2). (C) the final distribution of the 900 random-searching birds when they have highest similarity to IFD (threshold=19 prey/m^2). (D) the final distribution of the 900 hybrid-searching birds when they have highest similarity to IFD (threshold=21 prey/m^2).

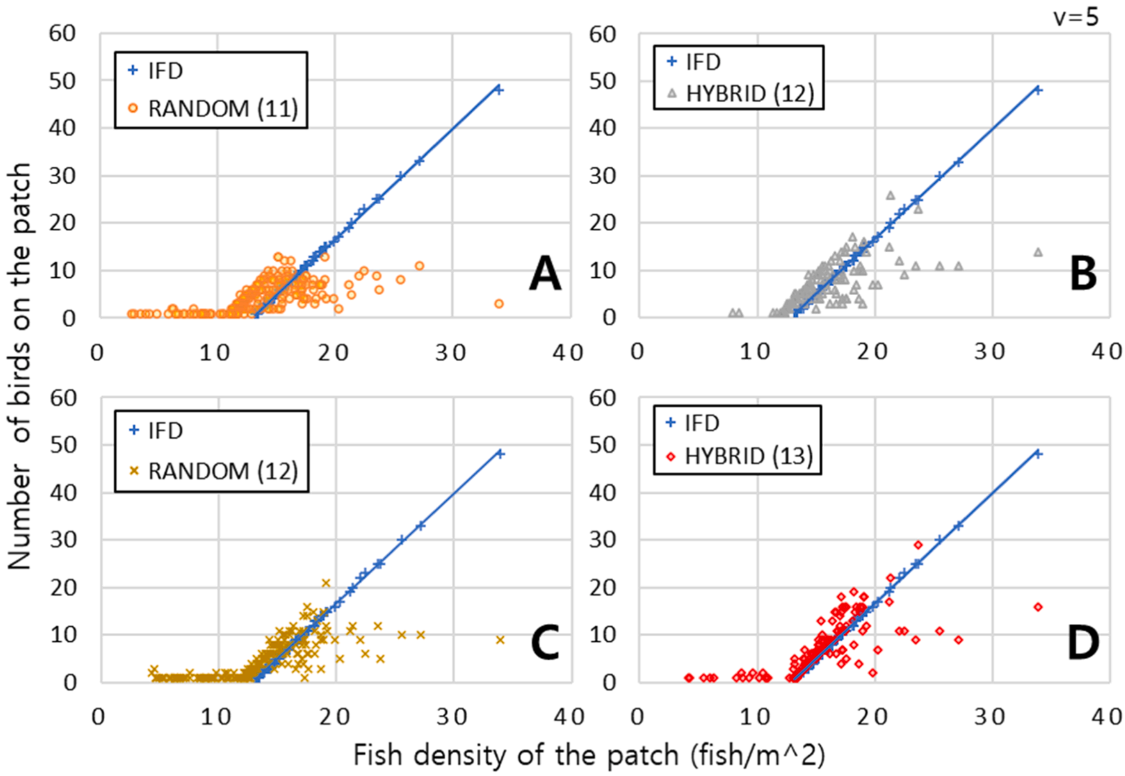


Fig. 11. Distribution of the wading birds with highest expected daily intake when $v = 5$. Blue crosses mark the plot of the IFD, and the blue line is the linear regression. (A) the final distribution of the 900 random-searching birds when they have highest daily intake (threshold=11 prey/m^2). (B) the final distribution of the 900 hybrid-searching birds when they have highest daily intake (threshold=12 prey/m^2). (C) the final distribution of the 900 random-searching birds when they have highest similarity to IFD (threshold=12 prey/m^2). (D) the final distribution of the 900 hybrid-searching birds when they have highest similarity to IFD (threshold=13 prey/m^2).

threshold than the ideal threshold. RANDOM shows the smallest BD when the threshold is 19 prey/m^2 (BD=0.190) (Fig. 10C), and HYBRID shows the smallest BD when the threshold is 21 prey/m^2 (BD=0.057) (Fig. 10D). HYBRID shows a stronger tendency to follow the IFD than RANDOM. RANDOM shows a tendency for wading birds to be more evenly distributed across patches. Also, the final wading bird distribution of the ideal threshold shows a smaller number of birds in low-quality patches than the final distribution with the minimum BD.

The gamma function parameter $v = 5$ shows a pattern similar to that of $v = 1$, where the smallest BD occurs at a higher threshold than the ideal threshold. RANDOM shows the highest daily intake at a threshold of 11 prey/m^2 (BD=0.251) (Fig. 11A) and the smallest BD when the threshold is 12 prey/m^2 (BD=0.143) (Fig. 11B). HYBRID shows the highest daily intake at a threshold of 12 prey/m^2 (BD=0.092) (Fig. 11C) and the smallest BD when the threshold is 13 prey/m^2 (BD=0.049) (Fig. 11D). In this case, the threshold where the smallest BD occurs is relatively closer to the ideal threshold compared to $v = 1$. The pattern of bird distribution of $v = 5$ shows similarity to that of $v = 1$, where HYBRID shows a stronger tendency to follow IFD than does RANDOM, and the final wading bird distribution of the ideal threshold shows a smaller number of wading birds in low-quality patches than the final distribution with the minimum BD. In summary, both the random and hybrid foraging strategies lead to spatial distributions of wading birds closer to the IFD when the prey density threshold is greater than the peak of the prey intake curve, with the hybrid distribution being closer to the IFD.

4. Discussion

We used a spatially explicit IBM with 900 wading birds foraging on 500 prey patches distributed on a heterogeneous landscape, where the prey distributions on the patches followed either of two gamma distributions with different shapes, v= 1 or v= 5 (Fig. 1). The wading birds followed a strategy of sampling patches until they found patches with prey densities above a threshold density sufficient for them to stay in those patches.

4.1. *Analytical expectation and individual variance*

First, assuming all wading birds had the same prey density threshold, the IBM was compared with a previous spatially implicit analytic model (Lee et al. 2022). The comparison of daily prey intake as a function of the prey density threshold indicated that the analytic model with its continuous distribution of prey densities was a good approximation of the IBM with a discrete number of prey patches (Fig. 2). However, when the wading bird population in the IBM was given a Gaussian distribution of prey density thresholds, the prey intake curves of the IBM and analytic model substantially differed, although in both cases the curves had a unimodal shape with an optimal prey density threshold at the peak (Fig. 3). In the IBM simulations, those in which the prey density distribution was described by a gamma distribution with v= 1 had larger means and standard deviations of total prey intake than those with v= 5, because the environment with v= 1 includes a higher proportion of high prey density patches. Both the unimodal prey intake curve and the difference between the v= 5 and v= 1 environments were characteristic of all simulation scenarios in this study.

4.2. *Interactions among individuals*

Two aspects of interactions among individuals were included in the simulations, wading birds following social cues of densities of other wading birds already on patches to find patches with high prey densities, and interference competition within the patches. When interference competition alone was in the IBM, the height of the prey intake curves decreased relative to that without competition, and the peaks of the curves also shifted towards smaller ideal prey density thresholds (Figs. 4 and 5). The results implied that a population of foragers experiencing intense competition should best lower their prey density thresholds compared to when competition was absent. In the simulations, that strategy led on average to individuals staying in lower-quality patches with lower competition. This resembles the effect of intra-specific competition found in eusocial bees by Walters et al. (2024). Those authors noted that high competition for floral resources at the end of the season led some bees to forage at the edge of their range, lowering their rate of energy intake. While the intensity of interference competition was fixed in the present study, it could be adjusted in the future by changing the interference competition parameter, *C*, of the BCM functional response. We predict that increasing the intensity of interference would lead to spatial distributions of wading birds in closer agreement with IDF (see Sutherland, 1983).

Use of social cues showed better performance than random searching (Fig. 6b, d), in agreement with Yurek et al. (2024), which did not include competition. This improvement in performance was much less in the presence of interference competition (Fig. 6a, c); as Beauchamp and Ruxton (2014) also found. Wading birds following cues could be led to crowded patches. Thus, individuals with a cue-searching strategy were more likely to face higher competition, decreasing the advantage of higher prey densities.

The relative rarity of a given strategy also affected its performance (Fig. 7). When both cue-searching and random searching occurred among the wading bird populations, each strategy showed better performance when their searching strategy was followed by only a small proportion of the wading birds. For example, when only a small proportion of the 900 wading birds used cue-following, those individuals likely found patches with high prey density, without the patches being crowded by other cue followers (see Parker, 1984). When only a small proportion of the 900 wading birds used random foraging, individuals were spread spatially and more likely to land on prey patches with few competitors.

When hybrid-searching, cue-searching, and random searching co-occurred, hybrid-searching individuals showed intermediate performance between cue-searching and random searching (Fig. 8). This pattern agrees with some predictions by game theory on social foraging. Parker (1984) predicted a frequency-dependent relationship between producers and scroungers, where the fitness of producers may increase when the proportion of scroungers increases (Giraldeau and Caraco, 2000). Buckley (1997) simulated colonial breeding in seabirds and found that this behavior is favored when resource patches are short-lived, suggesting that social interactions are more effective under those conditions. In this present study, prey density remained constant during the simulation; however, it was assumed that patches did not last more than a day, meaning the birds did not have prior knowledge of prey distribution at the start of each day. Buckley's study also showed that social interactions are more beneficial when patch sizes are large, which implies low competition. That pattern aligns with the results of this study. Smolla et al. (2015) also noted that social learning is favored when competition is weak. Additionally, they found that social aggregation is highly effective when resources are unevenly distributed, which is consistent with the findings of this study, as it was more successful when ν= 1 than ν= 5 (see Yurek et al., 2024 also). The accuracy of the information is also an important factor for effective social learning (Smolla et al. 2015). When there were larger numbers of cue-searching individuals, the accuracy of the information decreased. That is, cue-searching individuals often led others to lower-quality patches by creating overly crowded patches, thereby reducing the overall performance of the strategy (Fig. 7).

4.3. *Ideal free distribution (IFD)*

IFD predicts the distribution of animals such that no individual can increase its fitness by relocating itself to another patch. The comparison between the final wading bird distribution from IBM simulation and the IFD indicates that the use of social cues can be an important factor in leading to an IFD when individuals have limited a *priori* information about the environment. In both $\nu = 1$, where there are a greater proportion of high prey density patches, and $\nu = 5$, where prey densities are unimodally distributed among patches, the final bird distribution of HYBRID showed greater similarity to IFD than did the RANDOM, when the prey density threshold was in the range of the ideal prey density threshold (Fig. 9). When the prey density threshold was lower than ideal, both RANDOM and HYBRID foraging showed a similar pattern because HYBRID birds were almost as likely as RANDOM to settle on one of the first patches they encountered. When the prey density threshold was high, RANDOM showed higher similarity to IFD than did HYBRID (Fig. 9). This is because high thresholds can lead cue-searching birds to inadvertently set a “trap” by forming unnecessarily crowded patches that lure cue-searching individuals.

Also, the results showed that the smallest Bhattacharyya distance (BD) occurred when the actual prey density threshold was higher than the ideal prey density threshold. This is because a slightly higher threshold than the ideal threshold creates a higher chance for birds to end up with better patches, though it causes birds to spend more time sampling before settling on a patch and the birds will thus have less foraging time. Moreover, when the threshold is high, there is an increased chance that the wading birds will not find a patch to settle in until the end of the day. The IFD requires individuals to have perfect knowledge of resource distribution. Although this assumption is often not met in empirical cases, approximations of the IFD are nevertheless observed in nature (Griffen 2009). This simulation offers theoretical support for the observed IFD in natural systems in terms of cue-following, even when there are violations of the underlying assumptions.

4.4. *Limitations*

Our study did not include potential strategies of foragers other than random, cue-following, or hybrid search. This excluded the possibility of memory and learning within the period of foraging. An earlier analytic model of Lee et al. (2022) included the strategy of wading birds sampling a fixed number of patches and returning to the patch they remembered as having the highest prey density. Chudzińska et al. (2016) used IBM to simulate both social foraging and individual learning about the resource environment by pink-footed geese in Norway. The authors' simulations indicated that individual learning improved energy input, but social foraging did not. A further example of learning among foraging waterfowl was studied by Miller et al. (2017). The authors simulated individual waterfowl using MVT for deciding how long to stay in a patch. They assumed that the individuals had imperfect knowledge, but through time accidentally correct decisions on how long to stay would be reinforced and the individual would improve its rate of energy intake through time. Either of these strategies could be plausibly used by the wading birds in our model and can be studied in future work.

This study contains several other limitations. Various critical factors, such as predation risk, distance from the nest, and environmental cues, were not considered. Additionally, during the simulations, patch and bird numbers were fixed, although the ratio between patch and bird numbers is a factor influencing the importance of competition. Regarding individual variability, we examined only searching strategies and thresholds, while other individual differences, such as dominance, were not tested. Factors such as the distances between patches, birds' traveling speed, energy expenditure during foraging, and the impact of interference and searching activities also warrant further investigation. We did not report on sensitivity analyses in our Results section.

However, we did extensive informal sensitivity analysis. Figure A1 (Supplementary Information) shows how both the daily prey intake and the ideal prey density threshold vary as functions of the evenness of the prey density distribution and strength of interference competition.

Our long-term goals are to employ modeling in support of environmental restoration, particularly that of the Everglades, through more realistic modeling of wading bird foraging. Lee et al. (2022) used a spatially implicit analytic model, and Yurek et al. (2024) used a spatially explicit IBM to study cue-following on different landscape types. Here we added to these features individual variability among wading birds' prey density thresholds and the interference competition. The inclusion of individual variability, in particular, which shows the advantages of IBM, produced new results that may have implications for modeling of foraging behavior in general**.** In the future we will strive to improve our modeling efforts in the future, particularly in following Good Modeling Practice, as outlined in Jakeman et al. (2024).

5. Conclusions

At key result of this study was that the following of social cues to patches with higher wading bird numbers tended to lead to better individual performance when high prey densities were skewed toward a small number of patches ($\nu = 1$ gamma distribution), interference competition was not occurring, or a relatively small proportion of birds were using the social cues. These conditions also led to a final distribution of wading bird individuals closer to an IFD than when searching randomly. Interference competition within prey patches decreased the advantage of cue following. Interference competition and aggregating behaviors shifted the intake rate curves. The final foraging distribution showed a closer alignment with the IFD when social cues were used, as, collectively, the wading birds had higher information about the prey environment, and when thresholds were near the ideal level. These findings provide theoretical evidence that aggregation behavior can be advantageous when resources are concentrated, interference competition is minimal, relatively few individuals use social cues, and the presence of aggregation brings the distribution of individuals closer to the IFD. These results may provide insights into how social foraging affects key wading bird species of the Everglades, such as the white ibis.

CRediT authorship contribution statement

Hyo Won Lee: Writing – review & editing, Writing – original draft, Methodology, Formal analysis, Data curation, Conceptualization. **Donald L. DeAngelis:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Formal analysis, Conceptualization. **Simeon Yurek:** Writing – review & editing, Methodology, Conceptualization. **Yannis P. Papastamatiou:** Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2025.111178.

Data availability

The data generated from the simulations and the associated code are available upon reasonable request from the first author.

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