

Pattern-oriented modeling of bird foraging and pest control in coffee farms

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ABSTRACT

We develop a model of how land use and habitat diversity affect migratory bird populations and their ability to suppress an insect pest on Jamaican coffee farms. Bird foraging—choosing which habitat patch and prey to use as prey abundance changes over space and time—is the key process driving this system. Following the “pattern-oriented” modeling strategy, we identified nine observed patterns that characterize the real system’s dynamics. The model was designed so that these patterns could potentially emerge from it. The resulting model is individual-based, has fine spatial and temporal resolutions, represents very simply the supply of the pest insect and other arthropod food in six habitat types, and includes foraging habitat selection as the only adaptive behavior of birds. Although there is an extensive heritage of bird foraging theory in ecology, most of it addresses only the individual level and is too simple for our context. We used pattern-oriented modeling to develop and test foraging theory for this across-scale problem: rules for individual bird foraging that cause the model to reproduce a variety of patterns observed at the system level. Four alternative foraging theories were contrasted by how well they caused the model to reproduce the nine characteristic patterns. Four of these patterns were clearly reproduced with the “null” theory that birds select habitat randomly. A version of classical theory in which birds stay in a patch until food is depleted to some threshold caused the model to reproduce five patterns; this theory caused lower, not higher, use of habitat experiencing an outbreak of prey insects. Assuming that birds select the nearby patch providing highest intake rate caused the model to reproduce all but one pattern, whereas assuming birds select the highest-intake patch over a large radius produced an unrealistic distribution of movement distances. The pattern reproduced under none of the theories, a negative relation between bird density and distance to trees, appears to result from a process not in the model: birds return to trees at night to roost. We conclude that a foraging model for small insectivorous birds in diverse habitat should assume birds can sense higher food supply but over short, not long, distances.

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1. Introduction

This study is about modeling how land use and habitat diversity determine the extent to which birds suppress pest insects on Jamaican coffee farms. The birds, mainly migratory warblers from North America, forage on a variety of arthropod prey in forest, large trees, and shaded coffee, so these habitat types and their food supplies control bird abundance. However, the birds are capable of switching to consumption of insect pests of coffee shrubs when those pests are abundant. Our model is designed to address such questions as how the relative area of forest and coffee habitat affect bird abundance and the economic value of pest suppression by birds. Bird foraging, therefore, is key to understanding and modeling this problem.

Bird foraging has long been a subject of ecological theory and modeling, and empirical evaluation of models. This heritage is often described as starting with the pioneering optimal foraging models of Emlen (1966) and MacArthur and Pianka (1966), which addressed the question of how an individual should select between alternative prey types. Charnov (1976) proposed the “marginal value theorem” model for how long an individual should deplete the food in a patch before moving to another, and this model was supported in empirical experiments with chickadees by Krebs et al. (1974). The same question was modeled in more complex ways by Oaten (1977) and Green (1980), and more recently by measuring giving-up densities (Shochat et al., 2004). Even by 1977, Pyke et al. (1977) were able to review a number of models (and tests of the models) of individual foraging decisions such as: (1) selection among food types, (2) selection among habitat types, (3) allocation of time among patches, and (4) how to move through habitat in search of food.

The great majority of this work has been in the tradition of behavioral ecology, with both models and empirical experiments

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addressing the decisions of a single bird in a somewhat (or highly) simplified setting. For our coffee farm problem, though, we need a foraging model in the tradition of individual-based ecology (Grimm and Railsback, 2005): a model of individual decisions in a population context, with individuals competing for resources in a complex, dynamic, and unpredictable environment. The traditional behavioral ecology literature provides an important foundation, but much of it is not directly useful in a population-level model because its fundamental assumptions are not met. A prime example is the assumption of the “marginal value theorem” (Charnov, 1976) that there is a constant “average” resource availability, whereas in a model with birds depleting resources throughout the habitat, a spatial average of resource availability changes constantly over time. Stillman et al. (2000), Amano et al. (2006), and Stillman and Goss-Custard (2010) provide important examples of bird foraging models that do work in this individual-based ecology context, but none of them apply to the kinds of birds and habitats we address.

Our objectives were to design a model of the Jamaican coffee farm system, and then to use it to develop theory for foraging by small insectivorous birds that is useful in this population-level context. Both the model design and theory development phases use the “pattern-oriented modeling” strategy (Grimm and Railsback, 2005; Grimm et al., 2005). Pattern-oriented modeling uses a set of characteristic patterns observed in the real system—along with the model’s purpose—as the basis for designing and testing a model. Observed patterns are almost always important in designing and testing models, but in pattern-oriented modeling their use is made explicit.

The first modeling phase we describe is the use of pattern-oriented modeling to design a model. In Section 2.2 we select a set of characteristic patterns observed in the Jamaican coffee farm system, and identify what the patterns tell us about the structure of a model of the system: its scales, entities, and processes. We then (Section 2.3) develop the full model, incorporating additional empirical information from our study site.

The second phase of our study (Section 3) uses pattern-oriented modeling to develop theory for bird foraging decisions. We hypothesize several alternative foraging theories, then conduct simulation experiments to test how well the model, using each alternative theory, reproduces the observed patterns. These experiments let us draw conclusions about which theory best represents the birds’ foraging behavior and how useful the entire model is for understanding and managing the coffee farm system.

2. Methods

2.1. Study site: the Jamaican coffee farm system

Coffee is the highest value agricultural commodity produced in the tropics (O’Brien and Kinnaird, 2003; Vandermeer, 2003), and its most important pest is a very small beetle, the coffee berry borer (CBB, *Hypothenemus hampei*, LePelley, 1973). Female CBB bore into coffee berries, where they deposit eggs; the next generation of females can emerge ready to infest additional berries in 4–5 weeks (Damon, 2000). Coffee farmers must sort out and discard berries infested with CBB, a significant loss of income. CBB occurs in almost all coffee-growing regions and it is notoriously difficult to control (Barrera et al., 1990; Batchelor et al., 2005; Jaramillo et al., 2005). However, we and colleagues discovered that migratory insectivorous warblers sometimes consume large numbers of CBB on Jamaican coffee farms and provide a substantial economic benefit (Johnson et al., 2010; Kellermann et al., 2008; Sherry et al., unpubl. manuscript: “Diet comparisons and the potential for interspecific competition in five Neotropical migrant warbler species

wintering in Jamaican shade coffee farms”, T. W. Sherry, Department of Ecology and Evolutionary Biology, Tulane University).

The ability of birds to control CBB appears to be mediated strongly by coffee farm management, especially the amount of forest-like vegetation that provides food and habitat for birds. Because CBB are small (<3 mm long) and only occasionally numerous, birds cannot subsist on them alone; instead, other habitat must provide food resources (generally larger insects and other arthropods) sufficient to attract and maintain birds until CBB become numerous enough to become a profitable food resource. Jamaican coffee farms are best described as commercial polycultures (Moguel and Toledo, 1999) and typically include a complex patchwork of forest, forest fragments, coffee mixed with larger “shade trees” that provide canopy cover (“high-shade” coffee), and coffee grown with by itself with few to no shade trees (“low-shade” or “sun” coffee; Johnson et al., 2006). In general, the forest-like habitat provides more food for birds than do coffee plants (Johnson, 2000).

The most common insectivorous bird species in the Jamaican coffee farm system is the black-throated blue warbler (*Dendroica caruelescens*), which migrates from breeding grounds in eastern North America. Diet analyses suggest this species is the most important bird predator of CBB in Jamaica (Sherry et al., unpubl. manuscript). However, a number of small insectivorous bird species in Jamaican share prey forage in similar ways (Johnson and Sherry, 2001; Kellermann et al., 2008). Hence, the “population” in our model represents the entire community of such birds, while parameter values and assumptions based on field observations are generally developed for *D. caruelescens*. Because our model is designed to evaluate the effects of changes in land use and habitat, it does not represent a specific study site. However, the model’s general land use characteristics and much of the information used to parameterize it are from our study sites at the Kew Park and Seven Rivers farms in Jamaica (Jirinec et al., 2011; Johnson et al., 2010).

2.2. Patterns and model structure

2.2.1. Characteristic patterns of the coffee farm system

The first step in pattern-oriented modeling is to identify a set of observed patterns that characterize the system’s behavior with respect to the problem to be modeled. These patterns are general, robust, and often qualitative responses that seem to result from the same mechanisms we think are important for our modeling problem. From our field studies in Jamaica we identified the following patterns that characterize interactions among habitat types, bird foraging, and CBB infestation. In these patterns, “CBB infestation rate” refers to the fraction of coffee berries infested with one or more beetles.

Pattern 1: CBB infestation rates increase over the coffee season and are higher with birds excluded. The coffee fruit ripening season and peak CBB foraging activity in our study region (Dec–May) largely overlap the season when migratory birds from North America are present in Jamaica (Oct–April). Experiments using “exclosures”—nets that exclude birds but not insects—showed that presence of birds reduces the CBB infestation rate. Over the bird season, the rate of CBB infestation in exclosures rose 50–400% by approximately April, and then remained relatively constant (Johnson et al., 2010; Kellermann et al., 2008). On plants outside exclosures and accessible to birds, end-of-season infestation rates were approximately 50–70% of rates inside exclosures.

Pattern 2: In the absence of birds, CBB infestation rates are higher in low-shade coffee. In exclosures, the CBB infestation rate was approximately the same between sun and high-shade coffee at the start of the season but rose to approximately twice as high (~0.4)

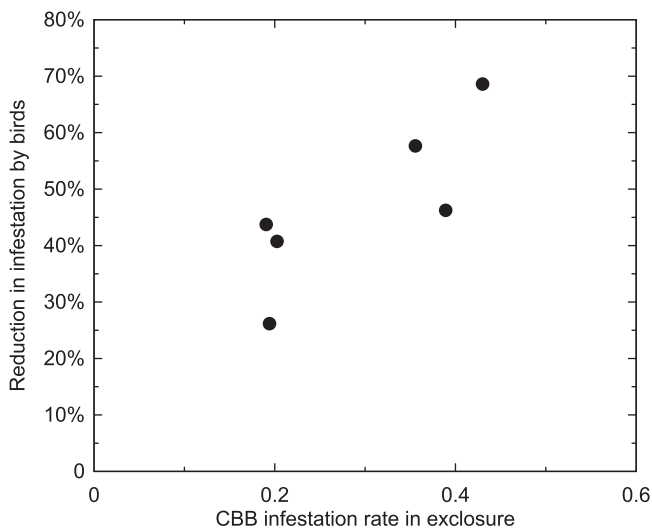


Fig. 1. Observed relation between bird reduction in CBB infestation and enclosure infestation rate. April, May, June mean results from Kew Park (M. Johnson, unpubl. data).

in sun coffee compared to high-shade coffee (~ 0.2 ; Johnson et al., 2010).

Pattern 3: Bird densities (number per area) are higher in high-shade than in low-shade coffee; Johnson et al. (2010) observed 2–3 times more birds in high-shade coffee at the Kew Park site.

Pattern 4: There is a positive relationship between (a) CBB infestation rate in enclosures and (b) the percentage by which birds reduce the infestation rate. This pattern is supported by unpublished data from enclosure experiments at our study site (Fig. 1). Birds appear more effective at suppressing CBB when CBB density is high.

Pattern 5: Birds respond quickly to local irruptions in their normal arthropod food supply. Short-term, sharp increases in food supply (approximately fivefold increases within 2 weeks) produced an immediate local increase in the density of feeding birds (Johnson and Sherry, 2001).

Pattern 6: Changes in bird densities over time within a season are related to changes in food supply. Over sites comparable in size to the entire spatial extent we model, Johnson and Sherry (2001; their Figure 5) observed that the rate at which bird densities changed between censuses was positively related to the rate at which arthropod food density changed, for both positive and negative changes.

Pattern 7: There is a weak relation between vegetation characteristics and bird density at intermediate scales. At 400 m² survey plots, there was a weak negative relationship between the distance to a patch of forest or tree habitat and the density of birds that prey on CBB (Kellermann et al., 2008). There was no relation at distances to forest or tree habitat less than 60 m, but low bird densities at distances of 70–120 m (Figure 2 of Kellermann et al., 2008).

Pattern 8: Bird movement distances measured at an hourly scale follow a log-normal distribution. Field observations in the winters of 2008–2009 and 2009–2010 identified locations of radio-tagged *D. caruelescens* at approximately hourly intervals (Fig. 2). The distribution of distances between hourly locations was highly skewed, with a peak (around 30 m) well below the mean (around 50 m) and occasional movements of between 200 and 500 m.

Pattern 9: Bird consumption of CBB is episodic. Our observations of bird feeding and stomach content samples indicate that CBB is a very small and highly variable part of the overall bird diet. On average, CBB composed $8 \pm 1.7\%$ SE of the identifiable prey in warbler diet samples, but these values ranged from 0 to 96% (Sherry et al.,

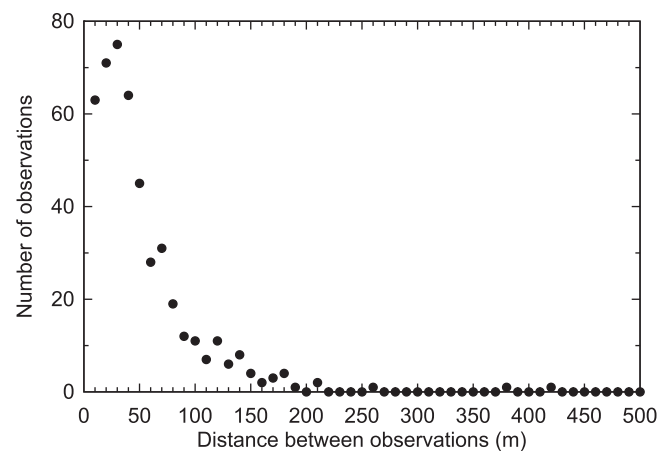


Fig. 2. Distribution of distances between hourly observations of individual birds at the Kew Park site (B. Campos, unpubl. data, Department of Wildlife, Humboldt State University).

unpubl. manuscript). Our energetic assumptions in Section 2.3.7.1 indicate that a bird would have to consume over 10,000 of these very small beetles to meet their daily food requirement. However, individual birds occasionally and briefly feed heavily on CBB.

2.2.2. What the patterns tell us about model structure

The second step of pattern-oriented modeling is to identify what the characteristic patterns indicate about the structure of a model of the system (Grimm et al., 2005). The model should use the same spatial and temporal scales as the empirical data that revealed the observed patterns, include the entities—kinds of things—that are in the patterns, and represent the processes believed to drive the patterns. Also, the model must produce outputs that let us test it by examining how well it reproduces the patterns. The following conclusions from the patterns strongly influenced the model structure described in Section 2.3.2.

- Many of the patterns concern changes over time, so the model needs to be dynamic.
- Many patterns concern differences among habitat types, so the model must be spatial with resolution fine enough to represent the small, irregular patches of low- and high-shade coffee, forest, and forest fragments that characterize Jamaican coffee farms.
- Foraging habitat selection by birds is a key process driving the patterns, so it needs to be included in the model explicitly. Because this individual behavior is important, individual-based modeling is a natural approach. Birds move among the small habitat patches rapidly, so the model needs a very short time step.
- Many patterns involve CBB infestation rate, so the model must represent this rate and how it is affected by bird feeding. Infestation rate is not a direct measure of CBB population but is the measure used to quantify CBB in the field and calculate its economic impact.
- Patterns 1, 2, and 4 are results of enclosure experiments, so the model needs to represent enclosures.
- Reproducing pattern 5 requires the ability to simulate irruptions of arthropod prey.
- Pattern 6 includes increases and decreases in bird populations. The model does not include the reproductive season, so reproducing population increases would require including immigration. Reproducing population decreases requires including mortality or emigration.
- Pattern 9 indicates that CBB are profitable as food only when infestation rates are higher than the average rate over time or

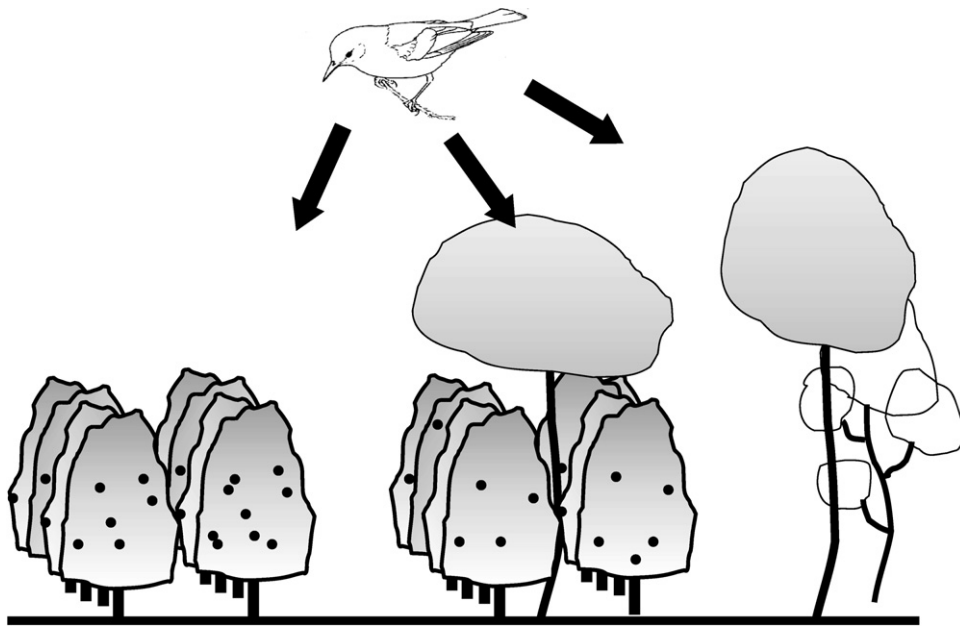


Fig. 3. Conceptual diagram of the coffee farm model. The model's outcomes (coffee berry infestation rate; bird survival) emerge from the spatial arrangement of habitat types and how birds decide which type to forage in. Key habitat types, left to right, are monoculture (low-shade) coffee, coffee mixed with overstory trees (high-shade coffee), and trees. Birds also decide whether to feed on general arthropods, which are especially abundant in trees, or on CBB (represented as dots), which are occasionally highly abundant and easy to catch on coffee plants.

space. Therefore, CBB infestation must be spatially and temporally variable.

2.3. Model description

This model description follows the ODD (Overview, Design concepts, Details) protocol for describing individual-based models (Grimm et al., 2006, 2010). The model was implemented in NetLogo (Wilensky, 1999) so we use some NetLogo conventions such as for variable names.

2.3.1. Purpose

The model's purpose is to explore the effects of changes in coffee farm management on suppression of CBB by birds. In particular it is designed to help us understand and predict how the relative area and spatial arrangement of several common habitat types, especially high- and low-shade coffee, affect local bird densities and the reduction of CBB infestation rates by birds (Fig. 3).

2.3.2. Entities, state variables, and scales

This section describes the model's structure.

2.3.2.1. Scales. The model's spatial extent is a square of 200×200 square cells, each $5 \text{ m} \times 5 \text{ m}$ in size; hence, the total area is 100 ha. This relatively fine resolution was chosen so the model can represent the effects of the small patches of trees and other habitat types that typify Jamaican coffee farms. The model's space is represented as bounded, not toroidal: birds at one edge of the space cannot jump to cells on the opposite edge.

The model runs at a 1-day time step, except that bird habitat selection and foraging is modeled at much shorter time step during daytime hours. This "foraging time step" is a parameter *forage-time-step* with value of 0.0167 h (1 min). The model does not represent night; it assumes all events occur during the day. The parameter *max-forage-hrs-per-day* specifies how many foraging hours there are per day, assumed constant at 12. Hence, birds can move and feed up to 720 times per day.

The time period modeled represents the period when CBB infest berries and when North American birds winter in Jamaica. The model runs for 151 days representing December 1 to April 30.

2.3.2.2. Habitat cells. The model landscape is made up of "clumps" of six different habitat types described here. (The more conventional term "patch" has a different meaning in NetLogo.) Each cell is assigned a habitat type, using methods that produce distinct but irregular clumps of each type (Fig. 4). All cells have the same equal



Fig. 4. Example model landscape with six habitat types. Dark green border on right: forest; grey: high-shade coffee; yellow: low-shade coffee; brown: unusable; orange: other; small green clumps: trees. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

tions for habitat processes but each habitat type has its own values for habitat parameters. The amount of area in each habitat type, and the number of clumps of each, are set by model parameters. The rules for assigning cells to the habitat types are explained in Section 2.3.5.1.

Forest habitat represents a single, large tract of forest. The size of the forest is controlled by the parameter *frac-forest*, the fraction (0–1) of all cells that are assigned the forest habitat type. The forest is arranged as a single clump that forms a ragged boundary on the right side of the space.

High-shade habitat represents coffee habitat with diverse vegetation and a relatively high canopy cover provided by shade trees above the coffee bushes. The fraction of cells that are high-shade coffee is determined by the parameter *frac-high-shade* (the fraction of all cells—except those of type *trees*, explained below—set to this type). High-shade habitat is arranged as a number of irregular clumps spread throughout the non-forest space. The number of high-shade clumps is set by the parameter *num-high-shade-clumps*.

Low-shade represents coffee habitat that has little to no shade-tree canopy cover, low vegetation diversity, and is effectively a monoculture. In Jamaica, coffee landscapes are diverse, with clumps of high-shade and low-shade coffee often within a single farm under one ownership. In other coffee growing regions, individual farms are often characterized along a shade gradient, such as that described by Moguel and Toledo (1999). The area of low-shade coffee is set by the parameter *frac-low-shade* (the fraction of all cells except those of type *trees* set to this type). The number of clumps is set by the parameter *num-low-shade-clumps*.

Unusable habitat represents land uses unusable for bird foraging, especially pasture. The parameter *frac-unusable* is the fraction of all non-trees cells set to this type, and the parameter *num-unusable-clumps* sets how many clumps there are.

Trees habitat represents non-coffee trees or forest fragments, dispersed among the other non-forest habitat types. The area of this habitat type is set by the parameter *frac-trees*, the fraction of the total area that is of this habitat type. The parameter *num-trees-clumps* sets how many clumps there are.

Other habitat represents non-forest and non-agricultural land use such as roads and housing.

Each cell has state variables for the supply (as biomass, g) of two kinds of invertebrate prey for birds. These variables do not represent the total biomass density of invertebrates but the amount of prey exposed and available for consumption by birds. The first prey type is CBB, the pest beetles that infest coffee berries. “Bugs” are all other prey for birds. The supply of these prey are contained in the cell variables *CBB-availability* and *bug-availability*. *CBB-availability* is calculated from cell variable *CBB-I*, the CBB infestation rate.

2.3.2.3. Birds. Birds are represented as mobile individuals with state variables for their location and energetic status. Location is tracked only as which cell the bird is in, and birds have a variable for their “home cell”, which does not change over time. The energetic state variable *daily-intake* is simply the grams of food consumed on the current day. (Several other variables are used only to generate output on how much time birds foraged in what kinds of habitat.)

2.3.2.4. Exclosures. The model represents exclosures—coffee habitat from which birds but not CBB are excluded. These are not treated as discrete objects located in space. Instead, the model simply calculates daily CBB infestation without bird consumption, in both low- and high-shade coffee. These calculations use the mean of the one CBB parameter that varies among cells (Section 2.3.5.2), and were shown experimentally to produce results very close to the mean over all coffee habitat when the model was run without birds.

2.3.3. Process overview and scheduling

On each daily time step, the following actions happen in this order. The order in which the individual cells and birds process each action is randomized each time the action is executed.

Bug production: Each cell re-sets its bug prey availability (Section 2.3.7.2).

CBB production: Each cell and exclosure updates its CBB infestation rate and biomass density of CBB prey (Section 2.3.7.3).

Bird updates: Birds re-set their *daily-intake* state variable (and other variables that track habitat use and food use for output) to zero.

Bird habitat selection and foraging: Each bird conducts its foraging action, selecting which cell to feed in and determining what kind (bugs or CBB) and how much food it consumes. The consumed food is subtracted from the cell's food availability. This action is repeated once for each foraging time step, up to the total number of foraging hours per day (details are in Section 2.3.7.1). The bird order is shuffled each foraging time step to represent the lack of any hierarchy or dominance in competition for habitat.

Birds return to home cell: At the end of the day's foraging, each bird returns to its home cell. This behavior imposes a kind of home range on the birds.

Bird mortality: At the end of each day, birds that have not obtained a minimum daily food intake of 5.0 g (Section 2.3.7.1) experience a daily risk of dying or leaving. Such birds have a random chance with probability 0.2 of being removed from the model. The process is necessary to allow changes in the bird population (pattern 6, Section 2.2.1). Mortality is also included because it, along with a high initial density of birds, is how we let local bird distribution patterns emerge at the start of a simulation (Section 2.3.5.2). This simple approach to starvation is not completely unrealistic for birds, which have high metabolic rates and little ability to store energy, and avoids the need to model energy reserves and balances. Emigration and immigration were not represented because (a) the period we simulate is after the end of migration so no more birds arrive from North America and (b) we assume that the area we model is large enough that emigration and immigration due to bird habitat selection balance each other and hence are negligible.

Observer updates: The last action executed each time step is an update of model outputs. The interface graphics are re-drawn, and current statistics on the birds and cells are written to an output file. The model also produces “virtual surveys” at a frequency selected via a model parameter; these produce observations comparable to some of our field surveys (Section 2.3.7.4).

2.3.4. Design concepts

This section describes the model at a conceptual level, using the 11 design concepts of the ODD protocol (Grimm et al., 2010).

Basic principles: In its foraging submodel (Section 2.3.7.1), this model poses a classical optimal foraging problem: how should an individual decide whether to stay in its cell and further deplete its food resource or move on to another? However, this question is posed in a more complex and realistic context than typically addressed in the foraging theory literature. We provide insight into this problem by contrasting four alternative theories for this decision by how well they reproduce observed patterns (Section 3).

Emergence: The model's primary results—CBB infestation rates—and intermediate results such as bird abundance and spatial distributions of birds and bug densities emerge from the amount and spatial distribution of the six habitat types, the number of birds, and the foraging behavior of birds. Of the characteristic patterns used to design and test the model, patterns 3, 4, 5, 7, and 8 especially emerge from bird foraging behavior and habitat characteristics. Patterns 1, 2, 6, and 9 are at least partially imposed by model rules and parameters.

Adaptation: Adaptive behavior is modeled only in birds. Their adaptive trait is foraging and habitat selection: deciding which cell to feed in and whether to eat CBB or bugs.

Objectives: The adaptive foraging trait uses implicit fitness-seeking. The trait assumes an objective of meeting a daily intake threshold in the shortest amount of time, by selecting habitat providing highest food intake. This objective is not a direct measure of bird fitness, if we consider “fitness” lifetime reproductive output. However, the objective is a strong indirect measure of fitness, for several reasons. First, the birds are overwintering so reproductive activities can be neglected. Instead, survival and energy accumulation are assumed to be the dominant fitness concern. Food intake is critical to bird survival: because of their high metabolic rate, birds starve rapidly when intake is inadequate. Indeed, there is evidence that annual survival rate is influenced by the capacity for wintering warblers to maintain body mass (Johnson et al., 2006), and effects of body mass appears to carry over into the migratory and breeding seasons for long-distance migratory songbirds (Norris et al., 2004; Bearhop et al., 2004). Second, predation risk can be neglected as a factor directly affecting selection of foraging sites. Potential predators on birds are rare at the field sites and we have rarely observed predation events. However, our assumption that birds cease feeding as soon as they meet their threshold intake is a form of predator avoidance, because birds are more vulnerable when feeding.

Learning and Prediction are not represented in the bird foraging trait.

Sensing: Birds are assumed able to perfectly sense the current availability of both bug and CBB prey in cells within a specified radius of their current cell (Section 2.3.7.1).

Interaction: There are no interactions among habitat cells; bug production and CBB infestation of each cell are not calculated from characteristics of neighboring cells. Birds interact with each other via competition for the available bug and CBB food, with asynchronous updating. When each bird occupies a cell, it immediately depletes its food consumption by subtracting it from the amount available for other birds in the current foraging time step or later on the same day.

Stochasticity: Stochasticity is used mainly in initializing the model (Section 2.3.5), to create irregular clumps of each habitat type, to assign each bird a home cell, and to impose variability among cells in CBB infestation rates (cells of the same habitat type do not vary in bug production; Section 2.3.7.1). During a simulation, the main uses of stochasticity are to (1) avoid a feeding hierarchy by randomizing the order in which birds execute their foraging trait each foraging time step (by using NetLogo’s “ask” primitive, which by default randomizes execution order), and (2) decide whether birds die if they did not make their daily intake requirement (Section 2.3.3). In bird foraging, several cells may offer exactly the same, highest, food intake rate; in such cases, the bird chooses one of these cells randomly.

Collectives: There are no collectives in this model.

Observation: Graphical output on the NetLogo interface shows the habitat type of each cell, via cell color. Bird locations are also shown. The model randomly selects one bird per day and displays a trace of its movement during the day, so foraging patterns can be observed. Summary statistics on the bird population, CBB, and bugs are provided via plots on the interface and output files. Virtual survey (Section 2.3.7.4) results are output to files.

2.3.5. Initialization

The model is initialized by assigning habitat types to cells, setting the CBB infestation rate of cells, then creating the birds.

2.3.5.1. Assignment of habitat types. The model’s landscape is created by assigning cells to the habitat types described in Section 2.3.2.2. This assignment uses the following steps, with parameters

Table 1
Habitat initialization parameter values.

Parameter	Standard value
<i>frac-forest</i>	0.10
<i>frac-high-shade</i>	0.28
<i>frac-low-shade</i>	0.28
<i>frac-unusable</i>	0.28
<i>frac-trees</i>	0.20
<i>num-high-shade-clumps</i>	20
<i>num-low-shade-clumps</i>	20
<i>num-unusable-clumps</i>	10
<i>num-trees-clumps</i>	1000
<i>clump-spacing</i>	200 m

defined in Section 2.3.2.2. The parameter values used here are in Table 1. These parameter values were chosen to represent the habitat characteristics (size and number of clumps of each habitat type) typical of the Jamaican high mountain coffee farms we have studied. The selection of parameter values was in particular guided by analysis of aerial photography of farms in the vicinity of Cambridge, Saint James Parrish, Jamaica.

First, the number of forest cells is calculated as *frac-forest* times the total number of cells. A rectangular border of forest cells is then created along the right boundary of the space, wide enough to include half of the total forest cells. Then one of the non-forest cells that is adjacent to a forest cell is chosen at random and turned into a forest cell. This process is repeated until the full number of forest cells has been created, producing a ragged border between the forest and coffee farms that is characteristic of Jamaica.

Second, high-shade coffee clumps are created by randomly selecting *num-high-shade-clumps* “seed” cells from among the unassigned cells, and turning them into high-shade cells. These seed cells must also be at least a specified distance (parameter *clump-spacing*, m) from any other seed cell. Then unassigned cells that are adjacent to a high-shade cell are chosen randomly and turned into high-shade cells, until the total number of high-shade cells is equal to *frac-high-shade* times the total number of cells.

Next, low-shade clumps are created using the same process as for high-shade; then unusable clumps are. Cells are not added to these clumps if they were already assigned a habitat type.

Fourth, tree clumps are created using a different process that creates a wide variety of clump sizes, with a few large clumps and many small ones. First, the mean clump size is calculated by dividing the total number of trees cells (*frac-trees* times the total number of cells) by *num-trees-clumps*. Then the clumps are created one at a time by (a) drawing a random size from an exponential distribution with this mean clump size, (b) selecting a seed cell randomly from among all non-forest cells (including cells already assigned to types high- or low-shade or unusable), and (c) randomly adding cells to the clump until its size is met. Cells are added in the same way they are to high-shade clumps.

Finally, all remaining unassigned cells are assigned the type “other”.

This process is complex and stochastic, so the exact area of habitat of each type varies slightly among implementations even when the parameters are not changed, and the actual fraction of area in each habitat type differs from the parameters *frac-high-shade*, etc. The expected actual fraction of the landscape in each habitat type is given in Table 2. Because this landscape generation process is computationally intensive and stochastic, the landscapes it produces can be saved and re-loaded in later model runs so multiple model runs can be initialized with the same landscape.

2.3.5.2. Initialization of CBB infestation and birds. The initial CBB infestation rate in each coffee habitat cell (types high-shade and low-shade) is set to the values of parameters *CBB-I-initial-*

Table 2Equations for expected actual fractions of landscape in each habitat type, and expected number of cells in the 200×200 cell landscape.

Habitat type	Expected fraction of total landscape	Expected number of cells
Forest	frac-forest	4000
High-shade	$\text{frac-high-shade} - \{\text{frac-trees} \times [\text{frac-high-shade}/(1 - \text{frac-forest})]\}$	8711
Low-shade	$\text{frac-low-shade} - \{\text{frac-trees} \times [\text{frac-low-shade}/(1 - \text{frac-forest})]\}$	8711
Unusable	$\text{frac-unusable} - \{\text{frac-trees} \times [\text{frac-unusable}/(1 - \text{frac-forest})]\}$	8711
Trees	frac-trees	8000
Other	One minus expected fraction of all other habitat types	1867

high-shade and *CBB-I-initial-low-shade*. The maximum infestation rate *CBB-I-K* described in Section 2.3.7.3 varies among cells and set during initialization by drawing its value randomly from a normal distribution with mean and standard deviation set by parameters *CBB-I-K-high-shade-mean*, *CBB-I-K-high-shade-SD*, *CBB-I-K-low-shade-mean*, *CBB-I-K-low-shade-SD* (Table 4). If the resulting value of *CBB-I-K* is greater than 1.0, it is set to 1.0 (infestation rates cannot be greater than 1.0). Likewise, infestation rates cannot decrease, so if the randomly drawn value of *CBB-I-K* is less than the initial infestation rate, it is re-set to that initial rate. Then the CBB dynamics methods in Section 2.3.7.3 are executed to calculate initial CBB availability values for each cell of coffee habitat.

The initial number of birds is the parameter *initial-bird-density* (birds/ha) multiplied by the total area of the space (ha). The home cell of each bird is chosen randomly, with equal probability for each cell (whether or not another bird has chosen the same cell), and the bird moves to its home cell. Birds are therefore spread relatively evenly, regardless of habitat type, at the start of a simulation. The model depends on a high initial bird density for the density of birds in various habitat types to emerge. The initial bird density should be a value that only the most productive habitat types (forest and trees) can support, so many initial birds in less-productive habitat types die of starvation in the first few time steps. However, extremely high initial densities can bias model results by causing unrealistically high CBB consumption and excess mortality early in model runs. The standard value of *initial-bird-density* is 20 birds/ha.

2.3.6. Input data

This model has no time-series inputs or external environmental drivers.

2.3.7. Submodels

The following subsections provide full detail on how model processes are simulated.

2.3.7.1. Bird habitat selection and foraging. This bird action is repeated each foraging time step of a day: each minute for up to 12 h. In Section 3 we describe four alternative theories for foraging; here, we describe the standard theory, “optimal cell selection over short range”, in detail. In its habitat selection and foraging action, a bird follows the steps depicted in the foraging conceptual diagram (Fig. 5).

First, if total daily foraging time exceeds *max-forage-hrs-per-day*, or if the bird's daily intake has already exceeded its daily minimum food requirement *daily-min-intake*, it does nothing.

Second, the bird identifies, as potential destinations, all the cells within a radius of its current cell determined by the bird parameter *forage-radius* (m). Cells are included within this radius if the straight-line distance from their midpoint to the midpoint of the bird's cell is less than *forage-radius*. The default value of 9 m causes the radius to include the bird's current cell and the eight adjacent cells.

The bird identifies which of these potential destination cells would provide the highest intake rate, as g/h of either bugs or CBB, and moves to that cell. (If multiple cells provide the same intake, one is chosen randomly.) The intake (g) is equal to the

current biomass availability of prey (bugs or CBB; g/m²) times the cell's catchability parameter (m²/h) times the forage time step (0.0167 h). As long as the catchability parameter is not unrealistically high (Section 2.3.7.2), intake cannot exceed the prey available in the cell.

Third, the bird consumes its intake by adding it to its daily intake and subtracting it from the availability of bugs or CBB remaining in the cell. The model does not exclude more than one bird from occupying the same cell on a time step, but the prey consumed by each bird is subtracted from the cell's availability as soon as the bird selects the cell, reducing the prey availability that subsequent birds use in deciding which cell to select.

The daily food requirement parameter *daily-min-intake* (g prey, as wet weight) is estimated for black-throated blue warblers to be 5 g. These birds typically weigh about 10 g (Holmes et al., 1979; Nagy et al., 2007). Holmes et al. (1979) estimated a daily energy

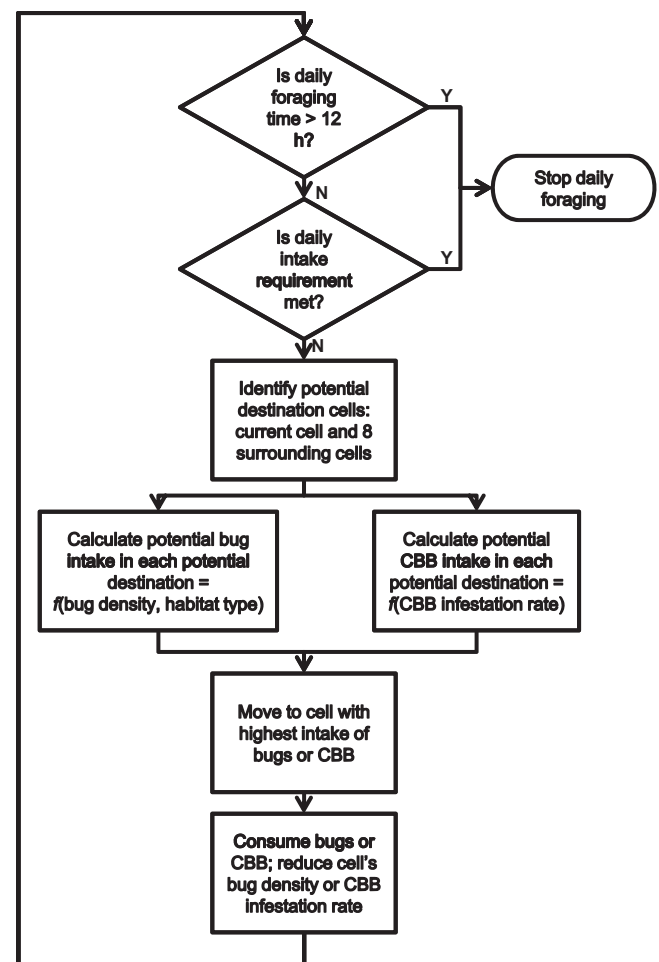


Fig. 5. Bird foraging under the standard “optimal cell selection over short range” theory. Each bird conducts this cycle every minute until one of the two stopping criteria (in diamonds) is met.

Table 3
Bug production and catchability parameter values.

Habitat type	Parameter name	Value
Forest	<i>forest-bug-prod</i> (g/m ²)	0.018
	<i>forest-bug-catchability</i> (m ² /h)	35
High-shade	<i>high-shade-bug-prod</i>	0.016
	<i>high-shade-bug-catchability</i>	90
Low-shade	<i>low-shade-bug-prod</i>	0.0054
	<i>low-shade-bug-catchability</i>	170
Unusable	<i>unusable-bug-prod</i>	0.00054
	<i>unusable-bug-catchability</i>	35
Trees	<i>trees-bug-prod</i>	0.018
	<i>trees-bug-catchability</i>	70
Other	<i>other-bug-prod</i>	0.0014
	<i>other-bug-catchability</i>	35

demand of 0.965 kcal/g/d for the pre-nesting period, equivalent to 40 kJ/d for a 10-g bird. To convert this demand to g insect prey, we assumed 25 kJ per g dry insect weight (similar to values for crickets reported by Levey and Karasov, 1989), a typical water content of 60%, and a typical energy assimilation efficiency of 75% (Levey and Karasov reported a metabolizable energy coefficient of 71–73% for robins and starlings consuming crickets and describe it as an underestimate). Therefore, each g (wet weight) of prey is assumed equivalent to 0.4 g dry weight and to provide 25 kJ \times 0.4 g \times 0.75 = 7.5 kJ. Therefore, 5 g/d of prey is needed by a 10-g bird, matching the general rule-of-thumb that insectivorous birds eat half their body weight per day. The other common migratory warblers in Jamaican coffee farms range in body mass from 6.5 to 12 g, so are reasonably represented by *daily-min-intake* of 5 g.

The intake rate is modeled with a simple, conventional, method. We assume a linear “functional response”: the intake rate is proportional to food availability, so birds must feed longer when availability is lower. The slope of intake rate vs. food availability differs among habitat types and is considered a “catchability” parameter (Section 2.3.7.2) that represents how much time and energy it takes to find and catch food in a particular kind of habitat. This simple approach has been supported as adequate (if not always the best compared to more complex alternatives) by empirical studies of birds including Whittingham and Markland (2002), Stillman and Simmons (2006), and Baker et al. (2009).

2.3.7.2. Bug production and catchability. Bugs are treated as a biomass density of available prey (g bugs/m²). Bugs are assumed to become available daily at a constant rate: at the start of each day, the initial bug density of each cell is reset to a “production rate” specific to the habitat type. This very simple representation assumes food production is equal to consumption by birds at a daily scale: at the start of each day, the bug biomass consumed on the previous day is replaced.

The daily bug production rates in each habitat type are specified by parameters provided in Table 3. Direct measurements of arthropod biomass per unit area or the rate of prey intake by birds were not available. Instead, parameter values for each habitat type were developed using these steps. The relative biomass density among habitat types was estimated from measurements of arthropod prey biomass per mass of vegetation, made at the study site in the 2009–2010 winter (Smith, C., et al., unpubl. manuscript “Predictors of aggression in Black-throated Blue Warblers wintering in Jamaican coffee farms,” Department of Wildlife, Humboldt State University), combined with vegetation volume estimates made by Johnson (1999). These observations indicate that bug availability is highest in forest and trees habitat types, is 90% of the forest value in high-shade coffee, 30% of the forest value in low-shade coffee, 3% in unusable habitat, and 8% in other habitat. The bug production in forest habitat was estimated inversely by assuming a bird foraging in unlimited forest, without competition, could obtain its daily

Table 4

Parameters for CBB dynamics. The parameters for *CBB-I-K* are explained in Section 2.3.5.2.

Parameter	Value
<i>CBB-I-initial-high-shade</i>	0.05*
<i>CBB-I-initial-low-shade</i>	0.05*
<i>CBB-I-r-high-shade</i>	0.05*
<i>CBB-I-r-low-shade</i>	0.05*
<i>CBB-I-K-high-shade-mean</i>	0.2*
<i>CBB-I-K-high-shade-SD</i>	0.05
<i>CBB-I-K-low-shade-mean</i>	0.4*
<i>CBB-I-K-low-shade-SD</i>	0.1
<i>CBB-berry-density-high-shade</i> (coffee berry density D_c)	220**
<i>CBB-berry-density-low-shade</i> (coffee berry density D_c)	270**
<i>CBB-borer-wt</i> (female borer weight W_b)	0.00049***

* Estimated from Figure 2 of Johnson et al. (2010).

** Estimated from harvest data for the Kew Park site and the assumption that low-shade coffee is 25% more dense than high-shade.

*** Mean weight of 100 gravid female CBB (pers. comm., J. Jaramillo, International Center for Insect Ecology and Physiology, ICIPE, Nairobi, Kenya, 2010).

energy requirement in 8 h. Bug production rates for other habitat types were then calculated from the forest rate using the above percentages.

The catchability parameter of the foraging intake submodel can be thought of as the habitat area over which a bird can remove all bugs in an hour (m²/h). Another way to think about this parameter is that it controls the time it takes a single bird to consume some percent of a cell's food, independent of the initial bug density. For example, the time (h) to reduce bug density by 50% is: $-\ln(0.5)A/C$ where A is the cell area and C is the catchability. To keep birds from overestimating their potential intake in foraging decisions, the catchability should be no higher than the value that lets a bird capture all the food in a cell in one time step, which is the area divided by the time step size (here, 1500 m²/h). We estimated the catchability parameter for bug prey in the various habitat types using judgment based on field observations of bird foraging and factors such as light levels, vegetation density and complexity, and insect color and camouflage. We estimated the time it takes a single bird to find and catch half the prey in a 5 m \times 5 m cell in the habitat types as: forest: 0.5 h, high-shade coffee: 0.2 h, low-shade coffee: 0.1 h, trees: 0.25 h, unusable and other: 0.5 h. These values produced the catchability parameters in Table 3.

2.3.7.3. CBB dynamics. Our formulation for the dynamics of CBB populations and availability as bird prey is based on several obser-

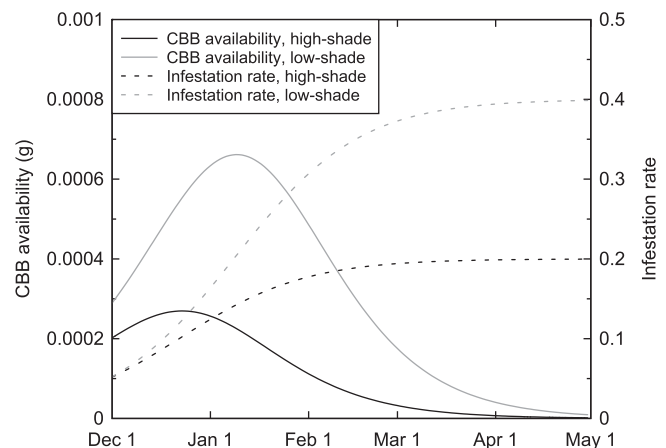


Fig. 6. Simulated CBB infestation rates (right axis) and availability (g CBB available as bird prey per cell per day; left axis), without bird consumption and *CBB-I-K* set to its mean value. Exclosures (Section 2.3.2.4) produce the infestation rates illustrated here.

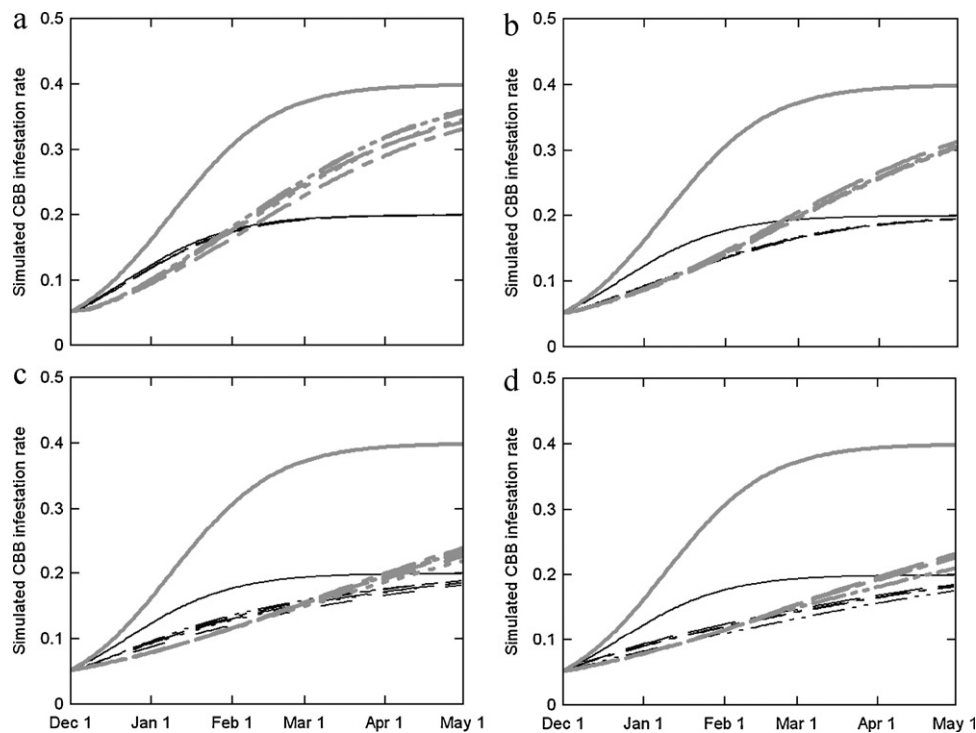


Fig. 7. Simulated CBB infestation rates over time, for (a) random, (b) optimal departure, (c) optimal cell-short distance, and (d) optimal cell-long distance foraging theories. Narrow black lines represent high-shade coffee habitat and wide grey lines represent low-shade coffee. Solid lines represent enclosures while the dashed and dotted lines represent results for the five replicate landscapes.

variations and assumptions. First, the model of CBB must represent the infestation rate (Section 2.2.2). Second, the only CBB available to birds as prey are gravid female beetles when drilling into an uninfested coffee berry. This assumption is supported by our observations of bird foraging, and the presumed difficulty of birds catching CBB while the beetles are flying or inside a berry. This assumption also links infestation rate to bird predation: each beetle captured by a bird while drilling can be equated with one berry kept from being infested. Third, we assume infestation rates in the absence of bird predation follow a logistic curve. This assumption is simple and convenient, but is also supported by field observations (Johnson et al., 2010; Kellermann et al., 2008), which show infestation rates in the absence of birds rising from an early low level until they reach a relatively constant high level. The logistic approach also makes conceptual sense: at low infestation levels the infestation rate should increase at an increasing rate because each infested berry can produce several gravid females to infest new berries; but at high infestation levels the rate of increase is limited by the supply of uninfested berries and should asymptotically approach 1.0 (when all berries are infested). Finally, this approach neglects the dynamics of coffee itself: production, development, and harvest of beans. Therefore, it may not be useful outside the season we simulate.

CBB dynamics are executed at the start of each day by cells of the high- and low-shade coffee habitat types. The following steps are used, with the variable *CBB-availability* (g) representing the biomass of CBB currently boring into berries, and hence available to birds, in the cell. Parameter values are in Table 4, and results of the submodel are illustrated in Fig. 6.

First, the cell's infestation rate *CBB-I* is updated by adding the change in infestation rate during the previous day (ΔI_P) to it: $CBB-I = CBB-I + \Delta I_P$ with $\Delta I_P = CBB-availability / (D_c \times W_b \times A)$. *CBB-availability* is the biomass of available CBB at the end of the previous day, D_c is the density of coffee berries (berries/m²), W_b is the weight of a female borer (g), and A is the cell area (m²). On the

first day simulated, the value of *CBB-availability* used in this step is zero.

Second, the current day's potential change in infestation rate (if no bird predation; ΔI_C) is calculated from the new value of *CBB-I* using the logistic assumption: $\Delta I_C = rI(1 - I/K)$. Here I represents *CBB-I*, r represents the infestation increase rate parameter *CBB-I-r*, and K represents the maximum infestation rate parameter *CBB-I-K*.

Third, *CBB-availability* is updated from the fraction of berries now being infested: $CBB-availability = \Delta I_C \times D_c \times W_b \times A$.

The bird foraging submodel requires a catchability parameter for CBB. Because female CBB boring into coffee berries are high exposed, obvious (black beetle on green or bright-red berry), and stationary, we assume their catchability is high. The parameter *CBB-catchability* is set to 1000 for both high- and low-shade coffee, so a bird can consume half of a cell's available CBB in 1 min.

2.3.7.4. Virtual bird surveys. "Virtual ecologists" are a technique for comparing simulation results to field data collected in specific ways (Zurell et al., 2010). We model virtual bird surveys to produce output comparable to the coffee farm bird surveys of Kellermann et al. (2008). The actual surveys are the basis of characteristic pattern 7 (Section 2.2.1). Kellermann et al. counted the birds in 30 plots within coffee plantations; the plots were circles with area 400 m² (radius = 11.3 m). Plots were placed randomly but with centers at least 10 m apart and 10 m from the plantation boundary. The distance from each plot's center to the nearest forest or group of trees was recorded.

The model's virtual bird surveys reproduce the actual survey protocol as closely as possible, with the most important difference being the survey plot area. The model tracks bird locations only by which cell they are in, so modeled birds can only be counted over a discrete number of cells. Therefore, the survey plot area was set to the 21 cells (total area of 525 m²) with centers within a distance of 11.3 m from center of the plot's central cell. The survey plots are created at the start of a model run. Thirty plot center cells are

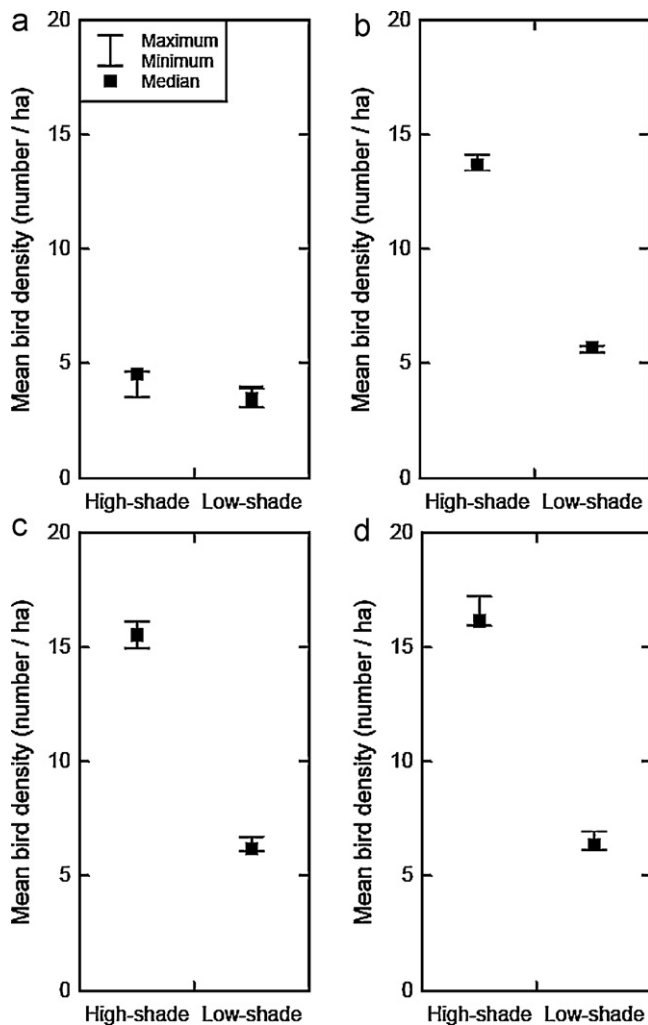


Fig. 8. Bird densities in high- and low-shade coffee, for (a) random, (b) optimal departure, (c) optimal cell-short distance, and (d) optimal cell-long distance foraging theories. The plots show the median and range of bird densities in each habitat type over one simulation each of the five replicate landscapes.

identified by selecting randomly from the cells that are of high- or low-shade coffee types, more than 10 m from the boundary of the model space, and at least 10 m from another plot center. The plot's distance to forest or trees is measured as the center-to-center distance from the plot to the nearest cell of habitat type "forest" or "trees".

Virtual surveys are conducted periodically, at an interval set by the model parameter *survey-frequency* (here: 30 days, for five surveys in a 151-day run; the first survey occurs *survey-frequency* days after the simulation starts). On a survey day, the model outputs the number of birds within the plot on each foraging time step.

2.3.7.5. Arthropod irruptions. Arthropod irruptions were added to the model to make it possible to reproduce pattern 5 in Section 2.2.1. Virtual arthropod irruptions can be started at any cell, at any time, from the model's graphical interface. Via NetLogo's "Agent Monitor" tool, the user can select the cell at the irruption's center and issue the command "start-irruption". The irruption occurs in all cells with center within a 25-m radius of the selected cell. For the next 10 days, no change is made except for output of data on the number of birds feeding in the irruption cells. Then the irruption cells' daily bug production (Section 2.3.7.2) is increased by a factor of five for another 10 days. For a final 10 days, bug production is returned to its normal value and output continues to be produced.

2.3.8. Software

The model's implementation used NetLogo's built-in representations of cells and mobile agents, and graphical interfaces. The code was spot-checked using NetLogo's "Agent Monitor" tool and by inspecting output files. The two most complex submodels, for CBB dynamics and bird foraging, were tested comprehensively by comparing output from them to an independent implementation of the submodel in spreadsheet software. One of the CBB dynamics tests verified the daily CBB availability in the exclosures, over each of the 151 days. A second test verified that each cell of coffee habitat calculated CBB availability correctly on each of 20 days (a total of 35,250 tests), and that the cells' values of *CBB-I-K* followed the bounded normal distribution specified in Section 2.3.5.2. The foraging submodel test compared output on each bird's evaluation of each potential destination cell on each move of 1 day, using a time step of 0.1 h, for a total of over 712,000 foraging calculations. This test verified that birds examined the correct number of potential destination cells, foraged for no longer than the value of *max-forage-hrs-per-day*, stopped foraging when the daily intake exceeded *daily-min-intake*, chose a cell with the best available intake rate, and chose between CBB and bugs to get the highest intake.

3. Theory

3.1. Analysis objective and theory alternatives

Once an individual-based model is designed and programmed, pattern-oriented analysis can be used to develop and test its theory for key individual behaviors and to demonstrate the model's suitability for its intended purpose (Grimm et al., 2005; see the examples of Railsback and Harvey, 2002; Railsback et al., 2005). The strategy is to test how well the model reproduces the characteristic patterns observed in the real system (Section 2.2.1) when using each of several alternative theories for the key behavior.

The theory we are interested in describes foraging of small, insectivorous birds in a population context: with individuals competing for and depleting food. Further, the theory must work in complex habitat and accommodate switching between alternative prey types. Our model provides an interesting laboratory for contrasting and evaluating foraging theory because it is more complex and realistic than most mathematical models yet still allows completely controlled experiments, and because we have a diverse set of observed patterns (Section 2.2.1) to test the model against. Patterns 3, 4, 5, 7, and 8 especially emerge from foraging decisions in response to static habitat characteristics, CBB supply, and dynamic changes in food supply.

We tested the model's ability to reproduce the patterns using four alternative foraging theories that differ in the degree to which they assume birds make "optimal" decisions about when to move to a new cell and which cell to select.

Random: Pattern-oriented theory development should include at least one "null" theory as a baseline against which the other alternative are compared (Railsback and Grimm, 2012). Analyzing this null model lets us see which patterns can and cannot be reproduced without assuming birds use some kind of "intelligent" decision-making. Our null model is random habitat selection: on each foraging time step, each bird chooses randomly among its current cell and the eight adjacent cells, no matter how much food is available there. Once in a cell, the bird still chooses to eat bugs or CBB by which is more profitable.

Optimal departure: This theory assumes birds select cells randomly but make "optimal" decisions of when to leave. The theory resembles the marginal value theory of Charnov (1976), which assumes individuals move to new habitat when they have depleted

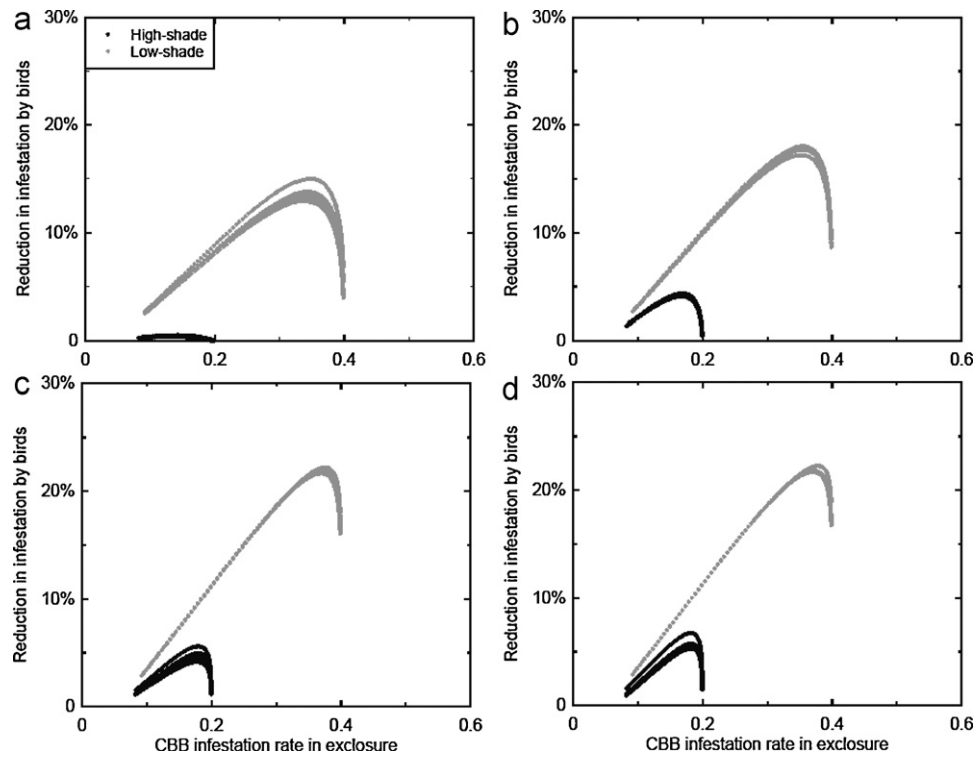


Fig. 9. Relation between the CBB infestation rate in enclosures and (y axis) reduction in infestation by birds (difference between infestation rates inside and outside enclosures), for (a) random, (b) optimal departure, (c) optimal cell-short distance, and (d) optimal cell-long distance foraging theories. Each point is 1 day's landscape-wide average; all five replicate simulations are included in each plot.

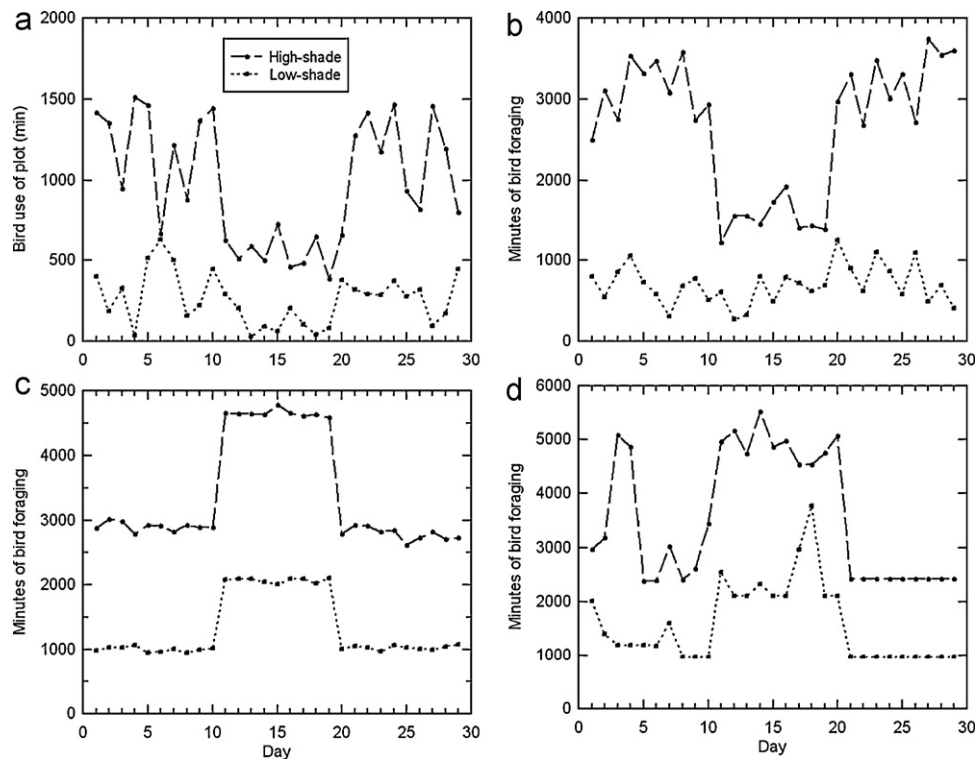


Fig. 10. Responses to simulated arthropod irruptions, for (a) random, (b) optimal departure, (c) optimal cell-short distance, and (d) optimal cell-long distance foraging theories. The x axis is the day within the irruption simulation; bug abundance is increased fivefold on days 11–19. The y axis is the daily total minutes of bird foraging in the irruption cells.

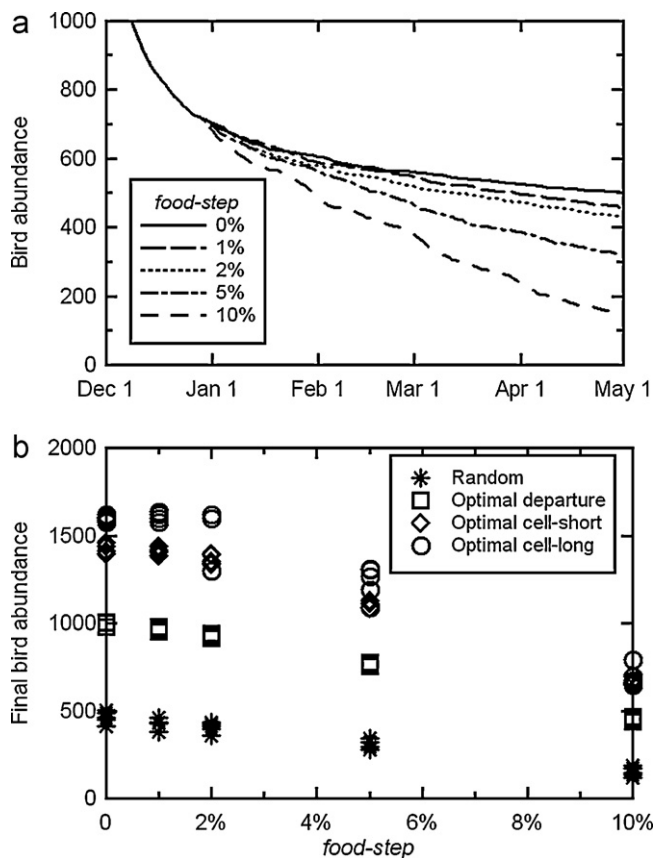


Fig. 11. Effects of reduced bug production on simulated bird abundance. (a) Bird abundance over simulated time under the random foraging theory, for five values of *food-step*. Under all foraging theories, abundance decreased stepwise when bug production was reduced each 30 days. (b) Final bird abundance vs. *food-step* for all four theories, with five landscapes simulated for each value of *food-step*.

the food at their current location down to the average available throughout their habitat. Marginal value theory is not clearly applicable to this model's context because it assumes that the habitat-wide average food availability is constant over time and unaffected by individual behavior; these assumptions are not true in our model. We retain the primary assumption of this theory, that individuals base habitat selection decisions on the state of their current cell, not nearby cells. However, we assume individuals base their departure decision on their own energetic state, which seems reasonable to assume birds can sense. We assume a bird leaves its cell when the food intake rate it would obtain in the next foraging time step falls below the rate needed to meet its daily intake requirement in the day's remaining foraging time. At any time t (h) during daily foraging, the intake rate (g/h) needed for a bird to meet its daily intake requirement is: $(I_D - I_C)/(T_F - t)$ where I_D is *daily-min-intake* (g), I_C is the intake so far on the current day, and T_F is *max-forage-hrs-per-day*. When a bird determines that this rate is greater than the intake in its current cell, it selects a new cell randomly from among the adjacent cells.

Optimal cell selection over short range: This is our standard theory (Section 2.3.7.1), which assumes birds can sense and select the cell offering highest intake rate, but only over a short distance. Birds depart their current cell whenever an adjacent one offers higher intake.

Optimal cell selection over long range: The fourth alternative theory is identical to the third except that birds are assumed to sense and select among cells over a much longer distance. Birds select among cells within a radius of 100 m of their current cell.

This alternative is designed to test the assumption that birds can sense widespread and detailed information about their habitat.

3.2. Theory testing methods

Each of the foraging theories was implemented in its own version of the model. To avoid bias due to calibration, the model was not calibrated to reproduce any of the patterns in Section 2.2.1 quantitatively or qualitatively. Instead, our independent, pre-calibration estimates of parameter values described in Section 2.3 were used in all analyses. We ran each version of the model five times, using five replicate landscapes produced by using the methods and parameters of Section 2.3.5.1 with five different random number seeds. We then analyzed the output to determine whether the patterns were reproduced. These analyses were generally qualitative and graphical because the patterns are generally qualitative and because the model was uncalibrated. Results from the first 14 days were excluded from most analyses because bird populations were still decreasing from their initial high density.

4. Results

4.1. Pattern 1: CBB infestation reduced by birds

Pattern 1 was reproduced to some extent with all four foraging theories (Fig. 7): the CBB infestation rate increased over time, and was reduced (compared to rates in exclosures) by bird foraging. However, the random foraging model resulted in very little reduction of CBB infestation in high-shade coffee (Fig. 7a). Birds reduced CBB infestation the most under the two optimal cell selection theories, with little difference between short- and long-range cell selection (Fig. 7c and d).

4.2. Pattern 2: CBB infestation higher in low-shade coffee

This pattern was met with all four theories (Fig. 7); it is strongly imposed by the model's parameters for CBB dynamics.

4.3. Pattern 3: Bird densities higher in high-shade coffee

This pattern was met with all foraging theories except random habitat selection (Fig. 8). With random selection, the difference in bird density between high- and low-shade coffee was very small or nonexistent; under the other theories bird densities were 2–3 times higher in high-shade than in low-shade, matching empirical observations.

4.4. Pattern 4: Bird reduction in CBB increases with infestation rate

The model generally reproduced the pattern that birds reduce CBB more at higher infestation rates (Fig. 9). The pattern is not clearly reproduced for high-shade coffee under the random selection and optimal departure foraging theories (Fig. 9a and b). However, these results also depict the model's assumption that the availability of CBB to birds decreases as the infestation rate approaches its maximum, because fewer females are boring into new berries (Fig. 6). If this assumption is realistic, then the model leads us to expect birds to be less effective at reducing CBB infestation rates as those rates reach their peak.

4.5. Pattern 5: Birds respond to local irruptions

To test this pattern, we started one arthropod irruption (Section 2.3.7.5) each in high- and low-shade coffee. The irruptions were started in cells chosen arbitrarily from a region relatively far from

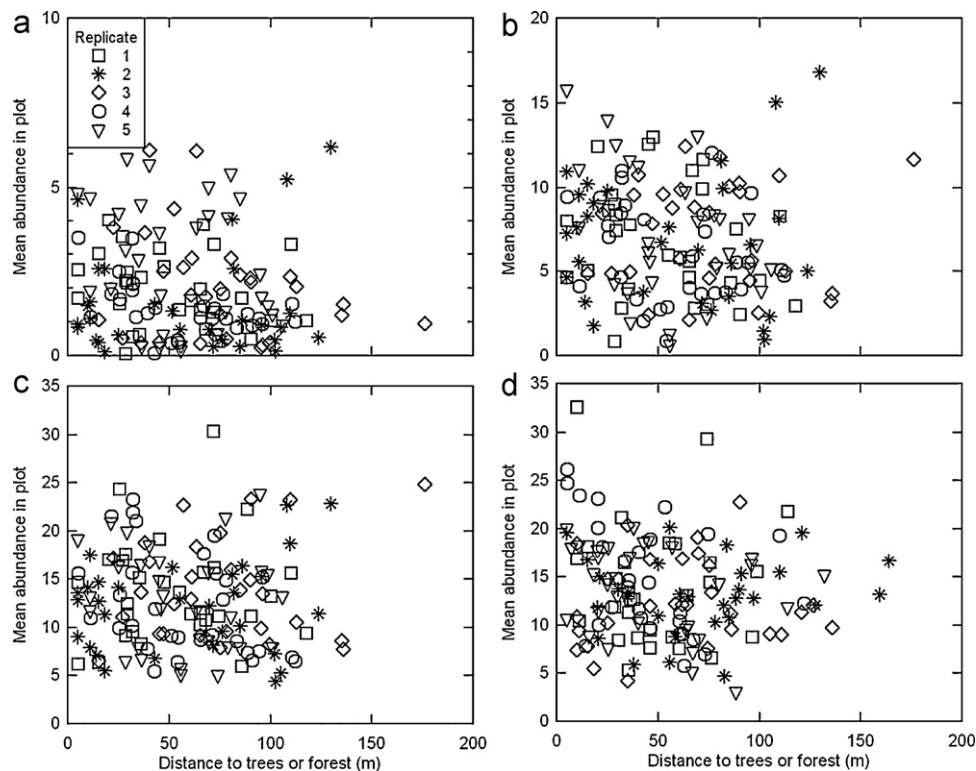


Fig. 12. Mean bird abundance vs. distance to nearest forest or trees habitat in simulated survey plots, for (a) random, (b) optimal departure, (c) optimal cell-short distance, and (d) optimal cell-long distance foraging theories. Each point represents the mean number of birds in the survey plot during one of the monthly survey days.

trees and forest. The observed pattern of higher bird feeding during the irruption was reproduced only with the optimal cell selection theories (Fig. 10c and d). Under random and optimal departure theories (Fig. 10a and b) the amount of bird feeding (minutes of bird feeding per day per cell) actually decreased instead of increasing when bug supply was higher. This unexpected outcome occurred because (a) birds that select cells randomly cannot actively seek highly profitable habitat, but (b) when they enter such habitat they meet their daily intake requirement and stop foraging earlier, which reduces the number of feeding birds.

4.6. Pattern 6: Changes in bird densities related to changes in food

We evaluated the model's ability to reproduce this pattern by stepping the daily bug production down, every 30 simulation days, by a percentage (variable *food-step*) applied to all habitats, and examining how bird abundance responded. Experiments varied *food-step* from zero (no change) to 10% (bug production reduced by 50% by day 150).

All four of the foraging theories reproduced the pattern. Each stepwise reduction in bug production resulted in a loss of birds due to mortality/emigration (Fig. 11a). Small reductions in food had small effects on bird abundance because birds could partially make up for lower bug supply by foraging longer each day; but large decreases in bug production produced substantial decreases in bird abundance (Fig. 11b). The lower effect of food supply at low values of *food-step* was clearer for the two optimal cell selection theories.

4.7. Pattern 7: Weak negative relation between distance to trees and bird density

This pattern was evaluated using data from the virtual bird surveys (Section 2.3.7.4). None of the theories produced a relationship

between the number of birds in a survey plot and its distance to the nearest trees or forest habitat. However, the highest distance to trees or forest was about 30 m, whereas the observed pattern occurred because of low bird densities at plots 70–120 m from forest-like habitat (Figure 2 of Kellermann et al., 2008). Therefore, we repeated the experiment using five new landscapes with smaller and fewer clumps of trees habitat (*frac-trees* = 0.02, *num-trees-clumps* = 50).

Even with these new landscapes, the model reproduced the observed lack of relationship between bird density and distance to trees over distances less than 60 m but not the observed low bird density at higher distances (Fig. 12). One process not in this model that may contribute to the pattern is overnight roosting in trees (Jirinec et al., 2011): if birds start their daily foraging in or near trees or forest, their use of habitat far from such habitat may be less likely.

4.8. Pattern 8: Log-normal movement distances

This pattern was evaluated by calculating, for each bird at the start of each hour (except the day's first), the straight-line distance from the cell it occupied at the start of the previous hour. (Keep in mind that simulated and real birds move many times within each hour.) These hourly movement distances were then displayed in histograms (Fig. 13), produced from results captured at an arbitrary time because the histograms change little during simulations. Results for all foraging theories were approximately log-normal, especially for random and optimal cell-short distance foraging. However, results for optimal departure and long-range cell selection are distinctly different from the observations in Fig. 2. The optimal departure (Fig. 13b) theory reproduced none of the observed long (>150 m) movement distances. With long-range cell selection (Fig. 13d), the peak and range of movement distances were far higher than in observations.

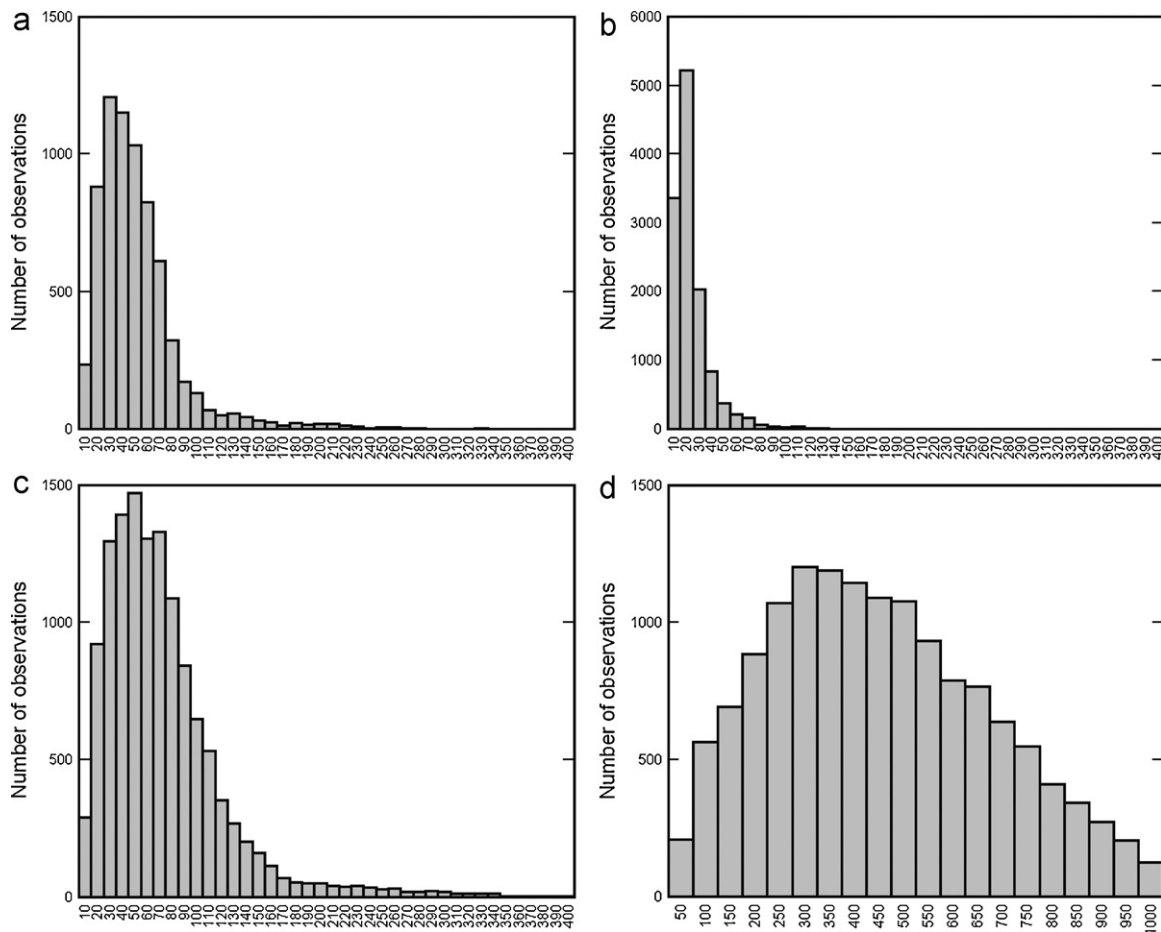


Fig. 13. Distributions of hourly movement distances, for (a) random, (b) optimal departure, (c) optimal cell-short distance, and (d) optimal cell-long distance foraging theories. The category (bar) labels are the distance (m) between a bird's current location and its location 1 h previously. The y axis is the number of birds observed in the distance category.

4.9. Pattern 9: Episodic consumption of CBB

This pattern was reproduced with all foraging theories. In all simulations, the 1-min foraging events consuming CBB were a small fraction of all foraging events. CBB was consumed most often with random foraging (mean: 2.1%), and least often with long-range optimal cell selection (mean: 1.7%).

5. Discussion

5.1. Progress in modeling foraging: from individual level to across-level

Foraging theory is a classic problem in ecological modeling, the subject of some of the earliest attempts to model decision-making by animals. The classic models (e.g., Charnov, 1976; Oaten, 1977) were in the tradition of behavioral ecology: they address how individuals make decisions, usually in a simplified context. As ecological modeling progresses to problems of individual-based ecology—understanding population ecology as a consequence of individual decisions—we often model contexts more complex and challenging than those of behavioral ecology (Stillman and Goss-Custard, 2010). Individual-based ecology is inherently across-level: we need theory for individual behavior that explains the dynamics of populations in which individuals interact, competing with and otherwise affecting each other, often in variable and dynamic environments.

We found the pattern-oriented process successful for developing foraging theory for insectivorous birds in a population context, with habitat that is spatially and temporally variable and with two prey types. Basing its design on a diverse set of observed patterns helped us develop a model with enough detail to reproduce the system's essential dynamics without excess complexity. By comparing how well four hypotheses for bird foraging behavior reproduced these patterns, we were able to show that at least one hypothesis—optimal cell selection over short distances—was useful for modeling the Jamaican coffee farm system. These experiments also pointed us to additional patterns that we could develop (via continued field studies) and simulation experiments that will let us further refine the theory.

5.2. Conclusions

Nine observed patterns characterizing habitat–bird–CBB relations on Jamaican coffee farms indicated that, on one hand, a model of these relations should be spatial, dynamic, and individual-based; and that foraging habitat selection needs to be represented in detail. Some additional details—exclosures, virtual surveys, and arthropod irruptions—were included to give the model the potential to reproduce patterns observed in the field. On the other hand, the patterns also showed that potentially complex processes such as predation and CBB population (instead of infestation) dynamics were not needed. The resulting model is relatively simple in concept: it represents six habitat types that differ only in parameter values, one type of bird with only one adaptive behavior, and an

insect pest represented only via a simple logistic equation. Yet the model could, with our standard foraging theory and no calibration, robustly reproduce almost all the observed patterns.

The pattern-oriented analysis of alternative foraging habitat selection theories illustrated that some of the nine patterns were strongly imposed or “hardwired”—especially, that CBB infestation rates increase over time and are higher in low-shade vs. high-shade coffee. Other patterns emerged robustly under several different foraging theories: that bird densities are higher in high-shade vs. low-shade coffee, that birds reduce infestation rates more when those rates are high, that hourly movement distances follow a log-normal distribution, and that CBB consumption is rare and episodic.

Some patterns, though, proved very useful for falsifying candidate foraging theories. The observed increase in local bird densities during arthropod food irruptions was reproduced only by theories that assume individuals actively seek good habitat cells instead of selecting cells randomly. Quantitative characteristics of the log-normal movement distribution were reproduced poorly by the optimal departure theory and, especially, by optimal cell selection over long distances.

These results indicate that a useful bird foraging theory, in this population-level context, needs to assume that birds have some ability to detect and select habitat where food intake is relatively high, but that this selection ability operates over short distances. Our optimal departure theory, which resembles classical models such as the marginal value theory, generally produced results similar to those of the optimal cell selection theory, but failed to reproduce patterns that illustrate the ability of birds to actively select better habitat when it is available nearby. Classical theory of behavioral ecology has also been shown inadequate for individual-based population models of fish (Railsback et al., 1999; Railsback and Harvey, 2002).

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