*Disentangling the role of predator hunting mode, spatial domain size, and habitat complexity: An agent-based examination of consumptive and nonconsumptive effects*

## The model description follows the ODD (Overview, Design concepts, Details) protocol for describing individual- and agent-based models (Grimm et al. 2006, 2010), as updated by Grimm et al. (2020).

## ***1. Purpose and patterns***

## The ultimate purpose of the model is to disentangle (i) how hunting mode and spatial domain size interact to influence the emergence of consumptive or nonconsumptive effects, and (ii) when nonconsumptive effects do dominate, how hunting mode and spatial domain separately or additively determine prey shifts in time, space, and habitat use. To do so, we build a model to explore three explicit aspects of the predator-prey relationships. First, we seek to add complexity to the current predator-prey theoretical framework; evaluating the nonconsumptive effect of prey habitat shift. The second purpose of the model is to predict which kinds of consumptive effects (CE) or nonconsumptive (NCE) (space shift, time budget shift, or habitat shift) occur in response to hunting mode (sit-and-wait, sit-and-pursue, active). The second purpose of the model is to predict which kind of CE/NCE dominates on the landscape in response to spatial domain size of both predators and prey. To address these questions, we modeled scenarios that simulated predator-prey dynamics on a complex landscape, allowing emergent consumptive and consumptive effects as a result of interaction between the prey and predator agents.

## **2. Entities, state variables, and scales**

We constructed a spatially explicit individual-based model in NetLogo version 6.1.1. We designed an environment to represent a 8 × 12 grid, which is neither wrapped vertically nor horizontally. Each patch represents physical landscape space in which predators and prey can transverse and interact.

## Our model consists of two agents, a predator and a prey agent. The initial units and state variables for each agent can be found below in Table 1. We have four different simulation experiments, in which the CE and NCE+CE model runs for 1 year (365 days) or 5 years (365 days x 5). In each simulation the day is broken into 24 time steps.

## Predators: Our model attempts to explore the theory of predator/prey dynamics generally and therefore our agents are built without a specific species in mind, but rather with general predator characteristics. In order to disentangle emergent prey responses to predation, prey-agents were the only agents which could change their spatiotemporal movements. At initiation, each predator-agent is assigned one of three hunting modes while initializing the model, as well as a specific spatial domain (large or small). Predators are always awake from hours 0-11.

Prey: As with the predator, the prey agent is not built to represent a specific prey species, but rather we aim to capture general prey characteristics. Each prey-agent is assigned a specific spatial domain (large or small) at initialization. To monitor the prey-agent’s spatial and habitat movement, each time the prey-agent is in a low or high detectability habitat, the presence is recorded within *count-detectability-low* and *count-detectability-high,* respectively*.* Each time the prey-agent is within the predator-agent spatial domain, it is recorded in the *count*-*domain-overlap*, while when the prey-agent is not within the predator-agent spatial domain it is recorded in the *count-prey-only-domain.* To monitor the temporal activity of the prey-agent, each hour the prey-agent is active is recorded in the *hours-active-table*. If the prey-agent dies, the *dead?* boolean becomes true.

Patch environment: The patches, i.e. the model environment, represent areas of different habitat types, determined by the *habitat* patch-value, arranged in a checkerboard fashion and split into groups of 2x2 which are each given an unique ID stored in the *local-spatial-unit*. Habitat types are mutually exclusive, with each cell in the habitat matrix identified as either “high detectability habitat” or “low detectability habitat”. The detectability of a habitat patch is described by their *detection-prob* and is a fixed value that describes the probability in which the prey-agent will be detected by the predator-agent while on that patch (Table 1). The number of habitat patches is also fixed, including the specific arrangement for each simulation. Patches also contain *risk* valueswhich is simply the number of times the prey-agent has interacted with predator-agent when on that patch type and in that hour of day. At each tick, interactions between predators and prey within each habitat type of each local spatial unit are recorded in *patch-interaction*. These are then added to a table stored in each patch under the *memory-high-detectability* and *memory-low-detectability*. At each hour, the *safer-hours* value reflects the lowest number between the *memory-high-detectability* and *memory-low-detectability*, to inform the prey-agent which type of patch is safest at the hour. Finally, patches contain booleans for *predator-domain?*and *prey-domain?* that determine which agent breed (predator or prey) is able to access that patch, which sets the spatial domain for each breed of agent.

Model entities are the square spatial units / habitat cells making up the landscape, the predator, and the prey. The central and only level of description in our model was individual prey and predator.

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## **Table 1. Summary of state variables in model for...**

| **Entity** | **Variable name** | **Description** | **Possible Values** | **Units** |
| --- | --- | --- | --- | --- |
| *Cell* | predator-domain? | Where the predator-agent is found | true/false |  |
| prey-domain? | Where the prey-agent is found | true/false |  |
| habitat | Checkerboard of habitat types | 0 / 1 |  |
|  | detection-prob | How detectable prey are on the patch. Based on Habitat-type/Checkerboard | .2 / .9 |  |
|  | risk | An hourly, habitat-specific risk of patch | 0 - infinity |  |
|  | memory-high-detectablity | A table which keeps track of the number of interactions which have occurred on the high-detectability patches based on hour. | First column [0 – 23] second column [ 0 – infinity] |  |
|  | memory-low-detectablity | A table which keeps track of the number of interactions which have occurred on the low-detectability patches based on hour. | First column [0 – 23] second column [ 0 – infinity] |  |
|  | local-spatial-unit | The unique ID for each local spatial unit | 0 - 24 |  |
|  | patch-interaction | The number of interactions that have occurred at that local spatial unit for a particular habitat type | 0 - infinity |  |
|  | safer-hours | Table used to store which hours each day that the prey-agent is active | First column [0 – 23] second column [ 0 – infinity] |  |
| *Prey* |  |  |  |  |
|  | count-detectability-low | Counts the number of ticks in which the prey-agent was found on a low-detectability patch | 0 - infinity |  |
|  | count-detectability-high | Counts the number of ticks in which the prey-agent was found on a high-detectability patch | 0 - infinity |  |
|  | count-prey-only-domain | Count the number of ticks in which the prey-agent was in a spatial domain which does not overlap with the predator-agent spatial domain | 0 - infinity |  |
|  | count-domain-overlap | Count the number of ticks in which the prey-agent was in a spatial domain which overlaps with the predator spatial domain | 0 - infinity |  |
|  | *hours-active-table* | A table that has each hour of the day and counts the number of ticks the prey-agent was active for the respective hour | First column [0 – 23] second column [ 0 – infinity] |  |
|  | dead? | Determines if the-prey agent has died or not | True / False |  |
| Globals | Attack-hours | List of hours which the prey-agent is hidden. Resets each day. | List of 12; range from 0 - 23 |  |
|  | hour | Keeps track of the hour of the day. Reset every 24 ticks. | 0 - 23 |  |
|  | day | Number of times the ‘hour’ global variable has reset. Keeps track of number of days. | 0 – length of simulation |  |
|  | Ranked-hours | Global variable which establishes which 12 hours to avoid. Resets every day | List of 12 values between 0 - 23 |  |
|  |  |  |  |  |

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## **3. Process overview and scheduling**

## Each time step (1 hour), the following processes are proceeded in the given order.

Overview and Scheduling processes:

To initialize the model, users choose a predator strategy, a predator spatial domain size and a prey spatial domain size. The model contains an internal clock and calendar, in which hours and days are kept track of, respectively. At initialization, the clock is set to hour = 0 and the calendar is set to day = 0. Following initialization, both the predator-agent and prey-agent are randomly distributed within their given spatial domain, with the prey-agent placed at least 4 patches away from the predator-agent.

The scheduling processes then begins as follows:

1. The spatial-temporal landscape is determined based on prey-agent’s past interactions with the predator-agent. At the beginning of each day the prey-agent evaluates how many times they had interacted with the predator-agent for each hour of the day and for each habitat type. For each hour, the prey-agent then evaluated the lowest number of interactions for each habitat type. These are then ranked from highest to lowest and the prey-agent disregard the hours with the 12 highest interactions. The disregarded hours are the hours which the prey-agent are inactive for that day. Each patch has an associated number based on the number of interactions the prey-agent has had with the predator-agent on that habitat type (i.e. higher detectability or low detectability) and during the current hour (hours 0-23). Thus, for each hour, each habitat type has a specific value which comprises the spatial-temporal landscape. This process allows the prey-agent to make informed movement decisions.
2. The model registers if the prey-agent has died or not. If it has, the simulation stops.
3. The Prey-Move submodel is activated where the prey-agent determines if they are awake, and if so the turtle becomes visible, otherwise it becomes hidden. If they are awake, the prey-agent will move. If the prey-agent moves:
   1. The prey-agent determines the movement for the next hour based on patches within its spatial domain and the *risk* value of the surrounding patches given the next hour.
   2. The Keeping-Track-Of-Habitat submodel is activated and the prey-agent records which type of habitat it has moved to within the *memory-high-detectability* or *memory-low-detectability* agent variable.
   3. The Keeping-Track-Of-Time submodel is activated and the prey-agent records the hour it is active within the *hours-active-table.*
   4. The Keeping-Track-Of-Space submodel is activated and the prey-agent records whether they are inside of or outside of the predator-agent spatial domain in either c*ount*-*domain-overlap* or *count-prey-only-domain*
4. The Predator-Move submodel is activated by which predator-agent then (1) determines if is awake and if so, the turtle becomes visible, (2) moves to a new location
5. The Detect submodel is activated in which the predator-agent attempts to detect the prey-prey agent (Feed-on-prey figure). The prey-agent has a change of detection based on the *detection-prob* for the habitat type and the predator-agent hunting mode. If the prey-agent is detected, the Hunt submodel is activated.
   1. If the Hunt submodel is activated, the predator-agent attempts to hunt the prey-agent. If the predator-agent is successful, the prey-agent dies. If the hunt is unsuccessful, the prey-agent increases their fear-value for that habitat type and that hour.
6. The internal clock in the model advances one hour. If the hour = 24, the internal calendar then advances one day.
7. The model stops either when a given time period has been reached or the prey-agent has died.

## **4. Design concepts**

Basic principles: Our model explores the theory behind spatial and temporal shifts in prey behavior as it relates to predator hunting strategy and the spatial domain size of both predator and prey individuals (Miller et al., 2014), while also adding new complexity - habitat type. By examining how the landscape of fear emerges, as a function of spatial domain and hunting mode on a complex landscape, we advance the theory of how consumptive and nonconsumptive effects emerge.

Emergence: The temporal and spatial behaviors of the prey-agent shifts to avoid predator-agent interactions.

Adaptation: The temporal and spatial behaviors of the prey-agent shifts as they respond to interactions with predator-agent.

Objectives: None.

Learning prediction: The prey-agent is able to “adapt” from previous interactions with the predator-agent, learning to avoid the spatial domain (when possible), habitat type, and time of predator-agent interactions. The strength of this learning is a function of the predator-agent hunting mode and spatial domain.

Sensing: The predator-agent is able to detect or “sense” the prey-agent. The ability to detect the prey-agent is a product of both the predator hunting mode and the *detection-prob* of the patch the prey-agent is on.

Stochasticity: The initial placement of the predator-agent and prey-agent on the landscape is random.

Collectives: None

Observation: To evaluate the consumptive effects in both the CE and NCE simulations we recorded the number simulations in which the prey-agent died due to an encounter with the predator-agent across all 100 simulations. To evaluate the NCE effects of various predator hunting strategies, we monitored spatial, temporal, and habitat selection in the prey-agent by counting the number presence of the prey-agent in each habitat type and spatial domain over the duration of the model as well as the hours in which they were active.

## **5. Initialization**

## Habitat used in the models were distributed equally across the Netlogo landscape. Each patch is assigned a *risk* value, which is the probability in which the predator-agent will detect the prey-agent, creating “high detectability” patches and “low detectability” patches. The *risk* values are distributed equally and alternatively, creating a checkerboard-like distribution. Next, the spatial domains are determined. Users select the spatial domain size (large or small) they wish to simulate for both the predator-anget and prey-agent breeds. When a “large” spatial domain size is chosen the all patches are determined available to the respective breed. When a “small” spatial domain size is chosen, only the top half of the world is available to the respective breed.

## The predator-agent is distributed randomly within their spatial domain. The prey-agent is then also distributed randomly within their spatial domain, however they are placed at least 4 patches away from the predator-agent. Number of encounters with the predator, the number of hours foraged that day, and patches to avoid are all set to zero.

The model runs in discrete time steps. We identify the following terms in this context: hour, day, and simulation run. Prey and predator agents operate on time steps of one hour, simulated by one tick. One day lasts 24 hours (i.e. 24 ticks) and a simulation covers 365 days.

## **6. Input data**

## The current model version does not include any input of data.

## **7. Submodels**

## All model parameters are listed in Table 2.

## Spatial-Temporal-Landscape

The Spatial-Temporal-Landscape submodel updates the risk value for each patch based on the time, local spatial unit, and habitat type in which previous interactions have occurred.

At the beginning of each day the prey-agent will determine which 12 hours they will be active that day by evaluating how many times they had interacted with the predator-agent for each hour of the day and for each habitat type. For each hour, the prey-agent then evaluated the lowest number of interactions for each habitat type (for example, if at hour 10 the prey-agent has had 5 interactions on a high detectability habitat patch and 1 on a low detectability habitat patch, it would select ‘1’). These were then ranked from highest to lowest and the prey-agent disregarded the hours with the 12 highest interactions. The disregarded hours were the hours which the prey-agent was inactive for that day.

At each hour during that day, the *risk* value of each patch is the sum of the number of interactions which have occurred on that *habitat* type for that upcoming hour and the *patch-interaction.*

Prey-Move:

The prey-agent first determines if this is one of the hours that they are or are not active based on *dangerous-hours*. If it is a *dangerous-hour* the prey-agent will become hidden and will not move. If they prey-agent is awake during the current hour, the prey-agent will choose the patch within a two-cell radius with the lowest *risk* value of that patch.

Keeping-Track-Of-Habitat

Each time the prey-agent is awake and moves to a new patch, either increase the *count-detectability-low* or *count-detectiablity-high* by 1 depending on if the prey-agent has moved to a low- or high-detectability patch.

Keeping-Track-Of-Time

Each hour the prey-agent is awake and moves to a new patch, increase the *hours-active-table* by one for that specific hour.

Keeping-Track-Of-Space

Each time the prey-agent is awake and moves to a new patch, either increase the *count-domain-overlap* or *count-prey-only-domain* by 1 depending on if the prey-agent has moved to a patch that is both in the predator and prey’s spatial domain, or if it is only in the prey’s spatial domain.

Pred-Move:

The predator-agent is active for 12 hours, 00:00-11:00, each day.

In sit-and-wait conditions, the predator-agent is initially randomly distributed on the landscape and within their spatial domain. They then remain in that patch for the duration of the day (24 hours/ticks). At the start of a new day, they move to a new, randomly selected patch within their spatial domain.

In sit-and-pursue conditions, the predator-agent is initially randomly distributed on the landscape and within their spatial domain. They then remain in that patch for the duration of the day (24 hours/ticks). At the start of a new day, they move to a new, randomly selected patch within their spatial domain.

In active conditions, the predator-agent is initially randomly distributed on the landscape and within their spatial domain. They then move each time period (each tick) in which they are active by randomly selecting a patch within their spatial domain and a radius of 2 from their current position and move to that patch.

Detect

The predator-agent can only detect the prey-agent if the following conditions are met: 1) the predator-agent must be active and 2) the prey-agent must be active. Additionally, there are other conditions which must be met based on hunting strategy type:

* In Sit and Wait conditions: The prey-agent must be on the same patch as the predator-agent.
* In Sit and Pursue and Active conditions: The prey-agent must be within the radius of 1 patch to the predator-agent.
* If these three conditions are met for each hunting strategy, there is then a probability of detection based on the patch in which the prey-agent is on.

If these three conditions are met, there is then a probability of detection based on the patch in which the prey-agent is on. If the predator-agent detects the prey-agent, it will activate the ‘Hunt’ submodel.

Hunt

The predator-agent can only hunt the prey-agent if the prey-agent is detected. The probability of a hunt being successful is 1 out of 100. If the predator-agent is successful, the prey-agent dies. If the hunt is unsuccessful, the prey-agent increases their *risk* value for that local spatial unit and that hour, based on habitat type.

To evaluate the non-consumptive effects of various predator hunting strategies, we monitor habitat shifts in prey-agent behavior due to interactions with the predator-agent. When the prey-agent is on a patch, the corresponding landscape type of that patch is recorded, creating a count of total presence of the prey-agent in each landscape type over the duration of the model. When the predator-agent successfully detect the prey-agent, the landscape type of the patch in which the encounter occurs adds a *risk* value.

To evaluate the non-consumptive effects of various predator hunting strategies, we also monitor temporal shifts in the prey-agent behavior due to interactions with the predator-agent. When the prey-agent is active, the corresponding hour of that activity is recorded, creating a temporal record of the prey-agent activity during the day. When the predator-agent successfully detects the prey-agent, the hour in which the encounter occurs adds to the *risk* value.

Time

For each tick, increase the *hour* by 1 until it reaches 24 hours, then reset *hour* to 0 and increase the *day* by 1.

Setting the *risk*/ Non-consumptive Effects

The prey-agent views each patch differently for each hour based on the number of interactions which have occurred previously through a combination of patch habitat type, the time which it occurred, and the patch area. This is determined through a series of steps:

(1) Patches determine what time it is; (2) each patch sets their *risk* value based on the number of interactions which have occurred at that time and on that habitat type; (3) patches then add the number of interactions which have occurred based on their local spatial unit and on that habitat type.

To evaluate the non-consumptive effects of various predator hunting strategies, we monitor spatial shifts in prey-agent behavior due to interactions with the predator-agent based on the respective size of spatial domains. Patches are grouped together into 2x2 grids, creating 24 patch-groups. Each patch-group can have overlapping spatial domains, where both predator and prey can be found on the landscape, or can be a prey-only spatial domain, where only prey are found. When a prey-agent is on a patch-group, the corresponding spatial domain type of that patch is recorded, creating a count of total presence of the prey-agent in overlapping spatial domain or prey-only spatial domain over the duration of the model. When the predator-agent successfully detects a prey-agent, the spatial domain type and vegetation type of the patch in which the encounter occurs increases the *risk* value by 1.

For the null model, regardless of the number of interactions which have occurred patches set their *risk* value for each hour to 0.