

ARTICLE

Predator–prey interactions across hunting mode, spatial domain size, and habitat complexities

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Abstract

Predator–prey interactions are a fundamental part of community ecology, yet the relative importance of consumptive and nonconsumptive effects (NCEs) (defined as a risk-induced response that alters prey fitness) has not been resolved. Theory suggests that the emergence and subsequent predominance of consumptive or NCEs depend on the given habitat's complexity as well as predator hunting mode and spatial domain sizes of both predator and prey, but their relative influence on the outcome of predator–prey interactions is unknown. We built agent-based models in NetLogo to simulate predator–prey interactions for three hunting modes—sit-and-wait, sit-and-pursue, and active—while concurrently simulating large versus small spatial domain sizes for both predators and prey. We studied (1) how hunting mode and spatial domain size interact to influence the emergence of consumptive or NCEs and (2) how, when NCEs do dominate, hunting mode and spatial domain separately or additively determine prey shifts in time, space, and habitat use. Our results indicate consumptive effects only dominate for active predators when prey habitat domains overlap completely with the predator's spatial domain and when sit-and-wait and sit-and-pursue predators and their prey both have large spatial domains. Prey are most likely to survive when they shift their time but most frequently shift their habitat. Our paper helps to better understand the underlying mechanisms that drive consumptive or NCEs to be most dominant.

KEYWORDS

active hunting, agent-based, consumptive effects, NetLogo, nonconsumptive effects, predator–prey, sit-and-pursue, sit-and-wait

INTRODUCTION

The behavioral response race (Sih, 1984) between predators and prey, where predators concentrate in areas of high prey densities and prey in turn avoid high-risk areas, have implications for population dynamics, ecosystem function, and evolution. Prey interactions with a predator are either consumptive or nonconsumptive

(Abrams, 2007; Miller et al., 2014). A consumptive outcome is straightforward: a predator eats a prey, resulting in the death of the individual prey and an energetic gain for the predator. A nonconsumptive outcome is more complicated: A predator individual and a prey individual interact, and though the prey is not eaten, the prey may experience energetic or stress-mediated costs (Boonstra, 2013; Hawlena & Schmitz, 2010; Lima, 1998;

Say-Sallaz et al., 2019). Prey that experience chronic stress from nonconsumptive interactions can reduce their interactions through risk avoidance, such as habitat shifts (Creel et al., 2005; Heithaus & Dill, 2006; Smith et al., 2019) and changes in activity patterns (Creel & Christianson, 2008; Gaynor et al., 2018). Risk avoidance responses can decrease time spent foraging, the quality of forage selection, or time spent breeding, any of which may incur corresponding fitness costs (Say-Sallaz et al., 2019). Current understanding of the dominance of consumptive effects (CEs) or nonconsumptive effects (NCEs) has mostly been gained through invertebrate experiments that collapse space-use into one or two dimensions (Preisser et al., 2007; Schmitz, 2008), precluding inference of predator–prey dynamics on a landscape level that can incorporate the full spectrum of movement and habitat use for predators with different hunting modes (Gorini et al., 2012). Knowing when CEs or NCEs dominate is important given the implications to provide insights regarding conservation and management (Abrams, 1984; Creel, 2011; Creel & Christianson, 2008; Matassa & Trussell, 2011; Sheriff et al., 2011).

The predominance of either CEs or NCEs is typically attributed to a combination of predator hunting mode and habitat domain (Schmitz, 2005; Schmitz et al., 2004, 2017). Hunting mode describes the way in which predators acquire their prey (McLaughlin, 1989) and is determined by a species' behavior, morphology, and physiology (Schmitz, 2017). While hunting mode for some predator species can change across ontogeny or differ by environmental context, the modes are generally categorized as active, sit-and-pursue, and sit-and-wait. Active hunters constantly roam to find prey (e.g., crabs, weasels); sit-and-pursue hunters remain in one location but will chase passing prey (e.g., dragonfly larvae, cheetahs); and sit-and-wait hunters remain in one location and ambush prey that come into the immediate vicinity (e.g., nursery web spiders, crocodiles; McLaughlin, 1989). Habitat domain describes the spatial extent in which an individual experiences an interspecific interaction (e.g., predator hunts or a prey forages; Burt, 1943; Schmitz, 2005; Schmitz et al., 2017). However, given that predators and prey may use a variety of habitat types while foraging or hunting (e.g., grasslands versus forests), we use the more general term *spatial domain* to characterize the spatial extent of foraging or hunting activities specifically. This distinction allows us to disentangle the relative importance of habitat structure from overlapping space use.

Current theory on the emergence of CEs and NCEs predicts that CEs should dominate when the predator is an active hunter with a large spatial domain; as the predator moves around, predation risk is unpredictable, and it

would be energetically inefficient for prey to invest in a consistent antipredator response (Schmitz, 2005). In contrast, NCEs should dominate when the predator is a sit-and-wait hunter; because the predator does not move, the risk of predation is more predictable, and it would be energetically efficient to employ some kind of chronic antipredator behavioral modification (Schmitz, 2005). Historically, predator spatial domain and predator hunting mode have been presented as nested concepts, with sit-and-wait predators having smaller domains, sit-and-pursue having larger domains, and active predators having the largest domains (Miller et al., 2014). This nested conceptualization works well at the invertebrate scale (Schmitz & Blake Suttle, 2001; Turner & Bernot, 1999), but recent large vertebrate studies have demonstrated that at the landscape level, hunting mode and the size of the predator's spatial domain may not necessarily be correlated (Gervasi et al., 2013; Lopes et al., 2021; Palmer & Packer, 2021). For example, sit-and-wait predators could select different ambush sites or hunting locations over time, meaning their spatial domain would be quite large across a landscape. Alternatively, sit-and-pursue predators could have a spatial domain equivalent to that of sit-and-wait predators if they did not encounter prey while hunting. Based on the requirements of their hunting mode, active hunters usually have a larger habitat domain but may also have a small habitat domain if they require a particular substrate to hunt within (e.g., crabs; Preisser et al., 2007).

Similarly to their predators, prey also have spatial domains that describe the spatial extent of foraging. Broadly speaking, the relative size and overlap of a prey spatial domain with a predator spatial domain is hypothesized to determine the type of antipredator response selected, whether prey will make a behavioral change to avoid predators in time (temporal shift) or in space (spatial shift) (Schmitz et al., 2017). When a prey has a spatial domain that completely overlaps with its predator, theory predicts that prey will shift their foraging activity temporally to minimize predation risk. When prey has a larger spatial domain than its predator, it should instead shift spatially away from the predator's domain (Schmitz, 2005; Schmitz et al., 2017).

Apart from predictions made by spatial domain overlap, habitat complexity can influence whether predators have CEs or NCEs (Holbrook & Schmitt, 1988; Schmidt & Kuijper, 2015; Smith et al., 2019; Trussell et al., 2006). Within any given spatial domain, there can be variable habitat types and, thus, variable detection probability. Prey that are unable to shift their use of space to move outside a predator's spatial domain can still shift their habitat selection to better avoid predators. This makes habitat complexity a more localized form of spatial

choice (Creel et al., 2005; Smith et al., 2019; Warfe & Barmuta, 2004) and another nonconsumptive shift.

Our objective was to understand how spatial domains and hunting mode influence the outcome of predator–prey interactions across a landscape with varying habitat complexity. While the concepts are theoretically clear, we know very little about the relative contribution of predator attributes in driving consumptive versus nonconsumptive fear effects. In addition, when the outcome is nonconsumptive, current theory does not allow us to predict whether prey will shift in space, in time, in habitat type, or in some combination of the three. We explore these questions using an agent-based model that allows us to (1) tease apart the interaction between spatial domain

and the hunting type and (2) quantify how hunting mode and spatial domain together determine prey shifts in time, space, or habitat use (Figure 1).

MATERIALS AND METHODS

Our model is a spatially explicit agent-based model (ABM), constructed using NetLogo version 6.1.1 (Wilensky, 1999). A detailed explanation of the NetLogo modeling platform can be found in the overview, design concepts, and details (ODD; Appendix S1), and the code and data generated from the simulations are archived in Orrick et al. (2024). We intentionally mimic the

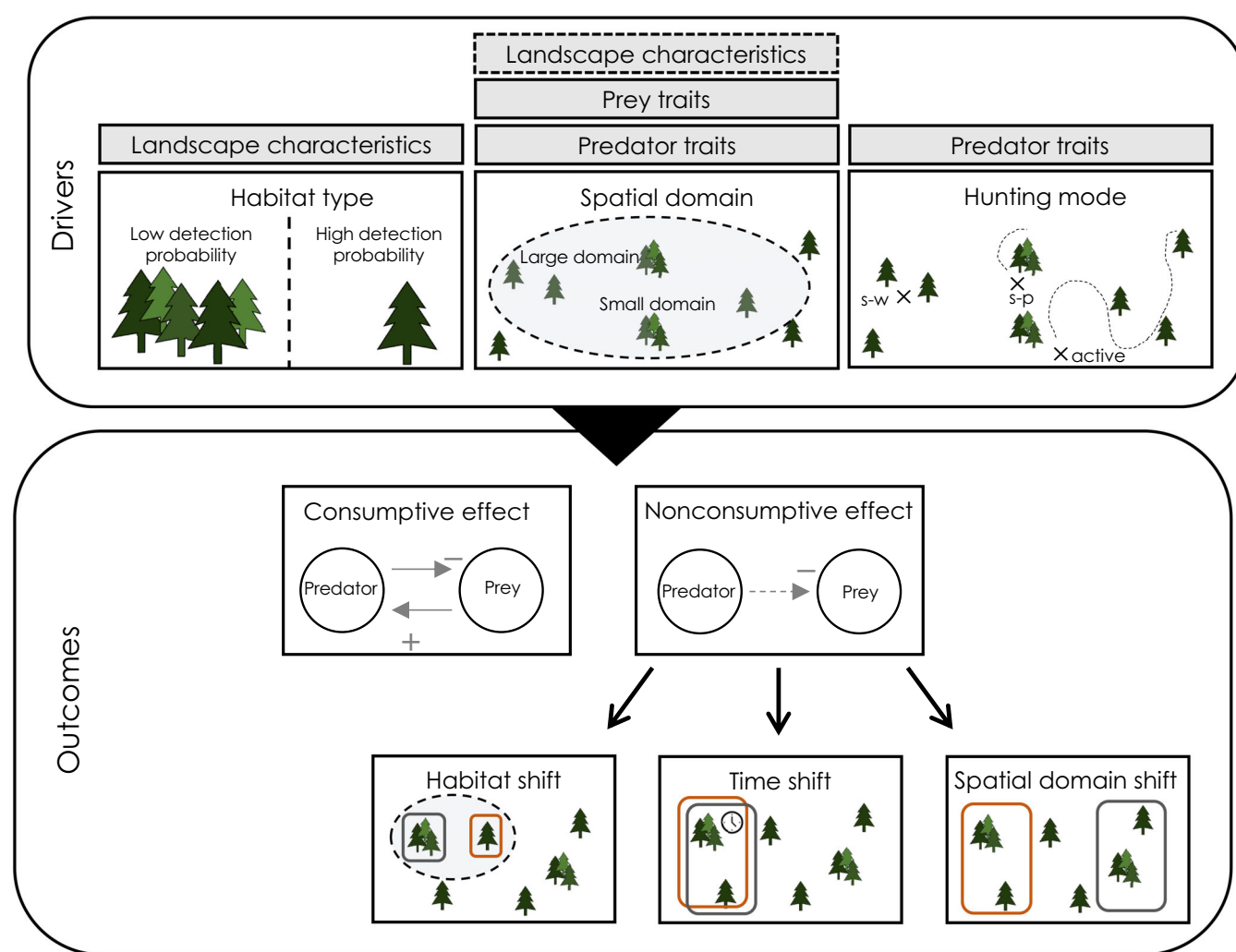


FIGURE 1 Theoretical framework that informs the design of our model depicting how habitat type, spatial domain, and hunting mode (s-w: sit-and-wait; s-p: sit-and-pursue; active) determine when consumptive or nonconsumptive effects (NCEs) are dominant. Hunting mode is a predator trait, while spatial domain is both a predator and a prey trait. Habitat type is a landscape characteristic. Spatial domain is indirectly influenced by major landscape characteristics (e.g., mountains, forests) by defining the parameter space in which it is possible for an individual to hunt or forage. We examine the three drivers to determine (1) when consumptive or NCEs dominate and (2) what type of behavioral shift occurs under nonconsumptive interactions. Under different types of shifts, the brown box indicates original behavior, while the gray box indicates shifted behavior.

conceptual model from Schmitz et al. (2017) and translate it to an ABM and add complexity by including habitat. Thus, based on Schmitz et al. (2017) our model is (1) not species-specific and (2) specifically examines nonconsumptive fear effects (Schmitz et al., 2017).

We created a hypothetical landscape arrayed as an 8×12 grid, resulting in 96 individual patches with one predator and one prey per simulation (Figure 2a). We use one prey and one predator because we are interested in the behavioral response of prey to predator interactions, which happen at the individual interaction scale. Therefore, while predators likely encounter many prey, and prey encounter many predators, it is each individual interaction that determines how prey may shift behaviors. Each patch represented landscape space that prey and predators could potentially occupy. To ensure prey's antipredator response had enough time to emerge, each model simulation emulated 5 years, with each year divided into 365 days.

Model simulations run for 1 year were too short in duration to induce many behavioral shifts (Appendix S2). Each day was divided into 24 discrete periods where predator and prey could move once each hour. Both predator agents and prey agents were required to be present on the landscape for 12 h in the day and absent for the other 12 h. Predator-agent hours did not change, with predator activity occurring from 00:00 to 11:00 h. The selection of these hours were slightly arbitrary and could have been any 12 h within the 24-h time period. Prey agents, however, could select any 12 h to be present.

Landscape environment and initial conditions

Predator and prey spatial domains were established at the start of each simulation. Predator and prey agents

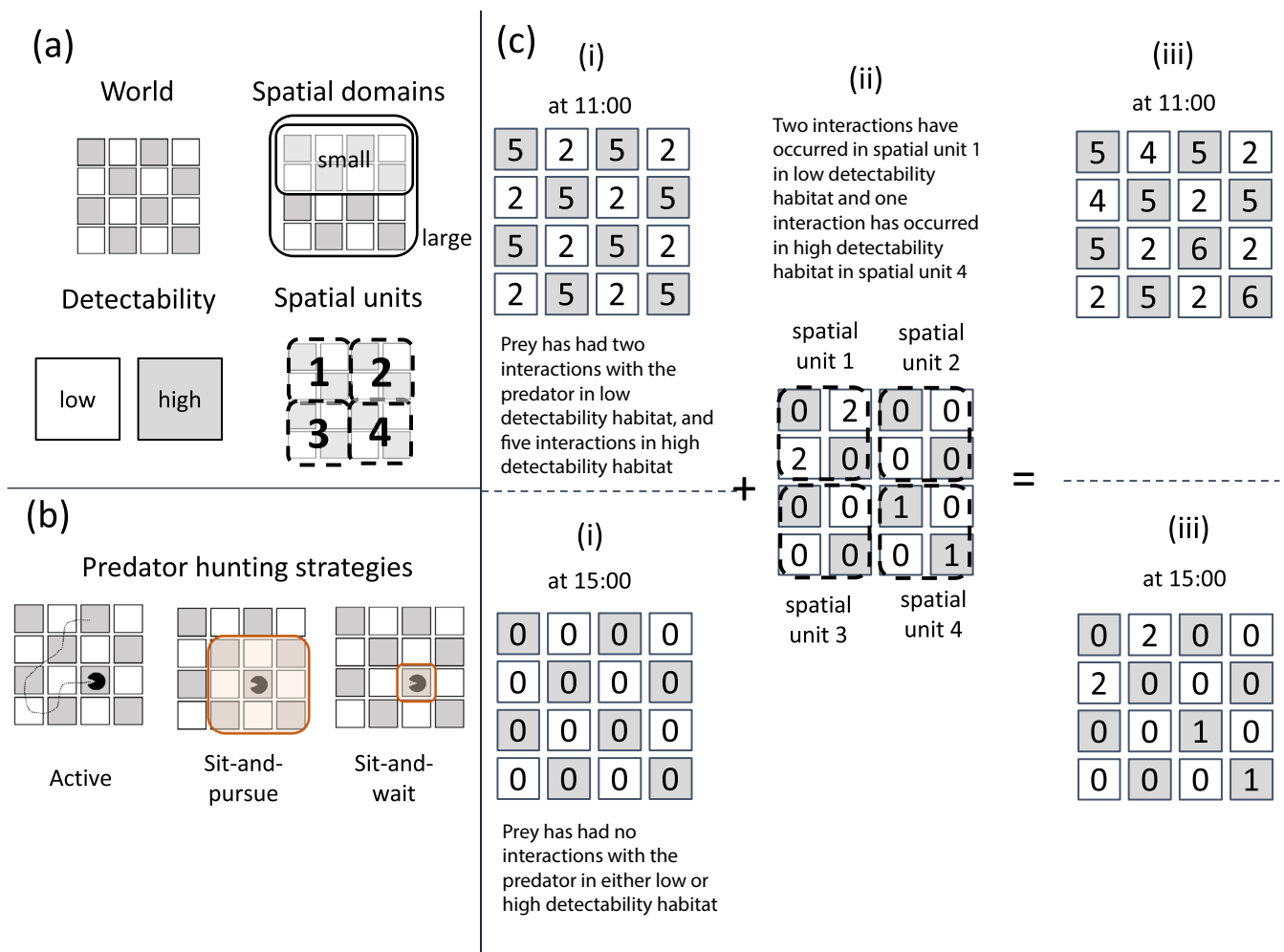


FIGURE 2 (a) Habitat distribution, spatial domain sizes, detectability, and local spatial units; (b) simulated active, sit-and-pursue, and sit-and-wait hunting modes; red box: range in which predators will hunt prey; and (c) visual depiction of how prey assesses risk value of each patch on landscape (iii), based on the habitat, time of day (i), and local spatial unit (ii). For the null model, regardless of the number of previous interactions, each risk value would remain at 0 for the duration of the simulation.

could each have large or small domains, creating four different possible conditions (Figure 2a), modeled after Schmitz et al. (2017). Large spatial domains encompassed the whole hypothetical landscape (96 patches) and were double the size of small domains. To create these different domains, each patch was assigned to a predator agent, prey agent, or both, commensurate with their domain size. Each agent type was only able to move on patches that were associated with them.

To avoid any spatial or temporal bias in prey-agent shifts, we created 24 unique local spatial units to match the 24 unique hours prey agents could choose from. Each local unit consisted of a 2×2 group of patches (Figure 2a). To explore shifts in habitat, prey could also choose between two mutually exclusive habitats arranged in a checkerboard pattern. Habitat patches had either a “high detectability” with a 0.9 probability of the predator agent detecting prey or a “low detectability” with a 0.2 probability of the predator-agent detecting prey (Figure 2a). These values were chosen to provide two distinct habitat detection rates while ensuring the prey was not completely hidden or visible in either habitat type. To tease apart emergent patterns of consumptive and NCEs it was assumed that both habitat types provided equal resources and that the only difference between the two was predation risk. Thus, any behavior modifications were shaped by the perceived risk of predation. For each simulation the habitat and local spatial area pattern and placement remained the same.

Predator–prey interactions

Both the predator agent and prey agent were initially randomly distributed within their respective spatial domains at the start of each simulation, which removed any bias that might have emerged from the initial agent placement. The prey agent and predator agent then began to move around the landscape. For all three hunting modes, if the predator agent detected the prey agent, it would hunt the prey. Detection was based on the low or high detection probability of the habitat patch in which the prey agent was located. If detected, predator agents had a 1 in 100 probability of successfully killing the prey agent, simulating the low rates of predator success often found in the wild (Witford et al., 2019). If the prey agent died, the simulation ended. If the hunt was unsuccessful, the prey agent recorded the time of day, the habitat type, and the local spatial unit where the attempted predation occurred.

All predator agents were present on the landscape for 12 h (00:00–11:00) and moved according to their specific hunting mode (Figure 2b). Active predator agents moved to a patch that was both within their spatial domain and within a radius of two patches from their current position.

To mimic predators pursuing nearby prey, active predator agents had the ability to detect and hunt a prey agent within a distance of one patch. Sit-and-pursue predator agents moved to a new, randomly selected patch within their spatial domain at the start of each day, mimicking the way in which sit-and-pursue predators move throughout their landscape, but without creating any spatial bias in predator–prey interactions due to predator-agent placement. They then remained on that patch for the duration of the day. Like active predator agents, sit-and-pursue predator agents were able to detect and hunt prey agents up to one patch away. Sit-and-wait predator agents also would move to a new, randomly selected patch in their spatial domain each day and then would remain there for the duration of the day. The predator agent could detect a prey agent only if the prey agent was on the same patch.

To tease out prey-specific NCEs, prey agents were the only agents that could change their spatiotemporal movements in response to interactions. At the beginning of each day (00:00) prey agents evaluated how many times they had interacted with the predator agent for each hour and for each habitat type. For each hour, the prey agent then selected the value and habitat type that had the lower number of interactions—for example, if at hour 10:00 the prey agent has had five interactions on a high detectability habitat patch and 1 on a low detectability habitat patch, it would select “1.” The selected values were then ranked from highest to lowest; the prey agent was then absent for the 12 h with the highest number of interactions. This allowed prey agents to adjust their temporal activity to account for previous predator-agent interactions, allowing for emergent temporal shifts in prey movement when predators were absent (12:00–23:00), as seen across multiple species and ecosystems (e.g., Bosiger et al., 2012; Courbin et al., 2019).

Once prey determined their 12 active hours on the landscape, prey agents assessed spatial risk. Prey agents viewed the “risk” value of a patch based on the number of interactions that occurred previously through a combination of patch habitat type, the time at which it occurred, and the patch spatial unit (Figure 2c). This was determined through a series of steps: (1) Patches determined the time; (2) each patch set its risk value based on the number of interactions that occurred at that time and on that habitat type (Figure 2ci); (3) patches then added up the number of interactions that occurred based on their spatial unit and on habitat type (Figure 2cii). If predator agents and prey agents had no previous interactions, then the risk value for all patches was 0 and the prey agent moved freely within its set spatial domain. If previous interactions had occurred, prey agents moved to the patch with the lowest risk value within a two-patch radius (i.e., prey cannot jump across the landscape) (Figure 2ciii).

This series of steps allowed for emergent spatial, temporal, and habitat shifts in prey foraging behavior through interactions with predators. In our model there was only the implicit cost of avoiding times or areas with a high number of predator interactions; there was no explicit cost for prey to engage in antipredator behavior.

Simulation experiments

We developed two different simulations. One which had both nonconsumptive and consumptive effects of predator agents impacting prey agents (CE + NCE) and one with only CEs that acted as our null simulation. In the CE + NCE simulations, prey agents could either be consumed by predator agents or have an interaction with a predator agent, which would create “risk” values at the patch and hour in which the interaction took place. This resulted in a change in prey-agent behavior through a combination of spatial, temporal, and habitat shifts to attempt to avoid predator agents in the future. Our CE scenarios had the same conditions, except that the “risk” values for each patch remain at 0 for the duration of each simulation. Accordingly, in the CE null simulations, prey agents did not change their behavior after interactions with a predator agent, and thus the CE model provided insight into how prey agents would behave without any antipredator behavioral responses—prey were only affected by predators when they were consumed. The CE + NCE model simulated how prey agents reacted when they were both able to be consumed by the predator and when they could induce antipredator responses, simulating real-life predator and prey interactions and prey-specific outcomes. We compared CE to CE + NCE simulations to determine survival rate curves. When NCEs dominated—identified when survival across time was significantly higher in the CE + NCE compared to the CE-only simulations—we then examined which type of antipredator behavioral modification was the most employed and which type most increased survival rate.

Both the CE and CE + NCE simulations contained 12 different experiments, four combinations of spatial domain size across the three different hunting modes, each replicated 100 times. The simulations were conducted using the Grace High Performance Computing Cluster at the Yale Center for Research Computing.

Outputs

Model output

To evaluate the CEs in both the CE and CE + NCE simulations, we recorded the number of simulations in which

prey agents died due to an encounter with predator agents across all 100 simulations. To evaluate the NCEs of various predator hunting modes, we monitored spatial, temporal, and habitat selection in the prey agent. When a prey agent was on a patch, the corresponding habitat type and local spatial unit of that patch were recorded, creating a sum occupancy of each patch type over the full duration of the simulation. We also created a count of which hours prey agents were active.

Sensitivity analysis

To evaluate the importance of the parameters in each of the hunting mode models, we conducted a sensitivity analysis using the nlrx package (Salecker et al., 2019) in R version 3.6.3 (R Core Team, 2021). We evaluated the model parameters according to the number of interactions predators had with prey, using a modified version of the elementary effects method (i.e., the Morris screening method; Campolongo et al., 2007; Morris, 1991; Salecker et al., 2019). We evaluated the sensitivity of detection probability of both types of habitat patches and the hours the predator was active, capturing a range of overlapping periods of activity for the prey and the predator. To evaluate a range of the parameter space for patch detection probability, we examined distributions within $\pm 10\%$ of the original value (10%–30% probability of detection for low detectability habitat and 80%–100% probability of detection for high detectability habitat patches). We explored a range of hours (12 ± 2 h) in which the prey and predators overlapped. We also used a sensitivity analysis on the null simulations with the same parameter ranges. The sensitivity of the model to each parameter was evaluated using the mean absolute value of elementary effects (μ^*), which measures the overall influence of a parameter on the results (Salecker et al., 2019). To measure higher-order effects, we used the SD of the elementary-effects values (σ) (Campolongo et al., 2007).

Statistics

We used the survival package (Therneau & Grambsch, 2000) in R to model the time to event (i.e., death) of the CE + NCE and CE null model conditions as Kaplan–Meier survival curves. We then plotted the survival curves using the survminer package (Kassambara et al., 2021). We used a Cox regression model to determine differences in survival between CE only and CE + NCE. If the survival curves were not statistically different at $\alpha = 0.05$, we took that as evidence that CEs were dominant. Next, we fit Cox proportional hazards models to each hunting mode \times

prey domain \times predator domain combination of the CE + NCE state. This allowed us to examine how behavioral modifications (i.e., shifts in habitat, time, and space) after unsuccessful predation attempts affected survival. These are reported as hazard ratios, where a number less than one indicates decreased risk of death.

RESULTS

Sensitivity analysis

The sensitivity analysis showed that within each simulated scenario, the parameters examined were all similarly influential, as indicated by their clustered μ^* and σ values (Appendix S3). However, for the active hunting mode and the sit-and-pursue hunting mode models, the range of overlapping hours of activity between predators and prey agents had a slightly greater influence on the model outputs relative to the other variables. Both the low detectability habitat and high detectability habitat patches were somewhat less influential, though the high detectability habitat was more influential than the low detectability habitat in both simulations. In the sit-and-wait hunting mode models, the opposite results were found. The high detectability habitat was the most influential parameter, followed by the low detectability habitat. The hours in which the prey and predators overlapped had the least influence. Of note, the parameters were less influential as predator movement decreased.

The parameters in the sensitivity analysis for the null models were similarly clustered (Appendix S3), indicating that the sensitivity of the model parameters was higher between models than within a model. Again, the active and sit-and-pursue hunting mode models followed a similar pattern to one another, though the most important parameters were different: In the null models, the high detectability habitat was slightly more influential than the other parameters, followed by the low detectability habitat, and then the hours overlapped between predators and prey. The sit-and-wait null model had a slightly different structure in which the low detectability habitat was slightly more influential, followed by the hours overlapped between prey and predators and, finally, the high detectability habitat. The pattern of parameter influence between models persisted, where parameters were more influential as models allowed for more predator movement.

Comparison of CE and CE + NCE survival

Across all models, overall survival was longer in the CE + NCE models when prey could employ an antipredator

response (median survival = 1.84 years, 95% CI [1.61, 2.03]), compared to the CE models (median survival = 1.23 years, 95% CI [1.13, 1.32]). Within each of the 12 CE + NCE model scenarios, only four had dominant consumptive effects: active small_{Pred}–small_{Prey}, active large_{Pred}–small_{Prey}, sit-and-pursue large_{Pred}–large_{Prey}, and sit-and-wait large_{Pred}–large_{Prey} (Figure 3a–c). For the other eight models, NCEs were dominant. Prey with active and sit-and-pursue predators had lower overall survival probabilities and were quicker to die (median survival \approx 1.5 years; Figure 3a,b) than prey with sit-and-wait predators (median survival \approx 3 years; Figure 3c). Prey spatial domain size did not affect survival in CE or CE + NCE models. When predators and prey both had small spatial domains, the survival decline was sharpest and median survival time was lowest (Figure 3a–c; Table 1).

When CE + NCE models were compared across hunting modes, sit-and-wait predators induced a hazard ratio that was half as strong as the other two modes (Table 1). For the CE models, sit-and-pursue predators were less likely to cause prey mortality than active predators, but in the CE + NCE models, when prey could respond, the active and sit-and-pursue predators were equivalent (Table 1). However, in the CE + NCE models, predator spatial domain was an important determinant of prey survival—prey had 40% lower mortality risk when predators had small spatial domains. In particular, predator and prey both having a small spatial domain size more than doubled the hazard ratio (Table 1).

Behavioral shifts in CE + NCE models

All antipredator responses (shifts in time, habitat, or space) strongly reduced the hazard ratio for prey, indicating a higher likelihood of survival, regardless of predator mode (Figure 4). Shifting active hours was most effective at reducing the hazard ratio by almost 10 orders of magnitude compared to shifting habitat type or spatial domain, but these time shifts only occurred after a number of years (Appendix S2; Figure 4) and had the largest error around them, indicating high variability in time shifts among prey (Figure 4). Across all combinations of spatial domain sizes, hunting modes, and avoidance behaviors, there was only one instance where the prey behavioral shift did not improve survival: habitat shifts for sit-and-wait small_{Pred}–large_{Prey} (Figure 4). Prey habitat shifts in small_{Pred}–small_{Prey} spatial domains significantly decreased their hazard ratio under active predators, relative to the other two hunting modes. Prey in this active small_{Pred}–small_{Prey} scenario had statistically equal hazard ratios regardless of whether they shifted habitat or time (Figure 4).

Prey exposed to sit-and-wait predators had a higher probability of shifting their time use to predator-free hours than prey in the other two predator modes. Prey with active predators were more likely to shift their habitat use. In the small_{Pred}–large_{Prey} scenario where prey could shift their space use to predator-free areas (i.e., when the spatial domains did not overlap completely), all three hunting modes caused shifts in space more than habitat or time (Figure 5).

DISCUSSION

General discussion

We found that predator hunting mode, spatial domain size, and habitat complexity all influenced when CEs or NCEs dominated in predator–prey interactions. Previous research hypothesized that nonconsumptive fear effects would dominate only for sit-and-wait or sit-and-pursue

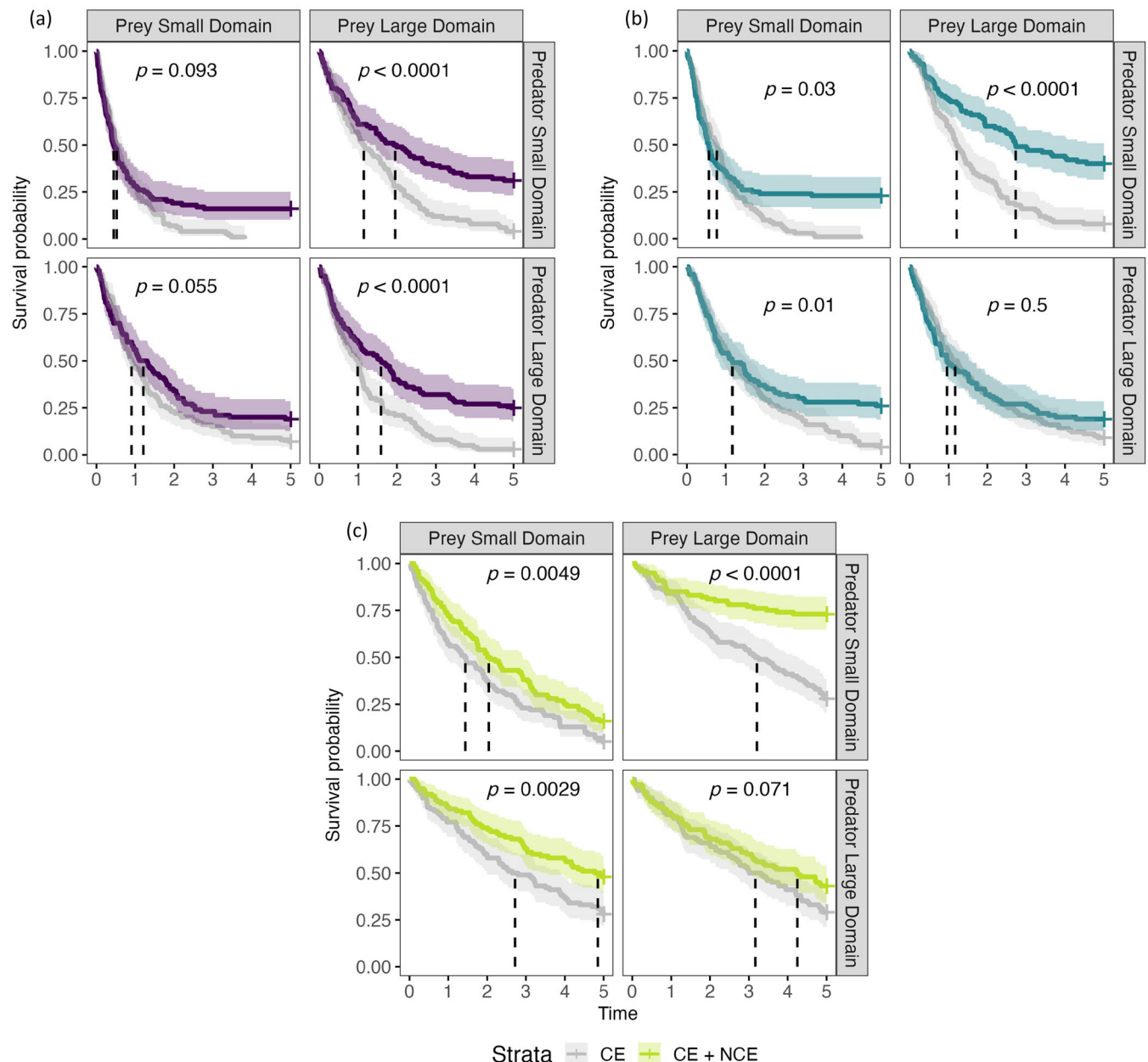


FIGURE 3 Survival curves for CE + NCE (color) and CE (gray) simulations for each combination of predator spatial domain and prey spatial domain over 5 years for (a) active, (b) sit-and-pursue, and (c) sit-and-wait hunting modes. Dashed vertical and horizontal lines indicate median survival of each curve. Cox regression model p -values for differences between survival curves are in each panel.

TABLE 1 Results for Cox proportional hazards models on how model scenarios affect the hazard ratio (HR) of prey.

Model scenario	Consumptive effects only			Consumptive and nonconsumptive effects		
	HR	95% CI	<i>p</i> -value	HR	95% CI	<i>p</i> -value
Hunting mode						
Active	
Sit-and-pursue	0.82	[0.71, 0.94]	0.006	0.88	[0.75, 1.04]	0.13
Sit-and-wait	0.37	[0.31, 0.43]	<0.001	0.45	[0.37, 0.53]	<0.001
Predator spatial domain						
Large	
Small	0.95	[0.80, 1.12]	0.50	0.60	[0.49, 0.74]	<0.001
Prey spatial domain						
Large	
Small	0.99	[0.83, 1.18]	0.90	0.97	[0.80, 1.18]	0.80
Predator × prey spatial domain						
Large × large	
Small × small	2.08	[1.64, 2.65]	<0.001	2.68	[2.03, 3.54]	<0.001

Note: HR > 1 means increased risk of mortality, HR = 1 is neutral on survival, and HR < 1 means better survival/lower risk. Within each modeled scenario, the results are compared to the baseline, which is set as the top entry (e.g., active hunting mode).

predators (Miller et al., 2014; Schmitz, 2005; Schmitz et al., 2017); however, we found that nonconsumptive fear effects could dominate with active predators. Our results also contradicted previous theory that CEs would dominate only when both predators and prey had large spatial domains (perhaps due to diffuse risk cues and fewer interactions; Luttbeg & Schmitz, 2000; Schmitz, 2007; Schmitz et al., 2017; Schmidt & Kuijper, 2015). We showed that consumptive effects could also dominate whenever active predators hunt prey with a small domain size. Further, active predators are not primary drivers of consumptive effects. In our simulations, active predators caused consumptive effects only when the spatial domains of prey were small. We corroborated existing work showing that prey with sit-and-wait predators had a higher survival rate than with other hunting modes, in part because the hunting radius was smaller than the other hunting modes (Figure 3). Overall, we found CEs were dominant either when antipredator behavior was ineffective (very high encounter frequency) or when antipredator behavior was not adopted (very low encounter frequency; Figure 3), which, as a mechanism, supports existing theory.

All three predator hunting modes created statistically nonsignificant differences in survival rate curves between models with and models without antipredator responses, thereby demonstrating that all three hunting modes could cause dominant CEs. When NCEs did dominate, irrespective of the hunting mode, prey were more likely to survive if they shifted in time as opposed to in habitat or

space (Figure 4). However, time shifts took longer than habitat or space shifts, meaning that shifts toward low detectability habitat and spatial shifts to move outside of a predator agent's domain occurred more frequently than time shifts (Figure 5). Our model corroborates Schmitz et al.'s (2017) prediction that spatial shifts would dominate when predators have small domains and prey have large domains. In contrast, Schmitz et al. (2017) proposed that temporal shifts would be most dominant whenever prey had small domains; however, our model found that if habitat type was also included, prey with small domains and active or sit-and-pursue predators were more likely to shift their habitat than to shift in time. This finding supports a general conclusion that heterogeneity in refugia (as a product of habitat type) should always be considered alongside temporal and spatial responses (Gorini et al., 2012).

Overall, active and sit-and-pursue predators caused similar NCEs on prey, while sit-and-pursue and sit-and-wait predators had similar consumptive effects. When NCEs dominated, prey would most effectively reduce their predation risk by shifting in time (Figure 4). However, prey did not always shift in time. Under active and sit-and-pursue predator scenarios, habitat shifts were more frequent than temporal shifts (Figure 5). Regardless of the hunting mode, prey consistently moved outside of a predator's domain when it was an available option, rather than shifting temporally or to a new habitat type (Figure 5).

In simulations where prey had the ability to make all three kinds of shifts in time, space, and habitat, prey had the highest likelihood of survival when they shifted their

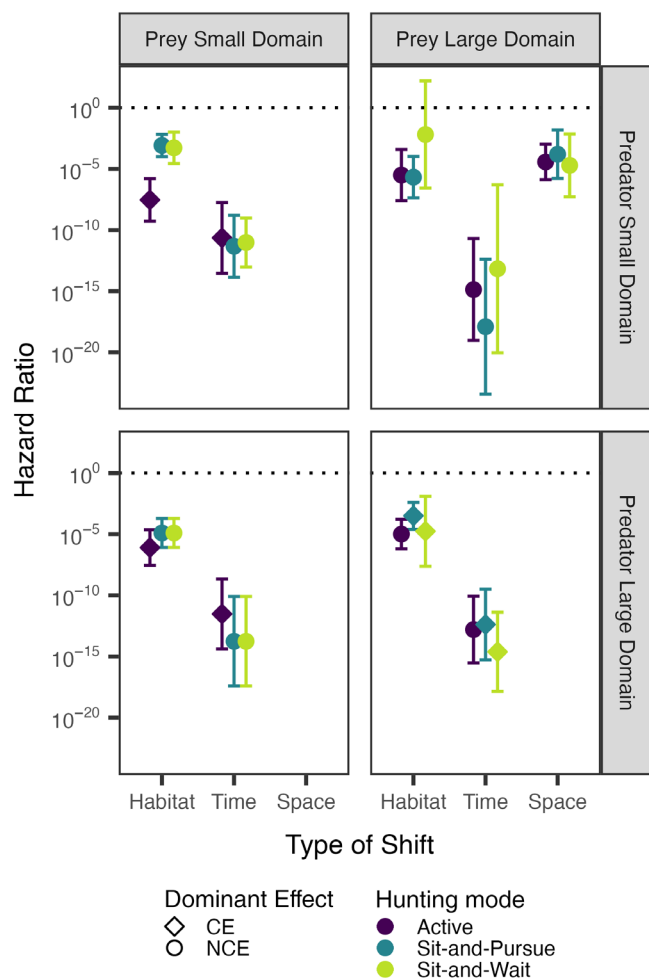


FIGURE 4 Each point represents the median ($\pm 95\%$ CI) of a proportional hazards regression model of 100 outcomes of a single combination of hunting mode \times prey spatial domain \times predator spatial domain ($n = 12$) when allowing for behavioral shifts (nonconsumptive effect) after an interaction with a predator. For each, we assessed how survival was influenced by behavioral shifts in habitat, time, or space. $HR = 1$ (no benefit or detriment to survival) is represented as a dotted horizontal line. $HR < 1$ indicates increased survival by the behavioral shift. Note the y-axis is log₁₀-scaled. A diamond (◇) represents when a consumptive effect was dominant. An open circle (○) represents when a nonconsumptive effect was dominant.

time (Figure 4), even though shifting their space to a predator-free area would reasonably have the same increase in survival probability. The slower time shifts are a product of the distance prey can move in a given time step relative to the hours available for activity. In the model, prey could select 24 discrete time steps for each habitat detection type, yet for each time step they are only able to choose between the eight surrounding patches. Thus, the prey were restricted in the distance they could travel but not by the hours they chose to be present and, consequently, would have more interactions

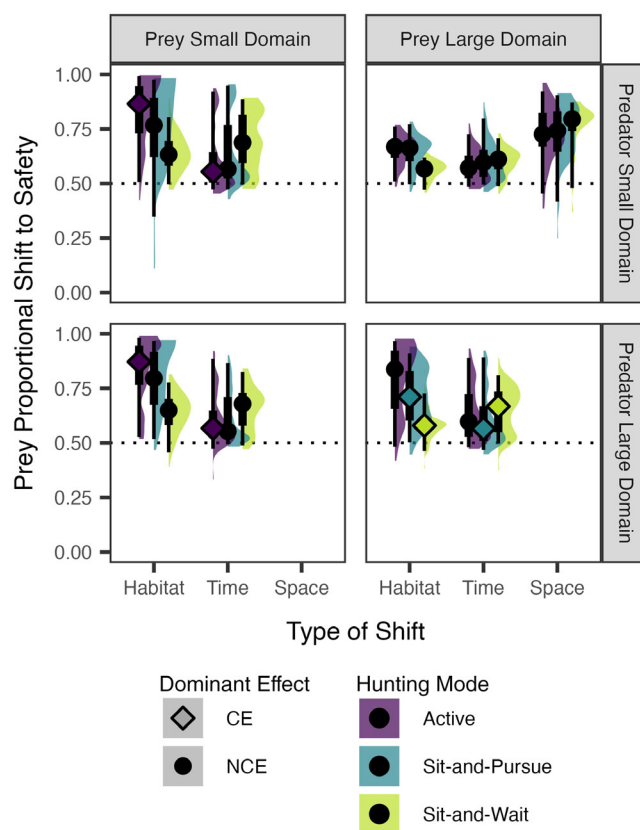


FIGURE 5 Antipredator responses in our 5-year simulations. Each point represents the median of all simulations for the proportion of habitat (more time on low-detection patches), time (predator-free hours), or predator-free space used. Thick lines show the 50% CIs and thin black lines the 95% CIs. A probability density function for a prey's behavior shift within each prey scenario, predator spatial domain, and hunting mode ($n = 100$ simulations for each scenario) is plotted to the right of each median and CI. A shift in spatial domain away from predators was only possible when the prey had a large spatial domain relative to a small spatial domain for predators. A diamond (◇) represents when a consumptive effect was dominant. An open circle (○) represents when a nonconsumptive effect was dominant.

on a certain patch or habitat than at a specific hour. This mimics, however, current theory, which states that prey first attempt to escape the predator by seeking refuge habitats and when prey are unable to do so, they will shift time (Schmitz et al., 2017). This finding does not include secondary costs or limitations to time shifts; however, despite the higher survival rate with time shifts, prey were more likely to engage in a spatial shift. The other simulations with limited possible risk aversion options had much higher shifts in habitat (Figure 5). This reflects a biological reality that the adaptive response to predation risk will depend on the context of the particular system (Wirsing et al., 2021), whether there is opportunity in time, space, or habitat to avoid predators.

The way we built our agent-based model directly links prey survival with predator hunting success rate, time, and number of interactions that occur on the landscape. But this approach is not without limitations in evaluating prey survival. Prey required time to effectively shift their behavior to avoid predators, but this finding is likely a product of having naive prey agents (Appendix S2). Prey in these models had zero initial information about their predators, which is not biologically accurate even in instances of captive reared prey. In reality, prey may engage in predator avoidance response more quickly.

Our model did not factor in that spatial domain sizes can change across seasons and years, and a constant domain size and area for 5 years might not be ecologically relevant. Any observed shift in dominance between CEs and NCEs over 10 and 20 years may be attributed to the inherent assumptions of the NetLogo model's world size (Appendix S2: Figures S3 and S5). It is important to note that these changes are contingent upon the model assuming a closed system, a condition not reflective of real-world dynamics. Of note, however, simulations that ran for 10 and 20 years resulted in the same behavioral responses, demonstrating that 5 years was a sufficient time period to be representative of the type of behavior shifts exhibited (Appendix S2: Figures S4 and S6). Additionally, our findings show the number of interactions in systems with large predator spatial domains is unaffected by the size of the prey domain and therefore would yield the same results regardless of the number of years.

Future directions

Agent-based models are useful in simulating complex behavioral patterns when a controlled experiment in real systems would be difficult to design (Carter et al., 2015; Ferraro et al., 2022; Pauli et al., 2013; Schmitz, 2001). We were able to use this agent-based modeling to further empirical syntheses by others and test their hypotheses. Nonetheless, these simulations do not encompass the entirety of ecologically significant traits exhibited by both prey and predator species. We developed a world that was resource-rich; prey were not restricted by food access and thus would not be impacted by other aspects that might shape alternative behavior shifts. There is also evidence that both short-term and long-term risk of predation has a strong impact in how prey alter their antipredator behaviors (Dröge et al., 2017). Prey agents were not designed able to “sense” and respond to the proximity of a predator; they were only able to adjust their temporal and spatial activity patterns after an

interaction occurred. While these models do not represent all the ways in which real predator and prey organisms interact with one another, they do yield important generalizations and contribute to predator–prey theory, especially for NCEs in systems where observations and experiments are difficult (DeAngelis & Diaz, 2019; Say-Sallaz et al., 2019).

For simplicity, our study did not incorporate multiple individuals or reproduction. As highlighted earlier, it also did not include costs for prey to shift their behavior. Combined, these aspects of prey underscore a more practical question: To what extent can NCEs alter prey population size? Changes in activity patterns can decrease time spent foraging, the quality of forage selection, or time spent breeding and may incur corresponding fitness costs, such as spending energy in grouping, vigilance, or reactive responses (Creel & Christianson, 2008; Hawlena & Schmitz, 2010; Ings et al., 2009; Palmer & Packer, 2021; Say-Sallaz et al., 2019; Werner & Peacor, 2003). Our current model does not include negative consequences for prey that shift their behavior, including competition among prey or decreased areas for refuge. Current literature is still debating the relevance of NCEs for prey demography (*sensu* Sheriff et al., 2020). Moreover, in multispecies systems, the functional traits of prey may provide a better understanding of predicting risk effects and predation (Creel, 2011). The contextual nuance of predator–prey dynamics in the real world makes it difficult to understand their significance. Further studies would need to scale up these models and allow for behavioral shifts from predators to determine their contribution to community demographics (Appendix S4).

Conclusion

The use of agent-based modeling to explore predator–prey CEs and NCEs revealed three important considerations. First, the sit-and-pursue hunting mode resulted in similar prey behavioral adjustments to that of active hunting. If these two hunting modes produce functionally equivalent NCEs on prey, then it is possible that hunting modes could effectively be collapsed into hunters versus ambush predators, allowing for a simplification of the theory. Second, hunting mode does not solely determine whether CEs or NCEs emerge. Our model shows that active predators, not only sit-and-wait predators, can cause NCEs. Third, habitat shifts should be considered alongside space and time shifts. Our results suggest that habitat shifts happen before time shifts, despite time shifts being more effective for predator avoidance.

This study provides stronger theoretical understanding of predator–prey CEs and NCEs as well as adding further nuance to current theory. Concomitant with landscape change due to anthropogenic activities (Findell et al., 2017), species range shifts due to climate change (Brooker et al., 2007; Thuiller, 2004), and rewilding conservation efforts (Fernández et al., 2017) is the need to understand general principles that underlie predator–prey relationships. We expand on previous attempts to generalize this context-dependent relationship by specifically exploring how consumptive and NCEs may dominate in different combinations of spatial domain sizes and predator hunting modes and by adding habitat complexity via detection probability.

AUTHOR CONTRIBUTIONS

Authors equally contributed to conceptualization, visualization, writing, and editing. Kaggie Orrick and Kristy Ferraro equally led contributions to the execution of software. Kaggie Orrick led data curation, investigation, and methodology. Kristy Ferraro led validation and supervision. Nathalie Sommer led in theoretical background. Freya Rowland led in formal analysis.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Orrick et al., 2024) are available in Zenodo at <https://doi.org/10.5281/zenodo.10928188>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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