









## RESEARCH ARTICLE

# Impersonating predators and prey to study trophic interactions through real-life simulations

David Bolduc<sup>1</sup>  | Frédéric Dulude-de Broin<sup>1</sup>  | Gabriel Bergeron<sup>1</sup> | Catherine Villeneuve<sup>2</sup> |  
 Matthieu Weiss-Blais<sup>1</sup>  | Clément Couloigner<sup>1</sup> | Rachel Dubourg<sup>1</sup> |  
 Maxime Fraser-Franco<sup>3</sup>  | Francis Banville<sup>3</sup> | Louis Moisan<sup>4</sup> | Pierre-Olivier Montiglio<sup>3</sup>  |  
 Daniel Fortin<sup>1</sup> | François Thibault<sup>5</sup> | Antoine Allard<sup>5</sup> | Camille Gaudreau-Rousseau<sup>1</sup> |  
 Irene Roca<sup>6</sup> | Audrey Durand<sup>2</sup> | Clément Massé<sup>7</sup> | Emmanuelle Barreau<sup>6</sup> |  
 Tamara A. Hiltunen<sup>7</sup> | Emily Madsen<sup>8</sup>  | Mathilde Lapointe St-Pierre<sup>9</sup> |  
 Alexandra Engler<sup>10</sup>  | Akiko Kato<sup>11</sup> | Morgane Le Goff<sup>1</sup> | Maria Isabel Arce-Plata<sup>3</sup> |  
 Norma Rocio Forero-Muñoz<sup>3</sup> | Sophie Gallais<sup>1</sup> | Dominique Gravel<sup>12</sup> | Pierre Legagneux<sup>1</sup> 

<sup>1</sup>Faculté des Sciences et de Génie, Université Laval & Sentinelle Nord, Québec, Québec, Canada; <sup>2</sup>Faculté de Génie Informatique et Génie Logiciel, Université Laval, Québec, Québec, Canada; <sup>3</sup>Faculté des Sciences, Sciences Biologiques, Université du Québec à Montréal, Montréal, Québec, Canada; <sup>4</sup>Biologie, Chimie et Géographie, Université du Québec à Rimouski, Rimouski, Québec, Canada; <sup>5</sup>Faculté des Sciences et de Génie, Physique, Génie Physique et Optique, Université Laval, Québec, Québec, Canada; <sup>6</sup>Département de Sciences Naturelles, Université du Québec en Outaouais, Gatineau, Québec, Canada; <sup>7</sup>Ecology and Genetics Research Unit, University of Oulu, Oulu, Pohjois-Pohjanmaa, Finland; <sup>8</sup>Department of Biology, University of Oxford, Oxford, UK; <sup>9</sup>Faculty of Agricultural and Environmental Sciences, McGill University, St-Anne-de-Bellevue, Québec, Canada; <sup>10</sup>Biology Department, Concordia University, Montreal, Québec, Canada; <sup>11</sup>Institut Pluridisciplinaire Hubert Curien, CNRS, Strasbourg, Grand Est, France and <sup>12</sup>Département de Biologie, Université de Sherbrooke, Sherbrooke, Québec, Canada

**Correspondence**

David Bolduc

Email: [david21bolduc@hotmail.com](mailto:david21bolduc@hotmail.com)

Frédéric Dulude-de Broin

Email: [frederic.ddb@gmail.com](mailto:frederic.ddb@gmail.com)**Funding information**

Natural Sciences and Engineering  
 Research Council of Canada; Sentinelle  
 Nord, Université Laval

Handling Editor: Timo Adam

**Abstract**

1. Predator–prey interactions are a fundamental aspect of ecology that has generated sustained research interests. Progress in the field stems from a diverse range of approaches, from highly controlled yet simplified mathematical and agent-based models, to grounded but data-limited field studies.
2. As a compromise between mathematical and observation-oriented methods, we introduce an original approach based on an outdoor game. In this game, biologged human players follow simple rules to impersonate predators and prey in a natural landscape augmented with synthetic resource patches and refuges. We investigated the behaviour, movement, functional response and spatial organization of over 25 players simultaneously monitored during nine simulations to determine whether the game could replicate realistic predator–prey dynamics.
3. Results derived from our real-life simulations were consistent with ecological patterns expected in natural systems. We found that (a) predator and prey

Frédéric Dulude-de Broin and David Bolduc equally contributed and share first authorship.

This is an open access article under the terms of the [Creative Commons Attribution-NonCommercial](https://creativecommons.org/licenses/by-nc/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited and is not used for commercial purposes.

© 2025 The Author(s). *Methods in Ecology and Evolution* published by John Wiley & Sons Ltd on behalf of British Ecological Society.

movements were driven by risk and reward trade-offs, (b) predators took advantage of linear features to travel at higher speed, making these areas risky for prey, (c) prey had nonlinear and risk-sensitive functional responses and (d) consumer–resource interactions were spatially modular and defined by players' movement rates and landscape features. Moreover, the comprehensive dataset generated through the game allowed for the exploration of phenomena that are challenging to study in natural settings, such as spatial memory and the influence of satiety on resource acquisition rates.

4. The approach offers a simple, computationally accessible and genuinely amusing way to explore the complex ramifications of predator–prey interactions and test otherwise data-deficient hypotheses. The strength and originality of the method lies in the use of living agents—players—making decisions in a real-world setting. This aspect alleviates the computational and empirical burden of defining and estimating decision-related parameters needed to build simulators, while generating extensive datasets in a flexible experimental framework that is generally out of reach for empirical studies. It also offers immersive insights into predator–prey interactions, making it an engaging pedagogical tool that encourages creative thinking. The numerous possible scenarios that can be explored are only constrained by the investigator's creativity in adapting game rules and the players' desire to win.

#### KEYWORDS

foraging, game, movement, predation risk, predator–prey, real-life simulations, spatial network, trophic interactions

## 1 | INTRODUCTION

Consumptive interactions among organisms, as well as their associated risk, can shape individual phenotypes (Grant & Bayly, 1981; Lima & Dill, 1990), population dynamics (Gilg et al., 2003), community assembly (Forsman et al., 2001) and ecosystem functioning (Schmitz, 2008; Suraci et al., 2022). Despite the widespread recognition of their importance, large gaps remain between trophic interactions theory and what can be studied in natural settings. For instance, the functional response of consumers (i.e. consumer acquisition rate as a function of resource density; Holling, 1965) is a central component of trophic dynamics, but the challenge of empirically measuring functional responses currently hampers our ability to properly model predator–prey interactions (DeLong, 2021). Similarly, the foraging behaviours of both vagile consumers and resources interact to shape when and where trophic interactions occur. Unfortunately, obtaining simultaneous behavioural information on a significant number of interacting individuals is rarely feasible. Moreover, interindividual interactions occur at spatial and temporal scales often finer than what biologging devices can capture. While this complexity brings a stimulating side to ecological research, it also limits our ability to explore and confront ecological theory with empirical observations.

To face these challenges, researchers routinely use an array of methods, from mathematical models to field studies. At one

end of the spectrum, mathematical models of ecological systems allow us to derive testable predictions and gain a global understanding of natural systems (Caswell, 1988; Grainger et al., 2022). They remain tractable by assuming simplified environments and individual behaviours, features that may largely impact their validity (McNamara et al., 2014). At the other end of the spectrum, field studies embrace the complexity of ecological systems and are used to test hypotheses and theories. However, their explanatory power is limited as the identification of causal mechanisms is often obscured by numerous confounding variables. Between these two types of methods, intermediate approaches with varying degrees of control and applicability exist. Mesocosm experiments, for example, can be tightly monitored and replicated, but can only accommodate relatively simple communities on a limited spatial scale that can tolerate confinement (Buckling et al., 2009; Srivastava et al., 2004). Manipulative experiments conducted in the field offer a higher level of realism and can provide robust inferences, but they are logistically challenging and hard to replicate at broad spatial and temporal scales (Fauteux et al., 2016; Krebs et al., 2018).

In some cases, games are harnessed as practical study systems in ecological research to investigate foraging behaviour (Fraser Franco et al., 2022; Holling, 1959) and determinants of survival (Céré et al., 2021; Lymbery et al., 2023). Indeed, board games and

virtual environments provide controlled settings in which emerging trophic interactions and their outcomes can be studied, integrating core principles from evolutionary, behavioural, functional and community ecology. A step closer to empirical field studies, real-life games can better capture the complexity of ecological systems by leveraging humans' cognitive and perceptual traits, which evolved to navigate the intricate, heterogeneous world animals inhabit. Freeing the investigators from many assumptions of theoretical models, these games benefit from the various possibilities of natural landscapes and can be defined using a simple set of rules. They represent a promising avenue to tackle the gaps in our understanding of predator–prey interactions while leaving plenty of room for insightful and unexpected discoveries (Doak et al., 2008).

Here, we introduce the *Trophic Interactions Experiment* (TrophIE) game, a real-life simulation where biologged players impersonate predators and prey interacting in a natural setting. TrophIE is based on the idea that humans, like other animals, can take foraging- and risk-related decisions to acquire resources and avoid predation. Hence, given a simple set of in-game rules governing consumer–resource interactions, players should optimize their decisions to maximize their in-game rewards. Harnessing the organismal nature of human players, this living 'agent-based model' removes the need for estimating numerous parameters otherwise necessary to generate realistic individual behaviour. In TrophIE, prey players must acquire resource points to reach reproductive status and avoid starvation while escaping predators in a landscape augmented with resource patches and refuges. Predator players must capture as many prey as possible during the allotted game time.

By altering game rules or changing the distribution of resources and refuges, investigators can generate countless scenarios to study consumer–resource interactions. The resulting high-resolution data can be used to explore hypotheses, gain insights on trophic interactions at the individual and population levels and foster the development of new methodologies. As an example, with only nine half-hour games, TrophIE generated 87.5h of tracking data, 1976 prey–resource and 130 predator–prey interactions describing the behaviour of 255 player-games. The method can also serve as a powerful resource for teaching predator–prey interactions through active, experiential and collaborative learning.

We tested the validity of our approach through a set of proof-of-concept case studies, investigating the movement, habitat selection, functional response and spatial organization of consumer–resource interactions. Broadly, we hypothesized that, as observed in non-human organisms, players' movement speed would vary according to the landscape (Dickie et al., 2020; McKenzie et al., 2012), that they would select gain prospects and avoid risks (Stephens et al., 2007), that their gain rates would saturate at high resource density due to handling and searching time (Holling, 1965; Stephens et al., 2007) and that their interactions would be spatially structured (Pasquaretta et al., 2019). Hence, we (1) describe TrophIE and show how it can reproduce ecological dynamics, (2) share an open-source

dataset generated by playing TrophIE and (3) discuss the benefits and limitations of the game for the study of trophic interactions.

## 2 | MATERIALS AND METHODS

### 2.1 | Simulation arena

Games occurred at the Parc Éco-Laurentides (46.0459°, –74.4757°) near Val-Morin, Québec, Canada. The eastern side of the area was bordered by a lake and a river, but there were otherwise no hard frontiers to the playable area. However, resource patches and refuges were distributed over 0.18km<sup>2</sup> and were never further than 85m from a trail, keeping most players within this area. The park consisted mostly of easily walkable mixed forest speckled with boulders, depressions and small hills and was crossed by a single large (width: 5m) trail and a network of smaller ones (width: 1.5m).

### 2.2 | Player roles

Players could choose between three roles each identified by a distinct colour jersey: prey, meso-predator or apex predator. Prey players' goal was to acquire resources, reproduce and avoid being killed by predators. They had to collect a predefined number of resources to survive (starvation threshold) and a larger number of resources to reproduce (reproduction threshold). They were never allowed to run, but they had access to refuges as shelters against apex predators. Meso-predators had to catch as many prey as possible while avoiding being killed by apex predators. Like prey, they were not allowed to run and could use refuges to find safety from apex predators. They could kill prey anywhere, including in refuges. Apex predators had to catch as many prey or meso-predators as they could during the designated game time. They could run, but they did not have access to refuges.

At the beginning of every game, organizers decided the number of apex predators and meso-predators in play. This number changed between games to create variations in predation risk. Players were then free to choose their role (prey, meso-predator or apex predator) until the desired amount of each role was filled.

### 2.3 | Resource patch and refuge locations

Resource patches and refuges (hereafter collectively designated as in-game features) consisted respectively of brightly coloured envelopes and forestry flags attached to one-meter-high metal poles. They were deployed by game organizers who walked the arena and chose their location as randomly as possible within the constraints imposed by site accessibility. Every game feature was given a unique ID and was georeferenced. In total, 73 resource patches and 39 refuge posts were deployed. They remained in the same locations across all games.

## 2.4 | Resource patch design

Resource acquisition was designed as a random draw. To obtain resources, prey players had to pull a card from the envelope attached to a resource patch (Figure 1b). The card consisted of a single column of 46 cells that each specified a random item (i.e. resource type A worth 5 points, type B worth 1 point, or X worth no points). Thus, a consumption attempt consisted of uncovering the next hidden cell by partially pulling the resource card out of the envelope in the hope that the cell would reveal a resource A or B instead of an X. Before each draw, prey players had to wait a short period of time reflecting within-patch search time. When their draw was successful, prey players had an additional predefined handling time for consumption and recorded the acquired resource on a mobile app (EarthRanger, see Data Logging and Box 2). Specific handling times used in our simulations are provided in Game parameters and Box 1.

Resource cards followed predefined probability distributions and were initially conceived to emulate diminishing returns (i.e. the gain rate declined as a function of exploitation). However, due to a coding error discovered only after data collection, resource cards provided gain rates that remained stable over time. Incorporating diminishing returns could be useful to explore questions related to optimal foraging.

## 2.5 | Game parameters

The number of players, competition intensity, prey resource acquisition thresholds and reproduction thresholds varied between games. In total, nine games were played, with a varying number of players ranging from 23 to 31, with 2–3 apex predators, 1–2 meso-predators and 18–26 prey players.

Competition among prey was introduced by modulating how the use of a patch by a player affected subsequent resource availability through three different scenarios: weak, mid and strong competition (Box 1). In the weak competition scenario, players arriving at a new resource patch were asked to start foraging from the top of the resource envelope, thus effectively resetting the envelope and avoiding any previous depletion of resources by other players. They could, however, not return to the same patch twice. In the mid-competition scenario, the envelopes were left as is after a visit, thus reducing the total amount of resources available for future players foraging at that resource patch. Finally, in the strong competition scenario, players were not allowed to forage from an already used resource patch at all.

Starvation and reproduction thresholds were set for prey at the beginning of each game. Prey had to collect a minimum of points to be considered 'alive' by the end of the game (between 30 and 40 in our simulations), and a larger amount to reach reproductive status (50 to 60 in our simulations). Once two players reached the reproduction threshold, they could find each other and record a reproduction event. Predators of both types had to catch at least one player to avoid starvation.

Handling times were fixed across games. Prey had to wait 10s for each resource consumption attempt (uncovering a resource cell), 10s for each consumption (when the uncovered cell contained A or B) and 30s when reproducing with another player. Predators capturing another player had to wait 30s at the kill site before hunting again.

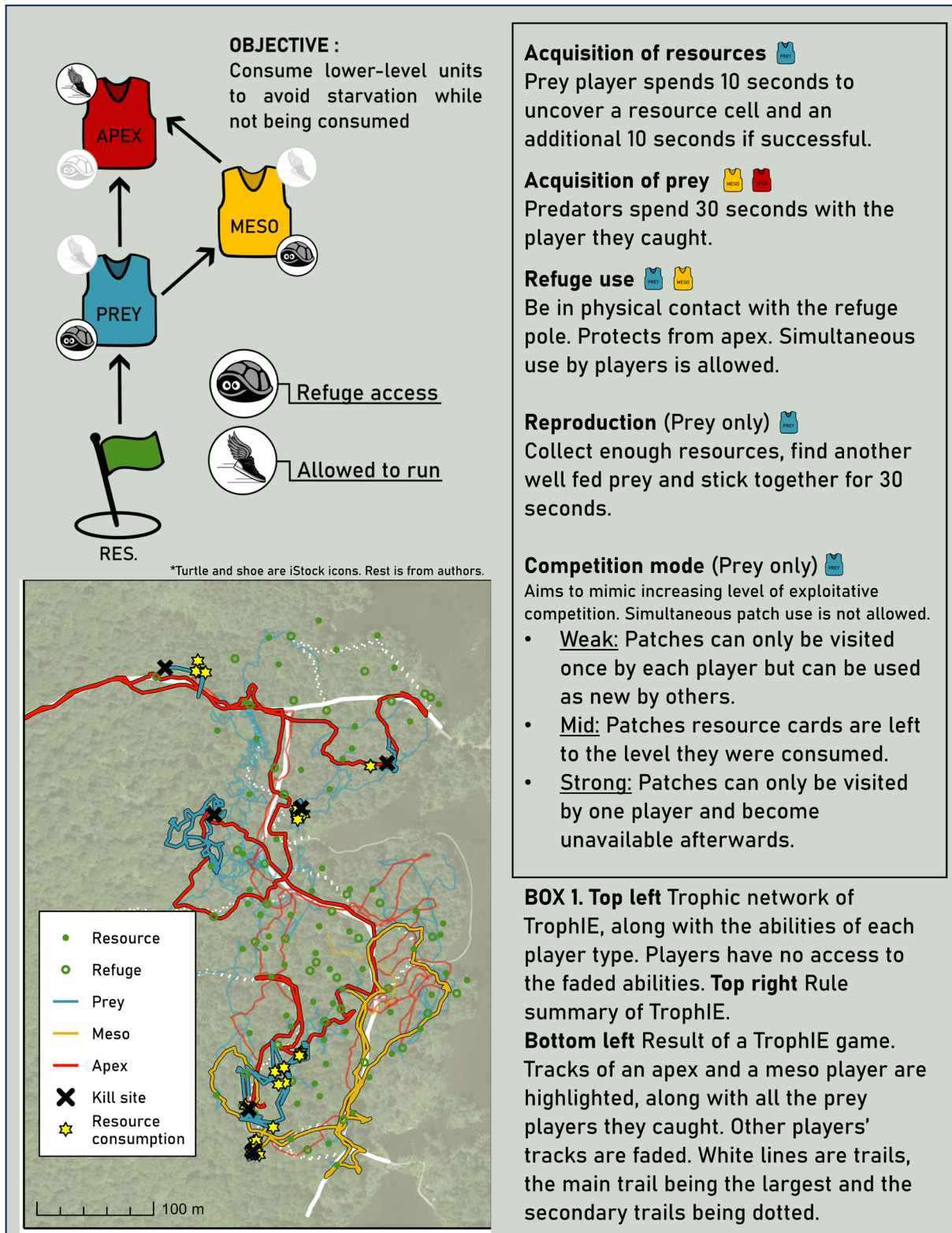
## 2.6 | Data logging

Each player carried a smartphone with two applications: GAIA GPS (TrailBehind Inc., 2023) and EarthRanger (Allen Institute for



**FIGURE 1** Study population. Panel (a) shows a rare feat in animal studies where most of the population was captured in a single frame, demonstrating the ease of working with docile members of the *Homo sapiens sapiens* species. However, no population bends perfectly to the expectations of experimenters and some members of the ssp. *principal investigators* (Inset c) will willfully adopt extreme behaviours. Panel (b) shows an anonymous prey foraging for resources. Note that here, prey players are wearing yellow jerseys, while apex predator and meso-predator players are respectively in red and blue.

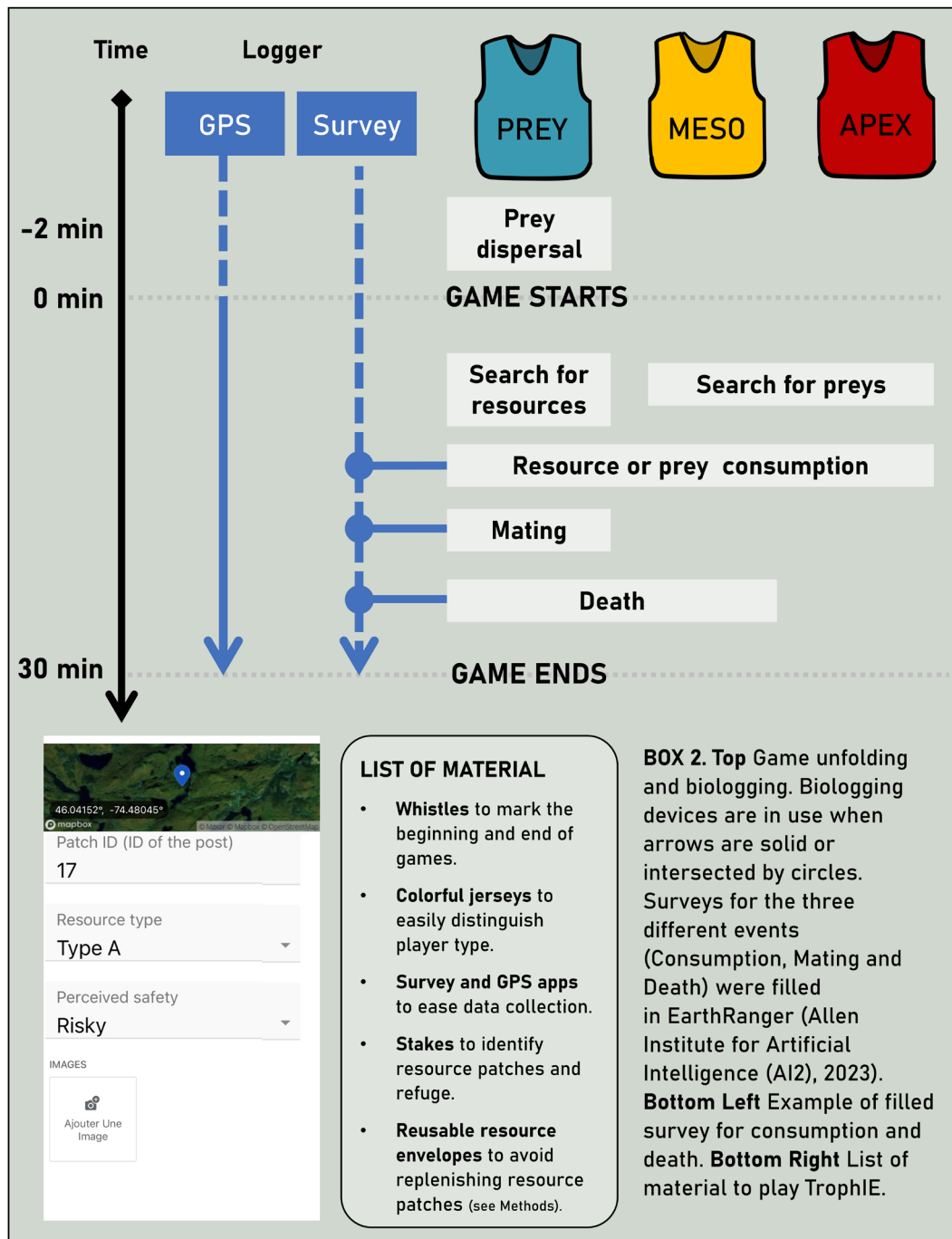
## BOX 1 TrophIE game rules and simulation parameters



**BOX 1. Top left** Trophic network of TrophIE, along with the abilities of each player type. Players have no access to the faded abilities. **Top right** Rule summary of TrophIE.

**Bottom left** Result of a TrophIE game. Tracks of an apex and a meso player are highlighted, along with all the prey players they caught. Other players' tracks are faded. White lines are trails, the main trail being the largest and the secondary trails being dotted.

## BOX 2 TrophIE game progression and setup material



AI, 2023; Wall et al., 2024). GAIA GPS was our primary way of tracking player movements, with an average logging frequency of 6 s (95% CI [2, 27]). Every player started the application at the beginning of each playing day and then sent their data to the organizers. During games 6–9, players were also equipped with the AxyTrek biologging device from TechnoSmArt, Italy. These

devices provided accelerometry data (not used in the paper) and fully substituted GPS tracks in 14% of player-games (i.e. a game record for a given player) where mobile app tracking was unavailable due to user error or outdated devices that did not meet app specifications. Both methods allowed the collection of tracking data for 94% of player-games.

We used EarthRanger to register events of resource consumption, death and reproduction (Box 2, bottom). For each of those events, a quick survey had to be completed, and both the location and time of the events were automatically registered. For example, after successfully acquiring a resource, a prey player opened the app, selected the 'Resource' survey, and registered the patch resource ID and the resource type (A or B). A 'perceived safety' field was added in Games 6 through 9 so that prey could rate how safe they felt when acquiring a resource using a Likert scale from 0 (very risky) to 5 (very safe).

## 2.7 | Game start and duration

Games were set to last 30 min. Timekeepers were equipped with a chronometer (or watch) and a whistle. They used whistles to indicate the beginning and end of each game. Prey were given 2 min to disperse before predators started playing the game, at the whistle blow.

## 2.8 | Analyses

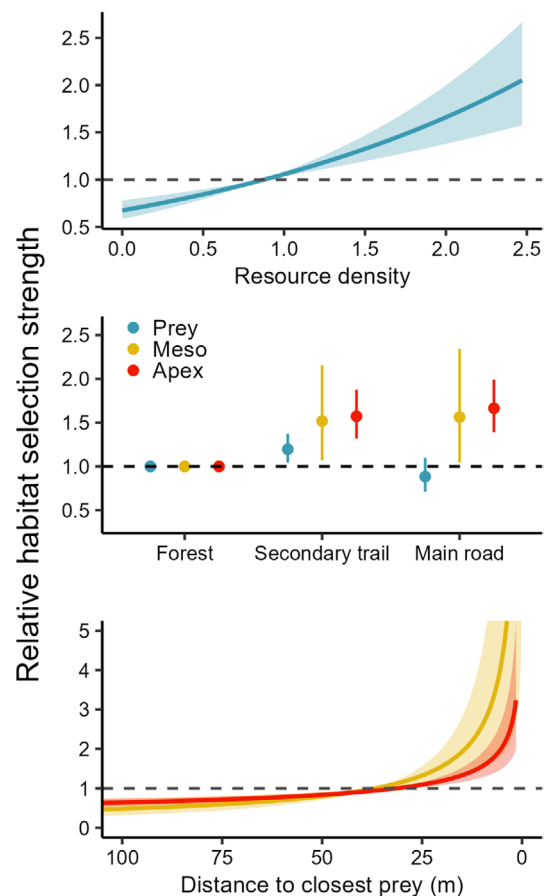
We investigated the movement, habitat selection, functional response and spatial organization of players throughout the games to assess whether TrophIE could reliably reproduce ecological dynamics expected in natural systems. Specifically, we assessed (1) how trade-offs between foraging, safety and search efficiency shaped players' habitat selection; (2) how terrain type and landscape features influenced player speed and predator kill location; (3) the shape of prey functional response and the influence of intrinsic and environmental variables on prey gain rates; (4) whether prey–resource interactions were spatially modular and influenced by landscape features. These diverse aspects of predator–prey interactions were investigated through (1) step-selection functions based on landscape features (refuge and resource density, distance to trails) and proximity to the nearest predator or prey, (2) linear mixed models linking player speed to terrain type (main or secondary trails, forest), along with habitat selection analysis comparing kill site locations to prey terrain use, (3) generalized linear mixed models relating prey player's gain rate to predator proximity, competition mode, number of already acquired resources, and trail proximity and (4) network analysis on a bipartite network built with prey and resource patches as nodes and feeding events as edges. The details of all analyses can respectively be found in Appendices A–D.

## 2.9 | Permits

The methods were approved by the ethics committee for research with humans of Université Laval (CÉRUL, Comité d'éthique de la recherche avec des êtres humains de l'Université Laval, # 2025-316/24-07-2025).

## 3 | RESULTS

TrophIE players were found to properly mimic the movement of complex biological agents and displayed trade-offs between resource abundance, safety and search efficiency. Indeed, players selected places with a high abundance of either prey or resource patches, avoided risky places and preferentially used linear features that facilitated movements (Figure 2; Appendix A). For instance, all players selected secondary trails, which allowed efficient exploration of the playground, but prey players—exposed to predation risk—showed the lowest selection towards secondary trails and avoided the main trail that was heavily patrolled by predators (Figure 2). Interestingly, TrophIE's extensive dataset allowed for the exploration of site familiarity, defined by the positive selection of known places, a mechanism that is often difficult to study in natural systems and which here



**FIGURE 2** Habitat selection of prey (blue), meso-predator (yellow), and apex predator (red) players assessed through an integrated step-selection function. The figure shows selection strengths predicted from an integrated step-selection model relative to the reference level, set to the average value for all covariates. Resource density was measured through quartic kernel density estimation on resource patch locations. The distance to the closest prey is the minimal distance between the player and a prey within the last minute before the considered step. Dots and lines are predicted values presented with their 95% confidence interval. Dashed lines represent the threshold value of neutral selection.

proved to be a strong determinant of player movement. Indeed, both predator types and prey strongly selected familiar sites, preferentially using areas visited in previous games rather than unexplored locations regardless of their previous roles.

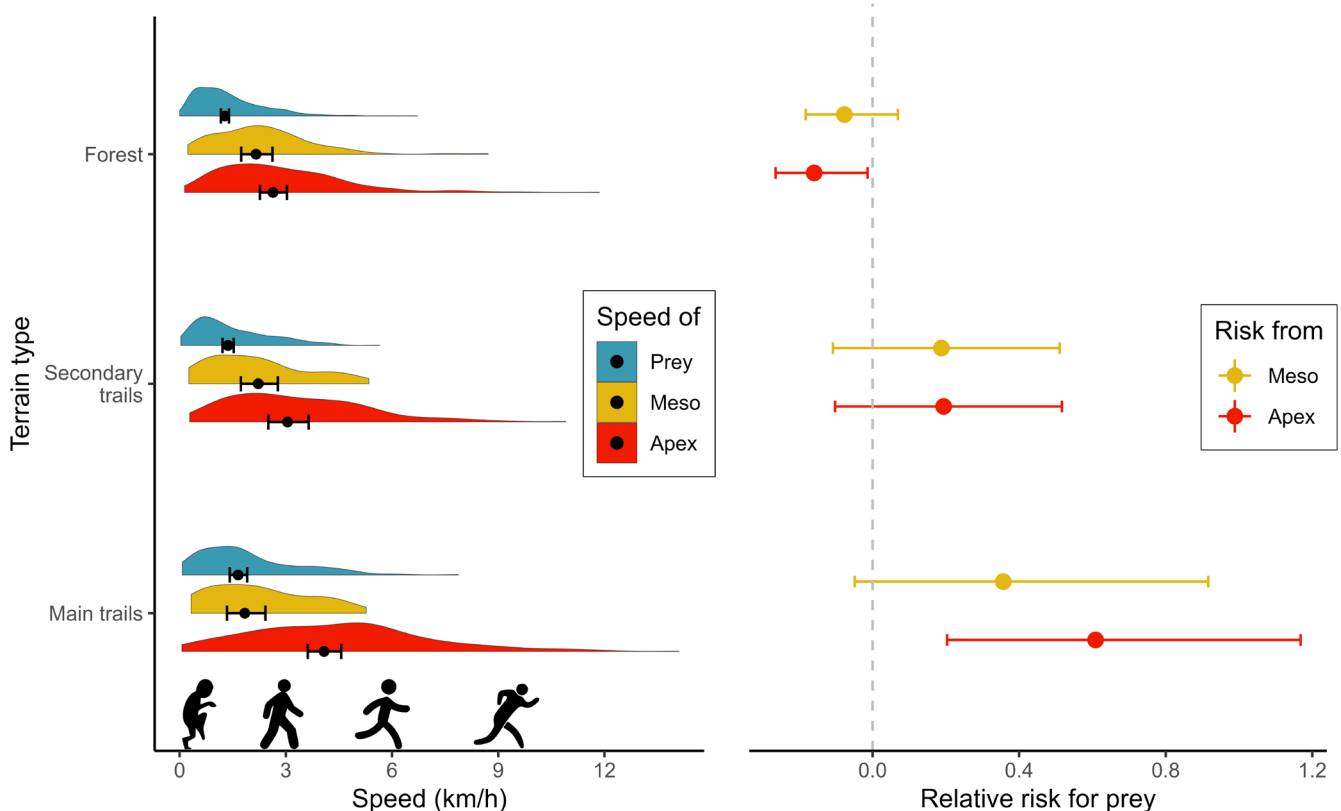
The behavioural consequences of player movement decisions were also reflected in the speed at which players moved and where prey players died (Appendix B). Indeed, predator speed and kill rates varied with landscape features as could be expected in natural systems. For example, apex predators, which strongly selected the main trail, moved twice as fast on this linear feature compared to the forest, leading to higher search efficiency and encounter rates (Figure 3; Appendix B). This made main trails the riskiest terrain for prey players (Figure 3; Appendix B).

Prey foraging rates followed a realistic functional response and were shaped by predator proximity, satiety level (the ratio between the current number of resources acquired and the reproduction threshold) and intraspecific competition (Appendix C). Prey players had lower foraging rates when either type of predator was nearby (Figure 4) and when intraspecific competition was high (Appendix C). The satiety level, which is particularly challenging to measure in the wild, also emerged as a driver of foraging decisions. Indeed, prey

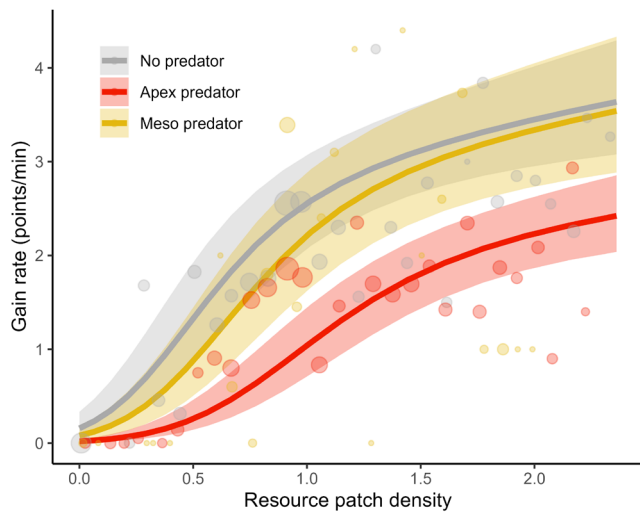
reduced foraging rates as they got closer to the resource threshold needed for reproduction (Appendix C).

The detailed dataset and large number of prey players provided an opportunity to scale up from individual behaviours to the spatial structure of consumer–resource interactions, something rarely feasible in natural systems. Indeed, prey–resource interactions were spatially modular, structured by prey players' limited movement rates and by their avoidance of the main trail (Figure 5; Appendix D). The high modularity of prey–resource interactions ( $Q=0.791$ ) could be expected given prey's low speed and need to avoid detection by predators. In addition, the main trail, which was risky and avoided by prey, partially structured prey–resource interactions and increased the modularity of the empirical network. Indeed, the probability that two resources separated by the main trail belonged to the same module was lower than expected based on distance alone.

The empirical results derived from TrophE case studies support our main hypothesis that predator–prey dynamics expected in natural systems can emerge from the behaviour of human players following a simple set of rules, at least with respect to habitat selection, movement, resource consumption and spatial organization. This statement represents the main result of our investigation.



**FIGURE 3** Left. Average speed of each player type in different terrains. Points and 95% CI are estimates of a random slopes model controlling for player ID. Right. Relative risk of each terrain type for prey. Coloured distributions are the raw data. The degree of risk was estimated by dividing the proportion of kills happening in a terrain type by the proportion of time spent by prey in this same terrain. Hence, a terrain where kills happen more often than expected based on the proportional use of this terrain by prey is considered risky (positive values).



**FIGURE 4** Functional responses of prey players when no predator is in the vicinity (grey), in the presence of a close meso-predator (yellow), or in the presence of a close apex predator (red). Gain rates were calculated as the number of resources acquired over 5-min intervals. Resource patch density and distance to the closest predators were estimated every 15 secs and averaged over the same 5-min interval. Predictions for each predator type were made by considering a short distance between the prey and the focal predator type (50 m) and a large distance between the prey and the other predator type (>200 m). Points are raw gain rates, averaged over 30 brackets, each one representing 1/30th of the x axis. Point size is proportional to the number of observations present in the bracket.

## 4 | DISCUSSION

We developed a game where players impersonate predators and prey in a natural landscape augmented with resource patches and refuges. We found that, given a minimal set of simple rules, the habitat selection, movement strategy, foraging behaviour and large-scale spatial organization of players replicated expected patterns of consumer–resource interactions found in non-human organisms. Using limited financial resources and few assumptions, the game produced a rich dataset that would be hard to obtain in natural systems, which can be used to test and explore complex hypotheses. Real-life games such as TrophIE offer a promising approach that could complement theoretical modelling and empirical studies to investigate the detailed ramifications of predator–prey interactions.

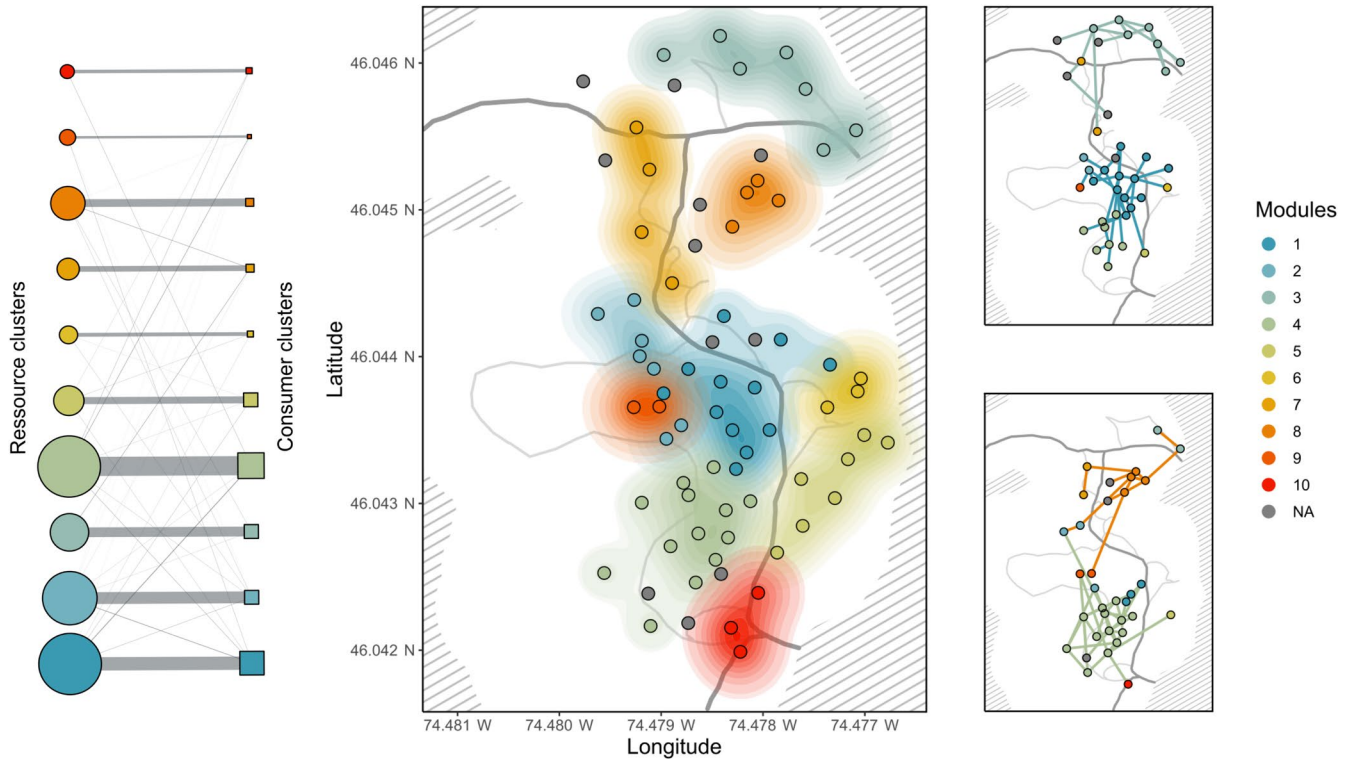
TrophIE is a simulation tool designed to explore ecological theories through artificial experiments similar to those performed with mathematical models. In TrophIE, the ecological context is manipulated by changing in-game rules. We manipulated predation risk by changing the number of predators in play and increased intraspecific competition by restricting access to resource patches after a single use. Researchers can thus compare the outcomes of different scenarios to explore ecological hypotheses. The approach offers great flexibility as new rules can be created quickly without the need to develop complex systems of equations or simulation software. In our simulations, we imposed a speed difference between players,

but other traits such as hearing, camouflage, anti-predator defence, diet and handling time can quickly be adjusted. Cryptic behavioural states such as site familiarity, satiety or perceived risk can also be easily monitored, providing opportunities to explore otherwise challenging mechanisms and hypotheses. While computer-based simulations may be better suited for long-term or large-scale processes requiring many iterations (e.g. evolutionary dynamics, species range limits), TrophIE offers a simple and complementary approach for exploring a broad range of research questions, including optimal behaviour, habitat selection and trophic interactions. We provide a non-exhaustive list of ideas for rule modifications in [Table 1](#) and a guide for readers to implement their own simulations in [Appendix E](#).

TrophIE distinguishes itself from other modelling approaches by relying on living agents—players—making decisions in a real-world setting. This aspect alleviates the computational and empirical burden of defining and estimating decision-related parameters needed to build simulators. It also provides a level of ecological realism that, for systems that can be roughly mimicked by players, cannot currently be matched by computer simulations. For instance, a prey player in TrophIE may hear a predator at a distance, move to cover, increase vigilance, detect the predator visually, assess risk, and decide whether it is safer to stay immobile or move to the nearest refuge. In natural systems, prey species can adopt similar behaviour, but calibrating such complex decision sequences in a computer simulation would be highly challenging.

The interesting level of ecological realism achievable through TrophIE can make simulations less tractable than simpler, more deterministic approaches and comes at a cost of few replicates. Environmental sources of variation such as landscape features or weather conditions, individual player heterogeneity and stochastic processes will impact the outcome of these experiments. This can complicate result interpretation, especially given that conducting a large number of simulations is often not logistically feasible. However, this complexity also provides interesting opportunities for hypothesis testing (e.g. whether the proportion of different personality traits among prey influence predation rates at the population level, or if adverse weather alters interaction frequencies). Indeed, variations among individuals, often exacerbated by the environment, are ubiquitous in natural systems, but challenging to incorporate in statistical models and theoretical approaches (Bolnick et al., 2011; Gimenez et al., 2018; Ning & You, 2019; Shoemaker et al., 2020; Vindenes & Langangen, 2015). It requires identifying and accurately modelling multiple sources of variability that often have scale-dependent effects on population and community dynamics (Gimenez et al., 2018; Ning & You, 2019). Many sources of such environmental and individual variations are implicitly included in TrophIE simulations. The approach could thus be used to assess whether ecological theory holds under individual and environmental stochasticity.

The use of human players is what makes TrophIE interesting but could backfire if human behaviour is too unique to be informative about biological fundamentals. However, as reviewed in Brosnan and Postma (2017), humans as model organisms have been informative in many fields and it has been argued that they can, in most



**FIGURE 5** Left: Bipartite representation of the prey (squares) and resources (circles) interaction network of the TrophIE games aggregated by modules (colours). Symbol size is proportional to the number of nodes in each module and edge width is proportional to cumulative edge weight (total number of prey–resource interactions between groups of nodes). Center: Spatial distribution of resource patches (circles) and their assigned modules (colours) within the TrophIE arena (white background). Trails found within the arena are illustrated as grey lines. Thick lines represent the main trails while thin lines are secondary trails. Density kernels were used to illustrate the spatial association of each module. Right: Highlight of the indirect interactions between resources of Modules 1 and 3 (top) and Modules 4 and 8 (bottom). Lines between resources indicate that at least one indirect interaction was created by a sequential movement of a prey player from one resource to the other.

cases, be considered as ‘just another mammal’ (Sterelny, 2017). Humans evolved facing trade-offs that are very similar to those that animals experience in the wild and, while the constraints we face have changed, resource allocation and risk trade-offs remain. As with studies on any taxa, species-specific traits must be kept in mind when interpreting results. Studies on mammals are often not directly transferable to fish, arthropods or micro-organisms, but can still be highly informative. Humans are visual, mobile, behaviourally plastic and have high cognitive capacity. The specific set of rules we presented might be more useful to study visual predators with good memory than static filter-feeding consumers. Yet, the scope of research questions addressed through such games can be broadened by adding new rules or constraints to emulate taxon-specific traits.

A main point of concern is that in-game motivations of humans differ from those of animals: We play for fun, while animals fight for survival and reproduction. This could lead to different behaviours related to resource acquisition and safety trade-offs (e.g. excessive risk-taking behaviours), at times fostering illogical choices (sensu McNamara et al., 2014) or behaviours that deviate from optimality. Interestingly, suboptimal behaviours seem common in animals (e.g. Aw et al., 2009; Shafir et al., 2002), and we know little about

how such behaviour can impact the validity of ecological theories. Moreover, there is always interindividual variability in game rules interpretation and level of compliance. For example, prey and mesopredator players were instructed to walk at all times, but their self-imposed speed limit varied from slow-paced to race walking. Large deviations from game rules could bias the outcome of TrophIE simulations, yet reasonable variability leads to individual heterogeneity and likely increases realism. The agency of human players working with few constraints can also have interesting outcomes as it may lead to emergent and biologically plausible strategies. An example of this is the production of mating calls: As moving was risky, some prey players who had reached the reproduction threshold started calling from a refuge to signal their location to potential partners. This biologically plausible behaviour emerged without being suggested by any specified rule.

Another underlying assumption is that participants' sole objective when playing is to reach the game goals (consume resources, reproduce and survive). Playing with specific hypotheses in mind could influence participants' behaviour in a scientifically undesirable manner. Also, boredom or curiosity about the game properties could lead to extreme behaviours that do not reflect natural variability. These drawbacks can be reduced through blind experiments, where

TABLE 1 List of ideas for future TrophIE simulations.

Interest in	Modifications	Possible outcomes
Information availability	<ul style="list-style-type: none"> <li>• Vary communication ability between players</li> <li>• Impede players' senses (e.g. wear ear plugs)</li> <li>• Players are omniscient (e.g. provide a map of resource patches)</li> </ul>	<ul style="list-style-type: none"> <li>• Access to public information benefits prey</li> <li>• Vocal prey players face higher predation risk</li> <li>• Omniscience favours the ideal free distribution of players</li> </ul>
Detection distance	<ul style="list-style-type: none"> <li>• Add auditory cues to resource patches, refuges or other players.</li> <li>• Impede players' senses.</li> </ul>	<ul style="list-style-type: none"> <li>• Increased detection distance of predators and resource patches respectively makes movement more risk-sensitive AND more selective of high patch density area.</li> </ul>
Patch quality	<ul style="list-style-type: none"> <li>• Patch quality varies and can be either known from a distance or from sampling.</li> </ul>	<ul style="list-style-type: none"> <li>• Residence time in each type of patch will vary according to patch quality, local variance in patch quality, the ability to know patch quality before sampling and travel cost between patches (e.g. predation risk).</li> </ul>
Patch aggregation	<ul style="list-style-type: none"> <li>• Vary the aggregation of resource patches</li> </ul>	<ul style="list-style-type: none"> <li>• Aggregation of resource patches should cascade to the aggregation of predator–prey interactions and loss of connectivity.</li> </ul>
Prey quality	<ul style="list-style-type: none"> <li>• Vary the quality, characteristics (ease of movement, access to refuges, handling time) and abundance of prey players</li> </ul>	<ul style="list-style-type: none"> <li>• Prey survival will depend on their selection by predators or their proximity to selected prey.</li> </ul>
Resource hoarding	<ul style="list-style-type: none"> <li>• Allow players to move resource patches and to take others' resources if undefended.</li> </ul>	<ul style="list-style-type: none"> <li>• Hoarding should favour survival and score when facing high predation risk.</li> <li>• Hoarding should also reduce prey players movement and lead to the active defence of territories.</li> </ul>
Central place foraging	<ul style="list-style-type: none"> <li>• Players must return to a given location every time they accumulate a given number of points.</li> </ul>	<ul style="list-style-type: none"> <li>• Predators' home range shrinks and the landscape of risk becomes more heterogeneous.</li> <li>• Score and survival of prey players becomes dependent on their central place location.</li> </ul>
Omnivory	<ul style="list-style-type: none"> <li>• Introduce omnivore players, which can consume prey and resources but with an equal or lower benefit than predators and prey.</li> </ul>	<ul style="list-style-type: none"> <li>• Diet of omnivore players will depend on prey and patch abundance as well as predation risk.</li> </ul>
Collaboration	<ul style="list-style-type: none"> <li>• Encourage players to collaborate by allowing resource sharing.</li> </ul>	<ul style="list-style-type: none"> <li>• The benefits of collaborating (sharing resources) will be greater in adverse conditions (e.g. high predation risk).</li> </ul>

the tested hypothesis is unknown to participants, by accentuating the importance of staying within the game's objectives, or simply by playing with non-ecologists.

We developed TrophIE by integrating core predator–prey principles, which are grounded in ecological theory and present in many systems (i.e. handling times, speed differences between predators and prey, and the presence of refuges) in order to explore emergent ecological properties. Our initial goal was to collect every interaction of every player during each game—a goal achieved with a 94% success rate, as some tracking devices failed to function properly. Even if based on only nine games of roughly 30min, the ability of this method to efficiently recreate plausible consumer–resource dynamics could make it a benchmark dataset for advanced methodological development. Such synthetic data can provide valuable insights to identify gaps in our knowledge of biological systems (Poisot et al., 2016). Although they cannot fully substitute the use of data collected in natural systems, synthetic datasets can serve as an efficient proxy when access to their real-world counterpart is

hindered by technological, financial, data sharing or fieldwork logistical challenges (Poisot et al., 2019; Roche et al., 2022).

While our simulations generated a comprehensive dataset that can be used to explore biological hypotheses, the main innovation of our study lies in the method itself. The approach is highly flexible, allowing for the exploration of a wide range of hypotheses limited only by players' traits, investigators' imagination and the logistical challenges posed by terrain availability and biologging devices. Playing TrophIE can also in itself generate interesting externalities. Rarely in our activities do we face situations similar to what a prey or a predator can experience, and these short immersions can make our understanding of predator–prey interactions more holistic. Indeed, having felt—a diluted version of—predation risk while having to forage, it becomes easier to understand the challenges prey can encounter, and how they may overcome them. For example, it became clear to most players that trails were a risky and defining feature of the area in which we played, even though absolutely no rules had been imposed in this regard. As animal behaviour is influenced by a plethora

of factors, immersing ourselves in games such as TrophIE can likely foster the generation of relevant and original ideas.

The immersive understanding gained by playing TrophIE also makes the game an interesting pedagogical tool to teach consumer–resource interactions. Contemporary learning theories propose that learning is most effective when it is active, experiential, situated, problem-based, and provides immediate feedback (e.g. Boyle et al., 2011; Freeman et al., 2014), since these approaches activate multiple cognitive processes (e.g. motivation, attention, memory, problem-solving) and engage students emotionally and/or socially (Dubinsky & Hamid, 2024). Indeed, games used in teaching have been shown to increase students' engagement, knowledge acquisition and conceptual learning (e.g. Connolly et al., 2012). TrophIE simulations incorporate all these elements. In our experience with undergraduate and graduate students, playing TrophIE frequently sparked animated discussions about predator–prey interactions and stimulated critical thinking among participants who contrasted their own playing experience with ecological theories. It also strengthened group cohesion among students and promoted a collaborative learning environment.

## 5 | CONCLUSION

In this paper, we introduced TrophIE, an innovative game where human players act as predators and prey within an augmented natural environment. Our findings demonstrate that, despite the inherent differences between humans and non-human organisms, the players' behaviours mirrored natural predator–prey dynamics with respect to habitat selection, movement strategies, foraging trade-offs and spatial organization. These behaviours emerged from the combination of simple game rules and the physical game setup, highlighting the potential of using real-life simulations to produce rich datasets that can serve as valuable proxies in ecological research. Additionally, the game's flexibility allows for adjustments to simulate various functional traits, making it a versatile tool for exploring different ecological scenarios.

While acknowledging the constraints of human behaviour and the artificial nature of the game environment, our study underscores the potential benefits of using human players in ecological simulations. The ability to collect detailed behavioural data, coupled with the insights gained from immersive participation, positions TrophIE as a promising approach to complement theoretical models and empirical studies. It also provides a powerful teaching tool, bringing ecological concepts to life through hands-on experiential learning. Ultimately, our method offers a novel avenue for ecological research and teaching, capable of generating valuable insights and fostering a deeper understanding of predator–prey interactions.

### AUTHOR CONTRIBUTIONS

*Conceptualization:* David Bolduc, Frédéric Dulude-de-Broin, Gabriel Bergeron, Matthieu Weiss-Blais, Catherine Villeneuve, Maxime Fraser-Franco, Pierre Legagneux, Dominique Gravel, Daniel Fortin,

Antoine Allard, Sophie Gallais, Pierre-Olivier Montiglio. *Methodology:* David Bolduc, Frédéric Dulude-de-Broin, Gabriel Bergeron, Matthieu Weiss-Blais, Catherine Villeneuve, Maxime Fraser-Franco, Clément Couloigner, Rachel Dubourg, Pierre Legagneux, Dominique Gravel, Daniel Fortin, Antoine Allard, Louis Moisan, Pierre-Olivier Montiglio. *Software:* David Bolduc, Frédéric Dulude-de-Broin, Gabriel Bergeron, Catherine Villeneuve, Francis Banville, Clément Couloigner, Rachel Dubourg, Matthieu Weiss-Blais. *Validation:* David Bolduc, Frédéric Dulude-de-Broin, Gabriel Bergeron, Matthieu Weiss-Blais, Catherine Villeneuve, Maxime Fraser-Franco, Francis Banville, Clément Couloigner, Rachel Dubourg, François Thibault, Louis Moisan. *Formal analysis:* David Bolduc, Frédéric Dulude-de-Broin, Gabriel Bergeron, Matthieu Weiss-Blais, Catherine Villeneuve, Maxime Fraser-Franco, Francis Banville, Clément Couloigner, Rachel Dubourg, François Thibault, Daniel Fortin, Louis Moisan, Irene Roca, Clément Massé, Tamara Hiltunen, Mathilde Lapointe St-Pierre, Pierre-Olivier Montiglio. *Investigation:* David Bolduc, Frédéric Dulude-de-Broin, Gabriel Bergeron, Matthieu Weiss-Blais, Catherine Villeneuve, Maxime Fraser-Franco, Francis Banville, Clément Couloigner, Rachel Dubourg, François Thibault, Louis Moisan, Camille Gaudreau-Rousseau, Clément Massé, Emily Madsen, Alexandra Engler. *Resources:* Pierre Legagneux, Daniel Fortin, Dominique Gravel. *Data Curation:* David Bolduc, Frédéric Dulude-de-Broin, Catherine Villeneuve. *Writing Original Draft:* David Bolduc, Frédéric Dulude-de-Broin, Gabriel Bergeron, Matthieu Weiss-Blais, Catherine Villeneuve, Maxime Fraser-Franco, Francis Banville, Clément Couloigner, Rachel Dubourg, François Thibault, Louis Moisan, Camille Gaudreau-Rousseau, Irene Roca, Emmanuelle Barreau, Mathilde Lapointe St-Pierre. *Writing Review & Editing:* David Bolduc, Frédéric Dulude-de-Broin, Gabriel Bergeron, Matthieu Weiss-Blais, Maxime Fraser-Franco, Francis Banville, Clément Couloigner, Rachel Dubourg, Pierre Legagneux, François Thibault, Dominique Gravel, Daniel Fortin, Antoine Allard, Louis Moisan, Camille Gaudreau-Rousseau, Audrey Durand, Emmanuelle Barreau, Morgane Le Goff, Mathilde Lapointe St-Pierre, Emily Madsen, Alexandra Engler, Sophie Gallais, Norma Rocio Forero Muñoz, Maria Isabel Arce Plata, Akiko Kato, Pierre-Olivier Montiglio. *Visualization:* David Bolduc, Frédéric Dulude-de-Broin, Gabriel Bergeron, Matthieu Weiss-Blais, Maxime Fraser-Franco, Francis Banville, Clément Couloigner, Rachel Dubourg, François Thibault, Louis Moisan, Camille Gaudreau-Rousseau, Irene Roca, Catherine Villeneuve. *Supervision:* Pierre Legagneux, Dominique Gravel, Daniel Fortin, Antoine Allard, Audrey Durand, Pierre-Olivier Montiglio, Akiko Kato. *Project Administration:* Pierre Legagneux, Dominique Gravel, Daniel Fortin, Antoine Allard, Sophie Gallais, Pierre-Olivier Montiglio. *Funding Acquisition:* Pierre Legagneux, Dominique Gravel, Antoine Allard, Audrey Durand, Sophie Gallais.

### ACKNOWLEDGEMENTS

We sincerely thank Alex Arkilian, Gabriel Dansereau, Fanny Thiery, Mélisande Teng, and Guillaume Blais for their enthusiastic participation in data collection. We also thank the Parc Éco-Laurentides team for making their wonderful site available to us.

## CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

## PEER REVIEW

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/2041-210X.70180>.

## DATA AVAILABILITY STATEMENT

Data and code to reproduce all analyses are available via GitHub [https://github.com/gabrielbouleau/TrophIE\\_pub.git](https://github.com/gabrielbouleau/TrophIE_pub.git) and Zenodo <https://doi.org/10.5281/zenodo.17236628> (Bolduc et al., 2025).

## ORCID

David Bolduc  <https://orcid.org/0000-0003-0851-2791>

Frédéric Dulude-de Broin  <https://orcid.org/0000-0003-4955-156X>

org/0000-0003-4955-156X

Matthieu Weiss-Blais  <https://orcid.org/0000-0002-8049-5271>

Maxime Fraser-Franco  <https://orcid.org/0000-0002-8687-8513>

Pierre-Olivier Montiglio  <https://orcid.org/0000-0002-1313-9410>

Emily Madsen  <https://orcid.org/0000-0003-4108-6608>

Alexandra Engler  <https://orcid.org/0000-0002-2495-9764>

Pierre Legagneux  <https://orcid.org/0000-0002-6366-0554>

## REFERENCES

- Allen Institute for AI. (2023). *EarthRanger* (Version 2023.1) [Software]. <https://allennai.org/earthranger>
- Aw, J. M., Holbrook, R. I., de Perera, T. B., & Kacelnik, A. (2009). State-dependent valuation learning in fish: Banded tetras prefer stimuli associated with greater past deprivation. *Behavioural Processes*, 81(2), 333–336.
- Bolduc, D., Dulude-de Broin, F., Bergeron, G., Villeneuve, C., Weiss-Blais, M., Couloigner, C., Dubourg, R., Fraser-Franco, M., Banville, F., Moisan, L., Montiglio, P.-O., Fortin, D., Thibault, F., Allard, A., Gaudreau-Rousseau, C., Roca, I., Durand, A., Massé, C., Barreau, E., ... Legagneux, P. (2025). Impersonating predators and prey to study trophic interactions through real-life simulations. Data at <https://doi.org/10.5281/zenodo.17236628>
- Bolnick, D. I., Amarasekare, P., Araújo, M. S., Bürger, R., Levine, J. M., Novak, M., Rudolf, V. H. W., Schreiber, S. J., Urban, M. C., & Vasseur, D. A. (2011). Why intraspecific trait variation matters in community ecology. *Trends in Ecology & Evolution*, 26(4), 183–192.
- Boyle, E. A., Connolly, T. M., & Hailey, T. (2011). The role of psychology in understanding the impact of computer games. *Entertainment Computing*, 2, 69–74.
- Brosnan, S. F., & Postma, E. (2017). Humans as a model for understanding biological fundamentals. *Proceedings of the Royal Society B: Biological Sciences*, 284, 20172146. <https://doi.org/10.1098/rspb.2017.2146>
- Buckling, A., Craig Maclean, R., Brockhurst, M. A., & Colegrave, N. (2009). The beagle in a bottle. *Nature*, 457(7231), 824–829.
- Caswell, H. (1988). Theory and models in ecology: A different perspective. *Ecological Modelling*, 43, 33–44. [https://doi.org/10.1016/0304-3800\(88\)90071-3](https://doi.org/10.1016/0304-3800(88)90071-3)
- Céré, J., Montiglio, P.-O., & Kelly, C. D. (2021). Indirect effect of familiarity on survival: A path analysis on video game data. *Animal Behaviour*, 181, 105–116. <https://doi.org/10.1016/j.anbehav.2021.06.010>
- Connolly, T. M., Boyle, E. A., MacArthur, E., Hailey, T., & Boyle, J. M. (2012). A systematic literature review of empirical evidence on computer games and serious games. *Computers & Education*, 59(2), 661–686.
- DeLong, J. P. (2021). *Predator ecology: Evolutionary ecology of the functional response* (p. 176). Oxford University Press.
- Dickie, M., McNay, S. R., Sutherland, G. D., Cody, M., & Avgar, T. (2020). Corridors or risk? Movement along, and use of, linear features varies predictably among large mammal predator and prey species. *Journal of Animal Ecology*, 89(2), 623–634.
- Doak, D. F., Estes, J. A., Halpern, B. S., Jacob, U., Lindberg, D. R., Lovvorn, J., Monson, D. H., Tinker, M. T., Williams, T. M., Wootton, J. T., Carroll, I., Emmerson, M., Micheli, F., & Novak, M. (2008). Understanding and predicting ecological dynamics: Are major surprises inevitable. *Ecology*, 89(4), 952–961.
- Dubinsky, J. M., & Hamid, A. A. (2024). The neuroscience of active learning and direct instruction. *Neuroscience & Biobehavioral Reviews*, 163, 105737.
- Fauteux, D., Gauthier, G., & Berteaux, D. (2016). Top-down limitation of lemmings revealed by experimental reduction of predators. *Ecology*, 97, 3231–3241. <https://doi.org/10.1002/ecy.1570>
- Forsman, J. T., Mönkkönen, M., & Hukkanen, M. (2001). Effects of predation on community assembly and spatial dispersion of breeding forest birds. *Ecology*, 82, 232–244. [https://doi.org/10.1890/0012-9658\(2001\)082\[0232:EOPOCA\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2001)082[0232:EOPOCA]2.0.CO;2)
- Fraser Franco, M., Santostefano, F., Kelly, C. D., & Montiglio, P.-O. (2022). Studying predator foraging mode and hunting success at the individual level with an online videogame. *Behavioral Ecology*, 33, 967–978. <https://doi.org/10.1093/beheco/arc063>
- Freeman, S., Eddy, S. L., McDonough, M., Smith, M. K., Okoroafor, N., Jordt, H., & Wenderoth, M. P. (2014). Active learning increases student performance in science, engineering, and mathematics. *Proceedings of the National Academy of Sciences of the United States of America*, 111, 8410–8415.
- Gilg, O., Hanski, I., & Sittler, B. (2003). Cyclic dynamics in a simple vertebrate predator-prey community. *Science*, 302, 866–868. <https://doi.org/10.1126/science.1087509>
- Gimenez, O., Cam, E., & Gaillard, J. M. (2018). Individual heterogeneity and capture–recapture models: What, why and how? *Oikos*, 127(5), 664–686.
- Grainger, T. N., Senthilnathan, A., Ke, P. J., Barbour, M. A., Jones, N. T., DeLong, J. P., Otto, S. P., O'Connor, M. I., Coblenz, K. E., Goel, N., Sakarchi, J., Szojka, M. C., Levine, J. M., & Germain, R. M. (2022). An empiricist's guide to using ecological theory. *The American Naturalist*, 199(1), 1–20.
- Grant, J. W. G., & Bayly, I. a. E. (1981). Predator induction of crests in morphs of the *Daphnia carinata* King complex. *Limnology and Oceanography*, 26, 201–218. <https://doi.org/10.4319/lo.1981.26.2.0201>
- Holling, C. S. (1959). Some characteristics of simple types of predation and parasitism. *The Canadian Entomologist*, 91, 385–398. <https://doi.org/10.4039/Ent91385-7>
- Holling, C. S. (1965). The functional response of predators to prey density and its role in mimicry and population regulation. *Memoirs of the Entomological Society of Canada*, 97, 5–60. <https://doi.org/10.4039/entm9745fv>
- Krebs, C. J., Boonstra, R., & Boutin, S. (2018). Using experimentation to understand the 10-year snowshoe hare cycle in the boreal forest of North America. *Journal of Animal Ecology*, 87, 87–100. <https://doi.org/10.1111/1365-2656.12720>
- Lima, S. L., & Dill, L. M. (1990). Behavioral decisions made under the risk of predation: A review and prospectus. *Canadian Journal of Zoology*, 68, 619–640. <https://doi.org/10.1139/z90-092>
- Lymbery, S. J., Webber, B. L., & Didham, R. K. (2023). Complex battlefields favor strong soldiers over large armies in social animal warfare. *Proceedings of the National Academy of Sciences of the United States of America*, 120, e2217973120. <https://doi.org/10.1073/pnas.2217973120>

- McKenzie, H. W., Merrill, E. H., Spiteri, R. J., & Lewis, M. A. (2012). How linear features alter predator movement and the functional response. *Interface Focus*, 2(2), 205–216. <https://doi.org/10.1098/rsfs.2011.0086>
- McNamara, J. M., Trimmer, P. C., & Houston, A. I. (2014). Natural selection can favour 'irrational' behaviour. *Biology Letters*, 10, 20130935. <https://doi.org/10.1098/rsbl.2013.0935>
- Ning, C., & You, F. (2019). Optimization under uncertainty in the era of big data and deep learning: When machine learning meets mathematical programming. *Computers & Chemical Engineering*, 125, 434–448.
- Pasquaretta, C., Jeanson, R., Pansanel, J., Raine, N. E., Chittka, L., & Lihoreau, M. (2019). A spatial network analysis of resource partitioning between bumblebees foraging on artificial flowers in a flight cage. *Movement Ecology*, 7, 1–10.
- Poisot, T., Bruneau, A., Gonzalez, A., Gravel, D., & Peres-Neto, P. (2019). Ecological data should not be so hard to find and reuse. *Trends in Ecology & Evolution*, 34, 494–496. <https://doi.org/10.1016/j.tree.2019.04.005>
- Poisot, T., Gravel, D., Leroux, S., Wood, S. A., Fortin, M.-J., Baiser, B., Cirtwill, A. R., Araújo, M. B., & Stouffer, D. B. (2016). Synthetic datasets and community tools for the rapid testing of ecological hypotheses. *Ecography*, 39, 402–408. <https://doi.org/10.1111/ecog.01941>
- Roche, D. G., Berberi, I., Dhane, F., Lauzon, F., Soeharjono, S., Dakin, R., & Binning, S. A. (2022). Slow improvement to the archiving quality of open datasets shared by researchers in ecology and evolution. *Proceedings of the Royal Society B: Biological Sciences*, 289, 20212780. <https://doi.org/10.1098/rspb.2021.2780>
- Schmitz, O. J. (2008). Effects of predator hunting mode on grassland ecosystem function. *Science*, 319, 952–954. <https://doi.org/10.1126/science.1152355>
- Shafir, S., Waite, T. A., & Smith, B. H. (2002). Context-dependent violations of rational choice in honeybees (*Apis mellifera*) and gray jays (*Perisoreus canadensis*). *Behavioral Ecology and Sociobiology*, 51, 180–187.
- Shoemaker, L. G., Sullivan, L. L., Donohue, I., Cabral, J. S., Williams, R. J., Mayfield, M. M., Chase, J. M., Chu, C., Harpole, W. S., Huth, A., HilleRisLambers, J., James, A. R. M., Kraft, N. J. B., May, F., Muthukrishnan, R., Satterlee, S., Taubert, F., Wang, X., Wiegand, T., ... Abbott, K. C. (2020). Integrating the underlying structure of stochasticity into community ecology. *Ecology*, 101(2), e02922.
- Srivastava, D. S., Kolasa, J., Bengtsson, J., Gonzalez, A., Lawler, S. P., Miller, T. E., Munguia, P., Romanuk, T., Schneider, D. C., & Trzcinski, M. K. (2004). Are natural microcosms useful model systems for ecology? *Trends in Ecology & Evolution*, 19(7), 379–384.
- Stephens, D. W., Brown, J. S., & Ydenberg, R. C. (2007). *Foraging: Behavior and ecology*. University of Chicago Press.
- Sterelny, K. (2017). Humans as model organisms. *Proceedings of the Royal Society B: Biological Sciences*, 284, 20172115. <https://doi.org/10.1098/rspb.2017.2115>
- Suraci, J. P., Smith, J. A., Chamaillé-Jammes, S., Gaynor, K. M., Jones, M., Luttbeg, B., Ritchie, E. G., Sheriff, M. J., & Sih, A. (2022). Beyond spatial overlap: Harnessing new technologies to resolve the complexities of predator–prey interactions. *Oikos*, 2022, e09004. <https://doi.org/10.1111/oik.09004>
- TrailBehind inc. (2023). GaiaGPS. (Version 2023.1) [Software]. <https://www.gaiagps.com/>
- Vindenes, Y., & Langangen, Ø. (2015). Individual heterogeneity in life histories and eco-evolutionary dynamics. *Ecology Letters*, 18(5), 417–432.
- Wall, J., Lefcourt, J., Jones, C., Doehring, C., O'Neill, D., Schneider, D., Steward, J., Krautwurst, J., Wong, T., Jones, B., Goodfellow, K., Schmitt, T., Gobush, K., Douglas-Hamilton, I., Pope, F., Schmidt, E., Palmer, J., Stokes, E., Reid, A., ... Wittmyer, G. (2024). EarthRanger: An open-source platform for ecosystem monitoring, research and management. *Methods in Ecology and Evolution*, 15(11), 1968–1979.

## SUPPORTING INFORMATION

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

**Appendix A.** Movement analysis on TrophIE data.

**Appendix B.** Search behavior and predation-risk analysis on TrophIE data.

**Appendix C.** Foraging analysis on TrophIE data.

**Appendix D.** Consumer-resource interaction network analysis on TrophIE data.

**Appendix E.** General guidelines for TrophIE game setup.

**How to cite this article:** Bolduc, D., Dulude-de Broin, F., Bergeron, G., Villeneuve, C., Weiss-Blais, M., Couloigner, C., Dubourg, R., Fraser-Franco, M., Banville, F., Moisan, L., Montiglio, P.-O., Fortin, D., Thibault, F., Allard, A., Gaudreau-Rousseau, C., Roca, I., Durand, A., Massé, C., Barreau, E., ... Legagneux, P. (2025). Impersonating predators and prey to study trophic interactions through real-life simulations. *Methods in Ecology and Evolution*, 00, 1–14. <https://doi.org/10.1111/2041-210X.70180>