Received: 20 January 2025 | Accepted: 26 September 2025

DOI: 10.1111/2041-210x.70180

RESEARCH ARTICLE

BRITISH ECOLOGICAL SOCIETY Methods in Ecology and Evolution

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

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

[1]Faculté des Sciences et de Génie, Université Laval & Sentinelle Nord, Quebec, Quebec, Canada; [2]Faculté de Génie Information et Génie Logiciel, Université Laval, Quebec, Quebec, Canada; [3]Faculté des Sciences, Sciences Biologiques, Université du Québec à Montréal, Montréal, Quebec, Canada; [4]Biologie, Chimie et Géographie, Université du Québec à Rimouski, Rimouski, Quebec, Canada; [5]Faculté des Sciences et de Génie, Physique, Génie Physique et Optique, Université Laval, Quebec, Quebec, Canada; [6]Département de Sciences Naturelles, Université du Québec en Outaouais, Gatineau, Quebec, Canada; [7]Ecology and Genetics Research Unit, University of Oulu, Oulu, Pohjois-Pohjanmaa, Finland; [8]Department of Biology, University of Oxford, Oxford, UK; [9]Faculty of Agricultural and Environmental Sciences, McGill University, St-Anne-de-Bellevue, Quebec, Canada; [10]Biology Department, Concordia University, Montreal, Quebec, Canada; [11]CEBC, UMR 7372, CNRS – La Rochelle Université, Villiers-en-Bois, France and [12]Département de Biologie, Université de Sherbrooke, Sherbrooke, Quebec, Canada

Correspondence
David Bolduc
Email: david21bolduc@hotmail.com

Frédéric Dulude-de Broin
Email: 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.

[Correction added on 04 December 2025 after first online publication: The affiliation of the co-author Akiko Kato has been updated.].

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 87.5 h 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 0.18 km^2 and were never further than 85 m 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: 5 m) trail and a network of smaller ones (width: 1.5 m).

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.

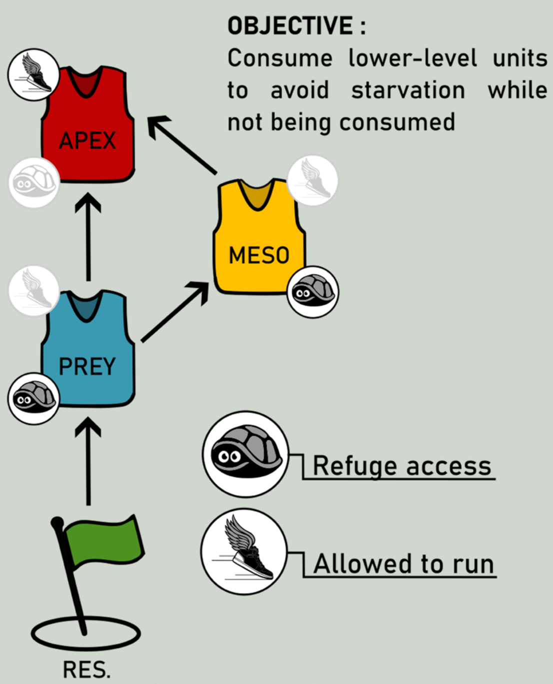
Handling times were fixed across games. Prey had to wait 10 s for each resource consumption attempt (uncovering a resource cell), 10 s for each consumption (when the uncovered cell contained A or B) and 30 s when reproducing with another player. Predators capturing another player had to wait 30 s at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

2.6 | Data logging

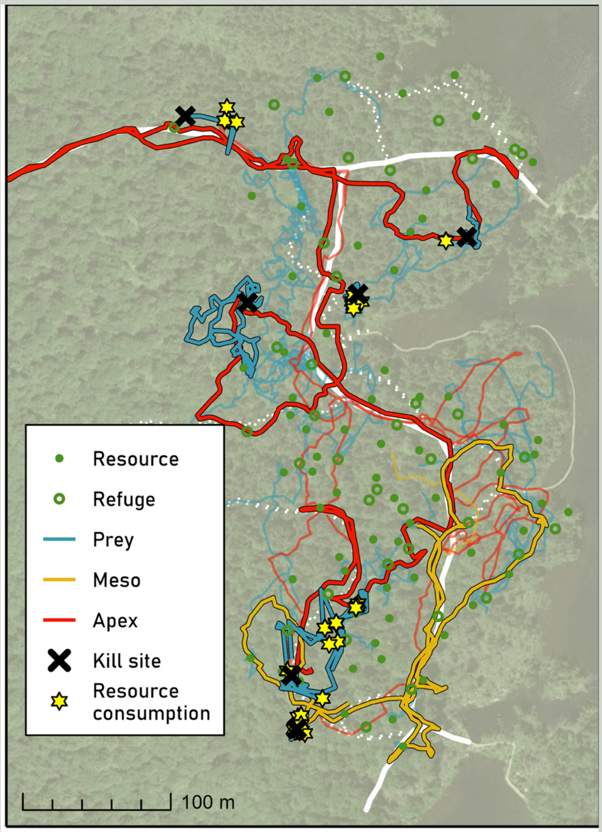
Each player carried a smartphone with two applications: GAIA GPS (TrailBehind Inc., 2023) and EarthRanger (Allen Institute for

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



*Turtle and shoe are iStock icons. Rest is from authors.



Acquisition of resources
Prey player spends 10 seconds to uncover a resource cell and an additional 10 seconds if successful.

Acquisition of prey
Predators spend 30 seconds with the player they caught.

Refuge use
Be in physical contact with the refuge pole. Protects from apex. Simultaneous use by players is allowed.

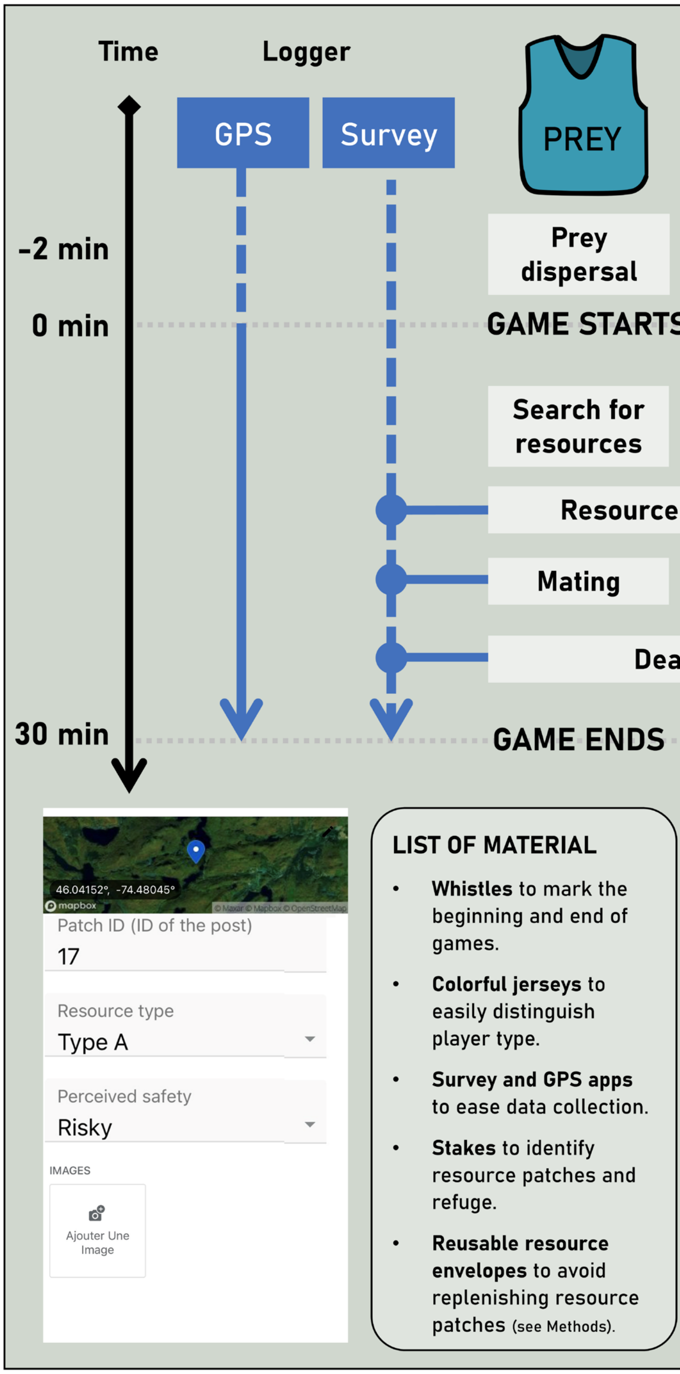
Reproduction (Prey only)
Collect enough resources, find another well fed prey and stick together for 30 seconds.

Competition mode (Prey only)
Aims to mimic increasing level of exploitative competition. Simultaneous patch use is not allowed.

- Weak: Patches can only be visited once by each player but can be used as new by others.
- Mid: Patches resource cards are left to the level they were consumed.
- Strong: Patches can only be visited by one player and become unavailable afterwards.

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



BOX 2. Top Game unfolding and biologging. Biologging devices are in use when arrows are solid or intersected by circles. Surveys for the three different events (Consumption, Mating and Death) were filled in EarthRanger (Allen Institute for Artificial Intelligence (AI2), 2023). **Bottom Left** Example of filled survey for consumption and death. **Bottom Right** List of material to play TrophIE.

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

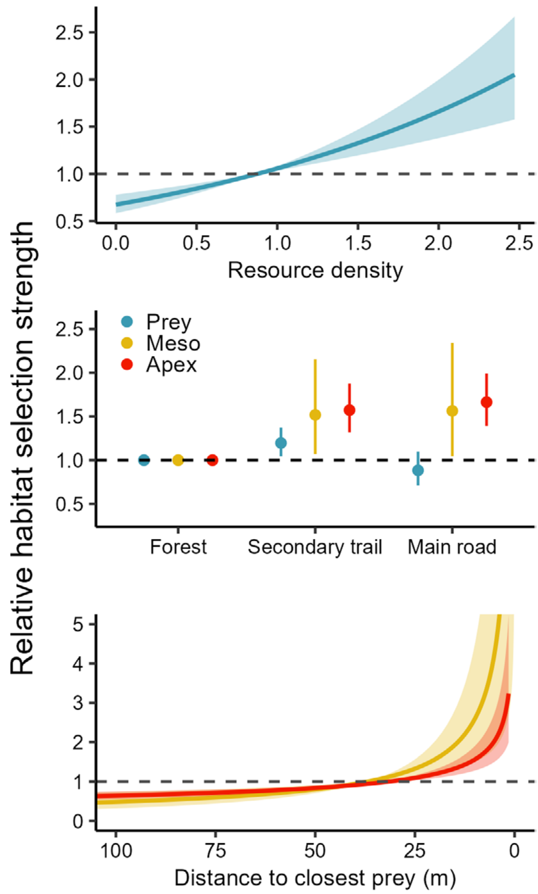


FIGURE 2 Habitat selection of prey (blue), meso-predator (yellow), and apex predator (red) players assessed through an integrated step-selection function. The figure shows selection strengths predicted from an integrated step-selection model relative to the reference level, set to the average value for 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.

which here 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 TrophIE 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.

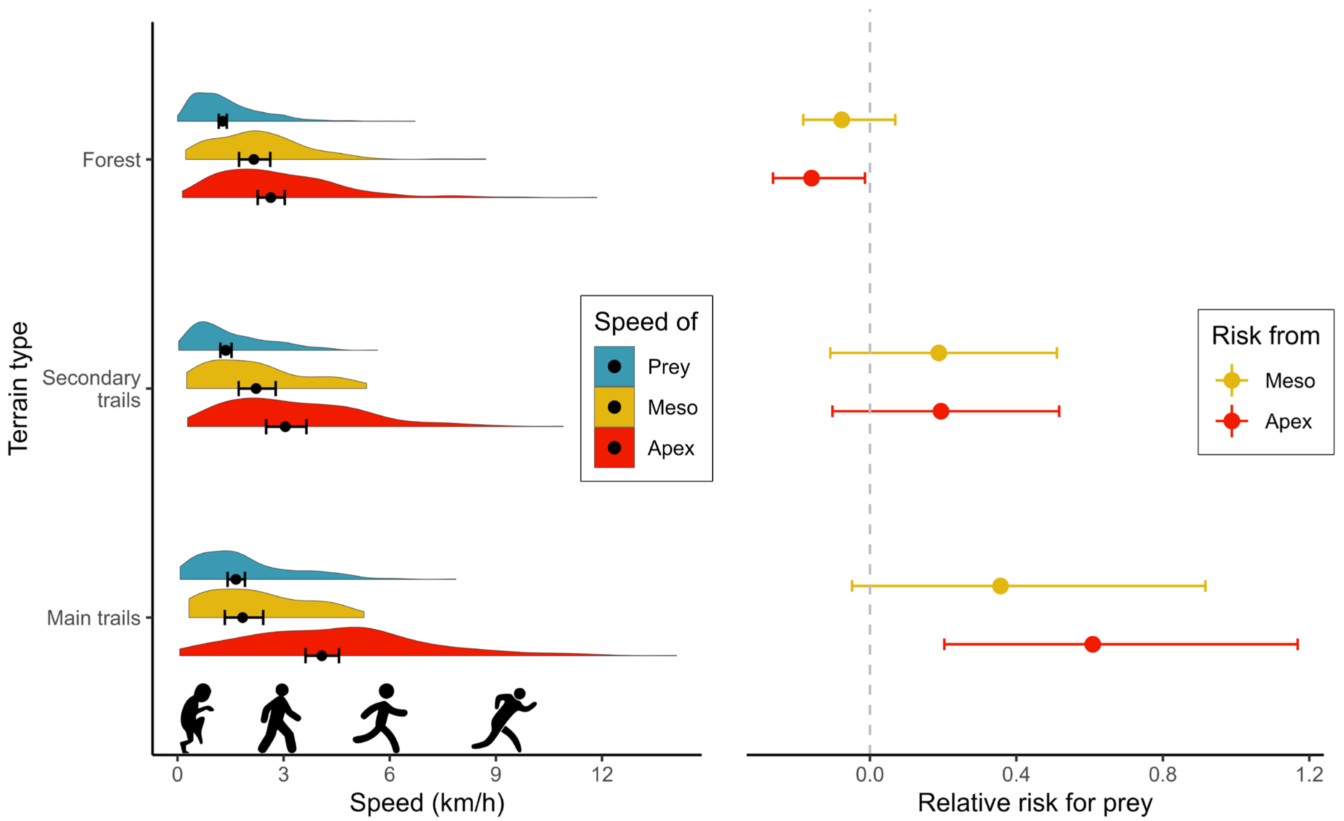


FIGURE 3 Left. Average speed of each player type in different terrains. Points and 95% CI are estimates of a random slopes model controlling for player ID. Right. Relative risk of each terrain type for prey. Coloured distributions are the raw data. The degree of risk was estimated by dividing the proportion 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).

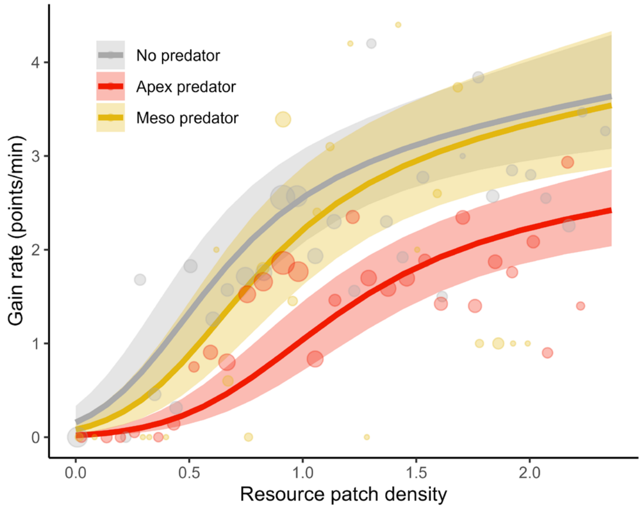


FIGURE 4 Functional responses of prey players when no predator is in the vicinity (grey), in the presence of a close meso-predator (yellow), or in the presence of a close apex predator (red). Gain rates were calculated as the number of resources acquired over 5-min intervals. Resource patch density and 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

BRITISH ECOLOGICAL SOCIETY Methods in Ecology and Evolution

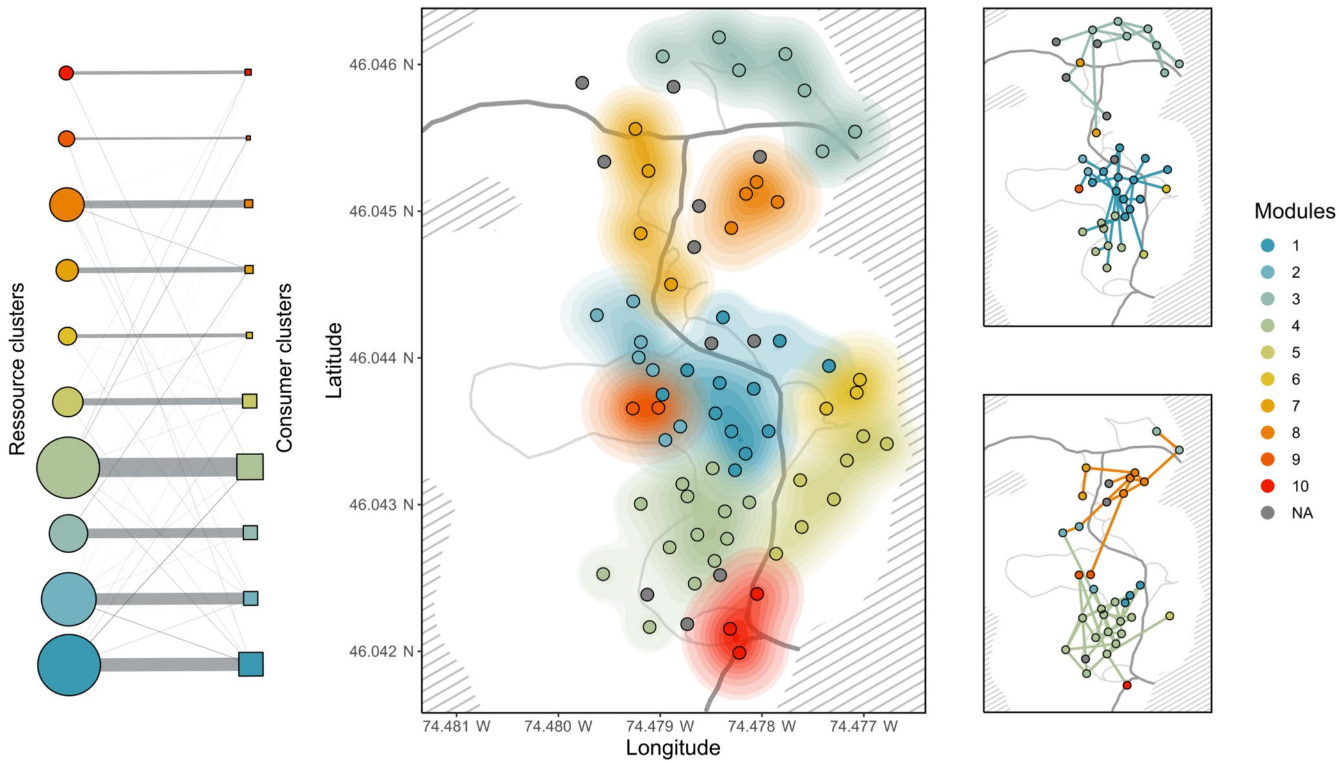


FIGURE 5 Left: Bipartite representation of the prey (squares) and resources (circles) interaction network of the TrophIE games aggregated by modules (colours). Symbol size is proportional to the number of nodes in each module and edge width is proportional to cumulative edge weight (total number of prey–resource 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	• Vary communication ability between players • Impede players' senses (e.g. wear ear plugs) • Players are omniscient (e.g. provide a map of resource patches)	• Access to public information benefits prey • Vocal prey players face higher predation risk • Omniscience favours the ideal free distribution of players
Detection distance	• Add auditory cues to resource patches, refuges or other players. • Impede players' senses.	• Increased detection distance of predators and resource patches respectively makes movement more risk-sensitive AND more selective of high patch density area.
Patch quality	• Patch quality varies and can be either known from a distance or from sampling.	• 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).
Patch aggregation	• Vary the aggregation of resource patches	• Aggregation of resource patches should cascade to the aggregation of predator–prey interactions and loss of connectivity.
Prey quality	• Vary the quality, characteristics (ease of movement, access to refuges, handling time) and abundance of prey players	• Prey survival will depend on their selection by predators or their proximity to selected prey.
Resource hoarding	• Allow players to move resource patches and to take others' resources if undefended.	• Hoarding should favour survival and score when facing high predation risk. • Hoarding should also reduce prey players movement and lead to the active defence of territories.
Central place foraging	• Players must return to a given location every time they accumulate a given number of points.	• Predators' home range shrinks and the landscape of risk becomes more heterogeneous. • Score and survival of prey players becomes dependent on their central place location.
Omnivory	• Introduce omnivore players, which can consume prey and resources but with an equal or lower benefit than predators and prey.	• Diet of omnivore players will depend on prey and patch abundance as well as predation risk.
Collaboration	• Encourage players to collaborate by allowing resource sharing.	• The benefits of collaborating (sharing resources) will be greater in adverse conditions (e.g. high predation risk).

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 30 min, 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

BRITISH ECOLOGICAL SOCIETY Methods in Ecology and Evolution

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 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
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://allenai.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., & Hainey, 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

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., Hainey, 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

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/arac063

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., Coblentz, 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., … Wittemyer, 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. (2026). Impersonating predators and prey to study trophic interactions through real-life simulations. *Methods in Ecology and Evolution*, *17*, 158–171. https://doi.org/10.1111/2041-210x.70180

Appendix A - Movement analysis on TrophIE data

Supplementary information to "Impersonating predators and prey to study trophic interactions through real-life simulations"

CONTEXT

Movement is a critical component of predator-prey interactions (Sih 1984; Sih 2005). It shapes spatial overlap between predators and prey, affecting their encounter rates, predation rates, and ultimately, population dynamics (Krivan 1997; Schmitz et al. 2017). In natural systems, animals face trade-offs between foraging and safety (Lima and Dill 1990; Brown 1999; Brown and Kotler 2004; Beltran et al. 2021; Ruprecht et al. 2021). They generally select areas that facilitate the acquisition of resources and avoid time and places where they are more likely to encounter predators (Heithaus and Dill 2002; Fortin et al. 2005; Valeix et al. 2009) or be killed (Kauffman et al. 2007; Kohl et al. 2018). For instance, cursorial predators tend to select linear features such as road or powerline clear-cuts that facilitate their movement, reduce energy expenditure and increase encounter rate with prey (Fahrig and Rytwinski 2009; Dickie et al. 2017; Dickie et al. 2020). On the other hand, most prey species avoid roads which are perceived as risky areas because they are selected by predators or associated to mortality induced by vehicle-collision (Gagnon et al. 2007; Fahrig and Rytwinski 2009; Leblond et al. 2013; Poulin et al. 2023). Despite the general avoidance of roads, prey may at time select linear features to reduce energetics costs of movement when risk is reduced such as when traffic intensity is low (Poulin et al. 2023) or when predators are less active (Fahrig and Rytwinski 2009; Smith et al. 2021). Patterns of space use can be further influenced by site familiarity. Site familiarity reflect the accumulation of knowledge by an individual about the unique features of a site it uses or inhabits (e.g. location of food and refuges, topography, vegetation, identity of neighbors). It is hypothesized that familiarity with a site promotes an individual's fitness because the perceived personal value of that site ('private value', Piper 2011) increases, as do the costs of moving elsewhere. Using movement data of players in TrophIE, we investigated habitat selection of predators and prey in relation to resource, risk, energy and site familiarity. We expected that: 1) prey would more frequently select areas of higher resource density and avoid risky places such as roads, 2) predators would select for proximity to prey and for features that facilitate their movement such as roads, 3) both predators and prey would preferentially use previously visited locations in which information could have been acquired.

METHOD

INTEGRATED STEP-SELECTION FUNCTION

We fitted an integrated *Step-Selection Function* (SSF; Fortin et al. 2005; Avgar et al. 2016) to assess habitat selection of prey, meso predators and apex predators. SSFs are *discrete choice models* that compare environmental attributes and movement characteristics of observed steps (the linear segment between two consecutive relocations) with alternative random steps taken from the same starting point. We fitted SSFs using generalised linear mixed models with a Poisson distribution and a stratum specific intercept to allow the inclusion of random slopes. This approach is likelihood-equivalent to SSF fitted with a conditional logistic regression as shown in Muff et al. (2020).

We used GPS data from 33 players over 9 TrophIE games representing 182 player-games for prey, 25 player-games for apex predators and 14 player-games for meso predators. Tracks were resampled to obtain continuous sequences (bursts) of relocations every 30 seconds with a 10 second tolerance. We generated 10 random steps for each observed step by sampling random step-lengths from a gamma distribution and random turning angles from a VonMises distribution fitted on the original tracks. Environmental covariates were extracted at the end of each step.

COVARIATES

We calculated the availability of resources for prey and refuges through quartic kernel density estimation on a grid of 10 m resolution and using a bandwidth of 30 m. This roughly corresponds to the average distance at which players could detect refuges and resources in the forest.

We quantified instantaneous prey availability for predators by calculating the distance to the closest prey in the last minute before each predator location.

We used a shapefile of the road network within the arena to test the effects of linear features on predator and prey movements. There were two types of trails in the arena. A large road (>5 m wide) paved with gravel and cleared from vegetation was categorized as the main road, while small unpaved paths in the forest with vegetation cover were categorized as secondary trails. We used a buffer of 5 meters around each linear feature to classify relocations as either on a main road, on a secondary trail or in the forest.

To account for topography, we used a High-Resolution Digital Elevation Model (HRDEM) from the CanElevation Series of Natural Resources Canada (Natural resources Canada 2024) from which we computed slopes on a 1 m resolution grid.

To explore the potential influence of site familiarity on player movements, we computed a map of site familiarity for each player based on a 30 meters resolution grid. We defined site familiarity as the total time spent by a player in a given cell in all previous games. Locations from the current game were not included in the calculation to avoid spatial autocorrelation issues. Therefore, site familiarity was always 0 for the first game and increased with the number of games played.

ANALYSIS

SSFs were fitted separately for prey, meso predators and apex predators. All models included landscape slope, whether the end location was on a main or secondary trail as well as step-length, log step-length and cos turning angle to inform the movement kernel. In addition, the prey model included resource density, refuge density, site familiarity and the interaction between resource density and site familiarity. The meso predator model included refuge density, distance to the closest prey, and site familiarity. The apex predator model included distance to the closest prey and site familiarity. To account for individual- and between-game variations in habitat selection, we added random slopes on each covariate, one for player and one for game identity for the prey and apex predator models.

For meso predators, there was not enough data to fit the model with both random slopes, so we included a single random slope corresponding to each player-game.

All analyses were conducted in R version 4.3.1 (R Core Team 2023). We used the R package amt (Signer et al. 2019) to resample tracks, generate random steps and extract covariates, terra (Hijmans 2024) to manipulate raster data and compute landscape slope, sf (Pebesma 2018) for spatial data and glmmTMB (Brooks et al. 2017) to fit the SSF with random effects.

RESULTS

The movement of prey were influenced by resource density, secondary trails, refuge density and site familiarity (**Figure 1**). Prey selected areas of high resource density (estimate[95%CI] = 1.3 [1.17, 1.44], **Figure 1**) with a 17% increase in the odds of choosing a step for each unit increase in resource density. They were also 20% more likely to take a step ending on a secondary trail (1.2 [1.04, 1.38]) compared to steps ending in the forest, but they did not select the main road (0.88[0.7, 1.1]) despite the ease of movement it provides. Prey tended to select areas with a higher refuge density although effect size was small to moderate and the confidence interval included neutral selection (1.1[0.91, 1.32]).

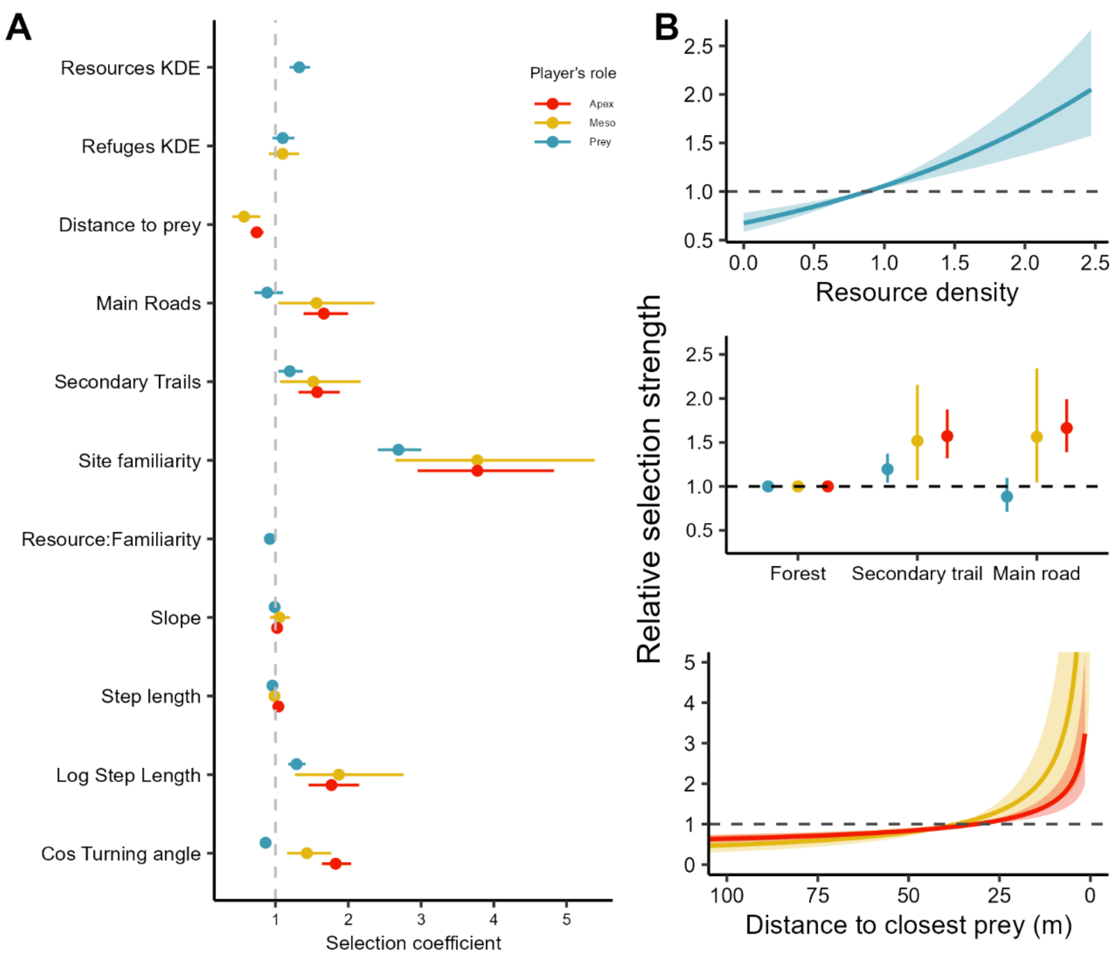


Figure 1. Step-selection function model results. A) Covariates included in the ssf models for prey, apex and meso-predators and their respective effect sizes (selection coefficients correspond to exponentiated model coefficients). B) Relative selection strength (exponentiated model coefficients) as a function of the covariates showing a statistically significant effect on prey, apex, and meso-predators respectively. Colored continuous lines and points represent model averages. Dashed lines and error bars depict 95% confidence intervals.

The movement of Apex and Meso predators were similar and mainly influenced by distance to prey, the main road, the secondary trails and site familiarity (**Figure 1**). They both minimised distance to prey (apex 0.74[0.66, 0.83], meso 0.57[0.41,0.79]) with a steep increase in the odds of choosing a step when it was within 30 meters of a prey. They also selected the main road (apex 1.66[1.38, 2.0], meso 1.56[1.04, 2.36]) and secondary trails (apex 1.57 [1.31, 1.88], meso: 1.52[1.06, 2.17], although selection of the main road was lower and more variable for meso predators compared to apex. Similar to prey, meso predator which were also exposed to predation risk by apex, tended to select areas with high relative refuge density (1.1[0.91, 1.32]), but the estimate for this variable was small to moderate, and the confidence interval included neutral selection.

Site familiarity strongly influenced prey, meso predator and apex predator movements (**Figure 2**). All players preferred to move in areas that were visited in previous games compared to unknown areas. Interestingly, there was a significant interaction between site familiarity and resource density for prey, with much lower influence of site familiarity when there were few resources in an area (**Figure 2**). Slope had no effect on the movement of players (prey 0.99[0.95,1.02], meso 1.05[0.92,1.19], apex 1.02[0.86, 1.09].

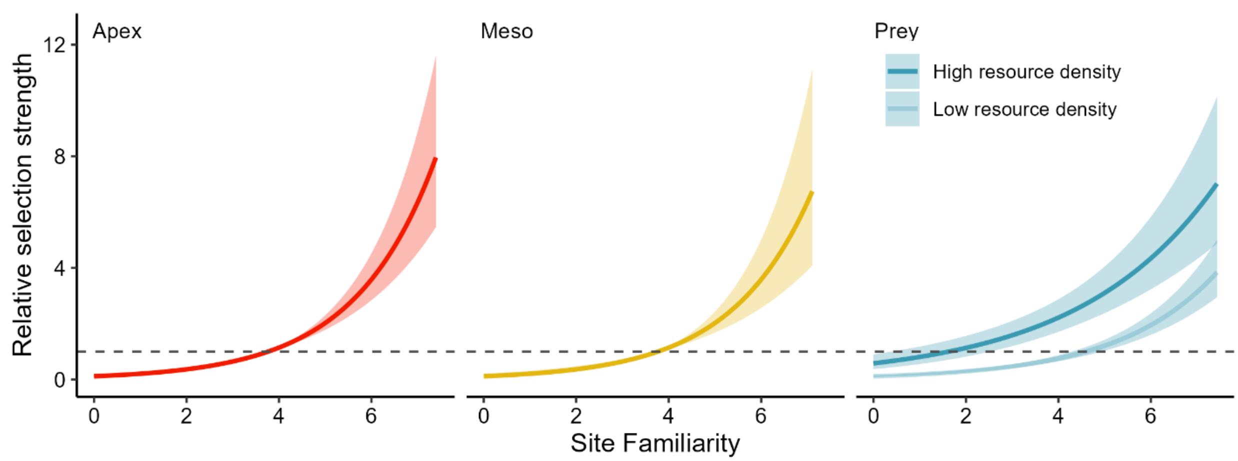


Figure 2. Influence of site familiarity on habitat selection by apex predator, meso predator and prey. Colored lines represent predicted selection strengths along with their 95% confidence intervals. Site familiarity was calculated as the total time spent by a player in a given cell in all previous games.

INTERPRETATION

TrophIE players exhibited movement behaviours comparable to the dynamics typically observed in natural systems. Indeed, prey and both types of predators maximised foraging opportunities by selecting patches of high resources density or proximity to prey.

Prey response to resource patch density was close to linear, while predators only selected prey proximity when a step would bring them under 30 meters of their target. This suggests that predators reacted to prey but were unable to predict their location over the study area. The lack of spatial anchor and heterogeneity in resource patch distribution could have made prey less predictable (Smith et al. 2019). Predators might have also been less likely to attempt a chase at larger distances as prey would be more likely to escape and reach a refuge.

Prey and both types of predators selected linear features that facilitate movements. The apex and meso-predator intensively used the main road and secondary trails to search for prey. Selection coefficients were higher for the main road which offered clear line-of-sight and paved surfaces to efficiently roam across the arena. This strategy likely minimised energy expenditure while maximising encounter rate with prey. Similarly, in natural systems, wolves and bears generally select linear features (Dickie et al. 2017; Dickie et al. 2020), presumably increasing prey acquisition (McKenzie et al. 2012). Interestingly, TrophIE players that had the role of prey selected secondary trails but tended to avoid the main road despite the ease of movement it confers. This suggests that they faced trade-offs between mobility and safety that differed between the type of road. Indeed, the main road was likely more risky than secondary trails as it was heavily used by predators and did not provide cover to prey. In non-human organisms, trade-offs between foraging and safety are common (Lima and Dill 1990). For instance, elk dynamically balance risks and rewards when choosing to cross linear features (Poulin et al. 2023).

Players did not avoid slopes. This could potentially be due to the general lack of steep cliffs or ledges that could act as impassable obstacles over the study area. In addition, while it could be energetically efficient to avoid slopes, other trade-offs such as those between foraging and safety could have been more important. This reinforce the idea that players in TrophIE acted as non-human organisms for which topography might have less impact than the risk of being killed or the need to forage. Indeed, humans walking in the arena without rules would likely choose the path of least resistance and avoid slopes, but players to which trade-offs were imposed did not seem to mind topography.

Landscape familiarity was an important driver of movement for all players. Familiarity can be challenging to measure in natural systems because it requires detailed tracking information over a prolonged period often including time prior to the capture of an animal. Nevertheless, some studies have shown that site familiarity can be an important driver of movement and fitness in both predators and prey (Piper 2011) especially when the cost of acquiring new information is high. In our TrophIE simulations, prey and meso predators risked being detected and killed every time they moved, and site familiarity likely helped finding resource efficiently while minimizing movement and detection probability. In keeping with this, the selection of known sites by prey players was higher when the quality of the site (resource density) was high. This suggests that players could, at least in part, remember the value of previously visited patches and that they used this knowledge to forage efficiently. As for predators, they were more likely to move to areas visited in previous games including those visited when they were playing as prey. Hunting in known areas could increase prey acquisition through higher encounter rates and lethality. For instance, it is likely easier to ambush or course prey for a predator that is familiar with the topography, visual cover, refuge location, and obstacles of an area.

CONCLUDING STATEMENT

TrophIE simulations reproduced movement dynamics that could be expected in natural systems. There were clear trade-offs between foraging, safety and movement efficiency. Interestingly, the extensive dataset was amenable to investigate the effect of variables that are often hard to measure in natural systems, such as site familiarity. Despite the inherent differences between animal and humans, the decisions of TrophIE players provided a level of realism that is often out of reach when using virtual simulation environments.

BIBLIOGRAPHY

Avgar T, Potts JR, Lewis MA, Boyce MS. 2016. Integrated step selection analysis: Bridging the gap between resource selection and animal movement. Methods Ecol Evol. 7(5):619–630. doi:10.1111/2041-210X.12528.

Beltran RS, Kendall-Bar JM, Pirotta E, Adachi T, Naito Y, Takahashi A, Cremers J, Robinson PW, Crocker DE, Costa DP. 2021. Lightscapes of fear: How mesopredators balance starvation and predation in the open ocean. Sci Adv. 7(12):eabd9818.

Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug HJ, Maechler M, Bolker BM. 2017. {glmmTMB} Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. R J. 9(2):378–400. doi:10.32614/RJ-2017-066.

Brown JS. 1999. Vigilance, patch use and habitat selection: foraging under predation risk. Evol Ecol Res. 1(1):49–71.

Brown JS, Kotler BP. 2004. Hazardous duty pay and the foraging cost of predation. Ecol Lett. 7(10):999–1014.

Dickie M, McNay SR, Sutherland GD, Cody M, Avgar T. 2020. Corridors or risk? Movement along, and use of, linear features varies predictably among large mammal predator and prey species. J Anim Ecol. 89(2):623–634.

Dickie M, Serrouya R, McNay RS, Boutin S. 2017. Faster and farther: wolf movement on linear features and implications for hunting behaviour. J Appl Ecol. 54(1):253–263.

Fahrig L, Rytwinski T. 2009. Effects of roads on animal abundance: an empirical review and synthesis. Ecol Soc. 14(1).

Fortin D, Beyer HL, Boyce MS, Smith DW, Duchesne T, Mao JS. 2005. Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. Ecology. 86(5):1320–1330.

Gagnon JW, Schweinsburg RE, Dodd NL. 2007. Effects of roadway traffic on wild ungulates: a review of the literature and case study of elk in Arizona.

Heithaus MR, Dill LM. 2002. Food availability and tiger shark predation risk influence bottlenose dolphin habitat use. Ecology. 83(2):480–491.

Hijmans RJ. 2024. terra: Spatial Data Analysis.

Kauffman MJ, Varley N, Smith DW, Stahler DR, MacNulty DR, Boyce MS. 2007. Landscape heterogeneity shapes predation in a newly restored predator--prey system. Ecol Lett. 10(8):690–700.

Kohl MT, Stahler DR, Metz MC, Forester JD, Kauffman MJ, Varley N, White PJ, Smith DW, MacNulty DR. 2018. Diel predator activity drives a dynamic landscape of fear. Ecol Monogr. 88(4):638–652.

Krivan V. 1997. Dynamic ideal free distribution: effects of optimal patch choice on predator-prey dynamics. Am Nat. 149(1):164–178.

Leblond M, Dussault C, Ouellet J--P. 2013. Avoidance of roads by large herbivores and its relation to disturbance intensity. J Zool. 289(1):32–40.

Lima SL, Dill LM. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Can J Zool. 68(4):619–640.

McKenzie HW, Merrill EH, Spiteri RJ, Lewis MA. 2012. How linear features alter predator movement and the functional response. Interface Focus. 2(2):205–216.

Muff S, Signer J, Fieberg J. 2020. Accounting for individual-specific variation in habitat-selection studies: Efficient estimation of mixed-effects models using Bayesian or frequentist computation. J Anim Ecol. 89(1):80–92. doi:10.1111/1365-2656.13087.

Natural resources Canada. 2024. High resolution digital elevation model (HRDEM). CanElevation Ser Specif Ed 11. https://open.canada.ca/data/en/dataset/957782bf-847c-4644-a757-e383c0057995.

Pebesma E. 2018. Simple Features for R: Standardized Support for Spatial Vector Data. R J. 10(1):439–446. doi:10.32614/RJ-2018-009.

Piper WH. 2011. Making habitat selection more “familiar”: a review. Behav Ecol Sociobiol. 65:1329–1351.

Poulin M-P, Cherry SG, Merkle JA. 2023. Dynamic balancing of risks and rewards in a large herbivore: Further extending predator--prey concepts to road ecology. J Anim Ecol. 92(10):1954–1965.

R Core Team. 2023. R: A Language and Environment for Statistical Computing.

Ruprecht J, Eriksson CE, Forrester TD, Spitz DB, Clark DA, Wisdom MJ, Bianco M, Rowland MM, Smith JB, Johnson BK, et al. 2021. Variable strategies to solve risk--reward tradeoffs in carnivore communities. Proc Natl Acad Sci. 118(35):e2101614118.

Schmitz OJ, Miller JRB, Trainor AM, Abrahms B. 2017. Toward a community ecology of landscapes: predicting multiple predator--prey interactions across geographic space. Ecology. 98(9):2281–2292. doi:10.1002/ecy.1916.

Signer J, Fieberg J, Avgar T. 2019. Animal movement tools (amt): R package for managing tracking data and conducting habitat selection analyses. Ecol Evol. 9:880–890.

Sih A. 1984. The behavioral response race between predator and prey. Am Nat. 123(1):143–150.

Sih A. 2005. Predator-prey space use as an emergent outcome of a behavioral response race. In: Ecology of predator-prey interactions. Vol. 256. Oxford university press New York. p. 78.

Smith JA, Donadio E, Pauli JN, Sheriff MJ, Bidder OR, Middleton AD. 2019. Habitat complexity mediates the predator--prey space race. Ecology. 100(7):e02724.

Smith JA, Gaynor KM, Suraci JP. 2021. Mismatch between risk and response may amplify lethal and non-lethal effects of humans on wild animal populations. Front Ecol Evol. 9:604973.

Valeix M, Loveridge AJ, Chamaillé-Jammes S, Davidson Z, Murindagomo F, Fritz H, Macdonald DW. 2009. Behavioral adjustments of African herbivores to predation risk by lions: spatiotemporal variations influence habitat use. Ecology. 90(1):23–30.

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

Supplementary information to "Impersonating predators and prey to study trophic interactions through real-life simulations"

CONTEXT

Species functional traits such as body size, predator hunting mode or prey escape behaviors are fundamental drivers of predator-prey interactions (Schmitz 2008, 2017, Miller et al. 2014). While some traits are relatively fixed over the lifetime of an individual (e.g. biomechanics, morphology), behavior is more flexible and can rapidly respond to the environmental context or habitat structure (Schmitz, 2017). For instance, predators may adopt ambush strategies in complex heterogeneous habitats providing ample cover to sit and wait, while favoring cursorial hunting in open and homogeneous habitats to maximize prey encounters (James and Heck 1994, Wasiolka et al. 2009, Donihue 2016).

A well-documented interaction between habitat features and predator hunting efficiency is the use of linear features which create open corridors facilitating predator movements and increasing their access to prey (Johnson-Bice et al. 2023). For instance, wolves travel faster on linear features than in the forest, allowing them to cover larger daily distances (Zimmermann et al. 2014, Dickie et al. 2017), which in turn can increase their prey encounter and acquisition rates (McKenzie et al. 2012). Prey and mesopredators may also benefit from using human-built features to move across the landscape (Frey and Conover 2006, DeMars and Boutin 2018, Cowan et al. 2024). However, being themselves exposed to predation, they tend to reduce their activity when they perceive an increase in the risk of encountering predators (Preisser et al. 2007, Brook et al. 2012, Gordon et al. 2015, Gaynor et al. 2019, Shores et al. 2019).

Using movement and kill site location data from TrophIE, we 1) compared the speed of apex predators, mesopredators, and prey, among three distinct terrain types and 2) assessed the predation risk associated with these terrain types. Terrain types that players encountered were a single large gravel trail (main trail), smaller wooded pedestrian trail (secondary trails) and the forest itself. Game rules allowed apex predators to run, but constrained meso-predators and prey to walk. We expected that 1) player speed would increase on trails, more so for the apex predators that have greater speed flexibility, and that 2) terrain types where predator movement speed was greater would be riskier for prey.

METHODS

SEARCH SPEED

DATA COLLECTION, PROCESSING AND ANALYSIS

We processed GPS data from players of all three trophic positions (apex, meso and prey). Data processing was done in R version 4.3.2 (R core Team, 2023) with libraries amt (version 0.2.1.0) and sf (version 1.0-14). Tracking data were filtered to exclude movements during predator chase or prey handling by removing 30 seconds before and after each predation events. This ensured that only search behaviour were included in the analysis.

We then split the tracks into steps of 30±10 seconds and assigned each step to one of the three terrain types. Steps were assigned to the main or secondary trails category if they were completely within a five-metre buffer of either side of the trail. If a step was fully outside any of these buffers, it was considered in the forest. Steps that overlapped multiple terrain types were excluded from the analysis. We computed the player's speed in km/h by dividing step length by step duration.

We ran linear mixed-effect models (lme4 version 1.1-35.1) separately for each trophic position (apex, meso & prey) to compare average speeds among the three terrain types. We included player ID as random intercepts to estimate among individual differences in speed. We also included game ID as random intercepts for apex predators exclusively, as there was no among-game variation for meso-predators nor prey. Speed was square-root transformed to satisfy model assumptions. The marginal and conditional R^2 values for the variation in player speed explained by terrain types were calculated using 1000 parametric bootstraps.

KILL SITE LOCATION

DATA COLLECTION, PROCESSING AND ANALYSIS

We recorded 122 kill sites throughout the games (n=96 for apex and n= 26 for meso) and assigned a terrain type for each kill site based on whether it fell within 10m of a trail or not (the forest).Here the buffer around main and secondary trails (10m) is larger than in the search speed analysis as kills happening close to either type of trails were thought to result from chases that occurred on trails. We then computed the proportions of kills that occurred in each terrain type.

We assessed prey habitat use by randomly sampling 122 prey players locations (i.e. the number of kill sites) and calculating the proportion of locations in each habitat type. This random sampling was repeated 5000 times (with replacement) to generate 95% confidence intervals through non-parametric bootstrap.

To quantify predation risk for each habitat type, we calculated the ratio of the proportion of observed kill sites to the proportion of prey positions in that habitat. Relative risk ratios were then log-transformed to facilitate interpretation. A value of zero indicates kills occurred in proportion to prey habitat use. Negative values suggest prey were killed less often than expected based on their use (safer), while positive values suggest they were killed more frequently than their use suggests (riskier).

We incorporated both aspects of this appendix to further evaluate whether differences in relative risk for prey in a given terrain type could be associated to predator speed in that same terrain type. For each predator and terrain type, we plotted the relative risk for prey against predator speed.

RESULTS

EFFECT OF TERRAIN TYPE ON PLAYERS' SPEED

As expected given game rules, player speed varied with their role. On average, movement speed increased with trophic position (prey : 1.43 km/h (95% CI: 1.30, 1.48), meso : 2.28 km/h (95% CI: 1.89, 2.74), apex : 3.36 km/h (95% CI: 2.96, 3.82)). We did not find evidence that prey nor meso-predators changed their speed across terrain features, as all 95%

confidence intervals were strongly overlapping (**Figure 1**). However, apex players' movement speed steadily increased as they moved through forests (2.64 km/h, 95% CI: 2.27, 3.03), secondary trails (3.05 km/h, 95% CI: 2.51, 3.64) and the main trail (4.08 km/h, 95% CI: 3.62, 4.56) (**Figure 1**).Terrain type explained 8.90% (95% CI: 5.21, 14.11) of the variation in apex predator movement speed, whereas it explained only 1.13% (95% CI: 0.24, 2.82) and 1.02% (95% CI: 0.068, 8.00) of that variation for prey and meso-predators, respectively.

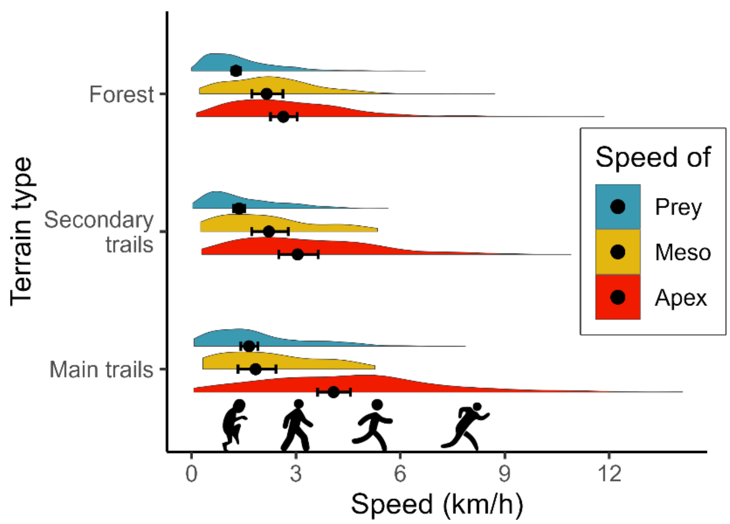


Figure 1. Average speed (x) of each trophic level as a function of the terrain types (y) predicted by the random slopes' models. The point estimates with their 95% confidence intervals are plotted alongside the raw speed data distribution for each trophic level and terrain type.

TERRAIN TYPE MEDIATED RISK

Out of 96 predation events by apex predators, 53% (n = 51) were in the forest, 27% (n = 26) were near secondary trails and 20% (n = 19) were near main trails (**Figure 2a**). Out of 26 predation events by meso-predators, 58% (n = 15) were in the forest, 27% (n = 7) were near secondary trails and 15% (n = 4) were near main trails. Prey spent 62% (95% CI: 54, 69) of their time in the forest, 22% (95% CI: 15, 29) near secondary trails and 10 % [(95% CI: 5, 15) near main trails(**Figure 2a**). The proportion of kill site in forest was lower than expected based on prey habitat use suggesting this terrain type provided safer habitat, whereas secondary trails were neutral and main trails were much riskier (**Figure 2b**). The simple visual analysis of the relationship between terrain type-mediated risk and predator speed for each terrain reveals a positive correlation between risk for prey and apex player speed, and the likely absence of correlation in the case of meso-predators. However, our results suggest that for similar speed (2.5 km/h or less), meso-predators represent a greater risk for prey players than apex predators (**Figure 3**).

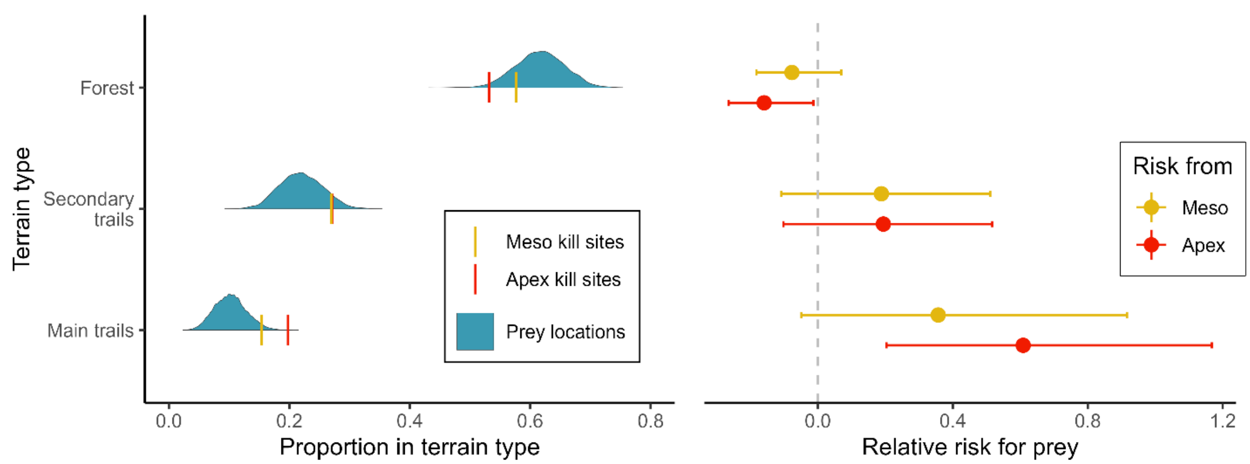


Figure 2. Left. Proportion of observed kill sites in each terrain type for apex and meso-predators, compared to the distribution of potential kill sites, namely prey terrain use, from the 5000 random sampling done in prey players track. **Right.** Relative risk of each terrain type for prey. Degree of risk is estimated by dividing the observed proportion of kills happening in a terrain type by the proportion of prey locations in that terrain type. Hence a

terrain where kills happen more often than chance based on the proportional use of this terrain by prey is considered risky (positive values). A negative value indicates the opposite. Median along with 95% confidence interval of these distributions are shown.

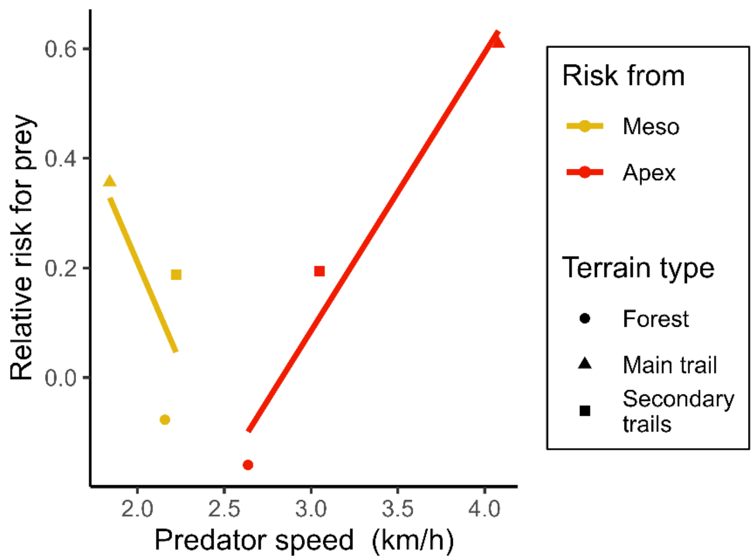


Figure 3. Relationship between relative predation risk associated with a given terrain type and the average speed of predators in that terrain. Yellow and red indicate meso and apex, respectively. Lines illustrate a linear model fitted with terrain type risk and speed data shown with circles, triangles and squares.

INTERPRETATION

We observed that trails increased apex predator movement speed, suggesting that these linear features promoted search efficiency. This speed increase, relative to speed in the forest, was higher in main than in secondary trails (**Figure 1**). It was indeed previously documented that roads, compared to small trails, could double (Zimmermann et al. 2014) or triple (Dickie et al. 2017) the speed of wild predators. However, meso-predator speed was not significantly different across terrain types. They could probably not positively respond to the ease of movement provided by trails because of their imposed speed limit and vulnerability to apex players (their speed was 20% lower on main trails than on secondary trails or in the forest).

These variations in speed parallel the relationship between prey terrain use and kill site locations. Indeed, we observed that apex kill site locations were more often in the vicinity of trails, and less often in the forest than what would be expected by prey terrain use (**Figure 2b**). This indicates that predation risk, emerging from both apex players habitat selection (Appendix A) and variations in apex lethality (as revealed by its speed), is higher near main trails than in secondary trails or the forest. Meso-predators showed a similar tendency, as kill sites were often close to trails, but confidence intervals of kill site to prey use ratio overlapped 0. For apex predators, predation risk experienced by prey in a given terrain seemed related to the traveling speed of the predator (**Figure 3**). This again was observed in large mammals, where snow conditions modulate predator speed which in turn generates various predation risk levels (Sullender et al. 2023).

Even though our observations are tainted by the fact that players play, whereas animals face life-or-death situations, it remains interesting that they concur with what is observed in natural systems where linear features or weather conditions impact organisms' movement.

CONCLUDING STATEMENT

TrophIE players reproduced terrain-driven speed variations observed in natural ecosystems (McKenzie et al. 2012, Dickie et al. 2017) without any in-game rules regarding the use of the different terrain types. Specifically, we found that apex predators increased their movement speed on linear features, leading to a higher predation risk near these trails. This behavior contrasts with meso-predators and prey, whose movement speeds remained mostly consistent across terrain types.

BIBLIOGRAPHY

Boyce, M. S., P. R. Vernier, S. E. Nielsen, and F. K. A. Schmiegelow. 2002. Evaluating resource selection functions. Ecological Modelling 157:281–300.

Brook, L. A., C. N. Johnson, and E. G. Ritchie. 2012. Effects of predator control on behaviour of an apex predator and indirect consequences for mesopredator suppression. Journal of Applied Ecology 49:1278–1286.

Cowan, M. A., J. A. Dunlop, L. A. Gibson, H. A. Moore, S. A. Setterfield, and D. G. Nimmo. 2024. Movement ecology of an endangered mesopredator in a mining landscape. Movement Ecology 12:5.

DeMars, C. A., and S. Boutin. 2018. Nowhere to hide: Effects of linear features on predator–prey dynamics in a large mammal system. Journal of Animal Ecology 87:274–284.

Dickie, M., R. Serrouya, R. S. McNay, and S. Boutin. 2017. Faster and farther: wolf movement on linear features and implications for hunting behaviour. Journal of Applied Ecology 54:253–263.

Donihue, C. M. 2016. Aegean wall lizards switch foraging modes, diet, and morphology in a human - built environment. Ecology and Evolution 6:7433–7442.

Frey, S. N., and M. R. Conover. 2006. Habitat Use by Meso-Predators in a Corridor Environment. Journal of Wildlife Management 70:1111–1118.

Gaynor, K. M., J. S. Brown, A. D. Middleton, M. E. Power, and J. S. Brashares. 2019. Landscapes of Fear: Spatial Patterns of Risk Perception and Response. Trends in Ecology & Evolution 34:355–368.

Gordon, C. E., A. Feit, J. Grüber, and M. Letnic. 2015. Mesopredator suppression by an apex predator alleviates the risk of predation perceived by small prey. Proceedings of the Royal Society B: Biological Sciences 282:20142870.

Johnson - Bice, S. M., T. D. Gable, A. T. Homkes, S. K. Windels, J. K. Bump, and J. G. Bruggink. 2023. Logging, linear features, and human infrastructure shape the spatial dynamics of wolf predation on an ungulate neonate. Ecological Applications 33:e2911.

L. James, P., and K. L. Heck. 1994. The effects of habitat complexity and light intensity on ambush predation within a simulated seagrass habitat. Journal of Experimental Marine Biology and Ecology 176:187–200.

McKenzie, H. W., E. H. Merrill, R. J. Spiteri, and M. A. Lewis. 2012. How linear features alter predator movement and the functional response. Interface Focus 2:205–216.

Michel, M. J., and M. M. Adams. 2009. Differential effects of structural complexity on predator foraging behavior. Behavioral Ecology 20:313–317.

Miller, J. R. B., J. M. Ament, and O. J. Schmitz. 2014. Fear on the move: predator hunting mode predicts variation in prey mortality and plasticity in prey spatial response. Journal of Animal Ecology 83:214–222.

Preisser, E. L., J. L. Orrock, and O. J. Schmitz. 2007. PREDATOR HUNTING MODE AND HABITAT DOMAIN ALTER NONCONSUMPTIVE EFFECTS IN PREDATOR–PREY INTERACTIONS. Ecology 88:2744–2751.

Schmitz, O. 2017. Predator and prey functional traits: understanding the adaptive machinery driving predator–prey interactions. F1000Research 6:1767.

Schmitz, O. J. 2008. Effects of Predator Hunting Mode on Grassland Ecosystem Function. Science 319:952–954.

Shores, C. R., J. A. Dellinger, E. S. Newkirk, S. M. Kachel, and A. J. Wirsing. 2019. Mesopredators change temporal activity in response to a recolonizing apex predator. Behavioral Ecology 30:1324–1335.

Sullender, B. K., C. X. Cunningham, J. D. Lundquist, and L. R. Prugh. 2023. Defining the danger zone: critical snow properties for predator–prey interactions. Oikos 2023:e09925.

Wasiolka, B., N. Blaum, F. Jeltsch, and J. Henschel. 2009. Behavioural responses of the lizard Pedioplanis l. lineoocellata to overgrazing. Acta Oecologica 35:157–162.

Zimmermann, B., L. Nelson, P. Wabakken, H. Sand, and O. Liberg. 2014. Behavioral responses of wolves to roads: scale-dependent ambivalence. Behavioral Ecology 25:1353–1364.

Appendix C – Foraging analysis on TrophIE data

Supplementary information to "Impersonating predators and prey to study trophic interactions through real-life simulations"

CONTEXT

Prey routinely adopt anti-predator strategies to balance risk-exposure and energy acquisition (Kotler *et al.* 2004, Kohl *et al.* 2018).This includes changes in habitat selection (Gilliam and Fraser 1987), activity budget (Sih and McCarthy 2002, Trussell et al. 2011) and behavior (Lima and Dill 1990, Kotler *et al.* 2004). The mere presence of predators can trigger anti-predator strategies limiting prey foraging ability and disrupting the energy flow within ecosystems (Schmitz *et al.* 1997).

Prey functional response (i.e., the intake rate as a function of resource availability) should reflect these behavioural trade-offs (Gude et al. 2006, Palmer et al. 2021). However, evaluating the impact of predation risk on prey functional response is challenging as it requires monitoring predator, prey, and resource dynamics at contrasted levels of resource density. Additionally, the functional responses can be influenced by confounding factors such as the satiety of the prey (Matassa and Trussell 2014), the intensity of intraspecific competition (de Villemereuil and López-Sepulcre 2011) and the physical landscape which provides safe and risky habitats (Gude *et al.* 2006; McKenzie *et al.* 2012, Appendix A).

TrophIE detailed dataset is well suited to evaluate the influence of predation-related metrics on prey gain rates. Here, we investigated whether the functional response of human players foraging under predation risk reflected trade-offs that could be expected in natural systems. Based on predator-prey literature, we tested a series of predictions regarding the impact of intrinsic and environmental variables on prey functional response. We expected that prey players would reduce their foraging efforts under high perceived predation risk, by giving up foraging to find refuge when predators are nearby or by reducing foraging intensity in favor of increased vigilance. We also expected the functional response to be influenced by other environmental and intrinsic covariates such as competition and prey satiety level. Specifically, we predicted that:

- **Density of resources** should correlate positively with both feeding probability and feeding rate and this correlation should lessen with time when competition between prey players is strong. Strong competition means that resource patches may no longer be available.
- **Density of refuge** should correlate positively with feeding probability and feeding rate, as it both reduces the risk of feeding and the required vigilance when doing so.
- **Distance to the closest apex predator** should correlate positively with feeding probability and feeding rates, especially when near main trails that favor apex predators' attacks. We thus expect a negative interaction between the predator distance and the trail distance.
- **Distance to the closest meso-predator** should correlate positively with feeding probability and feeding rate.
- **Satiety level** should correlate negatively with feeding probability and rate, as players approaching the reproduction threshold should be risk-averse.
- **Competition** should mostly reduce feeding probability and then rate, given that used patches are either visibly depleted or simply unusable. We expect that the effect of competition should increase with time.
- **Diet** —specialist or generalist— should modulate the feeding rate but not the probability of feeding. We predict a higher feeding rate for generalists than specialists because generalist resource patches had higher total "resource points" than specialists.

Therefore, in this Appendix, we estimated the relationship between prey feeding rate and these variables.

METHODS

Data acquisition and management

This analysis is based on the GPS tracks from GAIA GPS or TechnoSmart loggers combined with the georeferenced events (consumptions and deaths) from Earth Ranger. The tracks were resampled every 15s to ensure equal sampling rate between players. Additionally, we used the positions of resource patches, refuges and trails.

The gain rate of prey players as well as its potential drivers were evaluated within five-minute intervals, starting from the beginning of the game going onwards. Here we present these intrinsic and extrinsic covariates, and how each of these covariates and the gain rate were calculated.

- **Gain rate:** The gain rate (points/minute) was calculated as the score at the end of the interval minus the score at the beginning divided by the interval duration. Interval duration can be cut short when the prey is killed or when the game ends.
- **State:** Ratio between the score at the beginning of the interval and the resource accumulation threshold for reproduction.
- **Density of resources and refuges:** Each position on a prey player track falls on a 10 m x 10 m pixel for which the kernel density of refuges and resources within a 30 m radius were calculated. Values of densities were obtained for each position and were averaged over the duration of the interval.
- **Distance to predators:** For each position, we calculated the distance at which the closest predator player of each type was. These distances were averaged over the duration of the interval.
- **Distance to trails:** For each position, we calculated the distance to the closest trails, considering only main trails, which were shown to increase the speed of apex predator players (Appendix A). The distances were averaged over the duration of the interval.
- **Time:** Rank of the 5-minute interval since the start of the game. For example, if the interval in question corresponds to the interval between the 5th and 10th minutes of the game, the time interval equals 2.

- **Diet:** Either specialist or generalist. Players choosing a generalist diet have access to all resources type (A or B), but must expand the same handling time even if their value differs.
- **Competition:** Either weak, mild or strong (see Box 1 in the main text for details).

Despite our best efforts, we were not able to properly register the consumption events and tracks of all players. Hence, we removed the data concerning players who, for a given game, had reported 50% more points than what had been registered by the app (e.g., we accepted 30 reported points for 21 registered, as the difference is less than 50% of 21). Moreover, intervals lasting less than 60 seconds and those for which the satiety limit was reached were removed from the analysis. The impact of these consecutive filters, as well as the filters necessary for the hurdle model analysis (see Statistical analysis), is presented in Table 1, which shows that removing player-games with problematic data logging still left us with 90% of player-games data.

Table 1. Effect of consecutive filters on prey player sample size

Filter	Number of prey players	Number of player-games	Number of intervals
None (full data)	34	213	-
With GPS tracks	33	199	966
With proper resource consumption data logging (for binomial model)	33	186	910
Lasting more than 60 seconds	33	185	885
With satiety < 1	33	185	766
Intervals with gain rate > 0	33	176	526

Statistical analysis

Zero values were overrepresented in the response variable, the gain rate. Indeed, players often went without feeding within the 5 min intervals. Therefore, we used a hurdle model and split the analysis into two parts. First, we used a binomial generalized linear mixed model to investigate how the decision to feed or not – feeding probability - was influenced by covariates. Then, we used a subsequent linear model to look at the influence of covariates on feeding rates once feeding was initiated. Therefore, zero values were not considered in this second model. We did not use a zero-inflated Poisson model as we only knew that players had initiated feeding once they had gained at least one resource point. We hence had no knowledge of unsuccessful feeding attempts. We added prey and game ID as random effects in the first but not the second model for which the limited data could not support the presence of random effects. The natural logarithm of the interval duration was included as a weight in both models to reduce the impact of extreme gain rates measured on short time intervals, as visual inspection of the relationship between gain rate and interval duration suggested that variance in gain rates increased exponentially towards shorter intervals. Also, some covariates were correlated with each other. As might have been expected, state and time were quite strongly positively correlated ($\rho = 0.75$) as the score of prey players could only increase with time. However, the numerous observations (Table 1) we have allowed for the simultaneous use of these two covariates, with the expectation that the model would properly partition the variance (Morrissey and Ruxton 2018). Resource density and refuge density were also somewhat positively correlated ($\rho = 0.42$), which is likely due to the fact that resource patches and refuges were placed according to site accessibility. No other obvious multicollinearity was observed. Here is how the models were formulated:

$$\begin{aligned} \textit{Feeding decision} \sim\ & \ln(\textit{Distance to predators}(\textit{Apex})) * \ln(\textit{Distance to trails}(\textit{Main})) \\ & + \ln(\textit{Distance to predators}(\textit{Meso})) + \ln(\textit{state}) \\ & + \ln(\textit{Density of resources}) + \ln(\textit{Density of refuge}) + \textit{Competition} \\ & * \textit{Time} + \textit{Diet} + (1|\textit{player.id}) + (1|\textit{game.id}), \\ & \textit{weights} = \ln(\textit{duration}) \end{aligned}$$

$$\begin{aligned} \textit{Feeding rate} \sim\ & \ln(\textit{Distance to predators}(\textit{Apex})) * \ln(\textit{Distance to trails}(\textit{Main})) \\ & + \ln(\textit{Distance to predators}(\textit{Meso})) + \ln(\textit{State}) \\ & + \ln(\textit{Density of resources}) + \ln(\textit{Density of refuge}) + \textit{Competition} \\ & * \textit{Time} + \textit{Diet}, \qquad \textit{weights} = \ln(\textit{duration}) \end{aligned}$$

RESULTS

In line with our predictions, we found that the probability of feeding and gain rates increased with resource density and distance to both types of predators. However, the effect of the apex predators is not did not increase with trail proximity (**Figure 1**).

As expected, the probability of feeding and gain rate decreased with increasing prey satiety (**Figure 2**), suggesting that prey was less likely to feed and did so to a lesser extent when approaching the reproduction threshold score. While the second model found no effect of the competition level on the feeding rate, feeding probability was negatively impacted by increasing competition (**Figure 2**). This result is consistent with our prediction that increased competition could reduce prey per capita access to resources. This impact was stronger as time passed. There was, however, no difference between weak and mild competition levels. Contrary to our prediction, refuge density had a negative impact on feeding probability and rate (**Figure 2**).

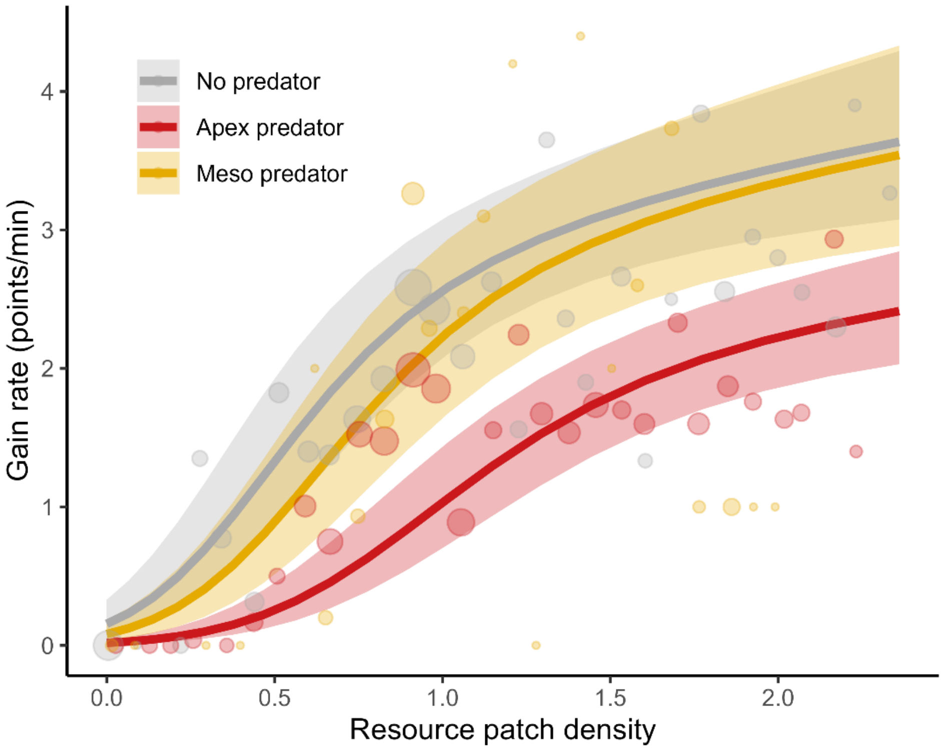


Figure 1. Functional responses of TrophIE prey players under predation risk. Gain rate and distance to the nearest apex and meso predator were calculated (and averaged for the latter) over 5 min intervals. The grey curve is the functional response for a prey player

far (200 m) from the nearest apex and from the nearest meso predator. The yellow curve is the functional response predicted for a prey far (200m) from the nearest apex and close (50 m) to the nearest meso predator. The red curve is the functional response for a prey far from the nearest apex and close (50 m) to the nearest meso predator. Points were generated by averaging raw gain rates over brackets corresponding to one 30th of the resource density axis. Points were split depending on proximity (closer or further than 100m) to both predator types. Point size is proportional to the number of observations present in the bracket.

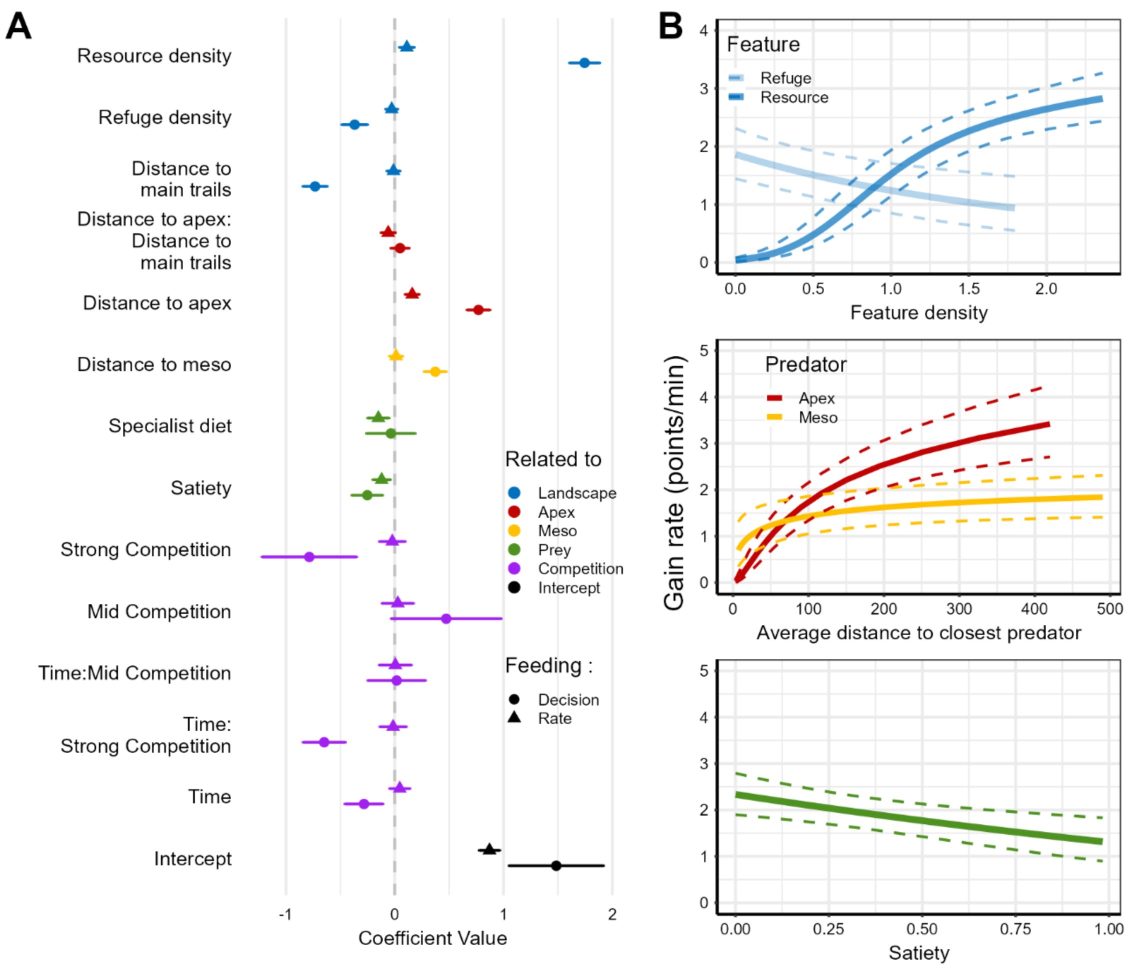


Figure 2. Results from the hurdle model linking gain rates to extrinsic and intrinsic prey player covariates. The left panel displays all the scaled coefficients from both the binomial (circle) and the normal (triangle) model. The right panels display the main

discussed effects (vertically: landscape feature density, average predator distance and satiety level). For both panels, colors refer to the type of covariates.

INTERPRETATION

Using data derived from TrophIE, we found that prey players' feeding decisions and gain rates varied as predicted by empirical studies on non-human organisms (Stephens et al. 2007). Prey players had reduced gain rates when predators were nearby, when they increased refuge use, when they got closer to the resource acquisition goal (i.e., satiety, Clark 1994) and when competition with other prey was stronger.

Specifically, we found that apex players triggered a stronger reduction in functional response (**Figure 2.B**), likely because these players produced plenty of reliable cues of their location -a prerequisite to fear- due to their faster and noisier movements. This result is in line with empirical research, where prey responds more to predators whose presence cues are more detectable and indicative of a direct danger of death (Sih 1992, Schmitz et al. 1997, Preisser et al. 2007). Contrary to our predictions, refuge density did not reduce the risk associated with foraging or the vigilance required when doing so enough to have a positive impact on the feeding rate. Rather, refuge density is likely related to refuge use, which precludes feeding. This is consistent with studies on predator-prey spatial games showing a trade-off for the prey between resource abundance and predation risk associated with foraging (Gilliam and Fraser 1987, Sih 1998, Aguiar et al. 2023).

Theory suggests that prey state should modulate risk-taking and that prey in need of resources should take higher risks than those that have reached or are close to reaching their foraging goals (Clark 1994, Matassa and Trussell 2014). Prey reduces their activity during periods when the risk of predation is high, but this phenomenon is less pronounced when they are starving. It is challenging, however, to estimate both animal state and risk-taking in the field. The detailed information we had about each player indeed suggests that prey players closer to their resource acquisition goals tended to forage less and thus likely exposed themselves less to risk.

Taking advantage of the plasticity of the TrophIE rules, we also highlighted the role of intraspecific competition on feeding probability. Strong competition (i.e competitive exclusion) negatively impacted the probability of feeding for the prey, because it reduced the availability of resources, which declined as the game went on. Our results show no differences between weak and mild competition, suggesting that neither constrained prey foraging efficiency.

Our models also produced results that are harder to interpret. Contrary to our predictions, we did not find an interaction between distance to apex players and main trails, even though main trails were shown to be riskier in the other analysis (see Appendix B). Moreover, a strong negative effect of distance to main trails appeared (the closer to main trails, the higher the gain rate). This might be because, when far from trails, prey players were mostly in transit between locations and not actively foraging, or that any correlation between resource density and distance to trails was not properly handled. Also, we might have overestimated the effect of resource density, as it was always higher in the immediate vicinity of the resources, where prey had to be when feeding. Despite our best efforts, even this highly detailed and complete dataset can provide its analytical challenges.

CONCLUDING STATEMENT

Using data derived from TrophIE – a rather simple human-based predator-prey model – we found that the functional response of prey players aligned with predictions from studies on non-human organisms (Stephens et al. 2007). This concordance with known phenomena highlights the methods' potential to complement traditional ecological research, as it provides a rich source of behavioral data.

REFERENCES

Aguiar, O., S. Sonnega, E. R. DiNuzzo, and M. J. Sheriff. 2023. Playing it safe; risk-inducedtrait
responses increase survival in the face of predation. Journal of Animal Ecology 92:690
697.

Clark, C. W. 1994. Antipredator behavior and the asset-protection principle. Behavioral Ecology 5:159–170.

Gilliam, J. F., and D. F. Fraser. 1987. Habitat selection under predation hazard: test of a model with foraging minnows. Ecology 68:1856–1862.

Gude, J. A., R. A. Garrott, J. J. Borkowski, and F. King. 2006. Prey risk allocation in a grazing
ecosystem. Ecological Applications 16:285–298.

Matassa, C. M., and G. C. Trussell. 2014. Prey state shapes the effects of temporal variation
in predation risk. Proceedings of the Royal Society B: Biological Sciences 281:20141952.

McKenzie, H. W., E. H. Merrill, R. J. Spiteri, and M. A. Lewis. 2012. How linear features alter
predator movement and the functional response. Interface Focus 2:205–216.

Morrissey, M. B., and G. D. Ruxton. 2018. Multiple Regression is Not Multiple Regressions:
The Meaning of Multiple Regression and the Non-Problem of Collinearity. Philosophy, Theory, and Practice in Biology 10.

Palmer, M. S., C. Portales-Reyes, C. Potter, L. D. Mech, and F. Isbell. 2021. Behaviorally-
mediated trophic cascade attenuated by prey use of risky places at safe times. Oecologia
195:235–248.

Preisser, E. L., J. L. Orrock, and O. J. Schmitz. 2007. Predator hunting mode and habitat domain alter nonconsumptive effects in predator–prey interactions. Ecology 88:2744–2751.

Schmitz, O. J., A. P. Beckerman, and K. M. O'Brien. 1997. Behaviorally mediated trophic cascades: effects of predation risk on food web interactions. Ecology 78:1388–1399.

Sih, A. 1992. Prey uncertainty and the balancing of antipredator and feeding needs. The American Naturalist 139:1052–1069.

Sih, A. 1998. Game theory and predator-prey response races. Pages 221–238 Game theory
and animal behavior. Oxford University Press.

Sih, A., and T. M. McCarthy. 2002. Prey responses to pulses of risk and safety: testing the
risk allocation hypothesis. Animal Behaviour 63:437–443.

Stephens, D. W., J. S. Brown, and R. C. Ydenberg. 2007. Foraging: Behavior and Ecology. University of Chicago Press.

Trussell, G. C., C. M. Matassa, and B. Luttbeg. 2011. The effects of variable predation risk on
foraging and growth: Less risk is not necessarily better. Ecology 92:1799–1806.

de Villemereuil, P. B., and A. López-Sepulcre. 2011. Consumer functional responses under
intra- and inter-specific interference competition. Ecological Modelling 222:419–426.

Appendix D – Consumer-resource interaction network analysis on TrophIE data

Supplementary information to "Impersonating predators and prey to study trophic interactions through real-life simulations"

CONTEXT

Trophic interactions are the driving force behind many ecological phenomena, from genetic differentiation and co-evolution (Guimarães et al. 2017) to community stability and resilience (McCann 2007, McCann 2011). Building networks from these interactions allows us to study the emergent properties of biological communities that would remain hidden if we were to analyze pairs of interacting individuals or species individually (Proulx et al. 2005). Food webs, as collections of trophic interactions within a community, are the principal network representation used in ecology. In many empirical food webs, groups of closely interacting species or individuals compartmentalize parts of the network. This within-food web compartmentalization of interactions is called modularity and grants important insights into the system's stability (Thébault and Fontaine 2010; Stouffer and Bascompte 2010, 2011). The presence of modules within a food web can increase the stability of the system by promoting asynchronous responses between groups following a perturbation (e.g., removal of a species, changes in interaction strength). A high value of modularity can also limit the propagation of perturbations throughout the network by constraining the consequences of the perturbation within some modules (Stouffer and Bascompte 2011; Grilli et al. 2016).

Trophic interactions are often defined on a population or species scale in empirical networks because of the difficulties associated with detecting, sampling and weighting interactions in the wild. Consequently, few systems have interactions defined on an individual scale (Pires et al. 2011), and even fewer have succeeded at recording all individuals. However, when modularity is successfully investigated in individual-based networks, it highlights the functional role of individuals in the network (i.e. module connector, hubs; Dupont et al. 2014) and the role of habitat patches for metapopulation persistence (Fletcher et al. 2013). In the specific case of spatial networks, it has been demonstrated that modularity naturally emerges from the movement and dispersal of individuals across the network (Gilarranz 2020). Modules of spatial networks are of particular interest as it is within their spatial boundaries that we should expect to find most processes linked to population dynamics. In contrast, processes such as dispersal and gene exchange happen between connected modules, which arguably explains why modules are seen by many as the most accurate representation of a population in both ecology and genetics (Albert, et al. 2013; Fletcher et al., 2013).

The TrophIE game offers an ideal setting to illustrate how a network approach can be used to identify modules of closely interacting individuals in a food web. In our ecological simulation, prey individuals move through space in search of stationary resources.

Herbivory-like interactions between prey individuals and resources may be represented as a bipartite network where prey and resources are the two types of nodes. Here we investigate the presence of modules in resource patches related by consumption, which could indicate limitations or preferences in prey movement. We expect that the spatial structure of resource patches, coupled with the limited speed of individual prey and game duration, will favor the composition of spatially aggregated resource modules. Moreover, we expect trails to restrict the movement of prey and contribute to aggregate prey-resource interactions into modules on either side of the road.

METHODS

Networks are defined by a set of nodes (e.g., individuals or species) connected by edges (e.g., trophic interactions) which can be represented by an adjacency matrix. Networks can present a single class of nodes, where all nodes could interact with each other, or multiple class of nodes where only interactions between nodes of different classes are allowed. Bipartite networks, which are networks comprising two classes of nodes, are commonly used in ecology (e.g., consumer-resource, plant-pollinator and host-pathogen networks). Edges connecting pairs of nodes can be treated as binary (i.e., unweighted) or weighted by a quantitative value (e.g., interaction strength). We can describe characteristics of individual nodes with metrics such as the degree, which represents the number of edges of a given node, or describe characteristics of the overall network with metrics such as the modularity coefficient, which increases as within-group interactions become more frequent compared to between-group interactions.

We represent interactions between prey and resource patches in TrophIE as a bipartite network. Prey nodes are players who were prey in a specific game. If a player played in six different games as a prey, it will be considered as six different nodes in the network. We thus refer to prey as player-game combinations. Resource nodes are the resource patches distributed across the arena and are not associated with a specific game. Edge information between prey and resource nodes is extracted from the EarthRanger report filed by each prey when successfully foraging at a resource patch. An edge between a prey and a resource patch is realized if the prey gathered resources from this patch at any point in the game. Edge weights correspond to the number of times this interaction was realized. In this bipartite network, we use data from all the games to encompass more broadly the emerging organization in ecological interactions between prey and resources throughout the arena.

The bipartite network is used to extract the number of prey nodes connected to each resource patch (i.e., resource degree) and to identify modules of closely interacting prey and resources. The modules are identified with the *walktrap* algorithm (Pons 2006). To assess the effect of trails on the spatial delimitation of modules, we extract for each pair of resource patches: the distance between them, whether they are separated by a main and/or secondary trail, and whether they are assigned to the same module. We then use a generalized linear model (GLM, family = binomial) to determine how the probability of resource patches being assigned to the same module is influenced by their spatial distance and the presence of trails.

We convert the bipartite network to a unipartite representation of the resource patches network (where an edge means that a prey moved directly from one patch to the other) and calculate the modularity index (Newman et al. 2004). This value is compared to the modularity values obtained from a purely spatial network where two resource patches are connected when their spatial distance is lower than a given threshold (see Figure 2). We also evaluate the distribution of the distances between each resource patch and its closest neighbor. Using the sequence of patches visited by each player, we also evaluate the distribution of the distances between each sequentially connected resource patch. Network analysis was performed with the *igraph* package (Csárdi and Nepusz, 2006) in R version 4.3.3.

RESULTS

We found that prey players and resource patches were partitioned in a total of 21 clusters out of which 10 were composed of more than two resource patches (**Figure 1, center**). We observed a high modularity in the network (Q = 0.791) illustrated by the strong within-modules and weak between modules interactions (**Figure 1, top**).

With the GLM analysis (**Figure 1, bottom**), we observed a significant effect of distance (Odds ratio = 0.98; $p<0.0001$) and the presence of main trails (Odds ratio = 0.31; $p<0.0001$), but not of secondary trails (Odds ratio = 1.25; $p = 0.20$), on the probability that resource patches are assigned to the same module of the bipartite network. Each meter separating two resource patches reduces the probability that they are assigned to the same module by 2%, and the presence of a main trail separating two patches reduces this probability by 69 %.

As for the unipartite network of resource patches, we also found a high modularity ($Q = 0.605$), which was expected as restrictions on prey movement prevent the connection of distant patches. This modularity value was higher than the modularity expected at all distances if connections in patches were only a function of a distance threshold (**Figure 2, bottom**). The distribution of distances between patches connected by player travels showed an average of more than double the distance to the nearest neighboring patch (73.45 m compared to 33.14 m). This implies that players often did not choose to move to the closest resource when leaving their current foraging patch. This is also shown by the relatively high number of travels of more than 100 metres (**Figure 2, top**).

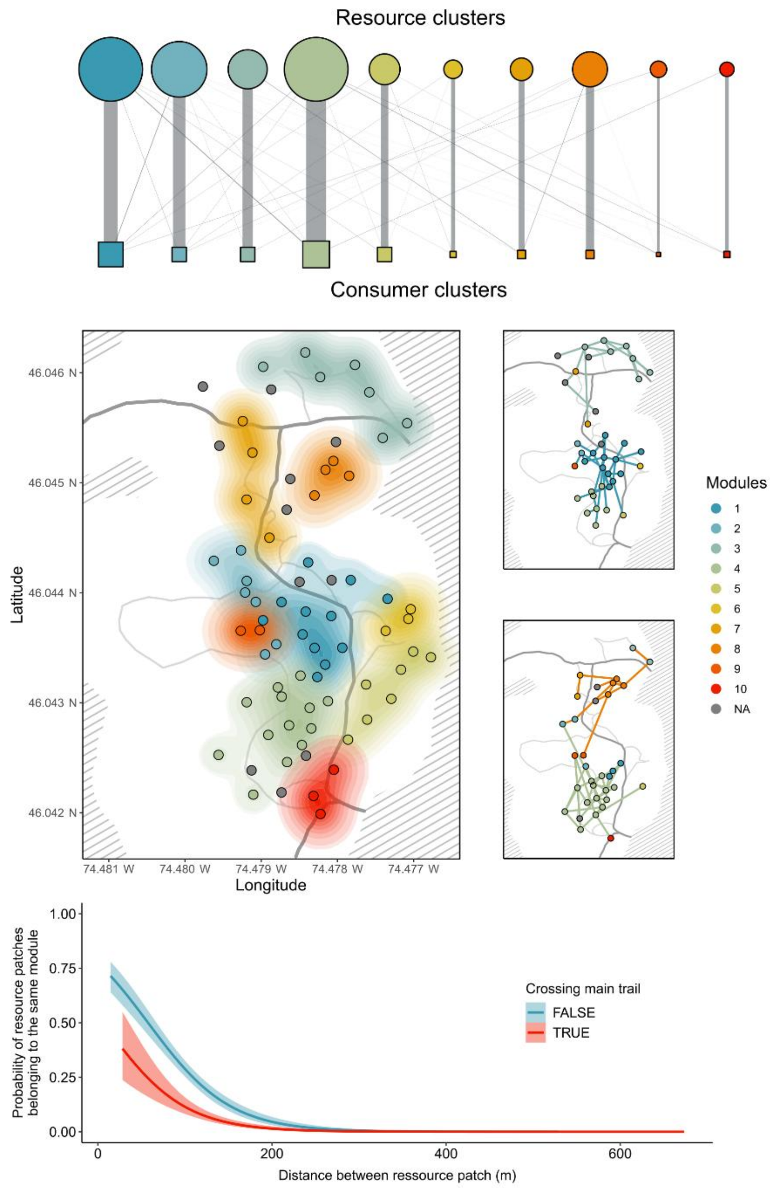


Figure 1. Top: Bipartite representation of the prey (squares) and resources (circles) interaction network of the TrophIE game aggregated by modules (colors). Symbol size is proportional to the number of nodes in each module and edge width is proportional to the cumulative edge weight (total number of prey-resource interactions between groups). **Center left**: Spatial distribution of resource patches (circles) and their assigned modules (colors) in the bipartite network within the TrophIE arena (white background). Trails found within the arena are illustrated as gray lines; thick lines represent the main trails while thin lines are secondary trails. Density kernels were used for illustration purposes to highlight the intensity of the spatial association to each module. **Center right**: Highlight of the indirect interactions between resources of modules 1 and 3 (top) and modules 4 and 8 (bottom). Lines between resources indicate a sequential movement of a prey from one resource to the other. Most links are between resources of the same module, but each module is connected to at least one other module, showing that the movement of

prey was not entirely restricted to a single module. Resources not connected to the highlighted modules are not shown for clarity. **Bottom**: Probability (obtained by the GLM) that two resource patches were in the same module according to the distance between them and whether they were separated by a main trail or not.

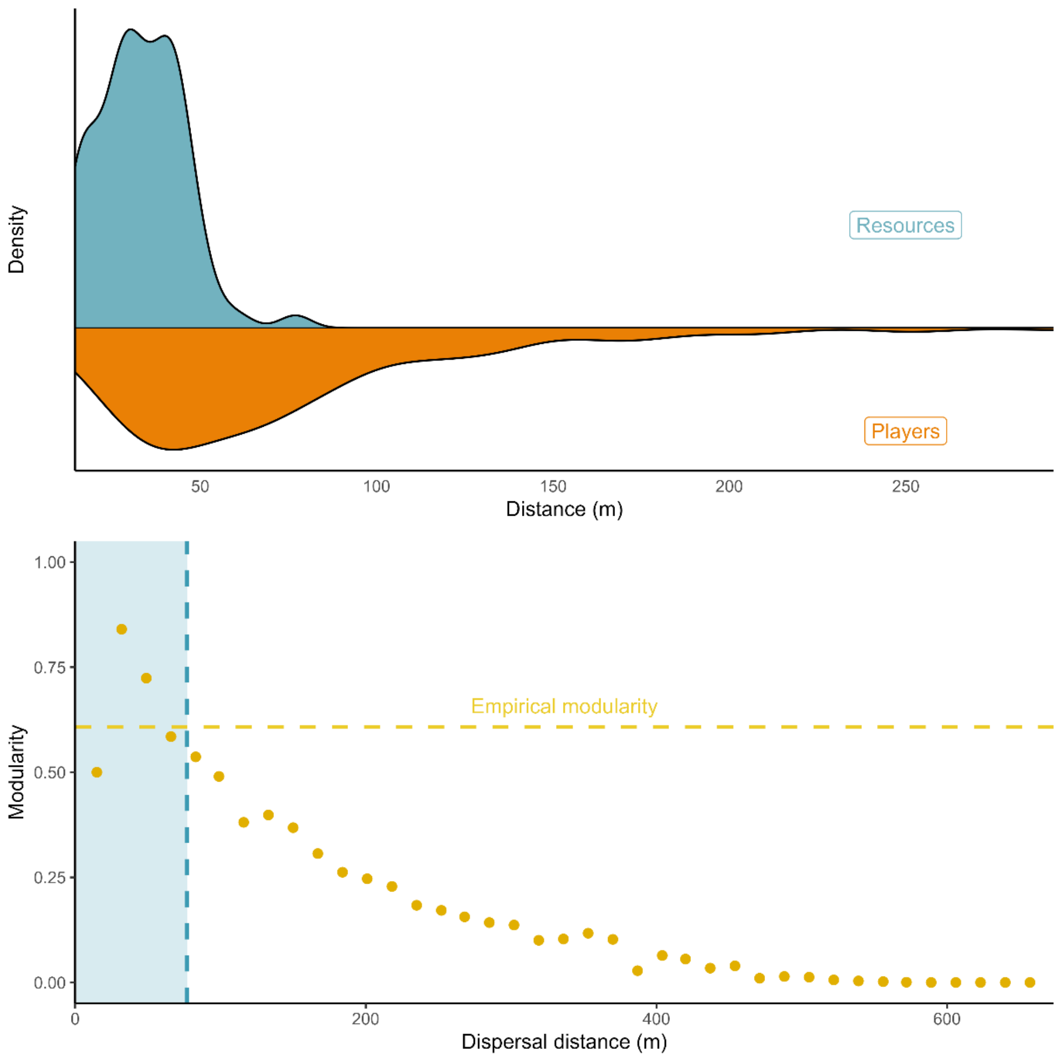


Figure 2. **Top:** Comparison between the distribution of distances to the nearest resource and the distribution of distances between resources connected by players. **Bottom:** Modularity of the purely spatial resource networks as a function of the distance threshold at which resource patches are connected. The horizontal line shows the empirical modularity of the unipartite network of resource patches, while the vertical line shows the distance threshold (14.6 m) to have a connected network (no isolated component in the network).

INTERPRETATION

Prey movement explains part of the modularity observed in the network. In spatial networks, modularity is a natural property that emerges from the restrictions imposed by the movement of individuals across a landscape (Gilarranz, 2020). In TrophIE, the short duration of the games and the walking speed imposed on prey could explain why resource modules are closely associated in space. This might have led to a relatively small prey home range, thus creating cores of highly connected resources. This hypothesis is further supported by the observed influence of distance on the probability that resource patches are found within the same module. However, the modularity value of the empirical unipartite network of resources is higher than what would be expected if edges were solely limited by the distance between the resources, as seen in **Figure 2 (bottom)**. This suggests that another factor, other than prey movement, could be responsible for increasing the modularity in the network. Further exploration shows that prey seemed to travel to resources usually farther than the closest one, supporting the idea that other factors than distance influenced the observed modularity (**Figure 2, top**). Notably, differences in perceived safety of resources, long-distance escape following predator detection and limited knowledge of the resource locations could also explain the high value of modularity.

We observed that the presence of large linear features (namely, main trails) in the arena influences the spatial organization of prey-resource interactions across the landscape. Linear features like trails can be perceived as risky environments by prey and therefore restrain their movement in the landscape (Whittington et al., 2011; Lendrum et al., 2018). Since modularity can influence the stability of food webs (Thébault and Fontaine, 2010; Grilli et al., 2016), the presence of linear features in the TrophiE arena could have positively impacted the overall stability of the system. However, we did not consider predators in our networks and the increase in their mobility provided by trails could, in fact, counterbalance the potential stabilizing effect of trails on the prey-resource network. Furthermore, we did not observe this influence from the secondary trails. Secondary trails were narrower and tended to have more vegetation cover, which might not have exposed prey moving between resources as much as the main trails. Another non-exclusive hypothesis is that the higher density of secondary trails in the arena compared to main trails could have forced prey to cross relatively often secondary trails within their home range.

While this study focused on prey-resource interactions, topography and refuge locations could also influence spatial use by prey and are generally important to gain an understanding of the landscape use patterns. In a case study with elephants, networks were used to reveal preferred rest locations, which allowed the characterization of spatiotemporal risk perception, and ultimately, provided a quantified landscape of fear (Wittemyer et al., 2017).

Besides predation, competitive effects could also play a role in the spatial structuring of prey and resource modules. During the games, prey foraging decisions changed under different scenarios of competition. Competition shapes how individuals select and use their spatial environment (Webber et al. 2023). Individuals may either join force or split in small groups depending on predation risk and resource density (Bonnell et al. 2019).

CONCLUDING STATEMENT

The extensive data provided by TrophIE allowed us to study trophic interaction networks at the individual level in a spatially explicit manner, something that is rarely feasible in natural systems. This high-resolution allowed us to unveil the principal mechanisms that shaped the spatial organization of consumer-resource interactions, namely the consumer mobility and the presence of linear features. Settings like TrophIE could greatly improve our understanding of spatio-temporal networks by providing means to test hypotheses on disease transmission, energy flow and even species rewiring and turnover. While we focused on prey-resource interactions, modularity and the effect of trails, there are still a lot of unexplored possibilities made possible by the game as is, or by slight modifications of the rules. Notably, further work could quantify more closely the effect of competition between prey, include the interactions of the predators in the network, or consider the temporal dimension of the interactions.

BIBLIOGRAPHY

Guimaraes Jr, P. R., Pires, M. M., Jordano, P., Bascompte, J., & Thompson, J. N. (2017). Indirect effects drive coevolution in mutualistic networks. *Nature*, *550*(7677), 511-514.

McCann, K. (2007). Protecting biostructure. Nature, 446, 29–29.

McCann, K.S. (2011). Food webs (MPB-50). In: Food Webs (MPB-50). Princeton University Press.

Pons, P., Latapy, M. (2005). Computing Communities in Large Networks Using Random Walks. In: Yolum, p., Güngör, T., Gürgen, F., Özturan, C. (eds) Computer and Information Sciences - ISCIS 2005. ISCIS 2005. Lecture Notes in Computer Science, vol 3733. Springer, Berlin, Heidelberg. https://doi.org/10.1007/11569596_31

Proulx, S. R., Promislow, D. E., & Phillips, P. C. (2005). Network thinking in ecology and evolution. *Trends in ecology & evolution*, *20*(6), 345-353.

Thébault, E., & Fontaine, C. (2010). Stability of ecological communities and the architecture of mutualistic and trophic networks. *Science*, *329*(5993), 853-856.

Stouffer, D.B.& Bascompte, J. (2010). Understanding food-web persistence from local to global scales. Ecology Letters 13, 154–161.

Stouffer, D.B. & Bascompte, J. (2011). Compartmentalization increases food-web persistence. Proceedings of the National Academy of Sciences of the United States of America 108, 3648–3652.

Grilli, J., Rogers, T., & Allesina, S. (2016). Modularity and stability in ecological communities. Nature communications, 7(1), 12031.

Pires, M. M., Guimarães Jr, P. R., Araújo, M. S., Giaretta, A. A., Costa, J. C. L., & Dos Reis, S. F. (2011). The nested assembly of individual ‐ resource networks. Journal of Animal Ecology, 80(4), 896-903.

Dupont, Y. L., Trøjelsgaard, K., Hagen, M., Henriksen, M. V., Olesen, J. M., Pedersen, N. M., & Kissling, W. D. (2014). Spatial structure of an individual ‐ based plant–pollinator network. Oikos, 123(11), 1301-1310.

Fletcher Jr, R. J., Revell, A., Reichert, B. E., Kitchens, W. M., Dixon, J. D., & Austin, J. D. (2013). Network modularity reveals critical scales for connectivity in ecology and evolution. Nature communications, 4(1), 2572.

Gilarranz, L. J. (2020). Generic emergence of modularity in spatial networks. Scientific reports, 10(1), 8708.

Pons, P., & Latapy, M. (2006). Computing communities in large networks using random walks. Journal of graph algorithms and applications, 10(2), 191-218.

Newman, M. E. J. and Girvan M. (2004). Finding and evaluating community structure in networks, Phys. Rev. E, 69, 026113

Csardi, G., & Nepusz, T. (2006). The igraph software. Complex syst, 1695, 1-9.

Olesen, J. M., Bascompte, J., Dupont, Y. L., & Jordano, P. (2007). The modularity of pollination networks. Proceedings of the National Academy of Sciences, 104(50), 19891-19896.

Guimera, R., & Nunes Amaral, L. A. (2005). Functional cartography of complex metabolic networks. nature, 433(7028), 895-900.

Whittington, J., Hebblewhite, M., DeCesare, N. J., Neufeld, L., Bradley, M., Wilmshurst, J., & Musiani, M. (2011). Caribou encounters with wolves increase near roads and trails: a time ‐ to ‐ event approach. Journal of applied ecology, 48(6), 1535-1542.

Lendrum, P. E., Northrup, J. M., Anderson, C. R., Liston, G. E., Aldridge, C. L., Crooks, K. R., & Wittemyer, G. (2018). Predation risk across a dynamic landscape: effects of anthropogenic land use, natural landscape features, and prey distribution. Landscape ecology, 33, 157-170.

Wittemyer, G., Keating, L. M., Vollrath, F., & Douglas ‐ Hamilton, I. (2017). Graph theory illustrates spatial and temporal features that structure elephant rest locations and reflect risk perception. Ecography, 40(5), 598-605.

Webber, Q. M., Albery, G. F., Farine, D. R., Pinter ‐ Wollman, N., Sharma, N., Spiegel, O., ... & Manlove, K. (2023). Behavioural ecology at the spatial–social interface. Biological Reviews, 98(3), 868-886.

Bonnell, T. R., Henzi, S. P. & Barrett, L. (2019). Functional social structure in baboons: modeling interactions between social and environmental structure in group-level foraging. Journal of Human Evolution 126, 14–23.

Albert, E. M., Fortuna, M. A., Godoy, J. A., & Bascompte, J. (2013). Assessing the robustness of networks of spatial genetic variation. Ecology Letters, 16, 86-93.

Appendix E – General guidelines for TrophIE game setup

Supplementary information to "Impersonating predators and prey to study trophic interactions through real-life simulations"

Our framework is highly flexible, and the following guidelines are not meant as prescriptions for how the game should be played. We offer this guidance based on our own experience to inspire implementation in other contexts. Readers may use the approach as is, but are also encouraged to develop their own unique version of the game based on the specific context or ecological phenomenon of interest.

Design game rules

What is the minimum set of rules you might need to create ecologically interesting patterns? What simple ecological trade-offs could be implemented? The simpler the better as emergent patterns can be particularly insightful. Also keep in mind that players having fun will stay motivated throughout the game, helping generate good data. We found that players stayed motivated when the rules were clear and when different options of physical involvement (e.g. roles where players could run and others where they had to walk) were available. Exhausted players means less fun and poor data.

Find a location

From our experience, having obvious landmarks (rivers, lakes, trails) is useful to set clear boundaries to the game arena. We looked for an arena large enough for players to roam freely, but small enough for players to occasionally meet and interact with each other. A heterogeneous terrain providing natural variability in detection distances, ease of movement, and concealment can increase realism and provide interesting study opportunity. Open terrains were often less suited for this game. When all players knew where other players were, they moved less and often avoided taking the necessary risks to make the game interesting.

Gather all necessary material

The specific material needed depends on the game rules and data of interest. Here is a list of material and considerations to inspire game implementation:

- Watch and whistle for timekeepers to clearly mark the beginning and end of games.
- Color jerseys to identify players' role.
- Markers and stakes to add features to the landscape (e.g. resources, refuges).
  We used small gardening stakes marked with forestry flag, but anything that is easy to deploy and visible from a reasonable distance works.
- Data recording material depending on the use case.
  - Collecting data at the end of the game: Players can report their score (number of resources, number of reproduction events, number of prey captured, etc.) to the

timekeepers at the end of each game. However, one line of data per player-game limits sample size and details compared to in-game data collection.

    - Collecting data during the game: There are various survey app compatible with most modern mobile phones that can help streamline in-game data collection. Alternatively, pen and paper forms fill out by each player during the game can also work, especially if it is possible for players to record the time and place of their interactions (e.g. resource patches have ID numbers).
    - Spatial data: Tracking apps work well on most modern mobile phones but should be tested on each phone beforehand to ensure they provide reasonable spatial and temporal resolution. Beware of battery-economy options which can interfere with GPS tracking. GPS devices are also an option but less affordable and sometimes harder to use.

Tips and tricks

- Keep the games short (<30 minutes) to maintain players' motivation. It's nice to know you'll get to play again even if you died within the first minutes of the game.
- Avoid having to reset the game setup at every new simulation. If you plan to move markers, consider playing in two areas so markers in one place can be moved and georeferenced while a game is occurring in the other place. One thing we did was to have two sets of resource envelopes at every resource patch, which we alternated between games. Players could reset the envelopes used in game 1 during game 2 so they were ready to use during game 3.
- Test the game with few players before going large scale. There are a lot of things you only realise when playing.
- Contact us (the corresponding authors). We like this game and will be please to chat about it.