

Lay summary

It is crucial that ecologists unravel the mechanisms driving predator hunting strategies to predict the impacts of predation on prey populations. With an online videogame simulating a predator-prey interaction, we demonstrate that prey behavior shapes the hunting tactics employed by predator players. While the predator players displayed a diversity of hunting strategies, they all achieved similar hunting success. Our results show that online videogames can be useful for ecological research.

Title: Studying predator foraging mode and hunting success at the individual level with an online videogame

Short title: Predator-prey interactions in virtual worlds.

Abstract

Predator-prey interactions are important drivers of community and ecosystem dynamics. With an online multiplayer videogame, we propose a novel system to explore within-population variation in predator hunting mode, and how predator-prey behavioral interactions affect predator hunting success. We empirically examined how four predator foraging behaviors covary at three hierarchical levels (among environments, among individuals, and within individuals) to assess the structure of predator hunting mode. We also investigated how prey activity affects the foraging behavior and hunting success of predators. We found that individual predators players displayed a diversity of hunting tactics that were conditioned by prey behavior. With prey movement, predator players specialized either as cursorial or ambush hunters along a continuum of their hunting traits, but also shifted their strategy between encounters. Both types of hunters were generally better against slower-moving prey, and they achieved similar prey captures over the sampling period. Our study supports key findings on predator foraging mode and predator-prey interactions from behavioral ecology. This suggests that virtual worlds supporting multiplayer online videogames can serve as legitimate systems to advance our knowledge on predator-prey interactions. We further discuss the insight they can provide for ecological research.

Keywords: individual specialization, environmental variation, hunting mode, hunting tactics, predator-prey interactions, online videogames.

Introduction

Predator hunting mode plays a crucial role in structuring ecological communities and ecosystems (Huey and Pianka 1981; Preisser et al. 2007; Schmitz 2008; Kersch-Becker et al. 2018) and is usually described as 1) active/cursorial when hunters search, follow, and chase prey for long distances, 2) sit-and-pursue, when hunters remain motionless and pounce on prey that are within chasing distance, and 3) sit-and-wait/ambush, when hunters wait for prey to be within immediate capture distance (McLaughlin 1989). Field studies show that contrasting hunting modes (e.g. cursorial vs ambush) found among and within predator species can lead to differences in the number of individuals or species, or in the type of prey captured (Miller et al. 2014; Donihue 2016; Glaudas et al. 2019). As a result, predators with contrasting hunting modes can cause opposing trophic cascades and act at different trophic levels (Schmitz 2008; Romero and Koricheva 2011).

Predator species are often classified either as active or sit-and-wait hunters based on their average behavior (Lima 2002; Miles et al. 2007; Pettorelli et al. 2015; Schmitz 2017). While such categorisation has proven useful to predict community and ecosystem dynamics (Wirsing et al. 2021), it ignores the complexities of predator foraging decision-making. Indeed, growing evidence suggests that behavioral variation among individual predators can have important consequences for predator-prey interactions (Pettorelli et al. 2015; Toscano et al. 2016; Schmitz 2017). For instance, individual predator behavioral type can mediate consumptive and non-consumptive effects during trophic interactions (Smith and Blumstein 2010; Griffen et al. 2012; Toscano and Griffen 2014). Yet, the extent to which predators within populations differ in their foraging mode and how these individual differences affect the outcome of predator-prey interactions remain unclear. It is therefore imperative that we quantify and account for individual variation in hunting mode during predator-prey interactions if we hope to understand the community consequences of predation.

Stable individual differences in hunting mode within populations can be driven by specialization when individuals experience temporal and/or spatial fluctuations in the distribution, availability, or behavior of their prey (Araújo et al. 2011; Carneiro et al. 2017; Phillips et al. 2017; Courbin et al. 2018). For instance, individual predators can specialize in specific tactics to meet the energy/time demands required to successfully capture the type of prey generally encountered (Bowen et al. 2002; Tinker et al. 2008; Arthur et al. 2016). According to the foraging syndrome hypothesis, these tactics are characterized by a continuum of morphological, physiological, and behavioral traits that are coordinately expressed by a predator to subdue its prey (Perry et al. 1990; Perry 1999; Butler 2005; Cooper 2005; Miles et al. 2007). The activity and movement

patterns of prey are major drivers of encounter rates with predators (Gerritsen and Strickler 1977; Huey and Pianka 1981; Scharf et al. 2006), which may therefore lead to nonrandom interactions between predator-prey behavioral types (Wolf and Weissing 2012). For example, the locomotor crossover hypothesis (Huey and Pianka 1981) predicts that ambush predators should be more successful when they hunt fast-moving prey, while cursorial predators should have greater success with sedentary prey (Scharf et al. 2006; Belgrad and Griffen 2016; Donihue 2016). Thus, in the presence of prey with diverse movement patterns, individual predators specializing in contrasting hunting modes might coexist within a population if they achieve similar hunting success (Araújo et al. 2011; Chang et al. 2017).

Habitat structure is a second important driver of predator foraging mode, as it shapes opportunities for prey encounter and prey capture (Robinson and Holmes 1982; James and Heck Jr. 1994; Sargeant et al. 2007; Wasiolka et al. 2009; Donihue 2016). A growing body of evidence points to predators who hunt in open and homogeneous habitats adopting a cursorial strategy, contrary to those hunting in heterogeneous and closed habitats that typically ambush their prey (James and Heck Jr. 1994; Wasiolka et al. 2009; Donihue 2016). Hence, the habitat components of a predator's hunting grounds can shape its hunting tactic. Heterogeneous habitats are expected to favor sit-and-wait/sit-and-pursue hunters as they offer perches and cover, which are useful for ambushes (James and Heck Jr. 1994; Laurel and Brown 2006). On the contrary, active hunters should benefit from higher encounter rates in open habitats as prey detection is easier, although, at the expense of being themselves more easily detected (Michel and Adams 2009). This suggests that habitat structure could mediate tradeoffs between hunting strategies.

Trophic interactions are dynamic processes that can also trigger flexible behavioral adjustments by individual predators (Helfman 1990; Heithaus et al. 2018). Predators can shift their hunting strategy in response to changes in prey density and heterogeneity (Inoue and Marsura 1983; Woo et al. 2008), prey behavioral type (McGhee et al. 2013), prey condition (Wignall and Taylor 2008), seasonality (Miles et al. 2007; Phillips et al. 2017), or habitat structure (Wasiolka et al. 2009). Foraging mode shifts might thus be crucial for predators to maintain capture rates when coping with prey antipredator behaviour and environmental change (Laurel and Brown 2006).

Longitudinal studies on predator-prey interactions often involve considerable financial, technical, and ethical challenges, especially when studying larger or elusive wildlife such as apex predators (Hertel et al. 2020). For instance, a major challenge impeding empirical investigations of individual variation in hunting mode is

the need for repeated behavioral measurements of numerous individuals in varying environmental settings (Dall and Griffith 2014; Dingemanse and Wright 2020). This also comes with the difficulty of identifying traits in predators and prey that are easily observable and ecologically relevant. Besides, numerous predator-prey studies are conducted under controlled laboratory conditions that may fail to capture the nuances and complexities of a predator's behavior in the wild (Carter et al. 2013; Niemelä and Dingemanse 2014). Consequently, few studies have investigated how prey movement shapes predator foraging syndromes at multiple hierarchical levels (i.e. within and among individuals or habitats) along with the relative importance of predator and prey behaviours for predator hunting success.

Here, we propose a novel approach to circumvent these challenges by studying individual variation in predator behavior that capitalizes on online multiplayer videogames (Balicer 2007; Lofgren and Fefferman 2007; Oultram 2013; Ahmad et al. 2014; Ross et al. 2015). Online multiplayer videogames could provide numerous opportunities for ecologists to study general ecological phenomena, including the mechanisms driving individual variation in behavior (Barbe et al. 2020; Beauchamp 2020; Céré et al. 2021; Duthie et al. 2021). First, online videogames provide abundant repeated measurements on millions of individual players across temporal and environmental gradients. Second, the structure of the virtual environment is known and can be used to evaluate how specific components affect the behavior of interest. Third, videogames can reproduce realistic ecological settings in which complex interactions occur among players. A classic example is the case of the “Corrupted Blood” epidemic in *World of Warcraft*, where transmission modes/vectors and human reactions to the disease were surprisingly similar to what would be expected in a real-world outbreak (Balicer 2007; Lofgren and Fefferman 2007). For these reasons, online multiplayer videogames could potentially constitute a complement to traditional field studies. They could allow ecologists (among other scientists) to bridge the gap between real-world ecological studies and large-scale computer simulations (Ross et al. 2015).

We used the videogame *Dead by Daylight* (DBD) as our study system. DBD is an asymmetrical online multiplayer horror game that pits a single player (predator) against a group of four players (prey). The predator's main objective is to search for and consume prey (figure 1A), whilst the preys' objective is to exploit resources while avoiding the predator. These resources consist of generators that need to be repaired so prey can escape and win. Thus, analogous to real prey that move across patches to exploit resources under predation risk, prey in DBD must move around the virtual environment and locate generators to repair them

(figure 1B). As described in classical ecological studies of patch use (Brown 1988; Kotler and Blaustein 1995; Brown 1999), prey must be wary of the time they spend repairing a generator (i.e. foraging in a patch) because investing too much time can increase the risks of being captured. Prey players can use a wide range of behaviors such as cooperation or hiding (Céré et al. 2021) to successfully escape (figure 1 B-C), providing opportunities for the predator to express a diversity of hunting tactics. Moreover, each match in *DBD* occurs within a specific virtual habitat such as forests, farmlands, and urban areas. These environments differ in their structure (McCoy and Bell 1991), such as in the availability of perches and refugia, vegetation density, or surface area (figure 1D). Predator players can exploit these habitat features to hunt their prey. Hence, they experience variability in the prey and habitats that they encounter, and are expected to benefit from changing their behavior accordingly to maximize hunting success. Lastly, although *DBD* is a virtual environment, we suggest that individual players express ecologically relevant decisions in response to predation or prey behavior, and the resulting complex interactions that are monitored can be valuable for ecological research. Therefore, an empirical approach can be adopted to study the player population (see these studies for examples on other games: Szell et al. 2010; Fuchs and Thurner 2014; Belaza et al. 2020), with methods equivalent to those used in observational studies of natural predators.



Figure 1: Images of the online videogame Dead by Daylight. (A) Image of the predator player’s first person vision. Here, we see a predator chasing a prey. (B) The prey (survivor) player’s third person vision. Prey can cooperate to repair generators. They can activate one of the two escape doors to flee and win the match when all generators are repaired. (C) Representative image of a prey player activating an escape door. (D) Representative pictures of the different game environments where matches take place. All the images were taken from the official Dead by Daylight wiki and forum web pages

In this study, we use an extensive dataset on the hunting behavior of predator players in *DBD* to empirically investigate environmental and individual variation in hunting mode, and how predator and prey behavior affect prey capture. We use four hunting-related behaviors as proxies of hunting mode: travel speed, the rate of space covered in the environment, the time spent guarding captured prey, and the time elapsed before the first prey capture. Predators adopting a cursorial hunting mode should travel faster and cover more space in the environment, but should spend less time guarding and have a shorter latency before the first capture. Predators with an ambush hunting mode should exhibit the opposite tendency. Thus, both strategies should represent the extremes of a continuum. We use multivariate mixed-modelling to quantify variation in these behaviors and their correlations as a way to decompose the hunting mode continuum at different hierarchical levels within the predator population (Dingemanse and Dochtermann 2013). These levels include behavioral differences among environments, consistent differences among individuals in their average hunting behavior, and differences arising from individuals adjusting their behavior over time in response to

temporal changes in environmental conditions or prey behavior. First, we hypothesize that habitats shape the hunting mode employed by predators. If there are among environmental behavioral differences, we expect correlated trait values associated with an ambush mode in smaller and heterogeneous environments, and correlated trait values associated with a cursorial mode in open/wider and homogeneous environments (i.e. among-environment behavioral correlations). Second, we hypothesize that predator players will consistently differ in their hunting mode over time, with some specializing as cursorial hunters and others as ambush hunters. Thus, if predator players differ in their average behaviors, we predict that their average trait values will be positioned along an ambush-cursorial continuum (i.e. among-individual behavioral correlations), where the position reflects their preferred hunting mode. Third, we expect that predator players will switch from cursorial to ambush tactics between foraging bouts (i.e. between matches). If there is within-individual behavioral variation, we predict negative relationships between hunting behaviours at this level (i.e. within-individual behavioral correlations). Fourth, following the locomotor crossover hypothesis, we predict that ambush and cursorial predator player-types will coexist in the population because both achieve similar hunting success by performing better against prey with the opposite locomotor tendency.

Materials and methods

Study system

The datasets used to test our hypotheses were provided by Behaviour Interactive Inc., the owner and developer of *DBD*. The company records the behavior of players for every match played online. During our study period, *DBD* offered 15 playable predator avatars. Players who adopt the predator's role choose their avatar before a match. Each predator avatar has unique abilities that may encourage different playstyles. Some have abilities that make them stealthier, while others can run faster, or have more powerful attacks. We thus controlled for the chosen avatar in our models since it may impact the playstyle of the predator player. In addition, the game environment where players compete is usually randomly assigned from a list of 27 maps differing in their physical components. For example, some maps have large playable surface areas with low vegetation density, which may favor the use of a cursorial strategy. Other maps have a smaller surface area with high vegetation density, which may impair visibility and alter prey detection, favoring the use of an ambush strategy. However, an important game feature to consider is that predators have constant visual cues that display the location of the generators. This could interfere with how the virtual environment affects the predator's behav-

ior or hunting success. For instance, predators might use these cues to approximate the distance/time required to travel between generators, which may relax the energy/concentration allocated to managing movement across the environmental features. For additional details on the game settings and map characteristics, refer to <https://deadbydaylight.com/en>, and https://deadbydaylight.gamepedia.com/Dead_by_Daylight_Wiki.

Data collection

The game developer provided us with raw datasets ranging from 20 March to 17 June 2019. Because the company records player data with automated scripts, technical issues or errors in the data compilation can occur. For instance players hacking the game or disconnecting during a match among other reasons can cause errors in the data compilation. We thus had to combine these datasets and apply filtering, cleaning, and verification procedures to obtain our synthetic dataset. First, we filtered for matches that were played exclusively against a group of unknown people. Second, we retained matches that lasted more than five minutes, as short matches are usually interrupted because of disconnexions or inactive players, and deleted any match where the match duration was missing or equal to zero. Third, we removed matches where predator players were obviously inactive, that is, when they had average speeds of or very close to zero while staying within two squares or less during the match. Fourth, based on our knowledge of the game, we deleted any matches where the observed behaviours were extreme and were most likely the result of hacking or players doing something different than playing how the game was intended to (e.g. farming for points).

Our synthetic dataset consists of a population of 2 378 new anonymous players who initiated their first match between 20 March and 22 March, with a total record of 77 047 matches (average: 187 matches per individual, range: 1 - 1047 matches). The average match duration was 11.13 minutes (range: 5 - 35 minutes). For every match, the date (date-hour-minutes), the duration (seconds), the predator player's anonymous ID, the prey players' anonymous ID, the predator's avatar, and the game environment was recorded along with the predator and prey behaviors.

Behavioral traits

We ran a principal component analysis on eight behavioral traits to identify the presence of structured hunting tactics in the predator player population (see figure S1 and table S1 in the Supporting information). We then selected four behaviors that summarized most of the variation in the observed tactics for all our analyses. We used this approach to ease the interpretation of the trait correlations in the multivariate models and allow

for future analyses to reuse the same variables as the present study. In fact, any new sample of observations would yield a different ordination with different principal components, precluding any comparison between studies. The behaviors we selected were the average travel speed (m/s) (mean = 3.30, sd = 0.45), the rate of space covered (square/s) (mean = 0.05, sd = 0.01), the total amount of time spent guarding captured prey (mean = 42.91, sd = 41.91), and the time predators took to capture their first prey (mean = 178.67, sd = 146.65).

Our proxies of activity were the predator's average travel speed representing the average number of meters per second traveled during a match, and space coverage describing the number of 16x16 meters squares entered per second in a grid that covers the whole virtual environment (similar to measures of activity in open field tests, Montiglio et al. 2010). The grids are drawn by the game developer to build the game environments, but are invisible to the players. Based on this data, we divided the number of times a square was visited by the match duration to obtain the rate of space covered. Unfortunately, it was not possible to know which specific square was visited. This variable is thus a raw estimate of the rate at which predators cover space in the environment. The time spent guarding prey describes the time a predator spent monitoring around capture sites to ambush prey players trying to rescue individuals that were captured. This trait is measured by drawing (invisible) 9-meter radius circles around all sites where the predator brings prey to be consumed (each site is at the center of a circle). Thus, whenever a predator brought prey to a capture site during a match, the time (in seconds) it spent monitoring within the site's circle area was recorded. We could then sum all the events where predators were monitoring capture sites to obtain the total amount of time spent guarding captured prey during a match. Lastly, the time before the first capture was calculated as the amount of seconds elapsed before a predator captured its first prey.

To test the locomotor crossover hypothesis, we were provided datasets that contained the average travel speed (m/s) and rate of space covered (square/s) of all the prey players for each match played by the predator. Both traits are measured using the same method described for predators. For both prey behaviors, we averaged the four individual prey player values within each match since we were interested in the average effect of prey behavior on the predator's hunting behavior and success. Thus, we used one average value per prey behavior for each match played by the predator.

Statistical analyses: Software and computer setup

224 We performed all statistical analyses using the R software (version 4.1.2, R Core Team, 2021) on a remote
 225 computer cluster (Cedar, Compute Canada, <https://docs.computeCanada.ca/wiki/Cedar>) running on CentOS
 226 Linux 7. All models were fitted using the R package ‘brms’ version 2.16.3 (Bürkner 2017). To ensure a mini-
 227 mum of reproducibility and transparency, we made all the R code and most outputs available along with the R
 228 sessions information on this GitHub repository ([https://github.com/quantitative-ecologist/predator-foraging-](https://github.com/quantitative-ecologist/predator-foraging-mode-videogames)
 229 [mode-videogames](https://github.com/quantitative-ecologist/predator-foraging-mode-videogames)).

230 *Statistical analyses: Variation in hunting mode*

231 We first parametrized a Bayesian multivariate mixed model (Dingemanse and Dochtermann 2013; Bürkner
 232 2018; Mitchell and Houslay 2020) (for an overview using ‘brms’, see [https://paul-buerkner.github.io/brms/](https://paul-buerkner.github.io/brms/articles/brms_multivariate.html)
 233 [articles/brms_multivariate.html](https://paul-buerkner.github.io/brms/articles/brms_multivariate.html)) to quantify the repeatability of hunting behavior, and evaluate among-
 234 environment, among-individual (specialization), and within-individual (flexibility) behavioral correlations.
 235 For each hunting behavior, we controlled for the predator’s population-response to prey behavior by adding
 236 the prey travel speed (x_1) and rate of space covered (x_2) as linear fixed effects. We also included the
 237 square-root of the match duration (x_3) as a fixed effect for the time spent guarding and the time before the
 238 first capture to control for differences in game length. We log transformed the time spent guarding and
 239 the time before the first capture to achieve normality and then defined each behavior ($y1$ = speed, $y2$ =
 240 space, $y3$ = guarding time, $y4$ = time 1st capture) as having a Gaussian distribution. All behaviors were then
 241 standardized to mean and unit variance (z-scores). The model is described by the following equations:

$$y1_{ghij} = (\beta_{0y1} + env_{0y1,g} + avatar_{0y1,h} + id_{0y1,i}) + \beta_{1y1}x_1 + \beta_{2y1}x_2 + \varepsilon_{0y1,ghij} \quad (1)$$

$$y2_{ghij} = (\beta_{0y2} + env_{0y2,g} + avatar_{0y2,h} + id_{0y2,i}) + \beta_{1y2}x_1 + \beta_{2y2}x_2 + \varepsilon_{0y2,ghij} \quad (2)$$

$$y3_{ghij} = (\beta_{0y3} + env_{0y3,g} + avatar_{0y3,h} + id_{0y3,i}) + \beta_{1y3}x_1 + \beta_{2y3}x_2 + \beta_{3y3}x_3 + \varepsilon_{0y3,ghij} \quad (3)$$

$$y_{4ghij} = (\beta_{0y4} + env_{0y4,g} + avatar_{0y4,h} + id_{0y4,i}) + \beta_{1y4}x_1 + \beta_{2y4}x_2 + \beta_{3y4}x_3 + \varepsilon_{0y4,ghij} \quad (4)$$

where g indexes the environment, h the predator avatar, i the individual player, and j the recorded match. The game environment ($env_{0y,g}$), the predator avatar ($avatar_{0y,h}$), and the player ID ($id_{0y,i}$) are random intercepts (among- environment, avatar, and individual variances), and ($\varepsilon_{0y,ghij}$) are the residuals (within-individual variance). Random intercepts and residuals were assumed to follow a multivariate Gaussian distribution with their associated variance-covariance matrices ($\Omega_{env}, \Omega_{avatar}, \Omega_{id}, \Omega_{\varepsilon}$) (equations S1-S4 in the Supporting information). For each combination of behaviors (y_n), we extracted the behavioral correlations among environments ($r_{env_{0,y_n} env_{0,y_n}}$), individuals ($r_{id_{0,y_n} id_{0,y_n}}$), as well as within-individual behavioral correlations ($r_{\varepsilon_{0,y_n} \varepsilon_{0,y_n}}$) (Dingemanse and Dochtermann 2013). The sample size of each parameter's posterior distribution is 1000 (see section 'Parametrization of the Bayesian multivariate mixed-model' in the Supporting information for details).

Statistical analyses: Effect of hunting behavior and prey behavior on prey capture

We first quantified the linear relationship between hunting success and predator behavior by fitting a Bayesian generalized linear mixed model. Since predators can capture a maximum of four prey, we fitted the model using the number of prey captured per total number of prey in a match (four) as a binomial response variable ($\omega_{hij} \sim Binom(max_{hij}, P_{hij})$) with a logit link function. The model fits a linear function ($\beta_{n,pred}x_{hi}$) where we could estimate if hunting success increased or decreased with increasing hunting behavior scores. We fitted the mean probability of capturing four prey (P_{hij}) in the environment h for individual i on its j match as a function of its travel speed, rate of space covered, time spent guarding, and latency before the first capture (equation S5 in the Supporting information). We computed a second model to account for variation in hunting success explained by prey behavior ($\beta_{n,prey}x'_{hi}$). We thus added prey travel speed and their rate of space covered in the model equation (equation S6 in the Supporting information). Both models had random intercepts for the game environment ($env_{0,h}$) and the predator player's ID ($id_{0,i}$) to partition the variance in hunting success explained by differences among players and the environments where matches occurred. The random intercepts for the game environment and the player ID were assumed to follow a Gaussian distribution with estimated variance ($env_{0,h} \sim N(0, V_{env}), id_{0,i} \sim N(0, V_{id})$). We included an observation-level random effect to account for overdispersion and compared the models to a beta-binomial model to

ensure that the estimates were robust (Harrison 2015). Trait values were standardized to mean and unit variance (z-scores). The sample size of each parameter's posterior distribution is 1000 for both models.

We built a third model with the same structure as the first model and included quadratic terms ($\frac{1}{2}\gamma_{n,pred}x_{hi}^2$), identified as lambda, to determine whether the relationships between hunting success and predator behavior are concave or convex (equation S7 in the Supporting information). Concave gradients suggest that individuals at the extremes of the trait distribution perform poorly while the opposite is true when the gradient is convex (Brodie et al. 1995). We also added interaction terms for each combination of predator traits ($\gamma_{n,pred}$) to estimate correlated effects on hunting success. Lastly, we computed a fourth model with the same structure as the third and included quadratic terms for prey behavior ($\frac{1}{2}\gamma_{n,prey}x_{hi}^2$), and interaction terms between predator and prey behaviors ($\gamma_{n,pred,prey}$) to test if predators perform better against prey with the opposite locomotor tendency (locomotor crossover) (equation S8 in the Supporting information). All trait values were standardized to mean of 0 and unit variance (z-scores). The sample size of each parameter's posterior distribution is 1000 for both models. For the four models, we included the square-root of the match duration as a fixed effect to control for differences in game length. We provide a detailed description of the model parametrization in the supporting information (Parametrization of the Bayesian mixed-models for hunting success).

We performed approximate leave-one-out cross-validation using Pareto smoothing importance sampling (PSIS-LOO) (Vehtari et al. 2017) with the 'loo' function in 'brms' to select the best out of the four candidate models. This method outlines the best model by comparing their predictive accuracy based on the difference of their expected log predictive density (elpd). The model with the highest elpd value should thus be the best at predicting the data. We also computed the marginal ($R_{marginal}^2$) and conditional ($R_{conditional}^2$) coefficients of determination (Nakagawa et al. 2017) of all the candidate models to assess the relative contribution of the predator behavior, the prey behavior, the behavioral interactions, and the random effects (differences among individuals and environments) on the predator's hunting success. We assumed that the relationship between hunting behavior and hunting success reached statistical significance when the 95% credible intervals of the fixed parameter values did not overlap zero (Nakagawa and Cuthill 2007).

Variance decomposition

Following the method by Nakagawa and Schielzeth (2010) for Gaussian response models, we calculated

each hunting trait's adjusted repeatability estimate (intra-class correlation coefficient, ICC) for the game environment, the predator avatar, and the player ID. To do so, we divided the mean variance (V) drawn out of the 1000 posterior samples of each specific random effect by the total behavioral variance (e.g. $ICC_{id_{y1}} = V_{id_{0,y1}} / (V_{env_{0,y1}} + V_{avatar_{0,y1}} + V_{id_{0,y1}} + V_{\varepsilon_{0,y1}})$). We computed the 95% credible intervals for each repeatability estimate using the highest posterior density intervals. We additionally calculated the ICC of the predator hunting success for the player ID and the game environment using the method by Nakagawa et al. (2017) for binomial models and computed their 95% credible intervals using the highest posterior density intervals.

Results

Variation in hunting mode: Repeatability of hunting behavior

Contrary to our predictions, neither the average travel speed ($ICC_{env_{y1}}$ [95% CI] = 0.002 [0.001, 0.003]), nor the time spent guarding ($ICC_{env_{y3}}$ [95% CI] = 0.014 [0.008, 0.021]) differed among the game environments (figure 2A, diagonal). We detected minimal differences among the game environments in the average rate of space covered ($ICC_{env_{y2}}$ [95% CI] = 0.040 [0.022, 0.061]) and latency before the first capture ($ICC_{env_{y4}}$ [95% CI] = 0.022 [0.012, 0.033]) (figure 2A, diagonal).

Predator avatars differed slightly in their average travel speed ($ICC_{avatar_{y1}}$ [95% CI] = 0.081 [0.039, 0.138]). We observed weak differences among avatars for the other three hunting behaviors ($ICC_{avatar_{y2}}$ [95% CI] = 0.020 [0.008, 0.035], $ICC_{avatar_{y3}}$ [95% CI] = 0.026 [0.008, 0.049], $ICC_{avatar_{y4}}$ [95% CI] = 0.027 [0.010, 0.048]).

As predicted, we found moderate among-individual differences in the average travel speed ($ICC_{id_{y1}}$ [95% CI] = 0.277 [0.256, 0.301]), the time spent guarding ($ICC_{id_{y3}}$ [95% CI] = 0.263 [0.240, 0.282]), and the latency before the first capture ($ICC_{id_{y4}}$ [95% CI] = 0.211 [0.195, 0.228]) (figure 2B, diagonal). Individual predators differed weakly in their average rate of space covered ($ICC_{id_{y2}}$ [95% CI] = 0.057 [0.049, 0.064]) (figure 2B, diagonal).

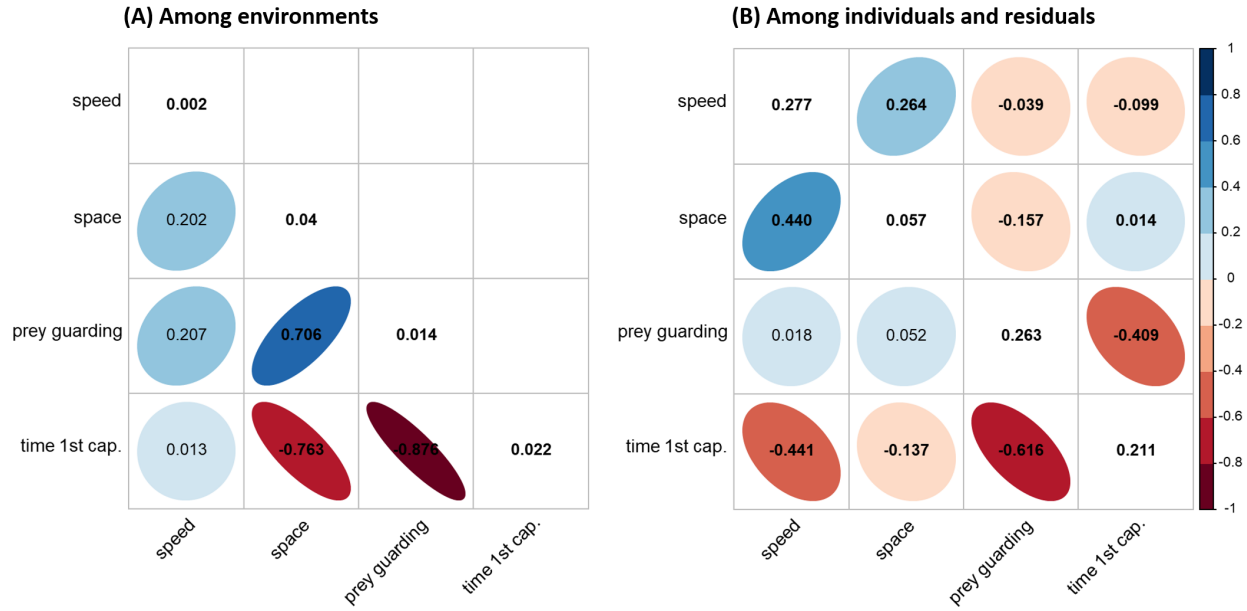


Figure 2: Correlations between combinations of hunting behaviors and their ICCs. For each panel, the posterior average ICC of the behavior is displayed on the diagonal. Darker red and darker blue colors represent stronger negative and positive correlations respectively. (A) Among-environment behavioral correlations on the lower off-diagonal. (B) Among-individual behavioral correlations on the lower off-diagonal, and (residual) within-individual behavioral correlations on the upper off-diagonal. Behavior names were shortened to simplify the plot.

Variation in hunting mode: Correlations between hunting behaviors

Environments where predators were faster were also those where they tended to spend more time guarding their prey ($r_{env_{0,y1}env_{0,y3}}$ [95% CI] = 0.207 [-0.124, 0.541]) (figure 2A, lower off-diagonal), but the relationship was not significant. We detected a similar yet stronger and significant relationship between space coverage and time spent guarding ($r_{env_{0,y2}env_{0,y3}}$ [95% CI] = 0.706 [0.51, 0.892]). Predators took on average less time to capture their first prey in environments where they covered space at a faster rate ($r_{env_{0,y2}env_{0,y4}}$ [95% CI] = -0.763 [-0.899, -0.61]) and when they spent more time guarding their prey ($r_{env_{0,y3}env_{0,y4}}$ [95% CI] = -0.876 [-0.952, -0.781]) (figure 2A, lower off-diagonal). Lastly, we did not detect significant among-environment correlations between travel speed and space coverage, or between travel speed and the latency to capture the first prey ($r_{env_{0,y1}env_{0,y2}}$ [95% CI] = 0.202 [-0.124, 0.536], ($r_{env_{0,y1}env_{0,y4}}$ [95% CI] = 0.013 [-0.316, 0.358]) (figure 2A, lower off-diagonal).

Contrary to our expectations, individuals that traveled faster did not spend less time guarding prey

($r_{id_{0,y1}id_{0,y3}}$ [95% CI] = 0.018 [-0.042, 0.077]) (figure 2B, lower off-diagonal). Similarly, the relationship between space covered and time spent guarding was weak and non significant ($r_{id_{0,y2}id_{0,y3}}$ [95% CI] = 0.052 [-0.035, 0.141]). Faster individuals covered space at a faster rate ($r_{id_{0,y1}id_{0,y2}}$ [95% CI] = 0.44 [0.376, 0.499]), and individuals who were faster or covered space at a faster rate took less time to capture their first prey ($r_{id_{0,y1}id_{0,y4}}$ [95% CI] = -0.441 [-0.489, -0.39], $r_{id_{0,y2}id_{0,y4}}$ [95% CI] = -0.137 [-0.221, -0.058]) (figure 2B, lower off-diagonal). Another result opposing our predictions was that hunters who spent more time guarding prey were faster to capture their first prey ($r_{id_{0,y3}id_{0,y4}}$ [95% CI] = -0.616 [-0.655, -0.579]) (figure 2B, lower off-diagonal).

At the within-individual level, we detected a moderate positive correlation between travel speed and the rate of space covered ($r_{\varepsilon_{0,y1}\varepsilon_{0,y2}}$ [95% CI] = 0.264 [0.257, 0.27]) so that predator players covered space at a faster rate (relative to their average) in matches where they traveled faster. Players barely spent less time guarding prey in matches where they traveled faster ($r_{\varepsilon_{0,y1}\varepsilon_{0,y3}}$ [95% CI] = -0.039 [-0.046, -0.032]). However, players spent less time guarding prey in matches where they were faster at covering space in the environment ($r_{\varepsilon_{0,y2}\varepsilon_{0,y3}}$ [95% CI] = -0.157 [-0.165, -0.148]) (figure 2B, upper off-diagonal). Individuals tended to be faster at capturing their first prey in matches where they traveled faster ($r_{\varepsilon_{0,y1}\varepsilon_{0,y4}}$ [95% CI] = -0.099 [-0.106, -0.092]), but not when they covered space at a faster rate ($r_{\varepsilon_{0,y2}\varepsilon_{0,y4}}$ [95% CI] = 0.014 [0.006, 0.023]) (figure 2B upper off-diagonal). In accordance with our observations at the among-individual level, predator players captured their first prey earlier in matches where they spent more time guarding their prey ($r_{\varepsilon_{0,y3}\varepsilon_{0,y4}}$ [95% CI] = -0.409 [-0.415, -0.404]) (figure 2B upper off-diagonal).

Effects of the predator and prey behavior on hunting success

The best model at predicting hunting success included a linear and quadratic effect of all the predator behaviors along with two-way interactions between predator behaviors and predator and prey behaviors (see table S4 in the Supporting information). Predators maximized their hunting success when they traveled at population-average speed values (figure 3A), suggesting that extreme speeds (either low or high) were at a disadvantage. Alternatively, predators were more successful when they covered space at a slower rate (figure 3B). Spending time guarding prey was positively related to hunting success and was maximized at values above the population average (figure 3C). The predators' hunting success decreased when they took more time to capture their first prey, implying that the more successful ones were those who secured captures earlier in a match. Predators optimized their hunting success when they encountered prey that were slower

than the population average (table 1). Matches where prey were faster at covering space in the environment were associated with significant reductions in the predators' hunting success (table 1).

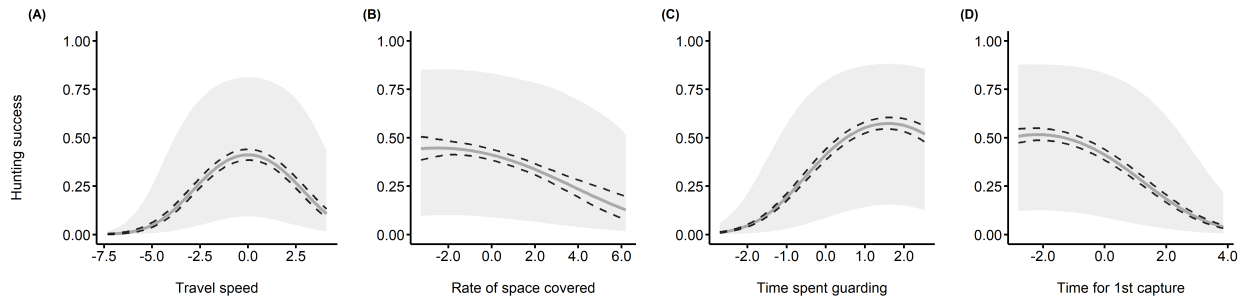


Figure 3: Relationships between predator hunting behavior and prey capture. Hunting success (i.e. the probability of capturing 4 prey) is on the y axis for all panels, and the standardized hunting behavior is on the x axis. The gray lines illustrate the posterior predicted values, the black dashed lines represent the 95% credible intervals for the predicted values, and the gray bands represent the 95% prediction intervals (variance in the fixed effects + variance in the random effects).

Predator behaviors also interacted to affect hunting success. Predators were more successful when they spent more time guarding while moving at average or lower speeds (figure S2B). This suggests that prey guarding might have been used as a successful ambush strategy. Predators that were faster than the average and secured a first capture earlier in a match were more successful (figure S2C). We observed a similar trend for space coverage although hunting success was optimized at higher rates and the optimum was larger (figure S2E). We also found that predators who spent more time guarding prey and captured their first prey earlier in a match were more successful (figure S2F).

Table 1: Posterior means and credible intervals of the estimates relating predator hunting success to predator hunting behavior, prey behavior, and their interactions.

Predictor	Linear (95% CI)	Quadratic (95% CI)	Predator trait interactions (95% CI)	Predator-prey trait interactions (95% CI)
travel speed	0.00 (-0.02, 0.02)	-0.10 (-0.09, -0.11)	-	-
space covered	-0.12 (-0.09, -0.15)	-0.02 (-0.01, -0.04)	-	-
time guarding	0.82 (0.80, 0.84)	-0.26 (-0.24, -0.28)	-	-
time 1st capture	-0.39 (-0.37, -0.40)	-0.09 (-0.08, -0.10)	-	-
prey travel speed	-0.25 (-0.24, -0.27)	-0.07 (-0.06, -0.08)	-	-
prey space covered	-0.68 (-0.65, -0.70)	-0.09 (-0.08, -0.11)	-	-
travel speed: space covered	-	-	0.00 (-0.02, 0.02)	-
travel speed: time guarding	-	-	-0.09 (-0.07, -0.11)	-
travel speed: time 1st capture	-	-	-0.04 (-0.03, -0.06)	-
space covered: time guarding	-	-	-0.01 (-0.04, 0.01)	-
space covered: time 1st capture	-	-	-0.11 (-0.10, -0.13)	-
time guarding: time 1st capture	-	-	-0.16 (-0.14, -0.18)	-
travel speed: prey travel speed	-	-	-	0.00 (-0.02, 0.01)
travel speed: prey space covered	-	-	-	-0.13 (-0.11, -0.15)
space covered: prey travel speed	-	-	-	-0.05 (-0.03, -0.06)
space covered: prey space covered	-	-	-	0.12 (0.09, 0.14)
time guarding: prey travel speed	-	-	-	-0.03 (-0.01, -0.05)
time guarding: prey space covered	-	-	-	-0.05 (-0.02, -0.08)

* The estimates are from the hunting success model with the highest elpd value (see table S4)

Effects of the predator and prey behavioral interactions on hunting success

We did not detect a significant interaction between predator and prey travel speed (table 1). Hence, predators moving at average travel speeds optimized their success against slower prey rather than locomotor opposites as we predicted (figure 4A). Contrary to our expectations, predators that covered space at slower rates opti-

mized their success against prey that covered space at slower rates (figure 4D), and predators that spent more time guarding prey optimized their success against prey that were generally slower in their travel speed and rate of space covered (figure 4E-F). However, faster predators were significantly more successful when they competed against prey that covered space at lower rates (figure 4B), which is in line with our predictions. Lastly, predators had relatively similar hunting success irrespective of the rate of space they covered when they encountered prey that were slower or close to the population average (figure 4C).

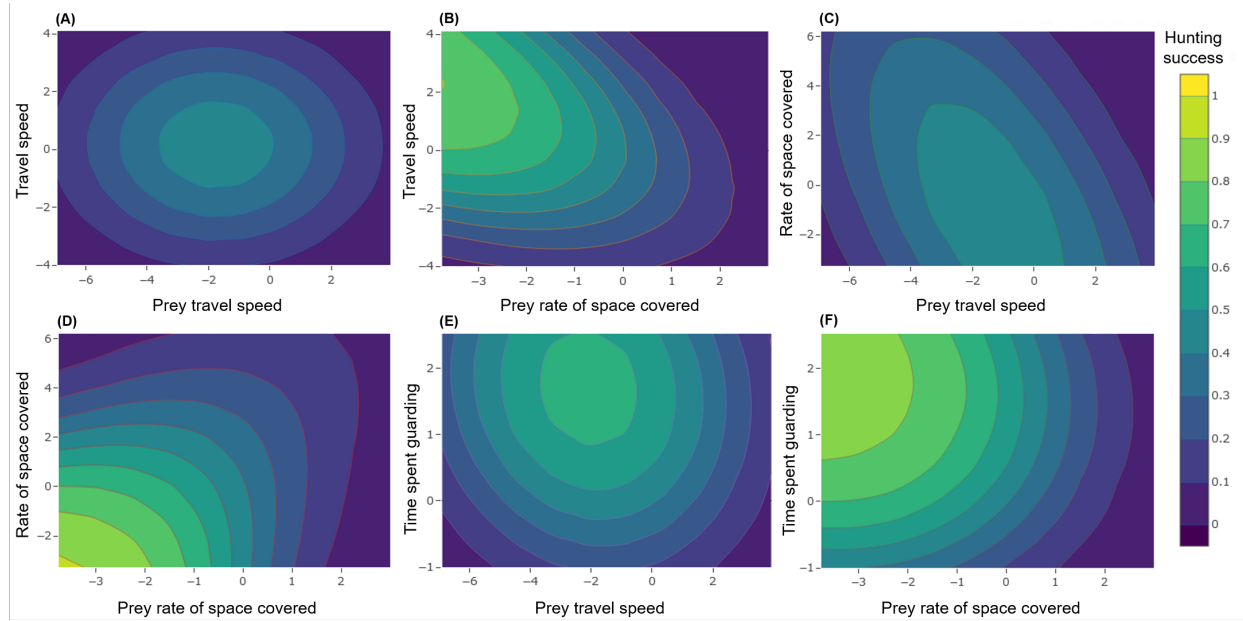


Figure 4: Influence of the predator and prey behavioral interactions on predator hunting success. The contour plots display the interacting influence of predator and prey behaviors on predator hunting success, represented by the color gradient. We computed the plots by predicting the mean probability of capturing four prey based on the best quadratic approximation of the predator and prey interaction terms. Here, we show interactions that enable us to assess if locomotor crossovers determine hunting success. (A) Predator and prey travel speed. (B) Predator travel speed and the prey's rate of space covered. (C) Predator space coverage and prey travel speed. (D) Predator and prey space coverage. (E) Predator time spent guarding and prey travel speed. (F) Predator time spent guarding and prey rate of space covered.

Relative contribution of predator and prey behavior to variation in hunting success

Predator behavior explained the highest portion of variation in hunting success ($R^2_{marginal-model1}$ [95% CI] = 0.322 [0.32, 0.325]), while prey behavior accounted for only ~5% of the total variation ($R^2_{marginal-model2}$ [95% CI] = 0.376 [0.372, 0.38]). The quadratic terms along with the predator trait interactions explained ~3% of the total variation in hunting success ($R^2_{marginal-model3}$ [95% CI] = 0.404 [0.401, 0.406]). ~5% of the differences in hunting success were explained by the behavioral interactions between predators and prey.

Overall, the best model which combined the effects of the predator and prey behaviors along with all the two-way interactions explained 45% of the total variation in hunting success ($R^2_{\text{marginal-model4}}$ [95% CI] = 0.451 [0.446, 0.454]). Hunting success was very similar among game environments (ICC_{env} [95% CI] = 0.012 [0.006, 0.019]) and players (ICC_{id} [95% CI] = 0.039 [0.035, 0.043]). Both collectively accounted for only 5% of the total variation in hunting success ($R^2_{\text{conditional-model4}}$ [95% CI] = 0.501 [0.497, 0.506]).

Discussion

Our study uses an online multiplayer videogame to quantify variation in predator foraging mode at multiple levels of organisation, and to investigate how predator and prey behavior affect hunting success. We found that individual players who adopted the predator role showed consistent differences in their foraging behavior while also displaying flexibility. The expression of some behaviors was consistent with shifts in the expression of other behaviors mostly at the within-individual level. However, the behaviors were generally not organized into foraging modes along a cursorial to sit-and-wait continuum. Contrary to our expectations, neither hunting behavior nor prey capture varied among the game environments. At the population level, the most successful predators were those that hunted at travel speeds closer to the average, covered space at lower rates, and those who spent more time guarding prey relative to the average. Predators that took more time to capture their first prey were less successful. Prey behavior also affected hunting success, such that predators generally captured more prey when they encountered prey that were on average less mobile. Moreover, the behavioral interactions between predators and prey revealed only partial evidence supporting the locomotor crossover hypothesis.

Our analyses show that individual predator players differed in their average travel speed and in the amount of time they spent guarding prey, but did not specialize as either cursorial or guarding (ambush) hunters along a continuum when we controlled for prey behavior. Faster players had higher rates of space use while those who guarded for longer periods were variable in their space use. In this case, fast space-covering players were efficient at capturing their first prey. However, these patterns were largely different when considering variability in prey locomotion (i.e. removing prey behavior as controls in the models), such that predator players specialized either at covering space or at guarding prey for longer periods, revealing the presence of a space-guard continuum (see table S3 in the Supporting information). In addition, travel speed was not associated with space use anymore, and predator players specializing exclusively as prey guarders were

more efficient at capturing their first prey than those specializing as fast space users. The predator players' preferred hunting strategies and their efficiency were thus conditioned in part by the movement of prey players encountered throughout the study period.

Predator players displayed flexibility in their foraging mode as they switched between high rates of space use in some matches to a guarding strategy in others. These foraging mode switches were accompanied by shifts in their movement as they were sometimes sedentary or otherwise highly mobile. This is most likely a consequence of pressures within a match that leave them with no choice but to guard or actively search. In nature, prey antipredator behavior can induce dynamic shifts in a predator's searching or attack behaviors (Savino and Stein 1989; McGhee et al. 2013). Here, prey behavior strengthened the shift between space use and prey guarding, but didn't seem to change the relationships among other behaviors at the within-individual level (table S3 in the Supporting information). Alternatively, other factors such as time constraints or reductions in prey abundance as individuals are captured could be at play. For example, starvation can force ambush hunters to adopt a cursorial mode (Inoue and Marsura 1983), while ambush hunters often switch to a cursorial mode when prey density is lower (Helfman 1990). Otherwise, foraging shifts may be advantageous when prey encounters are unpredictable (Woo et al. 2008; Ceia and Ramos 2015; Phillips et al. 2017) that is, when predators can successfully adjust their strategy to varying types of prey.

Surprisingly, hunting behavior was very similar across the different environments. This contrasts with studies showing that predators exploit habitat characteristics such as vegetation density to choose their hunting strategies (James and Heck Jr. 1994; Warfe and Barmuta 2004; Wasiolka et al. 2009). Because hunting success was also very similar among the game environments, we cannot exclude the possibility that this may be a consequence of the game's design aiming to minimize differences in success resulting from changes between environments. In addition, we mentioned earlier that predators have visual cues on the generators, which could hinder the effect of the environment if all they have to do is travel between generators to capture prey. While the environments do differ esthetically and in some features that affect prey escape rates (e.g. distance between generators, exit gates, surface area), we did not observe clear differences in important criteria such as heterogeneity (personal observations). Instead, habitat structure could have affected prey behavior, for instance, by altering their perception of predation risk or their fear (Preisser et al. 2007; Heithaus et al. 2009; Gaynor et al. 2019). However, when we did not account for prey behavior, differences among the game environments in the rate of space covered slightly increased, but differences in the other behaviors re-

mained very low (table S2 in the Supporting information). Experiments also suggest that differences in prey antipredator responses to the environment can negate its effects on predator behavior or success (Warfe and Barmuta 2004). This could have occurred if, within matches, individual prey players had distinct responses to the virtual environment (e.g. some increase their activity in heterogeneous habitats while others do the opposite). Alternatively, field observations show that predators can alter their hunting behavior at larger scales according to prey behavior, but seek prey accessibility at finer scales by killing them in specific areas (Hopcraft et al. 2005). Quantifying this would require fine-scale environmental variables that are currently not monitored by the game designer.

We hypothesized that predator-prey locomotor crossovers could act as a mechanism maintaining the diversity of hunting tactics in the population. However, we found that both cursorial and guarding (ambush) predators had greater success when they encountered sedentary prey. This could be caused by the trait itself (prey guarding) not being a proper proxy of ambush behavior (predators need to capture a prey to guard it), or because we failed to capture other important prey strategies involved in the interaction by focusing solely on prey movement. Other studies have used taxonomic classification for predator hunting mode or prey boldness rather than the interaction between predator and prey activity to test the locomotor crossover hypothesis (Belgrad and Griffen 2016; Donihue 2016; Chang et al. 2017). Hence, using prey boldness could have generated different patterns. Otherwise, it is well established that predators often target juvenile/unexperienced prey (Quinn and Cresswell 2004; Kauffman et al. 2007; Gaynor et al. 2019; Wirsing et al. 2021), and that appears like a plausible scenario assuming that slower prey were less experienced. For instance, novice prey could be more prone to inadequately respond to predator cues (e.g. exposing themselves instead of hiding or moving away), and thus, be more vulnerable to predation since prey need to move and repair generators to escape. Altogether, similar to theoretical and empirical observations, specific predator and prey behavioral attributes may lead to non-random predator-prey encounters in this system.

While the foraging mode paradigm has proven useful to understand the mechanisms driving predator-prey interactions, there is some consensus that a dichotomous view may be too simplistic, and that a wider diversity of modes exist within populations (Butler 2005; Cooper 2005; Beaupre and Montgomery 2007; Miles et al. 2007). So far, the underlying causes and mechanisms of this diversity remain poorly understood. Our results suggest that prey behavior can mediate individual specialization as either cursorial or ambush hunters rather than differences in hunting success, and predator experience might have played a role because hunting

strategies are often developed by learning (Wilson-Rankin 2015; Heithaus et al. 2018). We thus ran separate analyses on novice and experienced players (see the “methods” section in the Supplementary information) and found that both displayed distinct hunting strategies that were not apparent when they were pooled together. Novice players that traveled faster spent more time guarding prey, so they probably aimed at capturing prey and securing their kill by preventing others from rescuing it. In contrast, experienced players displayed clear specialization as either cursorial or guarding (ambush) hunters (table S3 in the Supporting information). Interestingly, novice hunters were more flexible at switching between ambush and cursorial modes compared to experienced players who didn’t display mode switching. These notable distinctions show that considering hunting experience can reveal important insights on the dynamics of predator-prey interactions (Weimerskirch et al. 2005; Woo et al. 2008; Tinker et al. 2009; Phillips et al. 2017) and we are presently investigating its effects for a follow-up study (Fraser Franco et al. in prep).

We are among the first ecologists (but see also Céré et al. 2021) to use an online multiplayer videogame to investigate how ecological mechanisms shape the dynamics of trophic interactions. As virtual worlds become increasingly present in our lives, understanding their ecology and our interactions within them will become an important topic of study (Duthie et al. 2021). We are convinced that online videogames will be valuable for testing hypotheses under realistic ecological scenarios, as they reduce several challenges associated with empirical studies, while providing rich and ecologically-relevant datasets on human decision-making. Besides, our results support this assertion as they were generally consistent with patterns reported in ecological studies of natural predators (Helfman 1990; Butler 2005; Miles et al. 2007; McGhee et al. 2013). However, videogames are not a panacea; they are potentially limited by player behavior not properly reflecting behavioral decisions made by real-life organisms in the wild, as the player cannot “die”. Hence, individuals may take greater risks in a videogame compared to natural predators (Lofgren and Fefferman 2007; Oultram 2013). Moreover, while *DBD* provides an interesting system to investigate predator-prey interactions, prey density is fixed at four players, which prevents the modelling of predator functional responses. Lastly, similar to mesocosm experiments with single predators, the game may not reflect natural systems where multiple predator species compete for the same prey. In light of these potential limitations, researchers should interpret results from online videogames with care, and aim to test specific ecological hypotheses with them. Individual variation in predator (and prey) behavior is increasingly recognized as a critical factor influencing the outcome of trophic interactions (Pettorelli et al. 2015; Toscano et al. 2016; Moran et al. 2017). Our

study is the first to investigate individual variation in predator foraging behavior using an online videogame. Our results corroborate patterns observed in natural systems and highlight complex relationships between predator foraging behavior, prey movement, and hunting success. Predator players specialized in diverse hunting strategies. These strategies varied among and within individuals along a continuum of correlated behaviors (foraging syndrome hypothesis), and were shaped by prey movement and predator experience. In addition, our results suggest that different predator behavioral types could coexist through the consumption of potentially vulnerable prey and in part by locomotor crossovers. Thus, investigating the effects of prey behavior on predator behavior and success at different hierarchical levels can provide a more comprehensive depiction of a predator's foraging ecology. We recommend that further studies consider these aspects when possible. To conclude, we provided support that virtual worlds can be used to identify how ecological mechanisms drive observable phenomena like individual behavioral decisions. While the potential of online multiplayer videogame data remains untapped for ecological research, we are confident that further studies employing them will provide valuable ecological insight for behavioral and community ecologists.

Competing interests

The authors declare no competing interests

Literature Cited

- Ahmad MA, Shen C, Srivastava J, Contractor N. 2014. On the problem of predicting real world characteristics from virtual worlds. In: Ahmad MA; Shen C; Srivastava J; Contractor N, editors. Predicting real world behaviors from virtual world data. Cham: Springer International Publishing. (Springer Proceedings in Complexity). pp. 1–18.
- Araújo MS, Bolnick DI, Layman CA. 2011. The ecological causes of individual specialisation. *Ecol Lett.* 14(9):948–958.
- Arthur B, Hindell M, Bester MN, Oosthuizen WC, Wege M, Lea M-A. 2016. South for the winter? Within-dive foraging effort reveals the trade-offs between divergent foraging strategies in a free-ranging predator. *Funct Ecol.* 30(10):1623–1637.
- Balicer RD. 2007. Modeling infectious diseases dissemination through online role-playing games. *Epidemiology.* 18(2):260–261.

Barbe L, Mony C, Abbott BW. 2020. Artificial intelligence accidentally learned ecology through video games. *Trends Ecol Evol.* 35(7):557–560.

Beauchamp G. 2020. Predator attack patterns influence vigilance in a virtual experiment. *Behav Ecol Sociobiol.* 74(4):49.

Beaupre SJ, Montgomery CE. 2007. The meaning and consequences of foraging mode in snakes. In: Miles DB; McBrayer LB; Reilly SM, editors. *Lizard Ecology*. Cambridge: Cambridge University Press. pp. 334–368.

Belaza AM, Ryckebusch J, Schoors K, Rocha LEC, Vandermarliere B. 2020. On the connection between real-world circumstances and online player behaviour: The case of EVE Online. *PLOS ONE.* 15(10):e0240196.

Belgrad BA, Griffen BD. 2016. Predator–prey interactions mediated by prey personality and predator hunting mode. *Proc R Soc B Biol Sci.* 283(1828):20160408.

Bowen WD, Tully D, Boness DJ, Bulheier BM, Marshall GJ. 2002. Prey-dependent foraging tactics and prey profitability in a marine mammal. *Mar Ecol Prog Ser.* 244:235–245.

Brodie ED, Moore AJ, Janzen FJ. 1995. Visualizing and quantifying natural selection. *Trends Ecol Evol.* 10(8):313–318.

Brown JS. 1988. Patch use as an indicator of habitat preference, predation risk, and competition. *Behav Ecol Sociobiol.* 22(1):37–47.

Brown JS. 1999. Vigilance, patch use, and habitat selection: Foraging under predation risk. *Evol Ecol Res.*:49–71.

Butler MA. 2005. Foraging mode of the chameleon, *Bradypodion pumilum*: A challenge to the sit-and-wait versus active forager paradigm? *Biol J Linn Soc.* 84(4):797–808.

Bürkner P-C. 2017. brms: An R package for Bayesian multilevel models using Stan. *J Stat Softw.* 80(1):1–28.

Bürkner P-C. 2018. Advanced Bayesian Multilevel Modeling with the R Package brms. *R J.* 10(1):395–411.

Carneiro APB, Bonnet-Lebrun A-S, Manica A, Staniland IJ, Phillips RA. 2017. Methods for detecting and quantifying individual specialisation in movement and foraging strategies of marine predators. *Mar Ecol*

554 Prog Ser. 578:151–166.

555 Carter AJ, Feeney WE, Marshall HH, Cowlshaw G, Heinsohn R. 2013. Animal personality: What are
556 behavioural ecologists measuring? Biol Rev. 88(2):465–475.

557 Ceia FR, Ramos JA. 2015. Individual specialization in the foraging and feeding strategies of seabirds: A
558 review. Mar Biol. 162(10):1923–1938.

559 Céré J, Montiglio P-O, Kelly CD. 2021. Indirect effect of familiarity on survival: A path analysis on video
560 game data. Animal Behaviour. 181:105–116.

561 Chang C-c, Teo HY, Norma-Rashid Y, Li D. 2017. Predator personality and prey behavioural predictability
562 jointly determine foraging performance. Sci Rep. 7(1, 1):40734.

563 Cooper WE. 2005. The foraging mode controversy: Both continuous variation and clustering of foraging
564 movements occur. J Zool. 267(2):179–190.

565 Courbin N, Besnard A, Péron C, Saraux C, Fort J, Perret S, Tornos J, Grémillet D. 2018. Short-term prey
566 field lability constrains individual specialisation in resource selection and foraging site fidelity in a marine
567 predator. Ecol Lett. 21(7):1043–1054.

568 Dall SRX, Griffith SC. 2014. An empiricist guide to animal personality variation in ecology and evolution.
569 Front Ecol Evol. 2:3.

570 Dingemanse NJ, Dochtermann NA. 2013. Quantifying individual variation in behaviour: Mixed-effect mod-
571 elling approaches. J Anim Ecol. 82(1):39–54.

572 Dingemanse NJ, Wright J. 2020. Criteria for acceptable studies of animal personality and behavioural syn-
573 dromes. Ethology. 126(9):865–869.

574 Donihue CM. 2016. Aegean wall lizards switch foraging modes, diet, and morphology in a human-built
575 environment. Ecol Evol. 6(20):7433–7442.

576 Duthie AB, Minderman J, Rakotonarivo OS, Ochoa G, Bunnefeld N. 2021. Online multiplayer games as
577 virtual laboratories for collecting data on social-ecological decision making. Conserv Biol. 35(3):1051–
578 1053.

579 Fuchs B, Thurner S. 2014. Behavioral and Network Origins of Wealth Inequality: Insights from a Virtual

World. PLOS ONE. 9(8):e103503.

Gaynor KM, Brown JS, Middleton AD, Power ME, Brashares JS. 2019. Landscapes of fear: Spatial patterns of risk perception and response. *Trends Ecol Evol.* 34(4):355–368.

Gerritsen J, Strickler J. 1977. Encounter probabilities and community structure in zooplankton: A mathematical model. *J Fish Board Can.* 34(1).

Glaudias X, Glennon KL, Martins M, Luiselli L, Fearn S, Trembath DF, Jelić D, Alexander GJ. 2019. Foraging mode, relative prey size and diet breadth: A phylogenetically explicit analysis of snake feeding ecology. *J Anim Ecol.* 88(5):757–767.

Griffen BD, Toscano BJ, Gatto J. 2012. The role of individual behavior type in mediating indirect interactions. *Ecology.* 93(8):1935–1943.

Harrison XA. 2015. A comparison of observation-level random effect and Beta-Binomial models for modelling overdispersion in Binomial data in ecology & evolution. *PeerJ.* 3:e1114.

Heithaus MR, Dill LM, Kiszka JJ. 2018. Feeding strategies and tactics. In: Würsig B; Thewissen JGM; Kovacs KM, editors. *Encyclopedia of marine mammals (third edition)*. Academic Press. pp. 354–363.

Heithaus MR, Wirsing AJ, Burkholder D, Thomson J, Dill LM. 2009. Towards a predictive framework for predator risk effects: The interaction of landscape features and prey escape tactics. *J Anim Ecol.* 78(3):556–562.

Helfman GS. 1990. Mode selection and mode switching in foraging animals. In: Slater PJB; Rosenblatt JS; Beer C, editors. *Advances in the study of behavior*. Vol. 19. Academic Press. pp. 249–298.

Hertel AG, Niemelä PT, Dingemanse NJ, Mueller T. 2020. A guide for studying among-individual behavioral variation from movement data in the wild. *Movement Ecol.* 8(30).

Hopcraft JGC, Sinclair ARE, Packer C. 2005. Planning for success: Serengeti lions seek prey accessibility rather than abundance. *J Anim Ecol.* 74(3):559–566.

Huey RB, Pianka ER. 1981. Ecological consequences of foraging mode. *Ecology.* 62(4):991–999.

Inoue T, Marsura T. 1983. Foraging strategy of a mantid, *Paratenodera angustipennis* S.: Mechanisms of switching tactics between ambush and active search. *Oecologia.* 56(2):264–271.

James PL, Heck Jr. KL. 1994. The effects of habitat complexity and light intensity on ambush predation within a simulated seagrass habitat. *J Exp Mar Bio Ecol.* 176(2):187–200.

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.

Kersch-Becker MF, Grisolia BB, Campos MJO, Romero GQ. 2018. Community-wide responses to predation risk: Effects of predator hunting mode on herbivores, pollinators, and parasitoids. *Ecol Entomol.* 43(6):846–849.

Kotler BP, Blaustein L. 1995. Titrating food and safety in a heterogeneous environment: When are the risky and safe patches of equal value? *Oikos.* 74(2):251–258.

Laurel BJ, Brown JA. 2006. Influence of cruising and ambush predators on 3-dimensional habitat use in age 0 juvenile Atlantic cod *Gadus morhua*. *J Exp Mar Bio Ecol.* 329(1):34–46.

Lima SL. 2002. Putting predators back into behavioral predator–prey interactions. *Trends Ecol Evol.* 17(2):70–75.

Lofgren ET, Fefferman NH. 2007. The untapped potential of virtual game worlds to shed light on real world epidemics. *Lancet Infect Dis.* 7(9):625–629.

McCoy ED, Bell SS. 1991. Habitat structure: The evolution and diversification of a complex topic. In: Bell SS; McCoy ED; Mushinsky HR, editors. *Habitat structure: The physical arrangement of objects in space.* Dordrecht: Springer Netherlands. (Population and Community Biology Series). pp. 3–27.

McGhee KE, Pintor LM, Bell AM. 2013. Reciprocal behavioral plasticity and behavioral types during predator-prey interactions. *Am Nat.* 182(6):704–717.

McLaughlin RL. 1989. Search modes of birds and lizards: Evidence for alternative movement patterns. *Am Nat.* 133(5):654–670.

Michel MJ, Adams MM. 2009. Differential effects of structural complexity on predator foraging behavior. *Behav Ecol.* 20(2):313–317.

Miles DB, Losos JB, Irschick DJ. 2007. Morphology, performance, and foraging mode. In: Miles DB; McBrayer LB; Reilly SM, editors. *Lizard ecology.* Cambridge: Cambridge University Press. pp. 49–93.

632 Miller JRB, Ament JM, Schmitz OJ. 2014. Fear on the move: Predator hunting mode predicts variation in
633 prey mortality and plasticity in prey spatial response. *J Anim Ecol.* 83(1):214–222.

634 Mitchell DJ, Houslay TM. 2020. Context-dependent trait covariances: How plasticity shapes behavioral
635 syndromes. *Behav Ecol.*(araa115).

636 Montiglio P-O, Garant D, Thomas D, Réale D. 2010. Individual variation in temporal activity patterns in
637 open-field tests. *Anim Behav.* 80(5):905–912.

638 Moran NP, Wong BBM, Thompson RM. 2017. Weaving animal temperament into food webs: Implications
639 for biodiversity. *Oikos.* 126(7):917–930.

640 Nakagawa S, Cuthill IC. 2007. Effect size, confidence interval and statistical significance: A practical guide
641 for biologists. *Biol Rev.* 82(4):591–605.

642 Nakagawa S, Johnson PCD, Schielzeth H. 2017. The coefficient of determination R² and intra-class corre-
643 lation coefficient from generalized linear mixed-effects models revisited and expanded. *J R Soc Interface.*
644 14(134):20170213.

645 Nakagawa S, Schielzeth H. 2010. Repeatability for Gaussian and non-Gaussian data: A practical guide for
646 biologists. *Biol Rev.* 85(4):935–956.

647 Niemelä PT, Dingemanse NJ. 2014. Artificial environments and the study of ‘adaptive’ personalities. *Trends*
648 *Ecol Evol.* 29(5):245–247.

649 Oultram S. 2013. Virtual plagues and real-world pandemics: Reflecting on the potential for online computer
650 role-playing games to inform real world epidemic research. *Med Humanit.* 39(2):115–118.

651 Perry G. 1999. The evolution of search modes: Ecological versus phylogenetic perspectives. *Am Nat.*
652 153(1):98–109.

653 Perry G, Werner YL, Lampl I, Rothenstein D, Sivan N, Lerner A, Shani E. 1990. Foraging mode in lacertid
654 lizards: Variation and correlates. *Amphib-Reptil.* 11(4):373–384.

655 Pettorelli N, Hilborn A, Duncan C, Durant SM. 2015. Chapter Two - Individual variability: The missing
656 component to our understanding of predator–prey interactions. In: Pawar S; Woodward G; Dell AI, edi-
657 tors. *Advances in ecological research.* Vol. 52. Academic Press. (Trait-based ecology - From structure to

function). pp. 19–44.

Phillips RA, Lewis S, González-Solís J, Daunt F. 2017. Causes and consequences of individual variability and specialization in foraging and migration strategies of seabirds. *Mar Ecol Prog Ser.* 578:117–150.

Preisser EL, Orrock JL, Schmitz OJ. 2007. Predator hunting mode and habitat domain alter nonconsumptive effects in predator–prey interactions. *Ecology.* 88(11):2744–2751.

Quinn JL, Cresswell W. 2004. Predator hunting behaviour and prey vulnerability. *J Anim Ecol.* 73(1):143–154.

Robinson SK, Holmes RT. 1982. Foraging behavior of forest birds: The relationships among search tactics, diet, and habitat structure. *Ecology.* 63(6):1918–1931.

Romero GQ, Koricheva J. 2011. Contrasting cascade effects of carnivores on plant fitness: A meta-analysis. *J Anim Ecol.* 80(3):696–704.

Ross TL, Castronova E, Knowles I. 2015. Virtual worlds as laboratories. In: *Emerging trends in the social and behavioral sciences.* American Cancer Society. pp. 1–15.

Sargeant BL, Wirsing AJ, Heithaus MR, Mann J. 2007. Can environmental heterogeneity explain individual foraging variation in wild bottlenose dolphins (*Tursiops* sp.)? *Behav Ecol Sociobiol.* 61(5):679–688.

Savino JF, Stein RA. 1989. Behavioural interactions between fish predators and their prey: Effects of plant density. *Anim Behav.* 37:311–321.

Scharf I, Nulman E, Ovadia O, Bouskila A. 2006. Efficiency evaluation of two competing foraging modes under different conditions. *Am Nat.* 168(3):350–357.

Schmitz O. 2017. Predator and prey functional traits: Understanding the adaptive machinery driving predator–prey interactions. *F1000Res.* 6:1767.

Schmitz OJ. 2008. Effects of predator hunting mode on grassland ecosystem function. *Science.* 319(5865):952–954.

Smith BR, Blumstein DT. 2010. Behavioral types as predictors of survival in Trinidadian guppies (*Poecilia reticulata*). *Behav Ecol.* 21(5):919–926.

- 683 Szell M, Lambiotte R, Thurner S. 2010. Multirelational organization of large-scale social networks in an
684 online world. *PNAS*. 107(31):13636–13641.
- 685 Tinker MT, Bentall G, Estes JA. 2008. Food limitation leads to behavioral diversification and dietary spe-
686 cialization in sea otters. *PNAS*. 105(2):560–565.
- 687 Tinker MT, Mangel M, Estes JA. 2009. Learning to be different: Acquired skills, social learning, frequency
688 dependence, and environmental variation can cause behaviourally mediated foraging specializations. *Evol*
689 *Ecol Res*. 11(6):841–869.
- 690 Toscano BJ, Gownaris NJ, Heerhartz SM, Monaco CJ. 2016. Personality, foraging behavior and specializa-
691 tion: Integrating behavioral and food web ecology at the individual level. *Oecologia*. 182(1):55–69.
- 692 Toscano BJ, Griffen BD. 2014. Trait-mediated functional responses: Predator behavioural type mediates
693 prey consumption. *J Anim Ecol*. 83(6):1469–1477.
- 694 Vehtari A, Gelman A, Gabry J. 2017. Practical Bayesian model evaluation using leave-one-out cross-
695 validation and WAIC. *Stat Comput*. 27(5):1413–1432.
- 696 Warfe DM, Barmuta LA. 2004. Habitat structural complexity mediates the foraging success of multiple
697 predator species. *Oecologia*. 141(1):171–178.
- 698 Wasiolka B, Blaum N, Jeltsch F, Henschel J. 2009. Behavioural responses of the lizard *Pedioplanis l. Li-*
699 *neocellata* to overgrazing. *Acta Oecol*. 35(2):157–162.
- 700 Weimerskirch H, Gault A, Cherel Y. 2005. Prey Distribution and Patchiness: Factors in Foraging Success
701 and Efficiency of Wandering Albatrosses. *Ecology*. 86(10):2611–2622.
- 702 Wignall AE, Taylor PW. 2008. Alternative predatory tactics of an araneophagic assassin bug (*Stenolemus*
703 *bituberus*). *Acta Ethol*. 12(1):23.
- 704 Wilson-Rankin EE. 2015. Level of experience modulates individual foraging strategies of an invasive preda-
705 tory wasp. *Behav Ecol Sociobiol*. 69(3):491–499.
- 706 Wirsing AJ, Heithaus MR, Brown JS, Kotler BP, Schmitz OJ. 2021. The context dependence of non-
707 consumptive predator effects. *Ecol Lett*. 24(1):113–129.
- 708 Wolf M, Weissing FJ. 2012. Animal personalities: Consequences for ecology and evolution. *Trends Ecol*

709 Evol. 27(8):452–461.

710 Woo KJ, Elliott KH, Davidson M, Gaston AJ, Davoren GK. 2008. Individual specialization in diet by a
711 generalist marine predator reflects specialization in foraging behaviour. J Anim Ecol. 77(6):1082–1091.