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15 Abstract

Predator-prey interactions are important drivers of community and ecosystem dynamics. In this 16 study, we propose a novel system that uses an online multiplayer videogame to explore withinpopulation variation in predator hunting mode, and how predator-prey behavioural interactions 18 affect predator hunting success. We examined how travel speed, space coverage, ambush time, 19 and latency to first capture correlate at three hierarchical levels (among environments, among 20 individuals, and within individuals) to assess the structure of the predator hunting mode. We 21 also investigated how these traits interact with prey travel speed and space coverage to affect 22 predator hunting success. We found that individual predators specialized either as cursorial or 23 ambush hunters along a continuum of these hunting traits, but also shifted their strategy between encounters. Predators were generally better against slower-moving prey, and both types of hunters 25 achieved similar prey captures over the sampling period. Our study brings additional evidence that 26 considering within-population variation in behavior and success during predator-prey interactions can increase our understanding of community stability. We further discuss the advantages and 28 scientific insight that online videogames can provide for ecological research, and develop on their weaknesses and potential biases.

Introduction

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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/cursioral 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 predators with contrasting hunting modes (e.g. cursorial vs ambush) differ in the number of individuals or species, or in the type of prey that they capture (Miller et al. 2014; Donihue 2016; Glaudas et al. 2019). As a result, they can cause opposing trophic cascades and act at different trophic levels (Schmitz 2008; Romero and Koricheva 2011).

Predator species tend to be 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). Despite that
categorising predators is still useful to predict community and ecosystem dynamics (Wirsing et
al. 2021), it essentially ignores the complexity of predator foraging decision-making. Growing
evidence suggest that individual predator behavioral variation can exert 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 community and ecosystem processes remains unclear. It is
therefore imperative that we 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). In sea predators, individuals specialize in specific tactics to meet the energy/time
demands that are required to successfully capture the type of prey generally encountered (Bowen
et al. 2002; Tinker et al. 2008; Arthur et al. 2016). Prey activity/mobility is an important trait

influencing encounter rates with predators (Gerritsen and Strickler 1977; Huev and Pianka 1981; Scharf et al. 2006). Therefore, individual variation in encounter rates with prey activity-types may lead to nonrandom interactions between predator-prey behavioral types (Wolf and Weissing 2012). For example, the locomotor-crossover hypothesis (Huev 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). Individual predators with contrasting hunting modes might thus coexist within a population if their tactics allow them to reach similar capture rates (Kobler et al. 2009; Michel and Adams 2009; Chang et al. 2017). Habitat structure is a second important driver of stable individual differences in 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

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

habitats are expected to favor sit-and-wait/sit-and-pursue hunters as they offer perches and cover,

easier, but, at the expense of being themselves more easily detected (Michel and Adams 2009).

80 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). For instance, predators can switch their hunting strategy in response to changes in prey density (Inoue and Marsura 1983), 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). Unfortunately, this type of research is often conducted under controlled laboratory conditions, which can fail to capture the nuances and complexities of a predator specie's behavior in the wild (Carter et al. 2013; Niemelä and Dingemanse 2014). Empirically investigating individual variation in hunting mode requires repeated measures

of behavior of numerous individuals under different environmental settings (Dall and Griffith 2014;
Dingemanse and Wright 2020). Such an approach may impose considerable financial, technical,
and ethical challenges when studying larger or elusive wildlife, such as apex predators (Hertel et
al. 2020). An additional challenge in empirical studies of predator-prey interactions is identifying
traits in predators and prey that are easily observable, but also ecologically relevant. For instance,
foraging mode is expected to vary along a continuum of morphological, physiological, and behavioral
traits (foraging syndrome hypothesis) (Perry et al. 1990; Perry 1999; Butler 2005; Cooper 2005;
Miles et al. 2007), but few studies have investigated how habitat- and prey-specific characteristics
jointly shape correlated foraging traits at different hierarchical levels.

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 100 videogames could provide numerous opportunities for ecologists to study general ecological phe-101 nomena, including the mechanisms driving individual variation in behavior (Barbe et al. 2020). 102 First, online videogames provide abundant repeated measurements on millions of individual play-103 ers across temporal and environmental gradients. Second, the structure of the virtual environment 104 is known and can be used to evaluate how specific components affect the behavior of interest. Third, 105 videogames can reproduce realistic ecological settings in which complex interactions occur among 106 players. A classic example is the case of the "Corrupted Blood" epidemic in World of Warcraft, 107 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). In 109 this sense, online multiplayer videogames could potentially constitute a complement to traditional 110 field studies. They could allow ecologists (among other scientists) to bridge the gap between real-111 world ecological studies and large-scale computer simulations (Cere et al., accepted, Ross et al. 2015). 113

We used the online multiplayer videogame *Dead by Daylight (DBD)* as our study system. This game
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 escaping the predator. Prey can use a wide range of behaviors such as cooperation or hiding

(Cere et al., accepted) to successfully escape (figure 1 B-C), which predators can exploit to lure them in an ambush. These situations offer the possibility for predators to express different hunting tactics. Moreover, each match in *DBD* occurs within a specific habitat, including forests, farmlands, and urban areas. These environments differ in the heterogeneity and complexity of their structures (McCoy and Bell 1991), such as in the availability of perches and refugia, vegetation density, or surface area (figure 1D). Hence, predators may encounter prey that express different behaviors, and are expected to benefit from changing their behavior accordingly to maximize hunting success.



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. Once all generators are repaired, prey may activate one of the two doors in order to escape and win the match. (C) Representative image of a prey player activating an escape door. (D) Representative pictures of the different game environments where matches take place. The game environments settings vary between urban, farmland, and forest areas. All the images were taken from the official Dead by Daylight wiki and forum web pages (https://deadbydaylight.fandom.com/wiki/Dead_by_Daylight_Wiki, https://forum.deadbydaylight.com/en/discussions)

In this study, we use an extensive and complete dataset on the hunting behavior of predator players in *DBD* to investigate environmental and individual variation in hunting mode, and how hunting mode affects prey capture. We use four hunting-related behaviors as proxies of hunting mode: travel

speed, the rate of space covered in the environment, the proportion of time spent in an ambush 128 position, and the time elapsed before the first prey capture. We use multivariate mixed-modelling 129 to quantify variation in multiple behaviors and their correlations at different hierarchical levels 130 (i.e. among and within-individuals, Dingemanse and Dochtermann 2013) as a way to describe the 131 variation in hunting mode within a population of predators (Perry et al. 1990; Perry 1999; Butler 132 2005; Cooper 2005; Miles et al. 2007). Within-population variation includes among-environment 133 differences in average hunting behavior, variation in tactic use arising when some individuals use 134 one tactic more often than others (i.e. individual specialization), and variation arising from individ-135 uals adjusting tactic use over time in response to temporal changes in environmental conditions or 136 prey behavior (i.e. individual flexibility). First, we hypothesize that predators use hunting tactics 137 according to habitat-specific characteristics. Therefore, we expect correlated trait values associ-138 ated with ambush tactics in smaller and heterogeneous environments, and correlated trait values 139 associated with cursorial tactics in open/wider and homogeneous environments (James and Heck 140 Jr. 1994; Wasiolka et al. 2009; Donihue 2016). Second, we hypothesize that individual predators 141 consistently differ in their hunting mode over time, with some specializing as cursorial hunters, and others as ambush hunters. Thus, we predict that individual predators should differ in their average 143 trait values along a continuum for all combinations of the four hunting traits (among-individual 144 behavioral correlations). Following the locomotor-crossover hypothesis (Huey and Pianka 1981), 145 we predict that ambush and cursorial predator-types will coexist in the population, because both 146 achieve similar hunting success by performing better against prev with the opposite locomotor ten-147 dency. Lastly, we hypothesize that individual predators will express flexible hunting behavior, by 148 switching from cursorial to ambush tactics between foraging bouts (i.e. between matches). Thus, 149 we predict that the individuals' residual trait values in contrasting hunting behaviors (ambush vs 150 cursorial) should be negatively correlated (within-individual behavioral correlations). 151

Materials and methods

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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 on-

line. 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 158 run faster, or have more powerful attacks. We thus controlled for the chosen avatar in our models 159 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, 162 which may favor the use of a cursorial strategy. Other maps have a smaller surface area with high 163 vegetation density, which may impair visibility and alter prey detection, favoring the use of an ambush strategy. For additional details on the game settings and map characteristics, refer to https:// 165 deadbydaylight.com/en, and https://deadbydaylight.gamepedia.com/Dead by Daylight Wiki. 166

Data collection 167

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The study period ranged from 20 March to 17 June 2019. Our population consisted of 2 171 new anonymous players who initiated their first match between 20 March and 22 March, with a total record of 70 831 matches (average: 177 matches per individual, range: 1 - 972 matches). The average match duration was 11 minutes (range: 5 - 58 minutes). For each match, we recorded the date (date-hour-minutes), the duration, the predator player's anonymous ID, the prey players' anonymous ID's, the predator's avatar, and the game environment where the match took place. We also recorded predator and prey behavior. We retained matches that lasted more than 5 minutes (short matches are usually interrupted because of technical issues). Players also score points during a match by performing different actions. To control for matches where players did not play, or for errors in the data collection, we removed matches where predators earned less than 1 point.

Behavioral traits

We selected four out of eight behavioral variables that summarized most of the variation in predator hunting tactics based on a principal component analysis (see figure S1 and table S1 in the Supporting information): average travel speed (m/s), the rate of space covered (square/s), the proportion of time spent in an ambush position over the match duration, and the proportion of time predators took to capture their first prey over the match duration. Travel speed and the rate of space covered differ in that speed describes the average distance traveled in meters per second, while space coverage desribes the number of 16x16 meters squares (from a grid that covers the whole virtual environment) entered per second in the environment (similar to the open field test, Montiglio et al. 2010). The proportion of time spent ambushing describes the total amount of time a predator spent monitoring around capture sites to ambush prey that try to rescue a conspecific (see section 'Behavioral traits measurements' in the Supporting information for details).

We quantified prey average travel speed (m/s) and rate of space covered (square/s). These two traits
were measured using the same method described for predators (refer to Supporting information).
For both traits, we averaged the four individual prey values within each match since we were
interested in the average effect of prey behavior on the predator's hunting behavior. Thus, we used
one average value per prey trait, for each match played.

Statistical analyses: Software and computer setup

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We performed all statistical analyses using the R software (version 4.0.2, R Core Team, 2020) on a remote computer cluster (Cedar, Compute Canada, https://docs.computecanada.ca/wiki/Cedar) running on CentOS Linux 7. All models were fitted using the R package "brms" version 2.14.4 (Bürkner 2017). We provide the R code and outputs on this GitHub repository (https://github. com/quantitative-ecologist/videogame_hunting_tactics-Rscripts) with the R sessions information to ensure reproducibility.

Statistical analyses: Variation in hunting mode

We first parametrized a multivariate Bayesian mixed model to quantify unadjusted repeatability of 203 hunting behavior, and evaluate among-environment, among-individual (specialization), and within-204 individual (flexibility) behavioral correlations. We included the predator's population-response to 205 prey behavior by adding prey travel speed (x_1) and rate of space covered (x_2) as linear fixed effects. 206 We square-root transformed the four hunting behaviors (y1 = speed, y2 = space, y3 = time in)207 ambush, $y4 = \text{time } 1^{\text{st}}$ capture) to achieve normality and then defined each as having a Gaussian 208 distribution. All traits were then standardized to mean and unit variance (z-scores). The model is 209 described by the following equations: 210

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

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

$$y3_{ij} = (\beta_{0y3} + id_{0y3,i} + env_{0y3,i} + avatar_{0y3,i}) + \beta_{1y3}x_1 + \beta_{2y3}x_2 + \varepsilon_{0y3,ij}$$
(3)

$$y4_{ij} = (\beta_{0y4} + id_{0y4,i} + env_{0y4,i} + avatar_{0y4,i})$$

$$+ \beta_{1y4}x_1 + \beta_{2y4}x_2 + \varepsilon_{0y4,ij}$$

$$(4)$$

ronment $(env_{0y,i})$, and the predator avatar $(avatar_{0y,i})$ are random intercepts (among- individual, 212 environment, and avatar variance), and $(\varepsilon_{0y,ij})$ are the residuals (within-individual variance). Ran-213 dom intercepts (BLUPs) and residuals were assumed to follow a multivariate Gaussian distribution 214 with their associated variance-covariance matrixes $(\Omega_{id},\,\Omega_{env},\,\Omega_{avatar},\,\Omega_{\varepsilon})$ (equations S1-S4 in Sup-215 porting information). For each combination of behaviors, we extracted the behavioral correlations 216 among- individuals, environments, and avatars, as well as within-individual (residual) behavioral 217 correlations (Dingemanse and Dochtermann 2013). The sample size of each parameter's posterior 218 distribution is 4000 (see section 'Parametrization of the bayesian multivariate mixed model' in the 219 Supporting information for details). 220 Following Nakagawa and Schielzeth (2010), we calculated each hunting trait's adjusted repeatability 221 estimate (intra-class correlation coefficient, ICC) for the player ID, the game environment, and the 222 predator avatar by dividing the variance of the specific random effect by the total phenotypic 223 variance (ex. $ICC_{id0,y1} = V_{id0,y1} / (V_{id0,y1} + V_{env0,y1} + V_{avatar0,y1} + V_{\varepsilon 0,y1})$). We computed the 95% 224 credible intervals for each repeatability estimate using the highest posterior density intervals. 225

where i indexes individual players and j the recorded match. Player ID $(id_{0y,i})$, the game envi-

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

Since predators can capture a maximum of four prey, we used the number of prey captured per 227 total number of prey in a match (four) as a binomial response variable $(\omega_{ij} \sim Binom(max_{ij}, P_{ij}))$. We first quantified the linear relationship between hunting success and predator behavior by fitting 229 a binomial Bayesian generalized linear mixed model (glmm) with a logit link function. The model 230 fits a linear function $(\beta_{n,pred}\mathbf{x}_i)$ where we could estimate if hunting success increased or decreased 231 with increasing hunting behavior scores. We fitted the mean probability of capturing four prey (P_{ij}) 232 for individual i on its j match as a function of its travel speed, rate of space covered, proportion of 233 time spent ambushing, and proportion of time before the first capture (equation S5 in Supporting 234 information). We computed a second model to account for variation in hunting success explained 235 by prey behavior $(\beta_{n,prey}\mathbf{x}_i^{'})$. We thus added prey travel speed and their rate of space covered in 236 the model equation (equation S6 in Supporting information). Both models had random intercepts 237 for the predator player's ID $(id_{0,i})$ and the game environment $(env_{0,i})$ to partition the variance in hunting success explained by differences among players and the environments where matches 239 occurred. Player ID and the game environment were assumed to follow a Gaussian distribution with 240 estimated variance $(id_{0,i} \sim N(0,V_{id}),\ env_{0,i} \sim N(0,V_{env}))$. We included an observation-level random effect to account for overdispersion and compared the models to a beta-binomial model to ensure 242 that the estimates were robust (Harrison 2015). Trait values were standardized to mean and unit 243 variance (z-scores). The sample size of each parameter's posterior distribution is 4000 for the first model and 6000 for the second model. 245

We built a third model with the same structure as the first model and included quadratic terms $(\frac{1}{2}\gamma_{n,pred}x_i)$ to determine whether the relationships between hunting success and predator behavior 247 are concave or convex (equation S7 in Supporting information). Concave gradients suggest that 248 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 250 of predator traits $(\gamma_{n,pred})$ to estimate correlated effects on hunting success. Lastly, we computed a 251 fourth model with the same structure as the third and included quadratic terms for prey behavior 252 $(\frac{1}{2}\gamma_{n,prey}\mathbf{x}_i^{'})$, and interaction terms between predator and prey behaviors $(\gamma_{n,pred\ prey})$ to test if 253 predators perform better against prev with the opposite locomotor tendency (locomotor crossover) 254 (equation S8 in 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 4000 for both models.

We calculated the models' ICCs following Nakagawa et al. (2017). For each model parameter, we computed the 95% credibility intervals using the highest posterior density intervals. We assumed the fixed effects and the ICCs reached statistical significance when the 95% credible intervals did not overlap zero (Nakagawa and Cuthill 2007).

262 Results

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Variation in hunting mode: Repeatability of hunting behavior

As predicted, we found moderate among-individual differences in average travel speed $(ICC_{id},$

average speed [95% CI] = 0.280 [0.254, 0.304]) and average proportion of time spent in ambush 265 position (ICC_{id} , time in ambush [95% CI] = 0.322 [0.301, 0.342]), while individuals differed weakly 266 in their time before the first capture $(ICC_{id}, \text{ time } 1^{\text{st}} \text{ capture } [95\% \text{ CI}] = 0.102 \text{ } [0.091, \text{ } 0.114])$ 267 (figure 2A, diagonal). Individual predators differed weakly in their average rate of space covered $(ICC_{id}, \text{ space covered } [95\% \text{ CI}] = 0.051 [0.044, 0.057]) \text{ (figure 2A, diagonal)}.$ 269 Contrary to our predictions, predators did not differ in their average travel speed $(ICC_{env}, average)$ speed [95% CI] = 0.002 [0.001, 0.003]), nor in their proportion of time spent ambushing (ICC_{env}), 271 time in ambush [95% CI] = 0.002 [0.001, 0.003]) in different game environments (figure 2B, diagonal). 272 We detected small differences among the game environments in the average rate of space covered and time before the first capture $(ICC_{env}, \text{ space covered } [95\% \text{ CI}] = 0.065 [0.036, 0.097])$ $(ICC_{env}, \text{ space covered } [95\% \text{ CI}] = 0.065 [0.036, 0.097])$ 274 time 1^{st} capture [95% CI] = 0.055 [0.029, 0.082]) (figure 2B, diagonal). Finally, predators displayed 275 weak among-avatar differences for the four hunting behaviors $(ICC_{avatar}, average speed [95\% CI])$ 276 = 0.091 [0.042, 0.153], ICC_{avatar} , space covered [95% CI] = 0.025 [0.010, 0.046], ICC_{avatar} , time 277 in ambush [95% CI] = 0.034 [0.012, 0.064], ICC_{avatar} , time 1st capture [95% CI] = 0.021 [0.008, 278 0.039]). 279

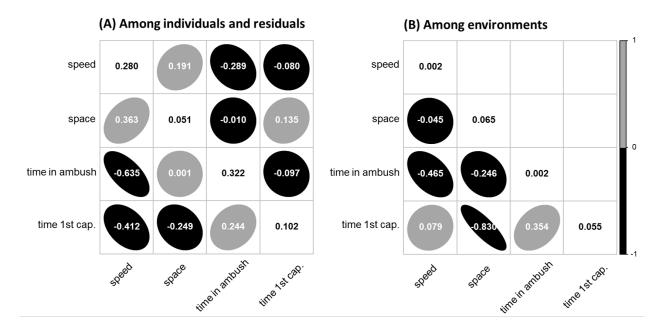


Figure 2: Correlations between combinations of hunting behaviors and their ICCs. For each panel, the ICC of the trait is displayed on the diagonal. Black and gray circles are negative and positive correlations respectively. (A) Among-individual behavioral correlations on the lower off-diagonal, and residual within-individual behavioral correlations on the upper off-diagonal. (B) Among-environment behavioral correlations on the lower off-diagonal. Behavior names were shortened to simplify the plot.

Variation in hunting mode: Correlations between hunting behaviors

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As we expected, the predators' average travel speed and proportion of time spent ambushing were 281 negatively correlated $(r_{id_{0,y_1}id_{0,y_3}}$ [95% CI] = -0.635 [-0.671, -0.597]). Thus, faster predators spent 282 less time ambushing prey (figure 2A, lower off-diagonal). Faster individuals covered space at a 283 faster rate $(r_{id_{0,u1}id_{0,u2}} [95\% \text{ CI}] = 0.363 [0.297, 0.434])$, and individuals who were faster or covered 284 space at a faster rate also took less time to capture their first prey $(r_{id_{0,y1}id_{0,y4}}$ [95% CI] = -0.412 285 $[-0.470,\,-0.350],\,r_{id_{0,y^2}id_{0,y^4}}\;[95\%\;{\rm CI}] = -0.249\;[-0.331,\,-0.163])\;({\rm figure}\;2{\rm A,\;lower\;off-diagonal}).\;\;{\rm There}\;(-0.470,\,-0.350)$ 286 was no relationship between space covered and time spent ambushing $(r_{id_{0,\eta_2}id_{0,\eta_3}} [95\% \text{ CI}] = 0.001$ 287 [-0.075, 0.079]), but ambush hunters required more time to capture their first prey $(r_{id_{0.n3}id_{0.n4}} [95\%])$ 288 CI = 0.244 [0.177, 0.310]) (figure 2A, lower off-diagonal). 289 At the residual within-individual level, we detected a weak positive correlation between travel 290 speed and the rate of space covered $(r_{e_{0,v1}e_{0,v2}}$ [95% CI] = 0.191 [0.184, 0.198]) and a negative 291 correlation between travel speed and the proportion of time spent ambushing prey $(r_{e_{0,n1}e_{0,n3}} [95\%$ 292

CI = -0.289 [-0.296, -0.282]) (figure 2A, upper off-diagonal). Hence, matches in which a predator 293 was faster (relative to its average) were also matches in which it covered space at a faster rate, while spending less time ambushing prey. Predators that covered space at a faster rate also took 295 more time before capturing their first prey $(r_{e_{0,y2}e_{0,y4}}$ [95% CI] = 0.135 [0.127, 0.142]). We did not 296 detect large correlations between travel speed or time spent ambushing and the time before the first $\text{capture } (r_{e_{0,y1}e_{0,y4}} \text{ [}95\% \text{ CI]} = -0.080 \text{ [}-0.088, -0.073], \ r_{e_{0,y3}e_{0,y4}} \text{ [}95\% \text{ CI]} = -0.097 \text{ [}-0.105, -0.090]).$ 298 Environments where predators were on average faster were also also those where they spent on average less time ambushing their prey $(r_{env_{0,y_1}env_{0,y_3}} [95\% \text{ CI}] = -0.465 [-0.767, -0.143])$ (figure 300 2B, lower off-diagonal). We detected a similar relationship between space coverage and time spent 301 ambushing, although it was not statistically significant as the credible intervals overlapped zero $(r_{env_{0,u2}env_{0,u3}}$ [95% CI] = -0.246 [-0.582, 0.071]). Predators took on average less time to capture 303 their first prey in environments where they covered space at a faster rate $(r_{env_{0,y2}env_{0,y4}}$ [95% CI] 304 = -0.830 [-0.937, -0.702]), while taking more time on average in environments where they used ambushes $(r_{env_{0,y3}env_{0,y4}}$ [95% CI] = 0.354 [0.025, 0.650]) (figure 2B, lower off-diagonal). Lastly, 306 we did not detect among-environment correlations between travel speed and space coverage, or 307 between travel speed and the time before capturing a first prey $(r_{env_{0,y1}env_{0,y2}} [95\% \text{ CI}] = -0.045$ 308 $[-0.404,\,0.291],\,(r_{env_{0,y1}env_{0,y4}}\,\,[95\%\,\,\mathrm{CI}]\,=\,0.079\,\,[-0.273,\,0.419])\,\,(\mathrm{figure}\,\,2\mathrm{B},\,\mathrm{lower}\,\,\mathrm{off\text{-}diagonal}).$ 309

Effect of predator and prey behavior on hunting success: Linear relationships

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Predator behavior alone (equation S5) explained 12.7% of the variation in hunting success 311 $(R_{marginal}^2 = 0.127)$. Travel speed and time spent ambushing were positively related to hunting 312 success (table I), suggesting that faster predators and ambush predators captured more prey 313 (figure 3A, C). Predators who covered space at a faster rate captured fewer prey (table I) (figure 314 3B). Predators that required more time to capture their first prey had lower hunting success (table 315 I) (figure 4D). Hunting success barely varied among game environments (ICC_{env0} [95% CI] = 316 0.005~[0.002,~0.008]). Differences among individuals in hunting success were low $(ICC_{id0}~[95\%~CI])$ 317 = 0.067 [0.060, 0.074]). 318

Adding prey behavior (equation S6) increased the explained variance in hunting success to 18%($R_{marginal}^2 = 0.181$). Predators that competed against cursorial prey had significantly lower hunting

success (table I). Prey that were faster at covering space in the environment significantly reduced the predators' hunting success (table I).

Table I: Estimates of the models relating predator hunting success to predator hunting behavior, prey behavior, and their interactions.

	Linear (95% CI)	Quadratic (95% CI)	Pred Interaction (95% CI)	Pred-prey Interaction (95% CI)
speed	0.07 (0.05, 0.08)	-0.11 (-0.10, -0.12)	-	-
space	-0.40 (-0.38, -0.42)	0.09 (0.08, 0.10)	-	-
ambush	0.38 (0.37, 0.40)	-0.12 (-0.12, -0.13)	-	-
time	-0.66 (-0.64, -0.67)	0.13 (0.12, 0.14)	-	-
prey speed	-0.20 (-0.19, -0.22)	-0.07 (-0.07, -0.08)	-	-
prey space	-0.63 (-0.60, -0.65)	-0.10 (-0.08, -0.11)	-	-
speed:space	-	-	-0.06 (-0.04, -0.07)	-
speed:ambush	-	-	-0.11 (-0.09, -0.12)	-
speed:time	-	-	-0.06 (-0.04, -0.07)	-
space:ambush	-	-	0.04 (0.03, 0.06)	-
space:time	-	-	-0.03 (-0.02, -0.05)	-
ambush:time	-	-	-0.02 (-0.01, -0.04)	-
speed:prey speed	-	-	-	-0.01 (-0.03, 0.00)
speed:prey space	-	-	-	-0.09 (-0.07, -0.12)
space:prey space	-	-	-	-0.05 (-0.03, -0.06)
space:prey space	-	-	-	0.10 (0.07, 0.12)
ambush:prey speed	-	-	-	-0.06 (-0.04, -0.07)
ambush:prey space	-	-	-	-0.01 (-0.03, 0.01)
time:prey speed	-	-	-	0.00 (-0.02, 0.01)
time:prey space	-	-	-	0.05 (0.03, 0.07)

Effect of predator and prey behavior on hunting success: Quadratic relationships

Relative to the first model, the model that included quadratic and interaction terms for predator behavior (equation S7) barely increased the explained variance in hunting success ($R_{marginal}^2 = 0.149$). However, we observed significant concave relationships for travel speed and time spent ambushing (table I), suggesting that hunting success was low at extreme behavioral values (figure 3E, G). There was a significant convex relationship between hunting success and space coverage (table I) (figure 3F), and the shape of the quadratic function relating hunting success to time before the first prey is captured was almost the same as the linear function (figure 3H). Hunting success

was still similar among game environments (ICC_{env0} [95% CI] = 0.010 [0.005, 0.016]), and varied slightly among individual players (ICC_{id0} [95% CI] = 0.072 [0.064, 0.079].

The model that included quadratic and interaction terms for predator and prey behavior (equation S8) had the highest explanatory power in hunting success ($R_{marginal}^2 = 0.212$). We detected concave relationships between hunting success and prey speed, as well as prey rate of space covered (table I). Thus, predators had a higher probability of capturing all prey during a match when they competed against prey that expressed average population values of these traits.

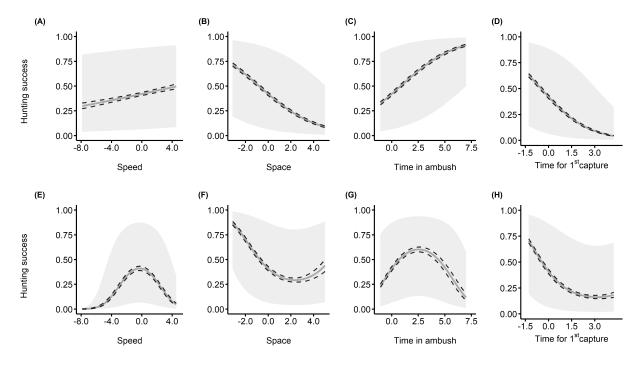


Figure 3: Effect of predator hunting behavior on prey capture. Hunting success (i.e. the probability of capturing four prey) is on the y axis for all panels, and the standardized hunting behavior is on the x axis. The black dashed lines represent the 95% credibility intervals for the predicted values, and the gray band represents the 95% prediction intervals (variance in fixed effects + variance in random effects). (A), (B), (C), (D) Linear functions. (E), (F), (G), (H) Quadratic functions.

Effect of predator and prey behavior on hunting success: predator and prey behavioral interaction

According to our predictions, faster predators were more successful when they competed against

sedentary prey (figure 4A). Predators had higher hunting success for the whole range of values

of space covered when they competed against slower-moving prey (figure 4C). Contrary to our

expectations, the most successful predators where those who covered space at a slow rate when

they competed against prey that were slower at covering space in the environment (figure 4D).

However, those who covered space at the fastest rate where more successful against prey that

were the slowest at covering space (figure 4D). There were no significant interactions between

predator and prey travel speed (figure 4B). Lastly, for the whole range of time spent ambushing

prey, predators had generally higher success against slower moving prey and prey that covered less

space in the environment (figure 4E-F), although the interaction with prey space covered was not

significant (table I).

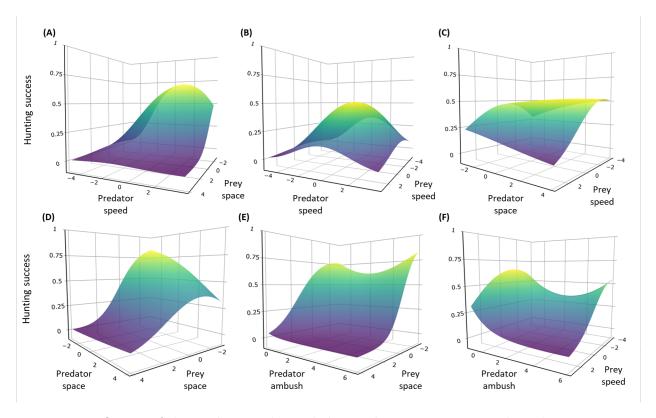


Figure 4: Influence of the predator and prey behavioral interactions on predator hunting success. The plots' 3D surfaces show the relationship between different combinations of predator-prey behaviors and predator hunting success. We fitted the surfaces by predicting the mean probability of capturing four prey based on the best quadratic approximation of the predator and prey interaction terms. Here, we show interactions that enable us to determine if there are predator-prey locomotor crossovers. (A) Predator travel speed and prey space coverage. (B) Predator and prey travel speed. (C) Predator space coverage and prey travel speed. (D) Predator and prey space coverage. (E) Predator time spent ambushing and prey travel speed.

350 Discussion

Our study is the first to use an online multiplayer videogame to investigate individual variation 351 in predator foraging mode, and how predator and prey behavior affect hunting success. We provide evidence that individuals who adopt the predator role display individual specialization and 353 flexibility in their foraging modes, varying along a continuum from cursorial to sit-and-wait. The 354 expression of these foraging modes was consistent with shifts in the expression of other behaviors 355 such as space use and the latency to first prey capture, matching the predictions of the forag-356 ing syndrome hypothesis at the individual level. Contrary to our expectations, neither hunting 357 behavior nor prey capture varied among game environments. Even if we found the presence of 358 competing foraging modes in the population, the most successful predators were those who hunted at average population values of travel speed, and those who spent an above population-average 360 of their time ambushing prey. Lastly, we found evidence for the locomotor-crossover hypothesis 361 for some predator-prey trait combinations. However, predators were generally less successful when they competed against fast traveling prey and those who covered space faster in the environment. 363 Our analyses revealed that predators differed in their average travel speed and in their proportion 364 of time spent ambushing prey. These behaviors were negatively correlated at the among-individual 365 level, suggesting that individuals may specialize as either cursorial or ambush predators. Cursorial predators displayed a shorter latency to first prey capture compared to ambush predators. These 367 results are similar to those of McGhee et al. (2013), who found that fast moving northern pike 368 (Esox lucius) were quicker to launch their initial attack. Interestingly, we found that hunting success 369 decreased significantly with increasing latency to first capture, but did not strongly interact with 370 time spent ambushing to affect hunting success. Thus, although ambush predators displayed a 371 longer latency to capture their first prey, they were as successful as cursorial predators. 372 Since individuals achieved similar hunting success across the study period, our observations sug-373 gest that ecological mechanisms such as locomotor-crossovers may favor the coexistence of both 374 foraging strategies within the DBD predator population. Indeed, we found that cursorial preda-375 tors had greater hunting success when they competed against more sedentary prey, which agrees 376 with empirical studies that tested the locomotor crossover hypothesis (Belgrad and Griffen 2016; 377 Donihue 2016; Chang et al. 2017). However, locomotor-crossovers did not seem to explain the

success of ambush predators, as they also displayed higher success against sedentary prey, or prey 379 travelling at speeds close to the population average. In addition, predators reached similar hunting success across the observed range of space coverage and time spent ambushing (figure 4. C-F). 381 A potential explanation is that by focusing solely on prev speed and space coverage, we failed to 382 capture other important prey strategies involved in the predator-prey interaction. For instance, 383 unpublished results by Santostefano et al. found four prey behavioral profiles in DBD, where faster 384 and exploratory individuals seemed distinct from bolder individuals that performed more coopera-385 tive/altruistic actions, and that were involved in longer chases with the predator. Hence, we can 386 hypothesize that the success of ambush predators might be explained, to a degree, by a higher 387 capture of bold prev. 388

Predators also displayed flexibility in their foraging mode, where individuals switched between a 389 cursorial or ambush strategy from one match to the other. These foraging mode switches were 390 accompanied by shifts in space coverage and in latency before a first capture, suggesting that 391 predators may adjust their behavior according to the type of prey encountered. Thus, the outcome 392 of the predator-prey interaction might not only be determined by the individual predator's preferred 393 hunting mode, but also by its flexibility from one encounter to the next (McGhee et al. 2013). 394 Although this falls outside the scope of this study, further analyses will need to investigate the 395 dynamics of the predator behavior within a match to determine if predators switch between sit-396 and-wait to cursorial strategies as prey density is reduced (Inoue and Marsura 1983). Short-term 397 switches in hunting mode are also expected to occur as predators make behavioral adjustments in 398 response to prey antipredator behavior (Helfman 1990), and should be favored when prey encounters 399 are unpredictable (Woo et al. 2008; Carneiro et al. 2017; Phillips et al. 2017). Comparing prev 400 selection and capture rates between specialist and flexible hunters could provide important insight 401 into the community-consequences of behavioral decisions made by predators. 402

An unexpected result in our study was that predator hunting mode did not change across 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). A potential explanation is that habitat structure may have instead affected prey behavior, for instance, by altering their perception of predation risk or

fear (Heithaus et al. 2009; Gavnor et al. 2019). Features of heterogeneous habitats can sometimes exert stronger predator cues, leading prey to avoid these habitats, or alter their activity to reduce predation risks (Preisser et al. 2007). In a seperate analysis, we found that predator space coverage 410 was largely explained by differences among game environments when prev behavior was excluded 411 from the model (Supplementary material), although the variance among game environments for the 412 other traits remainded the same. Alternatively, prey individuals in DBD might differ in the way 413 they respond to habitat changes, as some could have increased activity in heterogeneous habitats by 414 exploiting refuges, thus, negating the effect of the environment on the predator's hunting strategy 415 (Warfe and Barmuta 2004). This could also explain why hunting success was similar among game 416 environments. Another explanation is that predators can alter their hunting behavior at larger 417 scales according to prev behavior (as we have found), but seek prev accessibility at finer scales 418 by killing them in specific areas in a given habitat (Hopcraft et al. 2005). Ultimately, we cannot 419 exclude the possibility that the game's design might not properly simulate real ecological habitats to 420 affect the predator's behavior. For instance, one feature of the game's design is that predators have 421 constant visual cues on the location of patches where prey forage. This offers them the opportunity 422 to approximate the distance/time required to travel among patches, while possibly relaxing the 423 energy/concentration allocated to managing movement across the habitat's features. Thus, further 424 investigation is required to properly understand the scale at which the environments shape predator 425 behavior in this particular system. 426

We are among the first ecologists (Cere et al. accepted; Barbe et al. 2020) to propose the use 427 of online multiplayer videogames to investigate how ecological mechanisms shape the dynamics of 428 trophic interactions. We are persuaded that videogames are poised to play a central role in testing 429 ecological hypotheses, as they reduce financial, statistical or logistical hurdles associated with empir-430 ical research while providing complex and ecologically-relevant datasets. However, videogames are 431 not a panacea and they come with their own biases. Perhaps the most important one is that player 432 behavior may not properly reflect behavioral decisions made by real-life organisms in the wild, as 433 the player cannot "die" (Oultram 2013). Hence, individuals may take greater risks in a videogame 434 compared to real predators (Lofgren and Fefferman 2007; Oultram 2013). Moreover, while DBD 435 provides an interesting system to investigate predator-prey interactions, prey density is fixed at 436

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 biases, researchers should
interpret results from online videogames with care, and aim to test specific ecological hypotheses
when using virtual systems.

To conclude, individual variation in predator (and prey) behavior is increasingly recognized as a 442 critical factor influencing the outcome of trophic interactions (Pettorelli et al. 2015; Toscano et 2016: Moran et al. 2017). Albeit our study being essentially descriptive, as it is the first 444 to investigate individual variation in predator foraging behavior using an online videogame, we 445 showed that individuals differed in contrasting hunting strategies that align with those used by wild predators. These hunting modes varied among- and within- individuals along correlated behaviors 447 (foraging syndrome hypothesis), and our results suggest that predator-prey locomotor-crossovers 448 may promote the coexistence of different predator and prey behavioral types. We are confident that further studies using online videogames will provide valuable ecological insight for behavioral 450 and community ecologists. 451

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Competing interests:

The authors declare no competing interests

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Data availability statement:

- 463 We could not openly share the data on open science/data web platforms due to ownership and
- 464 privacy restrictions. However, upon request, we will provide the data used to conduct our analyses.
- 465 In addition, the project's R scripts and results are freely available on this GitHub repository:
- 466 https://github.com/quantitative-ecologist/videogame hunting tactics-Rscripts.

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