

Lay summary

Understanding the hunting strategies and prey preferences of predators is crucial to predict their impact on natural populations. With an online videogame simulating a predator-prey interaction, we demonstrate that some predator players specialize as active hunters, while others prefer to use ambushes. Both types of hunters differ in the type of prey that they capture, enabling them to achieve 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 an online videogame.

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 travel speed, space coverage, ambush time, and latency to first capture covary at three hierarchical levels (among environments, among individuals, and within individuals) to assess the structure of predator hunting mode. We also investigated how these traits interact with prey travel speed and space coverage to affect predator hunting success. We found that individual predators specialized either as cursorial or ambush hunters along a continuum of these 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.

Data: Here is an anonymized link to our data for reviewing purposes that we deposited on the Open Science Framework: https://osf.io/wyvrt/?view_only=8449b28df2314f24958702532dc4bbee

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 that are 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 the predator to subdue its prey (Perry et al. 1990; Perry 1999; Butler 2005; Cooper 2005; Miles et al. 2007). Prey ac-

tivity/mobility is an important trait influencing 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 when prey vary in their activity patterns (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). 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).

this paragraph should be integrated somewhere or stand on its own For instance, foraging mode is expected to vary along a continuum of morphological, physiological, and behavioral traits according to the foraging syndrome hypothesis (Perry et al. 1990; Perry 1999; Butler 2005; Cooper 2005; Miles et al. 2007). 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 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.

The paragraph starting at L73 was a bit less cohesive and unfocused, alternating between research approaches, behavioral syndromes, and other topics. One point that is probably worth mentioning in the context of videogames is that in this simulation predator has no direct competition. If I understand correctly, only a single predator exists in any game, and hence the only consideration is the time before prey escape. This is different than most realistic scenarios. (True, I think that flexibility could be integrated in parts where I talk about the prey and same thing with responses to habitat structure. I could thus distinguish between stable differences and plasticity and give examples that compare both.

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flexibility should be integrated in parts where I talk about habitat and prey 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 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).

However, this type of research is often conducted under controlled laboratory conditions, which can fail to capture the nuances and complexities of a predator's behavior in the wild (Carter et al. 2013; Niemelä and Dingemanse 2014). Empirically investigating individual variation in hunting mode requires repeated behavioral measurements for numerous individuals in varying 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. Unfortunately, few studies have investigated how habitat- and prey-specific characteristics jointly shape correlated foraging traits within and between individuals or habitats. A paramount challenge is to test the foraging syndrome hypothesis at multiple hierarchical levels, if we are to assess the importance of these levels of variation in hunting mode for predator-prey interactions.

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; 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 Feffer-

man 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).

Here, 2 things need to be made clear 1. talk about predators seeing the patches (clint suggests to make analogies like predators can use cues to locate the patches 2. other limitations of the game?

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., accepted) 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 habitat such as 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). 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. However, an important aspect of the game to consider is that predators have constant visual cues that display the location of the generators. We outline this game design feature as it may interfere with how the virtual environment affects the predator's behavior, for instance, if it only needs to think about travelling between each generator to capture prey. Lastly, although *DBD* is a virtual environment, we suggest that individual players express "real" predator-prey behaviors within it, 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 proportion of 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, while spending less time ambushing and having 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 among-environment differences in average hunting behavior, variation in hunting mode arising when individuals differ in their average hunting behavior (i.e. individual specialization), and variation arising

from individuals adjusting their hunting mode over time in response to temporal changes in environmental conditions or prey behavior (i.e. individual flexibility). First, we hypothesize that habitats shape the hunting mode employed by predators. 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. Second, we hypothesize that individual predators 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 will differ in their average trait values along a continuum for all hunting trait combinations (among-individual behavioral correlations). Third, we expect that individual predators express flexible hunting behavior by switching from cursorial to ambush tactics between foraging bouts (i.e. between matches). Thus, we predict that the individuals' residuals in contrasting hunting behaviors (e.g. travel speed vs ambush time) will be negatively correlated (within-individual behavioral correlations). Fourth, following the locomotor-crossover hypothesis, we predict that ambush and cursorial predator-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. 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 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, as short matches are usually interrupted because of technical issues (disconnexions, players in a match that don't play, etc.). 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 did not earn points.

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 further 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 selected behaviors were the average travel speed (m/s), the rate of space covered (square/s), the proportion of time spent ambushing over the match duration, and the proportion of time predators took to capture their first prey over the match duration.

We quantified the predator's average travel speed as the average number of meters per second traveled during a match. Space coverage describes 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). These grids are drawn by the videogame developer to build the game environments, but are invisible to the players. Unfortunately, it was not possible to know which specific square was visited. Based on this data, we could divide the number of times a square was visited by the match duration to obtain the rate of space covered. The proportion of time spent ambushing describes the total amount of time a predator spent monitoring around capture sites to ambush prey players that try to rescue individuals that were captured. We quantified this trait with help from the developer who drew (invisible) circles of 9-meter radiuses around all sites where the predator brought prey to be consumed (each site is at the center of a circle). Predators in *DBD* monitor these sites to ambush prey that come to rescue the prey that it captured. Thus, each time a predator brought prey to a site during a match, the time (in seconds) it spent monitoring inside the area of a circle was recorded. We could then sum the total amount of time spent ambushing during a match and divide it by the match duration (in seconds) to have the proportion of time spent ambushing over the match duration. Lastly, the time before the first capture was calculated as the amount of seconds elapsed before a predator consumed its first prey, divided by the match duration.

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. 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 and success. Thus, we used one average value per prey trait, for each match played.

224

Statistical analyses: Software and computer setup

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

230

Statistical analyses: Variation in hunting mode

231 We first parametrized a multivariate Bayesian mixed model to quantify unadjusted repeatability of hunting
 232 behavior, and evaluate among-environment, among-individual (specialization), and within-individual (flex-
 233 ibility) behavioral correlations. We included the predator’s population-response to prey behavior by adding
 234 prey travel speed (x_1) and rate of space covered (x_2) as linear fixed effects. We square-root transformed
 235 the four hunting behaviors (y_1 = speed, y_2 = space, y_3 = ambush time, y_4 = time 1st capture) to achieve
 236 normality and then defined each as having a Gaussian distribution. All traits were then standardized to mean
 237 and unit variance (z-scores). The model is described by the following equations:

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

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

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

$$y4_{ghij} = (\beta_{0y4} + env_{0y4,g} + avatar_{0y4,h} + id_{0y4,i}) + \beta_{1y4}x_1 + \beta_{2y4}x_2 + \varepsilon_{0y4,ghij} \quad (4)$$

238 where g indexes the environment, h the predator avatar, i the individual player, and j the recorded match.
 239 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 matrixes ($\Omega_{env}, \Omega_{avatar}, \Omega_{id}, \Omega_{\varepsilon}$) (equations S1-S4 in the Supporting information). For each combination of behaviors (y_n), we extracted the behavioral correlations among- environments ($r_{env_{0,y_n} env_{0,y_n}}$), avatars ($r_{avatar_{0,y_n} avatar_{0,y_n}}$), and 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 4000 (see section ‘Parametrization of the Bayesian multivariate mixed model’ in the Supporting information for details).

Following Nakagawa and Schielzeth (2010), 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, by dividing the variance of the specific random effect by the total phenotypic 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.

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 total number of prey in a match (four) as a binomial response variable ($\omega_{hij} \sim \text{Binom}(\max_{hij}, P_{hij})$). We first quantified the linear relationship between hunting success and predator behavior by fitting a binomial Bayesian generalized linear mixed model 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, proportion of time spent ambushing, and proportion of time 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 4000 for the first model and 6000 for the second model.

We built a third model with the same structure as the first model and included quadratic terms ($\frac{1}{2}\gamma_{n,pred}x_{hi}$) 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 ($\frac{1}{2}\gamma_{n,prey}x'_{hi}$), 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 4000 for both models. We calculated the models' ICCs following Nakagawa et al. (2017). For each model parameter, we computed the 95% credible intervals using the highest posterior density intervals. We assumed that the fixed effects and the ICCs reached statistical significance when their respective 95% credible intervals did not overlap zero (Nakagawa and Cuthill 2007).

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 proportion of time spent ambushing ($ICC_{env_{y3}}$ [95% CI] = 0.002 [0.001, 0.003]) differed among the game environments (figure 2B, diagonal). We detected small differences among the game environments in the average rate of space covered ($ICC_{env_{y2}}$ [95% CI] = 0.065 [0.036, 0.097]) and time before the first capture ($ICC_{env_{y4}}$ [95% CI] = 0.055 [0.029, 0.082]) (figure 2B, diagonal).

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