Analysing individual specialisation and flexibility in predator hunting mode and its effect on hunting success using an online multiplayer videogame

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# Abstract

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# 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/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).

To this day, predator species tend to be classified either as active or sit-and-wait hunters based on their average behaviour (Lima 2002; Miles et al. 2007; Pettorelli et al. 2015; Schmitz 2017), despite growing evidence that individual predator behavioural variation can exert important consequences for predator-prey interactions (Pettorelli et al. 2015; Toscano et al. 2016; Schmitz 2017). Indeed, studies report that individual predator behavioural type can mediate consumptive and nonconsumptive 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 community-level consequences of predation.

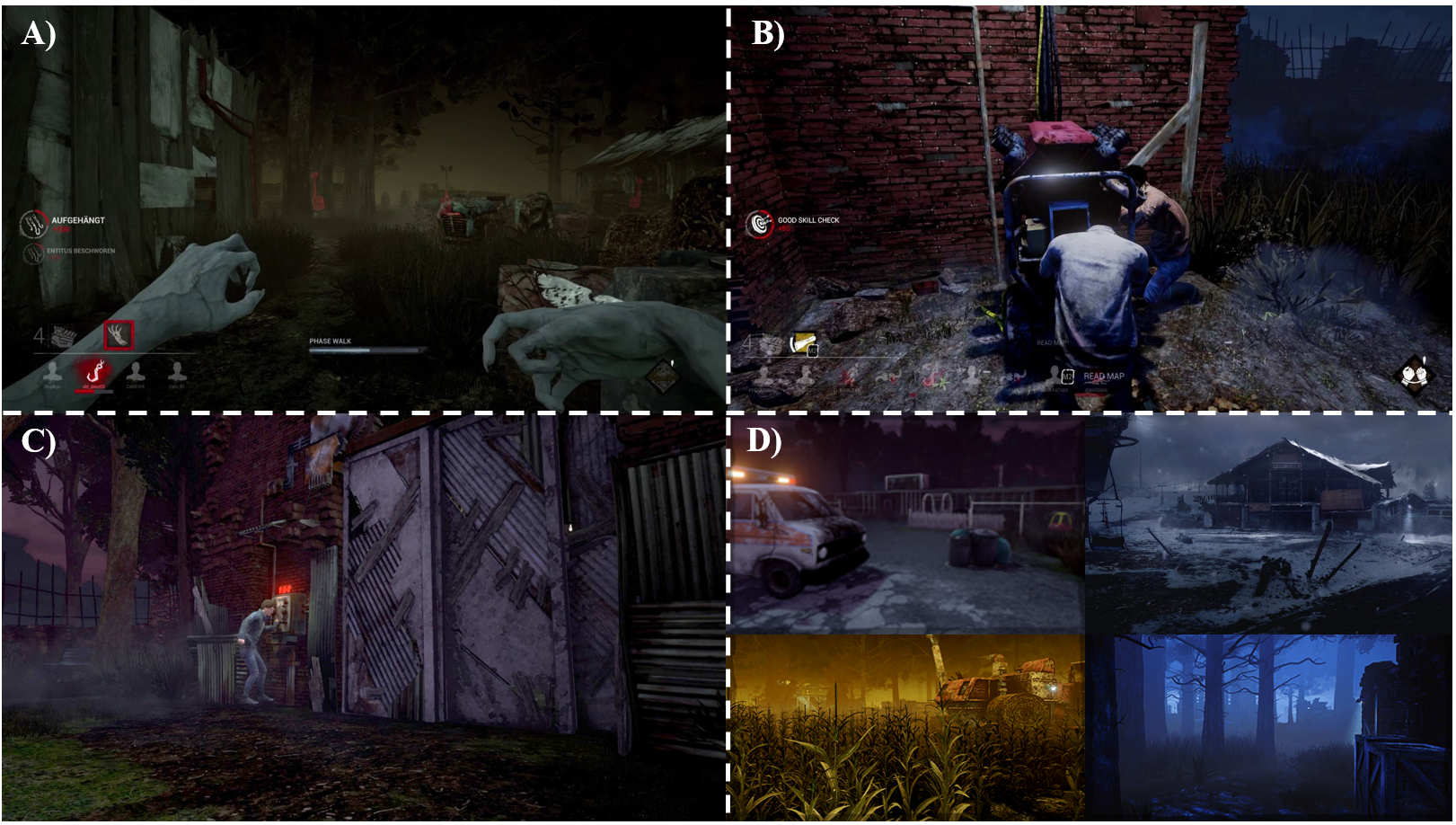
Stable individual differences in hunting mode within populations can be driven by specialisation when individuals experience temporal and/or spatial fluctuations in the distribution, availability, or behaviour of their prey (Araújo et al. 2011; Carneiro et al. 2017; Phillips et al. 2017; Courbin et al. 2018). In sea predators, individuals specialise 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; Huey 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 behavioural 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). 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 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, but, at the expense of being themselves more easily detected (Michel and Adams 2009). This suggests that tradeoffs could mediate individual differences in hunting strategies as a function of habitat structure.

Trophic interactions are dynamic processes that can also trigger flexible behavioural responses of individual predators (Helfman 1990; Heithaus et al. 2018), for instance, to changes in prey density (Inoue and Marsura 1983), prey behavioural type (McGhee et al. 2013), prey condition (Wignall and Taylor 2008), seasonality (Miles et al. 2007; Phillips et al. 2017), or in habitat structure (Wasiolka et al. 2009). Unfortunately, most of this research is conducted under controlled laboratory conditions, which can fail to capture the nuances and complexities of predator species’ ecology in the wild (Carter et al. 2013; Niemelä and Dingemanse 2014). Empirically investigating individual variation in hunting mode requires repeated measures of behaviour 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 behavioural 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 caracteristics 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 behaviour 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 behaviour (Barbe et al. 2020). First, online videogames provide abundant repeated measurements on millions of individual players across temporal and environmental gradients. Second, the structure of the virtual environmental is known and can be manipulated to assess the effect of specific environmental components on the behaviour of interest. Third, videogames can reproduce realistic ecological settings in which complex interactions occur among players. A classic example of this approach is the analysis of the “Corrupted Blood” epidemic in *World of Warcraft*, where precise epidemiological parameters, such as transmission rate, were used to predict the outbreaks (Balicer 2007; Lofgren and Fefferman 2007). In this sense, online multiplayer videogames potentially constitute a complement to traditional field studies. We suggest that they will permit ecologists (among other scientists) to bridge the gap between real-world ecological studies and large-scale computer simulations. Online videogames are of interest to social, economic, and epidemiological sciences (Ross et al. 2015), but to our knowledge, ours is the second study (see Cere et al., accepted) to use an online videogame to test ecological hypotheses.

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), where the predator’s objective is to capture prey (Fig. 1). The predator’s main objective is to search for and consume prey, while the preys’ objective is to escape the predator. Prey can use a wide range of behaviours such as cooperation or hiding to successfully escape (Fig. 1 B-C). For example, they can cooperate to help conspecifics escape from capture (Cere et al., accepted), which predators may 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 (Fig 1. D). Hence, predators may encounter prey that express different behaviours, and are expected to benefit from changing their behaviour accordingly to maximize hunting success.



**Figure 1. Images of the online videogame Dead by Daylight** **A)** The predator player’s first person vision. **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 **C)** doors in order to escape and win the match. **D)** Representative pictures of the different game environments where matches take place. The game environments settings vary between urban, farmland, and forest areas.

In this study, we used an extensive and complete dataset on the hunting behaviour of predator players in *Dead by Daylight* to investigate environmental and individual variation in hunting mode, and how hunting mode affects prey capture. We used four hunting-related behaviours as proxies of hunting mode: travel speed, the rate of space covered in the environment, the proportion of time spent in an ambush position, and the time elapsed before the first prey capture. We applied the recent advances in multivariate mixed-modelling to quantify variation in multiple behaviours and their correlations at different hierarchical levels (i.e. among and within-individuals, Dingemanse and Dochtermann 2013) as a way to describe the variation in hunting mode within a population of predators (Perry et al. 1990; Perry 1999; Butler 2005; Cooper 2005; Miles et al. 2007). Within-population variation includes a) among-environment differences in average hunting behaviour, b) variation in tactic use arising when some individuals use one tactic more often than the others (i.e. individual specialisation), and c) the variation arising from individuals adjusting tactic use over time in response to temporal changes in environmental conditions or prey behaviour (i.e. individual flexibility). First, we hypothesized that predators would use hunting tactics according to habitat-specific characteristics. Therefore, we expected correlated trait values associated with ambush tactics in smaller and heterogeneous environments, and correlated trait values associated with cursorial tactics in open/wider and homogeneous environments (James and Heck Jr. 1994; Wasiolka et al. 2009; Donihue 2016). Second, we hypothesized that individual predators would consistently differ in their hunting mode over time, with some specialising as cursorial hunters, and others as ambush hunters. Thus, we predicted that individual predators would differ in their average trait values along a continuum for all combinations of the four hunting traits (among-individual behavioural correlations). Following the locomotor-crossover hypothesis(Huey and Pianka 1981), we predicted that ambush and cursorial predator-types may coexist in the population, because both achieve similar hunting success by performing better against prey with the opposite locomotor tendency. Lastly, we hypothesized that individual predators would express flexible hunting behaviour, by switching from cursorial to ambush tactics between foraging bouts. Thus. we predicted that the individuals’ residual trait values in contrasting hunting behaviours (ambush vs cursorial) would be negatively correlated (within-individual behavioural correlations).

# Materials and methods

## (a) Study system

The datasets used to test our hypotheses were provided by Behaviour Interactive Inc., the creator and administrator of *DBD*. The company records the behaviour of players for every match played online. During our study period, *DBD* offered 15 playable predator avatars. Players who incarnate the predator choose their avatar before a match takes place. Each predator avatar has unique abilities that may encourage different playstyles. Some have abilities than 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>.

## (b) Data collection

The study period ranged from March 20 to June 17 2019. Our population consisted of 2 171 new anonymous players who initiated their first match between March 20 and March 22, 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 behaviour. 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.

## (c) Behavioural traits

### (i) Predator hunting behaviour

We selected four out of eight behavioural variables that summarized most of the variation in predator hunting tactics based on a principal component analysis (see Fig. S1 and Table S1 in Supporting information): average travel speed (meter/sec.), the rate of space covered (square/sec), the proportion of time spent in an ambush position during the match, and the proportion of time the predator took to capture his first prey during the match (see section ‘Behavioural traits measurements’ in the Supporting information for details).

### (ii) Prey behaviour

We quantified prey average travel speed (meter/sec.) and rate of space covered (square/sec.). 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 behaviour on the predator’s hunting behaviour. Thus, we used one average value per prey trait, for each match played.

## (d) Statistical analyses

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.

### (i) Variation in hunting mode

We first parametrized a multivariate Bayesian mixed model to quantify unadjusted repeatability of hunting behaviour, and evaluate among-environment, among-individual (specialisation), and within-individual (flexibility) behavioural correlations. We included the predator’s population-response to prey behaviour by adding prey travel speed and rate of space covered as linear fixed effects. We square-root transformed the four hunting behaviours ( = speed, = space, = time in ambush, = time 1st capture) to achieve normality and then defined each as having a Gaussian distribution. All traits were then standardised to mean and unit variance (z-scores). We parametrised the model as (see section ‘Parametrisation of the multivariate mixed model’ in the Supporting information for details):

where *i* indexes individual players and *j* the recorded match. Player ID (), the game environment (), the predator avatar (), and the residuals () are respectively random intercepts (among- individual, environment, and avatar variance) and residuals (within-individual variance) assumed to follow a multivariate Gaussian distribution, with their associated variance-covariance matrixes (, , , ) (refer to equations S1-S4 in Supporting information). We extracted among- individual, environment, avatar, and residual within-individual behavioural correlations from the variance-covariance matrixes by dividing the random effect covariances with the square root of the product of the random effect variances, for each combination of behaviours (according to equation 7c-d in Dingemanse & Dochtermann, 2013).

Following Nakagawa and Schielzeth (2010), we calculated each hunting trait’s adjusted repeatability estimate (intra-class correlation coefficient, ICC) for the player ID, the game environment, and the predator avatar by dividing the variance associated with the random effect by the total phenotypic variance (ex. ). We computed the 95% credibility intervals for each repeatability estimate using the highest posterior density intervals.

### (ii) Effect of hunting behaviour and prey behaviour on prey capture

Since predators can capture a maximum of four prey, we used the number of prey captured on the total number of prey in a match (four) as a binomial response variable ( ~ ). We first quantified the linear relationship between hunting success and predator behaviour by fitting a binomial Bayesian generalized linear mixed model (glmm) with a logit link function. The model fits a linear function where we could estimate if hunting success increased or decreased with increasing hunting behaviour scores. We fitted the mean probability of capturing four prey () for individual *i* on its *j* match as a function of its travel speed, rate of space covered, proportion of time spent in an ambush position, and proportion of time before the first capture (upper part of equation 1). We computed a second model to account for variation explained by prey behaviour. We thus added prey travel speed and their rate of space covered in the model equation (lower part of equation 1). Both models had random intercepts for the predator player’s ID () and the game environment () to partition the variance in hunting success explained by differences among players and environments where matches occurred. We included an observation-level random effect to account for overdispersion (Harrison 2015) and compared the models to a beta-binomial model to verify that the estimates were robust. Trait values were standardised to mean and unit variance (z-scores). The models were fitted as:

where player ID and the game environment come from a normal distribution with estimated variance (~, ~).

We built a third model within the same structure as the first model and included quadratic terms to determine whether the relationships between hunting success and predator behaviour are concave or convex. 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 to estimate correlated effects on hunting success. Lastly, we computed a fourth model that included quadratic terms for prey behaviour, and interaction terms between predator and prey behaviours to test if predators perform better against prey with the opposite locomotor tendency (locomotor crossover). This model was built within the same structure as the third model. All trait values were standardised to mean of 0 and unit variance (z-scores). The models had the following structure:

where the upper part of the equation shows the third model which includes quadratic and interactions terms for predator behaviour only, and the lower part the fourth model accounting for quadratic and interactions terms for predator and prey behaviour. are the quadratic terms for the predator traits (), are the quadratic terms for the prey traits (), are the interaction terms between predator behaviours, and are the interactions terms between predator and prey behaviours.

The reported estimates are partial coefficients which are the effect of the behaviour on hunting success while holding the other behaviours constant. 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% credibility intervals did not overlap zero (Nakagawa and Cuthill 2007).

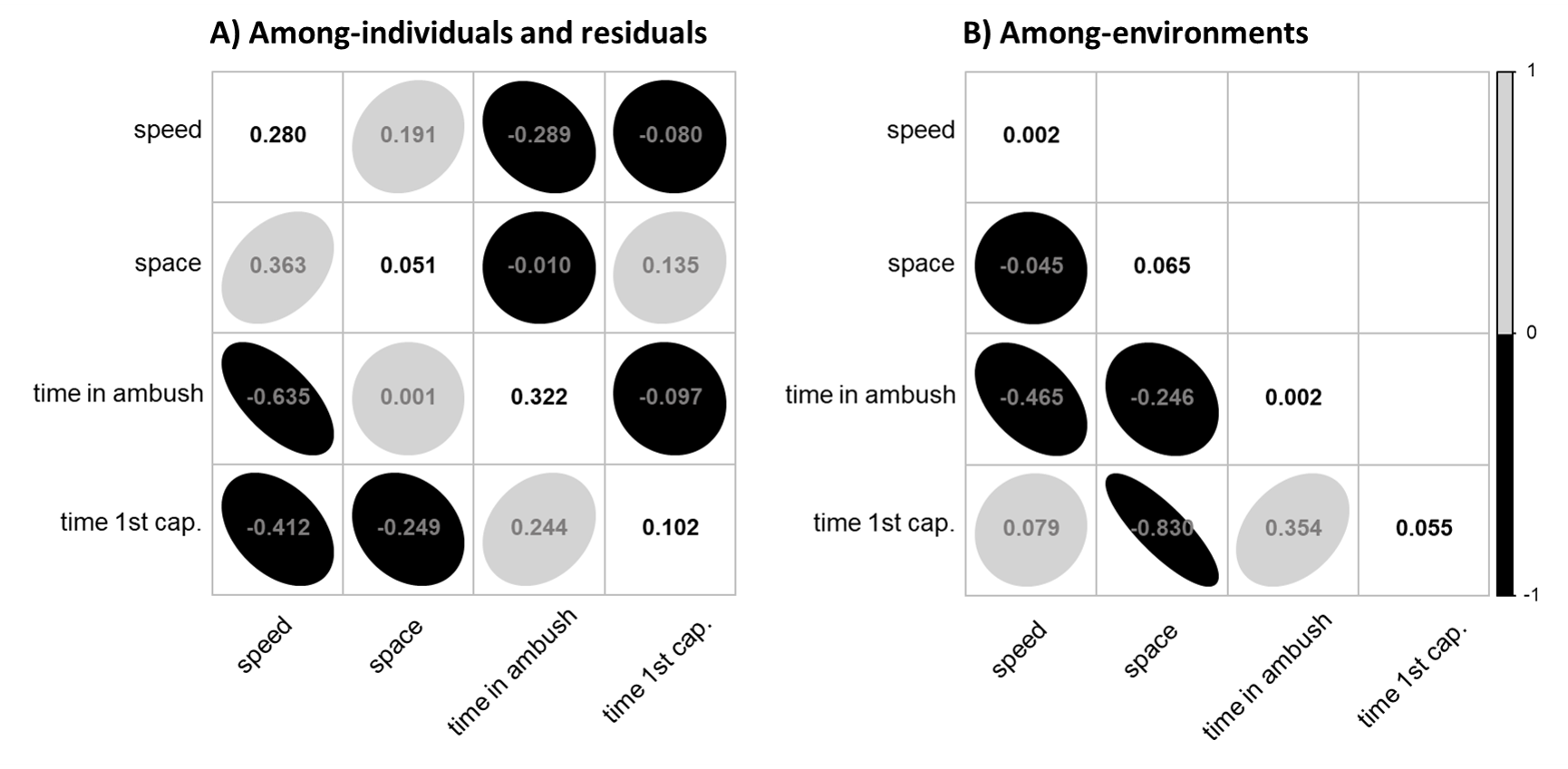
# Results

## (a) Variation in hunting mode

### (i) Repeatability of hunting behaviour

As we predicted, we found moderate among-individual differences in average travel speed (, average speed [95% CI] = 0.280 [0.254, 0.304]) and average proportion of time spent in ambush position (, time in ambush [95% CI] = 0.322 [0.301, 0.342]), while individuals differed weakly in their time before the first capture (, time 1st capture [95% CI] = 0.102 [0.091, 0.114]) (Fig. 2A, diagonal). Individual predators differed weakly in their average rate of space covered (, space covered [95% CI] = 0.051 [0.044, 0.057]) (Fig. 2A, diagonal).

Contrary to our predictions, predators did not differ in their average travel speed (, average speed [95% CI] = 0.002 [0.001, 0.003]), nor in their proportion of time spent in ambushing (, time in ambush [95% CI] = 0.002 [0.001, 0.003]) in different game environments. However, we detected small differences among the game environments in the average rate of space covered and time before the first capture (, space covered [95% CI] = 0.065 [0.036, 0.097]) (, time 1st capture [95% CI] = 0.055 [0.029, 0.082]) (Fig. 2B, diagonal). Finally, predators displayed weak differences among the predator avatars they played with for the four hunting behaviours (, average speed [95% CI] = 0.091 [0.042, 0.153], , space covered [95% CI] = 0.025 [0.010, 0.046], , time in ambush [95% CI] = 0.034 [0.012, 0.064], , time 1st capture [95% CI] = 0.021 [0.008, 0.039]) (*Fig. SX in Supplementary material*).



**Figure 2. Correlations between combinations of hunting behaviours and their ICCs.** The multivariate model was run on a sample of 70 831 matches played by 2 171 individuals across 27 different game environments, and who used up to 15 avatars. The sample size of each parameter’s posterior distribution is 4000. Each correlation is computed using the BLUPs of the random effect of interest. For each panel, the ICC of the trait is displayed on the diagonal. Black and gray circles are negative and positive correlations respectively. **A)** The left panel shows among-individual behavioural correlations on the lower off-diagonal, and residual within-individual behavioural correlations on the upper off-diagonal. **B)** The right panel displays among-environment behavioural correlations on the lower off-diagonal. We shortened the behaviour names to simplify the plot.

### (ii) Correlations between hunting behaviours

As we expected, the predators’ average travel speed and proportion of time spent ambushing were negatively correlated ( [95% CI] = -0.635 [-0.671, -0.597]). Thus, faster predators spent less time ambushing prey (Fig. 2A, lower off-diagonal). Faster individuals covered space at a faster rate ( [95% CI] = 0.363 [0.297, 0.434]), and individuals who were faster or covered space at a faster rate also took less time to capture their first prey ( [95% CI] = -0.412 [-0.470, -0.350], [95% CI] = -0.249 [-0.331, -0.163]) (Fig. 2A, lower off-diagonal). There was no relationship between space covered and time spent ambushing ( [95% CI] = 0.001 [-0.075, 0.079]), but ambush hunters took more time to capture their first prey ( [95% CI] = 0.244 [0.177, 0.310]) (Fig. 2A, lower off-diagonal).

At the residual within-individual level, we detected a small positive correlation between travel speed and the rate of space covered ( [95% CI] = 0.191 [0.184, 0.198]) and a negative correlation between travel speed and the proportion of time spent ambushing prey ( [95% CI] = -0.289 [-0.296, -0.282]) (Fig. 2A, upper off-diagonal). Hence, matches in which a predator was faster (relative to its average) were also matches in which he covered space at a faster rate, while spending less time ambushing prey, suggesting individual flexiblity in hunting mode. Predators who covered space at a faster rate also took more time before capturing their first prey ( [95% CI] = 0.135 [0.127, 0.142]). We did not detect substantial correlations between travel speed or time ambushing and the time before the first capture ( [95% CI] = -0.080 [-0.088, -0.073], [95% CI] = -0.097 [-0.105, -0.090]).

At the environment-level, predators who were faster in certain environments spent less time ambushing their prey ( [95% CI] = -0.465 [-0.767, -0.143]) (Fig. 2B, lower off-diagonal). This suggests that the environment could determine whether predators employ a cursorial or ambush tactic. We detected a similar relationship for space coverage and time ambushing, although not significant as the credibility interval overlapped zero ( [95% CI] = -0.246 [-0.582, 0.071]). Predators who covered space at a high rate in certain environments took less time to capture their first prey ( [95% CI] = -0.830 [-0.937, -0.702]), while those who used ambushes took more time to capture their first prey ( [95% CI] = 0.354 [0.025, 0.650]) (Fig. 2B, lower off-diagonal). Lastly, we did not detect among-environment correlations between travel speed and space coverage, or between travel speed and the time before capturing a first prey ( [95% CI] = -0.045 [-0.404, 0.291], ( [95% CI] = 0.079 [-0.273, 0.419]) (Fig. 2B, lower off-diagonal).

## (b) Effect of predator and prey behaviour on prey capture

### (i) Linear relationships between predator/prey behaviour and predator hunting success

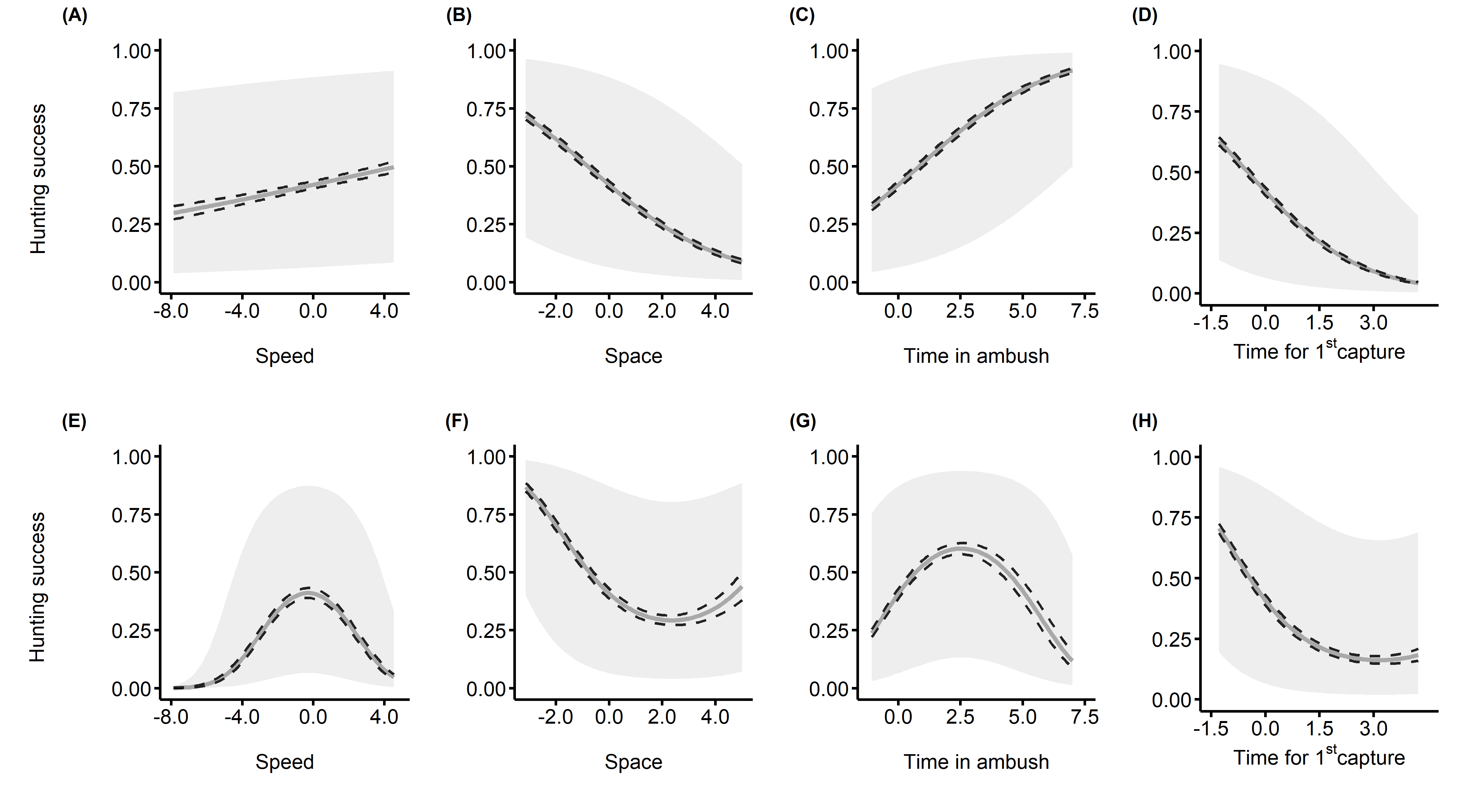
Predator behaviour alone explained 12.7% of the variation in prey capture ( = 0.127). Travel speed ( [95% CI] = 0.07 [0.05, 0.08]) and time spent ambushing ( [95% CI] = 0.38 [0.37, 0.40]) were positively related to prey capture, suggesting that faster predators and ambush predators captured more prey (Fig. 3A-C). Predators who covered space at a faster rate captured fewer prey (Fig. 3B, [95% CI] = -0.40 [-0.42, -0.38]) (Fig. 3B). Predators who took longer to capture their first prey had a lower probability of capturing all four prey [95% CI] = -0.66 [-0.67, -0.64] (Fig. 4D). The probability of capturing all prey barely varied among game environments ( [95% CI] = 0.005 [0.002, 0.008]). Differences among individuals were low ( [95% CI] = 0.067 [0.060, 0.074]).

By adding prey behaviour, the model explained 18.1% of the variation in prey capture ( = 0.181). Predators who competed against prey that were cursorial had a significantly lower probability of capturing all prey ( [95% CI] = -0.20 [-0.22, -0.19]). Prey who were faster at covering space in the environment significantly reduced the probability of capturing all prey for the predator ( [95% CI] = -0.63 [-0.65, -0.61]). All the model parameter values are reported in Table *SX* in Supporting information.

### (ii) Quadratic relationships between predator/prey behaviour and predator hunting success

The model that included quadratic and interaction terms for predator behaviour did not significantly increase explained variance in prey capture ( = 0.149). However, we observed significant concave relationships for travel speed ( [95% CI] = -0.11 [-0.12, -0.10]) and time in ambush ( [95% CI] = -0.12 [-0.13, -0.11]) (Fig. 3E-G), suggesting that predators maximized hunting success around the behaviours’ population averages. There was a significant convex relationship between prey capture and space coverage (Fig. 2F) ( [95% CI] = 0.09 [0.08, 0.10]), and the shape of the quadratic function relating prey capture to time before the first prey is captured was almost the same as the linear function ( [95% CI] = 0.13 [0.12, 0.14]) (Fig. 3H). The probability of capturing all prey was still similar among game environments ( [95% CI] = 0.010 [0.005, 0.016]), and varied slightly among individual players ( [95% CI] = 0.072 [0.064, 0.079].

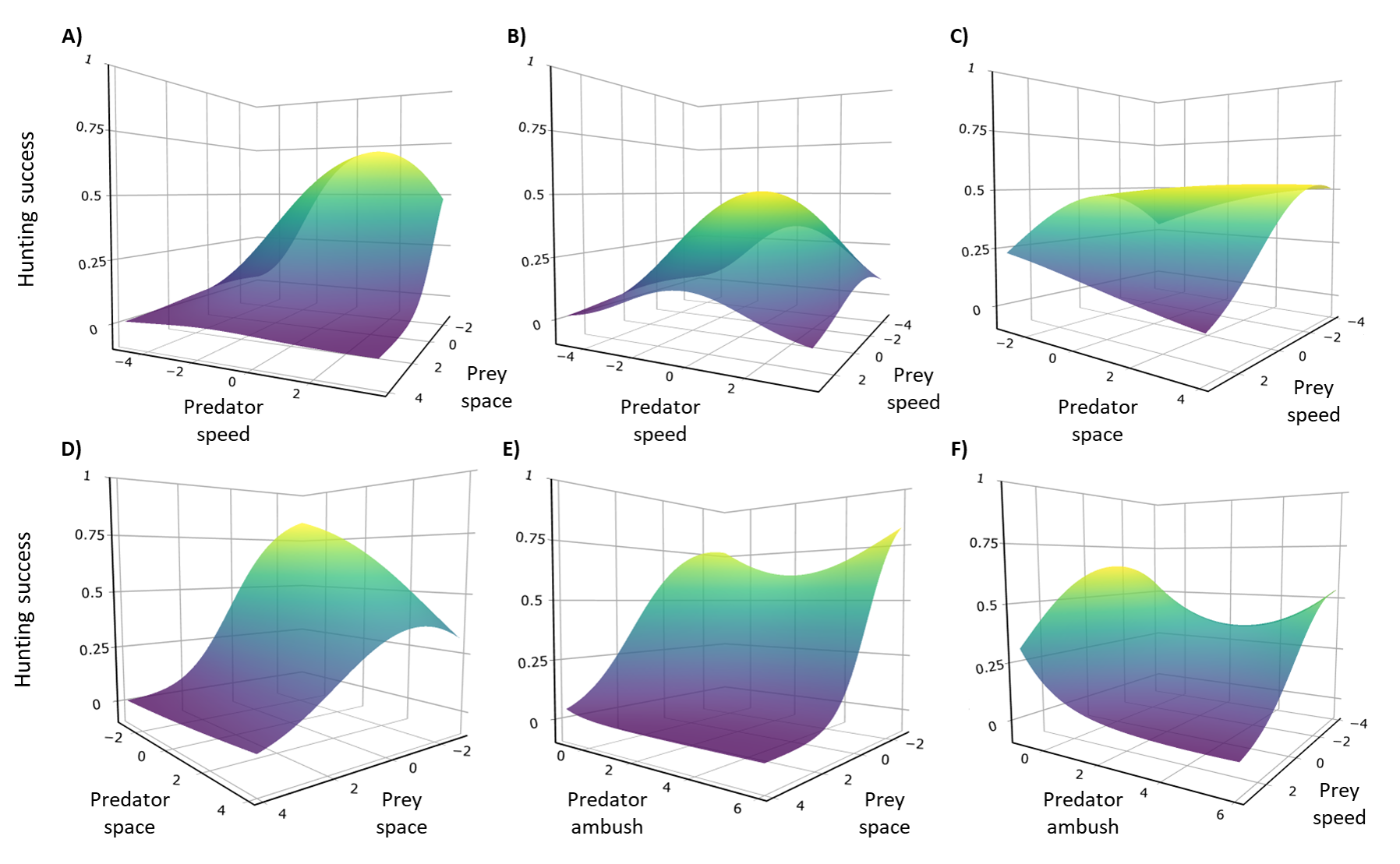
The model that included quadratic and interaction terms for predator and prey behaviour had the highest explanatory power ( = 0.212). Prey capture by predators as a function of prey speed and prey rate of space covered was described by concave relationships ( [95% CI] = -0.07 [-0.08, -0.07], [95% CI] = -0.10 [-0.11, -0.08]), thus, predators had a higher probability of capturing all prey during a match when they competed against prey who expressed average population values of these traits. All the quadratic model parameter values are reported in Table *SX* in Supporting information.



**Figure 3. Effect of predator hunting behaviour on prey capture.** Hunting success (i.e. the probability of capturing four prey) is on the y axis for all panels, and the standardised hunting behaviour 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). Both models were run on the same sample of 70 831 matches played by 2 171 players across 27 different game environments. The sample size of each parameter’s posterior distribution is 6000 for the base model, and 4000 for the quadratic model. **(A)**, **(B)**, **(B)** Linear functions. **(D)**, **(E)**, **(F)** Quadratic functions.

### (iii) Effect of the predator-prey behavioural interaction on predator hunting success

According to our predictions, faster predators were more successful when they competed against sedentary prey ( [95% CI] = -0.09 [-0.11, -0.07]) (Fig. 4A). Predators had higher hunting success for the whole range of values of space covered when they competed against slower-moving prey ( [95% CI] = -0.05 [-0.06, -0.03]) (Fig. 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 ( [95% CI] = 0.10 [0.07, 0.12]) (Fig. 4D). However, those who covered space at the fastest rate where more successful against prey that were the slowest at covering space (Fig. 4D). There were no significant interactions between predator and prey travel speed ([95% CI] = -0.01 [-0.03, 0.00]) (Fig. 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, although the interaction with prey space covered was not significant ( [95% CI] = -0.06 [-0.07, -0.04], [95% CI] = -0.01 [-0.03, 0.01]) (Fig 4E-F). All the interaction parameter values are reported in table *SX* in Supporting information.



**Figure 4. Incluence of the predator and prey behavioural interactions on predator hunting success.** The plots’ 3D surfaces show the relationship between different combinations of predator-prey behaviours 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. **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 space coverage. **F)** Predator time spent ambushing and prey travel speed.

# Discussion

Our study is the first to use an online multiplayer videogame to investigate individual variation in predator foraging mode, and how predator and prey behaviour affect hunting success. We provide evidence that individuals who incarnate the predator display individual specialisation and flexibility in competing foraging modes (cursorial vs sit-and-wait). The expression of these foraging modes was consistent with shifts in the expression of other behaviours such as space use and the latency before a first prey capture, matching the predictions of the foraging syndrome hypothesis at the individual level. Contrary to our expectations, neither hunting behaviour nor prey capture varied among the game environments. Although we found the presence of 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 of their time ambushing prey. Lastly, we indeed found evidence for the locomotor-crossover hypothesis for some predator-prey trait combinations. However, predators were generally less successful when they competed against fast traveling prey, and those who covered space in the environment.

Our analyses revealed that predators differed in their average travel speed and in their proportion of time spent ambushing prey. These behaviours were negatively correlated at the among-individual level, suggesting that individuals may specialise as either cursorial or ambush predators. Cursorial predators displayed a shorter latency before capturing their first prey compared to ambush predators who took more time as ambush time increased. These results are similar to those of McGhee et al. (2013), who found that fast moving pyke were quicker to launch their initial attack. Interestingly, hunting success decreased significantly with increasing latency before a first capture, but did not strongly interact with time spent ambushing to affect hunting success. Globally, the most succesful predators were those who moved at average population values of travel speed, while spending at least an above average of their time ambushing prey.

Since individuals reached similar hunting success across the study period, our observations suggest that ecological mechanisms may favor the coexistence of both foraging strategies within the *Dead by Daylight* predator population. Indeed, we found that cursorial predators had greater hunting success when they competed against more sedentary prey, which concords with empirical studies who tested the locomotor crossover hypothesis (Belgrad and Griffen 2016; Donihue 2016; Chang et al. 2017). However, ambush predators did not fit with its predictions as they also displayed higher success against sedentary prey, or prey that traveled around average population speed values. In addition, predators reached similar hunting success across the observed range of space coverage and time spent ambushing (Figure 4. C-F). A potential explanation is that we failed to capture other important prey strategies involved in the predator-prey interaction by focusing solely on prey speed and space coverage. Unpublished results by Santostefano et al. found four prey behavioural profiles in *DBD*, where faster and exploratory individuals were distinct from bolder individuals who performed more cooperative/altruistic actions with conspecifics, and who were involved in longer chases with the predator.

Predators also displayed flexibility in their foraging mode, where individuals switched between a cursorial or ambush strategy from one match to the other. These foraging mode switches were accompagnied by shifts in space coverage and the latency before a first capture, suggesting that predators adjusted their behaviour according to the type of prey encountered. Thus, the outcome of the predator-prey interaction might not only be determined by the individual predator’s preferred hunting mode, but also by its flexibility from one ecounter to the next (McGhee et al. 2013). Altough this falls outside the scope of this study, further analyses will need to investigate the dynamics of the predator behaviour within a match to determine if predators switch between sit-and-wait to cursorial strategies as prey density is reduced (Inoue and Marsura 1983). Mode swithing is also expected to occur within a foraging bout as predators make behavioural adjustments in response to prey antipredator behaviour (Helfman 1990), and should be favored when prey (encounters, distribution, behaviour) are unpredictable (Carneiro et al. 2017; Phillips et al. 2017). Comparing prey selection and capture rates between specialist and flexible hunters could provide important insight on the community-consequences of behavioural decisions made by predators.

An unexpected result was that predator hunting mode did not change as a function of the environment. This contrasts with studies showing that predators exploit habitat characteristics such as vegetation density to chose 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 behaviour, for instance, by altering their perception of predation risk or fear (Heithaus et al. 2009; Gaynor 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). Prey individuals in *DBD* might differ in the way they respond to these habitat changes, as some could have increased activity in heterogeneous habitats by exploiting refuges, thus, negating the effect of the environment on the predator’s hunting strategy (Savino and Stein 1989; Warfe and Barmuta 2004). This could also explain why hunting success was similar among game environments. Predators can also alter their hunting behaviour at larger scales according to prey behaviour (as we have found), but seek prey accessibility at finer scales by killing them in specific areas in a given habitat (Hopcraft et al. 2005). We will need to investigate kill sites in the environment to see if these habitat scale-dependent effects on hunting behaviour occur in *DBD*. Altogether, our observations emphasize the importance of investigating the interacting effects of environmental and individual-level factors of predators and prey to better understand trophic interactions.

We are among the first ecologists (Cere et al. accepted; Barbe et al. 2020) to propose the use of online multiplayer videogames to investigate how ecological mechanisms shape the dynamics of trophic interactions. Altough we are persuaded that videogames are poised to play a central role in testing ecological hypotheses, as they reduce financial, statistical or logistical hurdles associated with empirical research while providing complex and ecologically-relevant datasets, they are not a panacea and they come with their own biases. For instance, player behaviour may not properly reflect behavioural decisions made by real-life organisms in the wild, as the player cannot “die” and can come back to play everytime (Oultram 2013). Hence, individuals may take greater risks in the videogame compared to what a real predator would do (Lofgren and Fefferman 2007; Oultram 2013). In addition, although *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, single predator systems such has this 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 should aim to test specific ecological hypotheses when using virtual systems.

To conclude, individual variation in predator (and prey) behaviour 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). Although our study is essentially descriptive, as it is the first to investigate individual variation in foraging behaviour using the *Dead by Daylight* system, we showed that individuals differed in contrasting hunting strategies that concord with those used by wild predators. These hunting modes varied among- and within- individuals along correlated behaviours (foraging syndrome hypothesis), and our results suggest that predator-prey locomotor-crossovers may promote the coexistence of different predator and prey behavioural types. We aim to investigate in future studies how learning and small scale environmental components affect variability in hunting modes and success within the population, and test wether flexible vs specialist predators differ in their prey selection. We are confident that these studies will provide valuable ecological insight for behavioural and community ecologists.

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# Author contributions:

MFF and POM conceived the study. MFF collected the data, conducted the analyses, and led the writing of the manuscript. All authors contributed to revisions and gave their final approval for the present manuscript.

# Competing interests:

The authors declare no competing interests

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# Data availability statement:

We could not openly share the data on open science/data web platforms due to privacy restrictions. However, upon reasonable request, we can provide the data used to conduct our analyses. In addition, the project’s R scripts and results are freely available on this GitHub repository: <https://github.com/quantitative-ecologist/videogame_hunting_tactics-Rscripts>.

# References

Ahmad, M. A., C. Shen, J. Srivastava, and N. Contractor. 2014. On the Problem of Predicting Real World Characteristics from Virtual Worlds. Pages 1–18 *in* M. A. Ahmad, C. Shen, J. Srivastava, and N. Contractor, eds. Predicting Real World Behaviors from Virtual World Data, Springer Proceedings in Complexity. Springer International Publishing, Cham.

Araújo, M. S., D. I. Bolnick, and C. A. Layman. 2011. The ecological causes of individual specialisation. Ecology Letters 14:948–958.

Arthur, B., M. Hindell, M. N. Bester, W. C. Oosthuizen, M. Wege, and M.-A. Lea. 2016. South for the winter? Within-dive foraging effort reveals the trade-offs between divergent foraging strategies in a free-ranging predator. Functional Ecology 30:1623–1637.

Balicer, R. D. 2007. Modeling Infectious Diseases Dissemination Through Online Role-Playing Games. Epidemiology 18:260–261.

Barbe, L., C. Mony, and B. W. Abbott. 2020. Artificial Intelligence Accidentally Learned Ecology through Video Games. Trends in Ecology & Evolution 35:557–560.

Belgrad, B. A., and B. D. Griffen. 2016. Predator–prey interactions mediated by prey personality and predator hunting mode. Proceedings of the Royal Society B: Biological Sciences 283:20160408.

Bowen, W. D., D. Tully, D. J. Boness, B. M. Bulheier, and G. J. Marshall. 2002. Prey-dependent foraging tactics and prey profitability in a marine mammal. Marine Ecology Progress Series 244:235–245.

Brodie, E. D., A. J. Moore, and F. J. Janzen. 1995. Visualizing and quantifying natural selection. Trends in Ecology & Evolution 10:313–318.

Butler, M. A. 2005. Foraging mode of the chameleon, Bradypodion pumilum: A challenge to the sit-and-wait versus active forager paradigm? Biological Journal of the Linnean Society 84:797–808.

Bürkner, P.-C. 2017. Brms: An R Package for Bayesian Multilevel Models Using Stan. Journal of Statistical Software 80:1–28.

Carneiro, A. P. B., A.-S. Bonnet-Lebrun, A. Manica, I. J. Staniland, and R. A. Phillips. 2017. Methods for detecting and quantifying individual specialisation in movement and foraging strategies of marine predators. Marine Ecology Progress Series 578:151–166.

Carter, A. J., W. E. Feeney, H. H. Marshall, G. Cowlishaw, and R. Heinsohn. 2013. Animal personality: What are behavioural ecologists measuring? Biological Reviews 88:465–475.

Chang, C.-c., H. Y. Teo, Y. Norma-Rashid, and D. Li. 2017. Predator personality and prey behavioural predictability jointly determine foraging performance. Scientific Reports 7:40734.

Cooper, W. E. 2005. The foraging mode controversy: Both continuous variation and clustering of foraging movements occur. Journal of Zoology 267:179–190.

Courbin, N., A. Besnard, C. Péron, C. Saraux, J. Fort, S. Perret, J. Tornos, et al. 2018. Short-term prey field lability constrains individual specialisation in resource selection and foraging site fidelity in a marine predator. Ecology Letters 21:1043–1054.

Dall, S. R. X., and S. C. Griffith. 2014. An empiricist guide to animal personality variation in ecology and evolution. Front. Ecol. Evol. 2:3.

Dingemanse, N. J., and N. A. Dochtermann. 2013. Quantifying individual variation in behaviour: Mixed-effect modelling approaches. Journal of Animal Ecology 82:39–54.

Dingemanse, N. J., and J. Wright. 2020. Criteria for acceptable studies of animal personality and behavioural syndromes. Ethology 126:865–869.

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

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

Gerritsen, J., and J. Strickler. 1977. Encounter probabilities and community structure in zooplankton: A mathematical model. Journal of the Fisheries Board of Canada 34.

Glaudas, X., K. L. Glennon, M. Martins, L. Luiselli, S. Fearn, D. F. Trembath, D. Jelić, et al. 2019. Foraging mode, relative prey size and diet breadth: A phylogenetically explicit analysis of snake feeding ecology. Journal of Animal Ecology 88:757–767.

Griffen, B. D., B. J. Toscano, and J. Gatto. 2012. The role of individual behavior type in mediating indirect interactions. Ecology 93:1935–1943.

Harrison, X. A. 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, M. R., L. M. Dill, and J. J. Kiszka. 2018. Feeding strategies and tactics. Pages 354–363 *in* B. Würsig, J. G. M. Thewissen, and K. M. Kovacs, eds. Encyclopedia of Marine Mammals (Third Edition). Academic Press.

Heithaus, M. R., A. J. Wirsing, D. Burkholder, J. Thomson, and L. M. Dill. 2009. Towards a predictive framework for predator risk effects: The interaction of landscape features and prey escape tactics. Journal of Animal Ecology 78:556–562.

Helfman, G. S. 1990. Mode selection and mode switching in foraging animals. Pages 249–298 *in* P. J. B. Slater, J. S. Rosenblatt, and C. Beer, eds. Advances in the Study of Behavior (Vol. 19). Academic Press.

Hertel, A. G., P. T. Niemelä, N. J. Dingemanse, and T. Mueller. 2020. A guide for studying among-individual behavioral variation from movement data in the wild. Movement Ecology 8.

Hopcraft, J. G. C., A. R. E. Sinclair, and C. Packer. 2005. Planning for success: Serengeti lions seek prey accessibility rather than abundance. Journal of Animal Ecology 74:559–566.

Huey, R. B., and E. R. Pianka. 1981. Ecological consequences of foraging mode. Ecology 62:991–999.

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

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

Kersch‐Becker, M. F., B. B. Grisolia, M. J. O. Campos, and G. Q. Romero. 2018. Community-wide responses to predation risk: Effects of predator hunting mode on herbivores, pollinators, and parasitoids. Ecological Entomology 43:846–849.

Kobler, A., T. Klefoth, T. Mehner, and R. Arlinghaus. 2009. Coexistence of behavioural types in an aquatic top predator: A response to resource limitation? Oecologia 161:837–847.

Laurel, B. J., and J. A. Brown. 2006. Influence of cruising and ambush predators on 3-dimensional habitat use in age 0 juvenile Atlantic cod Gadus morhua. Journal of Experimental Marine Biology and Ecology 329:34–46.

Lima, S. L. 2002. Putting predators back into behavioral predator–prey interactions. Trends in Ecology & Evolution 17:70–75.

Lofgren, E. T., and N. H. Fefferman. 2007. The untapped potential of virtual game worlds to shed light on real world epidemics. The Lancet Infectious Diseases 7:625–629.

McCoy, E. D., and S. S. Bell. 1991. Habitat structure: The evolution and diversification of a complex topic. Pages 3–27 *in* S. S. Bell, E. D. McCoy, and H. R. Mushinsky, eds. Habitat Structure: The physical arrangement of objects in space, Population and Community Biology Series. Springer Netherlands, Dordrecht.

McGhee, K. E., L. M. Pintor, and A. M. Bell. 2013. Reciprocal behavioral plasticity and behavioral types during predator-prey interactions. The American Naturalist 182:704–717.

McLaughlin, R. L. 1989. Search modes of birds and lizards: Evidence for alternative movement patterns. The American Naturalist 133:654–670.

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

Miles, D. B., J. B. Losos, and D. J. Irschick. 2007. Morphology, performance, and foraging mode. Pages 49–93 *in* D. B. Miles, L. B. McBrayer, and S. M. Reilly, eds. Lizard Ecology. Cambridge University Press, Cambridge.

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

Moran, N. P., B. B. M. Wong, and R. M. Thompson. 2017. Weaving animal temperament into food webs: Implications for biodiversity. Oikos 126:917–930.

Nakagawa, S., and I. C. Cuthill. 2007. Effect size, confidence interval and statistical significance: A practical guide for biologists. Biological Reviews 82:591–605.

Nakagawa, S., P. C. D. Johnson, and H. Schielzeth. 2017. The coefficient of determination R2 and intra-class correlation coefficient from generalized linear mixed-effects models revisited and expanded. Journal of The Royal Society Interface 14:20170213.

Nakagawa, S., and H. Schielzeth. 2010. Repeatability for Gaussian and non-Gaussian data: A practical guide for biologists. Biological Reviews 85:935–956.

Niemelä, P. T., and N. J. Dingemanse. 2014. Artificial environments and the study of “adaptive” personalities. Trends in Ecology & Evolution 29:245–247.

Oultram, S. 2013. Virtual plagues and real-world pandemics: Reflecting on the potential for online computer role-playing games to inform real world epidemic research. Medical Humanities 39:115–118.

Perry, G. 1999. The evolution of search modes: Ecological versus phylogenetic perspectives. The American Naturalist 153:98–109.

Perry, G., Y. L. Werner, I. Lampl, D. Rothenstein, N. Sivan, A. Lerner, and E. Shani. 1990. Foraging mode in lacertid lizards: Variation and correlates. Amphibia-Reptilia 11:373–384.

Pettorelli, N., A. Hilborn, C. Duncan, and S. M. Durant. 2015. Chapter Two - Individual variability: The missing component to our understanding of predator–prey interactions. Pages 19–44 *in* S. Pawar, G. Woodward, and A. I. Dell, eds. Advances in Ecological Research, Trait-Based Ecology - From Structure to Function (Vol. 52). Academic Press.

Phillips, R. A., S. Lewis, J. González-Solís, and F. Daunt. 2017. Causes and consequences of individual variability and specialization in foraging and migration strategies of seabirds. Marine Ecology Progress Series 578:117–150.

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

Robinson, S. K., and R. T. Holmes. 1982. Foraging behavior of forest birds: The relationships among search tactics, diet, and habitat structure. Ecology 63:1918–1931.

Romero, G. Q., and J. Koricheva. 2011. Contrasting cascade effects of carnivores on plant fitness: A meta-analysis. Journal of Animal Ecology 80:696–704.

Ross, T. L., E. Castronova, and I. Knowles. 2015. Virtual Worlds as Laboratories. Pages 1–15 *in*Emerging Trends in the Social and Behavioral Sciences. American Cancer Society.

Sargeant, B. L., A. J. Wirsing, M. R. Heithaus, and J. Mann. 2007. Can environmental heterogeneity explain individual foraging variation in wild bottlenose dolphins (Tursiops sp.)? Behav Ecol Sociobiol 61:679–688.

Savino, J. F., and R. A. Stein. 1989. Behavioural interactions between fish predators and their prey: Effects of plant density. Animal Behaviour 37:311–321.

Scharf, I., E. Nulman, O. Ovadia, and A. Bouskila. 2006. Efficiency evaluation of two competing foraging modes under different conditions. The American Naturalist 168:350–357.

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

Schmitz, O. J. 2008. Effects of predator hunting mode on grassland ecosystem function. Science 319:952–954.

Smith, B. R., and D. T. Blumstein. 2010. Behavioral types as predictors of survival in Trinidadian guppies (Poecilia reticulata). Behavioral Ecology 21:919–926.

Tinker, M. T., G. Bentall, and J. A. Estes. 2008. Food limitation leads to behavioral diversification and dietary specialization in sea otters. PNAS 105:560–565.

Toscano, B. J., N. J. Gownaris, S. M. Heerhartz, and C. J. Monaco. 2016. Personality, foraging behavior and specialization: Integrating behavioral and food web ecology at the individual level. Oecologia 182:55–69.

Toscano, B. J., and B. D. Griffen. 2014. Trait-mediated functional responses: Predator behavioural type mediates prey consumption. Journal of Animal Ecology 83:1469–1477.

Warfe, D. M., and L. A. Barmuta. 2004. Habitat structural complexity mediates the foraging success of multiple predator species. Oecologia 141:171–178.

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

Wignall, A. E., and P. W. Taylor. 2008. Alternative predatory tactics of an araneophagic assassin bug (Stenolemus bituberus). acta ethol 12:23.

Wolf, M., and F. J. Weissing. 2012. Animal personalities: Consequences for ecology and evolution. Trends in Ecology & Evolution 27:452–461.