

**Hunting experience and prey behaviour jointly shape  
individual foraging specialization in a predator-prey  
videogame**

5    **ABSTRACT**

6    Keywords: foraging behaviour, individual specialization, experience, learning, prey predictability, online  
7    videogames

8

## 9 INTRODUCTION

10 Individual variation in predator foraging behaviour is increasingly recognized as a major driver of trophic  
11 interactions and community dynamics (Griffen *et al.* 2012; Michalko & Pekár 2016; Moran *et al.* 2017;  
12 Michalko *et al.* 2021). Indeed, predator populations often comprise assemblages of individuals  
13 specializing in different foraging strategies or resources irrespective of sexual, morphological, or age-  
14 related differences (Estes *et al.* 2003; Tinker *et al.* 2008; Kernaléguen *et al.* 2015; Phillips *et al.* 2017). A  
15 growing body of evidence suggests that ecological interactions, such as predator-prey interactions, can be  
16 major drivers of such individual foraging specialization (Araújo *et al.* 2011; Toscano *et al.* 2016). When  
17 they hunt, predators often use techniques that are fine-tuned to the type of prey that they encounter  
18 (Davoren *et al.* 2003; Estes *et al.* 2003; Woo *et al.* 2008; Courbin *et al.* 2018), and their capacity to use  
19 them effectively is contingent on periods of extensive practice (i.e. experience). While hunting experience  
20 may be essential to maintain or improve foraging success, we have limited empirical assessments of its  
21 role in predator foraging specialization (Dukas 2019), nor its consequences on predator-prey interactions.

22 The integration of individual behavioural variation in the study of predator-prey interactions has gained  
23 traction in recent years, with empirical studies revealing important consequences for habitat use,  
24 functional responses, prey choice, and foraging rate (Kobler *et al.* 2009; Patrick & Weimerskirch 2014b;  
25 Toscano & Griffen 2014; Matsumura & Miyatake 2022). However, an important and recurring challenge  
26 impeding research on predator-prey behavioural interactions, at the individual level, is the need to collect  
27 data simultaneously on both the predator and prey. We recently demonstrated with behavioural data from  
28 an online predator-prey videogame that virtual systems can overcome this challenge and help uncovering  
29 the mechanisms that shape predator-prey interactions (Fraser Franco *et al.* 2022). For instance, we found  
30 that the classical locomotor crossover hypothesis (Huey & Pianka 1981) applied only for cursorial hunters  
31 (see also: Matsumura & Miyatake 2022), suggesting that virtual systems could be useful in identifying  
32 general ecological patterns, which might in turn help to advance the current gaps in predator-prey  
33 research. Other studies on virtual predator-prey systems show that predation regimes can drive individual

variation in risk perception (Beauchamp 2020), that familiarity between prey has a positive indirect effect on survival (Céré *et al.* 2021), and that prey face contrasting natural and social selection regimes (Santostefano *et al.* in prep). Because virtual predator-prey systems generate large volumes of data on interacting players throughout their lifetime in the game, they offer the opportunity to tackle fundamental questions about the role of experience and prey behaviour on individual predator foraging specialization along with its potential fitness consequences.

The development of foraging strategies is crucial for young predators to reach adulthood and survive (Phillips *et al.* 2017; Heithaus *et al.* 2018). Theory predicts that foraging specialization may emerge via learning, limitations in memorizing multiple complex hunting skills, and expertise (Tinker *et al.* 2009; Dukas 2019). Dukas (2019) defines expertise as the characteristics, skills, and knowledge allowing individuals with extensive experience to outperform novices on complex tasks. This body of work suggests that the development of expertise is an optimizing process that promotes foraging specialization. Empirical studies on human and non-human hunters show that experience optimizes the efficiency (e.g. search and handling times, return rates) of their foraging tactics potentially via associative images or reliance on prey and environmental cues (Edwards & Jackson 1994; Morse 2000; MacDonald 2007; Reid *et al.* 2010; Wilson-Rankin 2015). Such optimization may thus reinforce the use of the same tactic (i.e. specialization) if its success is constant each time a prey is encountered. It may also be costly to attempt different hunting tactics by trial and error when prey are scarce or highly unpredictable (Dukas 1998; Estes *et al.* 2003; Mery & Burns 2010). An alternative mechanism is that the costs/risks faced by hunters when switching foraging tactics may be offset by gaining experience and information on their prey, leading to increased individual foraging flexibility (Ishii & Shimada 2010; Mery & Burns 2010; Snell-Rood 2013). To develop proper responses to fluctuating resources, individuals would need to sample their environment broadly during an extensive period of time, followed by higher performance at later stages of development (reviewed in Snell-Rood 2013).

There is currently a lack of consensus on the fitness advantages of specialized vs flexible foraging (REFERENCES). Importantly, we have limited information on the ecological contexts - except for competition - that favour one strategy over the other. This is reflected in the literature showing contrasting results in the links between specialization and fitness. For instance, some studies report increasing benefits of specialization (Patrick & Weimerskirch 2014a; van den Bosch *et al.* 2019), some report that flexible foraging has greater benefits (Paull *et al.* 2012; Manlick *et al.* 2021), and others find equal benefits depending on timescales (Woo *et al.* 2008; Potier *et al.* 2015). While quantifying the fitness consequences of specialization is a daunting task, in predator-prey systems, some clues indicate that fluctuations in the predictability of prey encounters throughout a predator's lifetime may be a key factor (Weimerskirch 2007; Woo *et al.* 2008; Chang *et al.* 2017; Phillips *et al.* 2017; Courbin *et al.* 2018). The resource-predictability hypothesis argues that when resources are predictable, individual specialists should have higher delivery rates by reducing the energy and time required to search for and handle prey. In contrast, individual generalists should benefit when resources fluctuate, as fine adjustments to resources are key for a predator's success and survival (Karkarey *et al.* 2017; Holm *et al.* 2019; Santoro *et al.* 2019). This hypothesis has, however, not been tested in systems where behavioural interactions are simultaneously monitored between predator and prey individuals. Thus, uncovering the mechanisms shaping direct predator-prey interactions would enable researchers to better predict the behavioural decisions of predators when they are hunting.

In this study, we analyze individual behavioural data from players in *Dead by Daylight (DBD)* to test how hunting experience and prey behaviour shape predator foraging specialization. *DBD* is an online videogame simulating a predator-prey interaction, where one predator player hunts four prey players in different virtual environments. The data grants a high degree of precision on the behavioural interaction as the behaviour of both the predator and the four prey is monitored simultaneously in each trial. First, we investigate how predators develop their individual hunting expertise. We hypothesize that predators should differ in the development of their expertise because they encounter varying levels of difficulty with

the prey that they pursue. For example, a predator may face more difficulty than other individuals if it encountered prey that were more elusive. Second, we test the hypothesis that individual variation in foraging behaviour will change with experience. If experience reduces the costs of switching between hunting tactics, we predict that individual predators should become more flexible with time. Alternatively, if experience enables the refinement of the hunting tactics, then individuals may instead specialize. Third, we evaluate how predator foraging specialization interacts with variation in prey behaviour. Whether predators specialize or not with experience may depend on the behaviour of their prey, for instance, as it may be harder to specialize when encounters are less predictable. Lastly, if individuals differ in their degree of foraging specialization, then we expect specialized hunters to fare better when prey variability is lower, while flexible hunters should fare better when prey variability is higher.

## MATERIALS AND METHODS

### Study system

*DBD* is a survival asymmetric multiplayer online game developed by Behaviour Interactive Inc. In this game, players can play as a predator or a prey. The objective of the predator is to hunt and capture the four prey across a virtual environment. The objective of the four prey is to forage for resources while avoiding the predator. The resources are in the form of power generators that, once they are all activated, will enable the prey to escape through one of two exit doors. The composition of the predator and prey group for a match is determined by a skill-based matchmaking algorithm. A match ends when the predator kills all the prey available (i.e. that have not escaped), or when the last remaining prey escapes the virtual environment. Each player, predator or prey, can choose an avatar with abilities that encourage specific play styles (e.g. bold vs cautious prey, or ambush vs roaming predator). During our study period, the game offered 23 predator avatars. The virtual environment where matches take place is composed of fixed and procedurally generated habitat components, such as vegetation, mazes, and buildings. Some of these environments are larger than others, with varying structural complexity. However, we have previously shown that predators display only minimal changes in behaviour and hunting success across the environments, probably due to a game feature enabling predators to have visual cues of the generators (Fraser Franco *et al.* 2022). There were 35 virtual game environments available for play during our study period.

In *DBD*, some individual predators specialize on hunting at high speeds and covering space in the environment, while others prefer to stalk and ambush their prey (Fraser Franco *et al.* 2022). Individuals are also flexible in the use of these tactics by switching between them across matches. The expression of these tactics and their success is also shaped by the behaviour of the prey group. The prey need to forage for resources while paying attention to the predator to avoid being detected and chased. Some prey contribute to the group's success by healing or helping others escape the predator, while others play alone and attempt to escape by themselves (Céré *et al.* 2021). Predators must be wary of how the prey behave to

choose the right way to capture them. Thus, *DBD* simulates a highly dynamic system where both predators and prey must constantly adjust to each other to be successful.

## Data collection

The videogame company provided data that spanned a period of 6 months of gameplay recorded for every player. The first recorded match was played on 2020-12-01, and the last one on 2021-06-01. We cleaned and filtered the raw data to produce a dataset appropriate for our analyses. We analyzed only matches where players did not know each other (i.e. “Online” mode). We filtered any matches where players were inactive, such as when speed values were equal to, or very close to, zero. Moreover, we used our knowledge of the game to remove any matches where players were potentially hacking, or not playing the game as it is supposed to be played. We then partitioned the player population by total experience, and sampled players that played 300 matches or more. To optimize the representation of gameplay experience at advanced levels, we set the maximum number of matches at 500 for these players. For instance, there could be a large difference in gameplay between 300-500 and 500-1000 matches. Players that played above 500 matches represented ~2% of the population.

Our population consists of 253 predator players with a total record of 100 412 matches. The predator-players’ experience varied between 301 and 500 matches played. These matches lasted between 3 and 70 minutes (mean = 11 minutes). The following information is collected and reported for every match : the player’s anonymous ID, its avatar, the game environment, the predator-player’s experience along with its speed, and the average speed of the group of prey it encountered.

## Variables

We analyzed the predator’s average speed and the average speed of the prey encountered by the predator. The predator’s average speed is measured as the average distance traveled per second during a match ( $\bar{x} = 3.31 \pm 0.49$ ). We measured the preys’ average speed as the average travel speed of the four individual prey within a match ( $\bar{x} = 2.40 \pm 0.32$ ). We defined hunting success as the number of prey consumed during the



match (min = 0, max = 4). Lastly, we defined the predator's cumulative experience as the number of matches played prior to the match being monitored. For example, the first match of a player would have a cumulative experience value of 0, while the tenth match would have a value of 9.

## **Statistical analyses**

### **Software and computer specifications**

All our statistical analyses were executed on Cedar (<https://docs.alliancecan.ca/wiki/Cedar>), a computer cluster maintained by the Digital Research Alliance of Canada. The operating system for Cedar is CentOS Linux 7. The models were fitted in R (version 4.1.2) using Markov chain Monte Carlo sampling with the package "brms" version 2.16.3 (Bürkner 2017), and "cmdstanr" version 0.4.0 (Gabry & Češnovar 2021) as the backend for estimation (cmdstan installation version 2.28.2).

### **Effect of experience on hunting success**

We tested whether predators varied in the development of their expertise using three Bayesian generalized additive mixed models (GAMM) with thin plate regression splines. These models estimate the relationship between hunting success (i.e. number of prey captured) and the predators' cumulative experience (i.e. number of matches played before the current match). We parametrized the models following the method of Pedersen *et al.* (2019). The first model was the simplest, with a common global smoothing function for all observations and random intercepts for the predator ID. In this model, we assume that individuals have the same development of expertise, with the model estimating a trend for the average individual (i.e. global smoother). For the second model, we included varying group-level smoothers for the predator ID. In this model, we assume that individuals share a similar relationship between success and experience, but that this relationship can vary (e.g. individual 1 has a steeper curve than individual 2). This enabled us to test whether predators differed in the development of their expertise. In the third model, we kept the group-level smoothers for the predators, but removed the global smoother. This allows each individual to have a unique relationship between success and experience without penalization by the

global smoother. Thus, this model assumes that predators do not share a common relationship between success and experience. We included match duration as a covariate in all three models.

Because a maximum of four prey can be captured in the game, and to control for overdispersion, we computed the three models using a modified version of the beta-binomial distribution implemented in “brms”. Thus, hunting success was estimated as the probability of capturing the four prey ( $\mu_i$ ), drawn from a Beta distribution ( $Beta(\mu_i, \phi)$ ) with mean ( $\mu \in [0,1]$ ) and precision ( $\phi > 0$ ) parameters. We used a logit link function to estimate  $\mu_i$  where  $\mu_i = \frac{\exp(\eta_i)}{\exp(\eta_i)+1}$  and  $\eta_i$  is the linear predictor, while the precision parameter ( $\phi$ ) was estimated with an identity link for all models.

We used the default number of basis functions (K) in “brms” for the models to estimate the relationship between hunting success and experience. We assumed that the random intercepts for the predator ID ( $id$ ) followed a Gaussian distribution with estimated variance ( $id \sim N(0, I \sigma_{id}^2)$ ). We estimated the parameters in all models using four MCMC chains with 1000 posterior samples for each parameter. To do so, we ran 2500 iterations for the first model with a thinning set to eight, and 1500 iterations with a thinning set to four for the second and third models; burn-in was set to 500 iterations in each model. We provide a description of how we specified the priors for each model in the supporting information. After fitting the three models, we proceeded to select the one with the best predictive accuracy using approximate leave-one-out cross-validation with Pareto-smoothed importance sampling (Piironen & Vehtari 2017; Vehtari *et al.* 2017; Vehtari *et al.* 2022).

### **Foraging behaviour and success, prey behaviour, and their relationships, at each level of experience**

We tested whether foraging behaviour changed with experience, and compared the success of generalists vs specialists, using a multivariate, double-hierarchical generalized linear model (MDHGLM) (Lee & Nelder 2006; Westneat *et al.* 2014; Cleasby *et al.* 2015; Mitchell *et al.* 2016; O’Dea *et al.* 2022). We categorized the predators by their experience based on the number of matches they played (i.e. their

cumulative experience). We assigned the status of “novice” to any predator-player that had a cumulative experience below 100 matches. For example, a predator player that played 500 matches in total would be labelled as a novice in its first 100 matches. Following this logic, we labelled predators as “intermediate” hunters when they had a cumulative experience between 100 and 299 and matches. For the third and last group, we defined predators as “advanced” hunters when they had a cumulative experience equal or above 300, with a maximum of 499 cumulated matches.

For each level of experience (i.e. novice, intermediate, advanced), we estimated the mean speed of individual predators, and a heterogeneous structure of the residuals such that we could estimate their intra-individual variation (IIV) in speed (i.e. specialization/flexibility). We followed the same structure for the preys’ speed to estimate among individual differences in the mean and variance in speed of the prey encountered by predators. For hunting success, we only modeled the mean part of the equation to estimate among individual differences in mean hunting success. For the predator and the prey’s speed, we controlled for the average rank of the prey that they encountered. The ranking system in *DBD* was implemented by the company to pair players in a match based on their skill (<https://deadbydaylight.fandom.com/wiki/Rank>). We used the mean rank of the four prey and applied a square-root transformation. For the predator’s hunting success, we controlled for the square-root of the duration of the match. The model has the following form, with each equation repeated three times (i.e. one for each level of experience) :

$$\begin{aligned} speed_{pred} &= X_m b_m + M env_m + N av_m + Z id_m + e \\ \log(\sigma_{e,pred}^2) &= X_d + Z id_d \end{aligned} \quad (1)$$

$$\begin{aligned} speed_{prey} &= X_m b_m + M env_m + N av_m + Z id_m + e \\ \log(\sigma_{e,prey}^2) &= X_d + Z id_d \end{aligned} \quad (2)$$

$$success_{pred} = X_m b_m + Z id_m + e \quad (3)$$

212 where  $env$ ,  $av$ , and  $id$  are the vectors of random environment, random avatar, and random individual  
 213 identity effects associated with their incidence matrices  $M$ ,  $N$ , and  $Z$ .  $b$  is the vector of fixed effects with  
 214 its incidence matrix  $X$ . The  $m$  and  $d$  subscripts indicate that an estimate is from the mean or dispersion  
 215 part of the model, respectively. We assumed that all random effects followed a Gaussian distribution with  
 216 estimated variance ( $env \sim N(0, I \sigma_{env}^2)$ ,  $av \sim N(0, I \sigma_{av}^2)$ , and  $id \sim N(0, I \sigma_{id}^2)$ ). The variance  
 217 parameters  $\sigma_{env}^2$ ,  $\sigma_{av}^2$ , and  $\sigma_{id}^2$ , correspond to the among environment, among avatar, and among  
 218 individual variances, respectively.  $I$  is the identity matrix, with  $I\sigma^2$  indicating that the random effects are  
 219 independently and identically distributed. Here, we assume that the residuals vary among individuals  
 220 where  $e \sim N(0, Diag[\sigma_e^2])$ ,  $\begin{bmatrix} id_m \\ id_v \end{bmatrix} \sim N\left(\begin{pmatrix} 0 \\ 0 \end{pmatrix}, \Sigma_{id} \otimes I\right)$ , and  $\Sigma_{id}$  is a variance covariance matrix of the  
 221 individual identity random effect. Equations (1) and (2) were parametrized with a Gaussian distribution  
 222 family (predator and prey speed), while equation (3) was parametrized with a beta-binomial distribution  
 223 family (predator hunting success). We parametrized the model to run four MCMC chains with 1000  
 224 posterior samples for each parameter. To do so, we ran 2500 iterations with a thinning set to 8, with the  
 225 first 500 iterations used as warmups. We explain how we specified the priors of the MDHGLM in the  
 226 supporting information.

227 We estimated the correlation between the individual random effect on the mean and on the dispersion  
 228 within each trait (e.g.  $cor(\sigma_{id_m pred}^2 \sigma_{id_d pred}^2)$ ) and among each trait (e.g.  $cor(\sigma_{id_m pred}^2 \sigma_{id_d prey}^2)$ )  
 229 within a level of experience. In the first case, this allows us to assess, for example, whether predators that  
 230 are on average slower/faster are more specialized or flexible. In the second case, the correlations enables  
 231 us to estimate, for example, whether predators that encountered prey that were faster/slower adopted a  
 232 slower/faster (or more specialized/flexible) strategy, or if slower/faster predators had lower/greater  
 233 hunting success. We also evaluated these correlations among the different levels of experience  
 234 (e.g.  $cor(\sigma_{id_m pred novice}^2 \sigma_{id_d pred intermediate}^2)$ ). The latter ‘‘character-state’’ approach (Via & Lande

1985; Via *et al.* 1995), enables us to investigate whether predators express similar behaviours across each developmental stage. The correlations were estimated assuming a multivariate Gaussian distribution.

Lastly we calculated the intra-class correlation coefficients (*ICC*, i.e. repeatability) of each random effect on the mean part of the predator's speed and prey speed to estimate the percentage of variation in speed attributed to differences among environments, avatars, and individuals. We also report the coefficient of variation in the mean (termed  $CV_I$ ) and dispersion (termed  $CV_p$ ) part of the predator and prey's speed, at each stage of experience, to report standardized effect sizes of individual variance for comparison across traits and studies (Cleasby *et al.* 2015; Holtmann *et al.* 2017; Dingemanse *et al.* 2022). This also allowed us to evaluate whether predators displayed increasing/decreasing differences in specialization at each stage of experience.

## RESULTS

### Effect of experience on hunting success

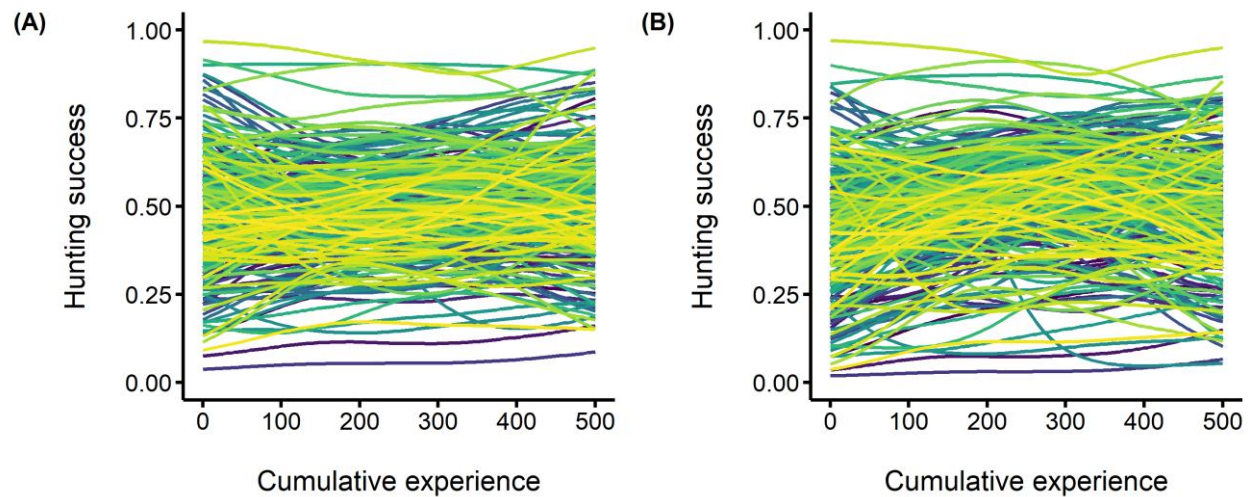
Our results confirm that individual predators displayed important differences in the development of their expertise, as the best model was the one with group-level smoothers exclusively (Table I). For instance, with experience, some predators steadily increased their hunting success while others displayed a decrease in prey capture (Figure 1A-S1A-S1B). Otherwise, there were players that maintained either a high or low success across their experience (Figure 1A). Another pattern that emerged was that some individuals optimized their success at an experience level that was below what we considered as “advanced” (i.e. >300 matches played).

**Table 1:** Leave-one-out cross-validation table of the three hierarchical GAMMs relating hunting success to player experience.

model	elpd difference	sd difference	elpd loo value	elpd loo standard error
Group-level smoothers only	0.00	0.00	-146 338.37	166.96
Global smoother + group-level smoothers	-101.47	6.28	-146 439.84	167.21
Global smoother only	-840.42	42.67	-147 178.79	163.31

\* 'elpd' refers to the 'expected log pointwise density' and is the value chosen to select the best model

We predicted that the relationship between hunting success and experience would differ among predators because they should encounter different prey. However, after controlling for prey speed, we did not find evidence confirming our hypothesis, such that differences among predators in the relationship between hunting success and experience remained mostly the same (Figure 1B).



**Figure 1.** Among individual differences in the development of hunting expertise. The predators' hunting success (i.e. the probability of capturing the four prey) is on the y axis, and the predators' cumulative experience (i.e. the number of matches played prior to each observation) is on the x axis. Each fitted curve represents an individual predator. (A) A generalized additive mixed model where we do not control for prey speed (B) A generalized additive model where we control for prey speed.

## Effect of experience on the development of behavioural specialization

We detected among individual differences in the average movement speed of predators (*ICC predator ID*, Table 2). These differences decreased at the intermediate stage, and increased at the advanced stage (Table 2). Among-individual differences in mean predator speed was slightly higher at the advanced stage compared to the novice stage (Table 2). However, the highest amount of variation in mean predator speed was due to differences among predator avatars, and differences increased with experience (*ICC avatar ID*, Table 2). We did not detect variation in mean predator speed among the virtual environments (*ICC environment ID*, Table 2). Individual predators displayed considerable differences in their degree of specialization, and these differences increased with experience (*CV<sub>p</sub> predator ID*, Table 2). Thus, the predator population is composed of individual specialists and generalists in their movement speed, and individuals further distinguish themselves in these strategies as they gain experience (Figure 2).

We predicted that, with experience, predators would become either increasingly flexible, or, more specialized. Our results do not support our prediction, as the pattern was more complex. Indeed, we found

280 that predators became more flexible with experience at the intermediate stage, but when they became  
281 advanced hunters, they returned to a level of flexibility similar to when they were novices (*Intercept*,  
282 Table 2, Figure 2). Thus, instead of increasing linearly, our results suggest that behavioural specialization  
283 changed in a nonlinear (quadratic) manner with experience.

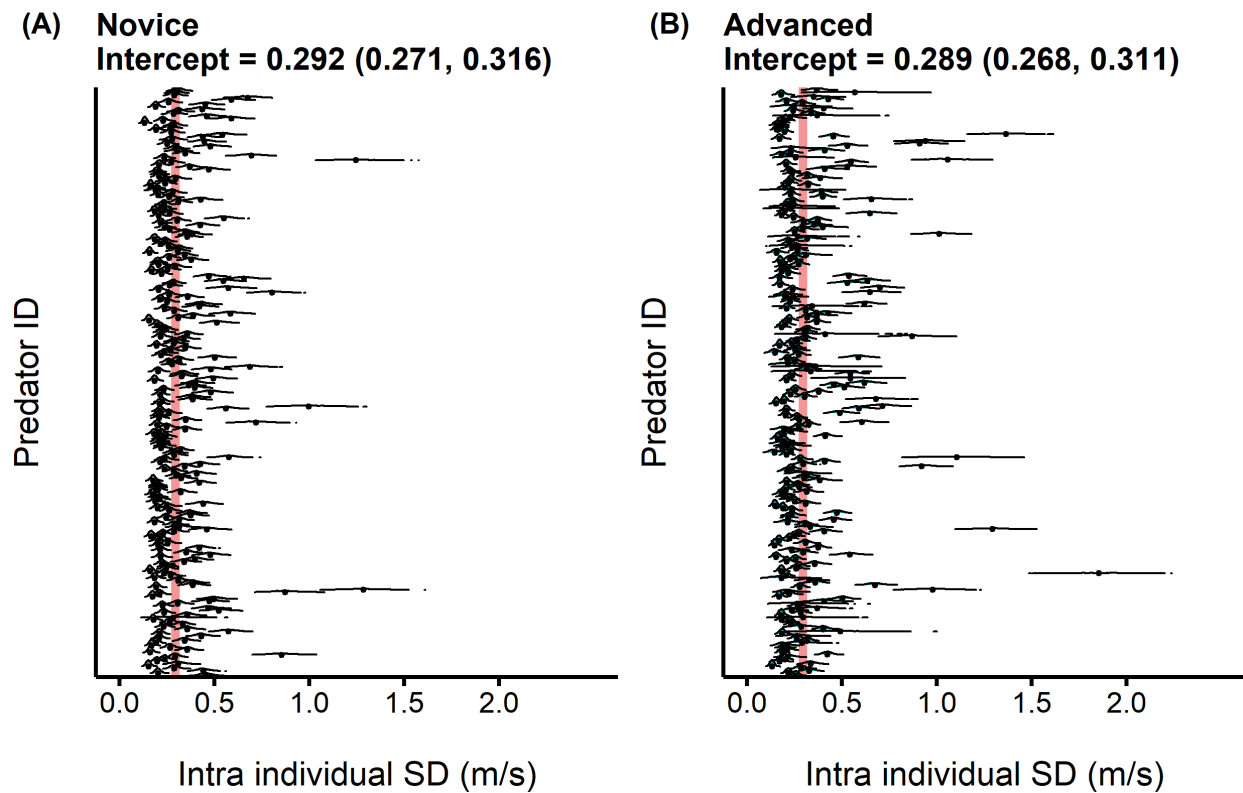


284 **Table 2:** Posterior mean estimates and 95% credible intervals computed by the multivariate double-  
285 hierarchical generalized linear model of predator speed, prey speed, and predator hunting success.

Trait	Parameter	Novice	Intermediate	Advanced
<i>Fixed effects</i>				
mu predator speed	Intercept	3.392 ( 3.283, 3.511)	3.387 ( 3.231, 3.559)	3.388 ( 3.242, 3.546)
mu predator speed	Mean prey rank	-0.030 (-0.036, -0.024)	-0.037 (-0.042, -0.033)	-0.045 (-0.052, -0.039)
mu prey speed	Intercept	2.948 ( 2.909, 2.986)	2.899 ( 2.864, 2.933)	2.837 ( 2.799, 2.873)
mu prey speed	Mean prey rank	-0.181 (-0.188, -0.174)	-0.171 (-0.176, -0.166)	-0.163 (-0.169, -0.156)
mu success	Intercept	0.018 ( 0.015, 0.021)	0.017 ( 0.015, 0.019)	0.018 ( 0.016, 0.021)
mu success	Match duration	0.539 ( 0.537, 0.540)	0.540 ( 0.539, 0.541)	0.540 ( 0.538, 0.541)
sigma predator speed	Intercept	0.292 ( 0.271, 0.315)	0.326 ( 0.307, 0.347)	0.289 ( 0.268, 0.311)
sigma predator speed	Mean prey rank	0.986 ( 0.969, 1.004)	0.967 ( 0.953, 0.980)	0.994 ( 0.978, 1.013)
sigma prey speed	Intercept	0.200 ( 0.189, 0.212)	0.201 ( 0.194, 0.209)	0.208 ( 0.199, 0.217)
sigma prey speed	Mean prey rank	1.116 ( 1.097, 1.134)	1.116 ( 1.102, 1.131)	1.107 ( 1.089, 1.124)
<i>Random effects</i>				
mu predator speed	ICC avatar ID	0.454 (0.322, 0.611)	0.500 (0.357, 0.662)	0.522 (0.384, 0.674)
mu predator speed	ICC environment ID	0.003 (0.001, 0.005)	0.003 (0.001, 0.005)	0.003 (0.001, 0.005)
mu predator speed	ICC predator ID	0.123 (0.085, 0.162)	0.091 (0.059, 0.120)	0.148 (0.095, 0.196)
mu prey speed	ICC avatar ID	0.051 (0.023, 0.086)	0.072 (0.035, 0.120)	0.063 (0.034, 0.098)
mu prey speed	ICC environment ID	0.060 (0.034, 0.092)	0.056 (0.031, 0.084)	0.048 (0.026, 0.072)
mu prey speed	ICC predator ID	0.149 (0.120, 0.175)	0.125 (0.104, 0.148)	0.192 (0.152, 0.224)
mu success	Variance predator ID	0.525 (0.429, 0.610)	0.331 (0.279, 0.387)	0.362 (0.298, 0.428)
<i>Coefficient of variation</i>				
mu predator speed	CVi predator ID	0.087 (0.079, 0.095)	0.085 (0.076, 0.091)	0.107 (0.096, 0.117)
mu prey speed	CVi predator ID	0.059 (0.053, 0.064)	0.053 (0.048, 0.057)	0.070 (0.063, 0.077)
sigma predator speed	CPp predator ID	0.412 (0.377, 0.450)	0.439 (0.398, 0.477)	0.487 (0.442, 0.533)
sigma prey speed	CPp predator ID	0.056 (0.043, 0.068)	0.080 (0.071, 0.089)	0.097 (0.085, 0.110)

\* We applied the exponent to the intercept values of sigma parameters, estimated on a log scale, and then squared them, such that values are mean posterior residual variances. We back-transformed the hunting success values, estimated on a logit scale, back to a probability scale.

As we predicted, individual predators encountered prey with varying levels of speed (*ICC predator ID*, Table 2). Similar to the predator's speed, prey encounters varied more among predators at the novice and advanced levels, and predators differed more in the mean speed of prey that they encountered at the advanced stage (Table 2). Thus, some individuals encountered prey that were on average slower, while others encountered prey that were on average faster. These encounters also varied slightly among the predator avatars and virtual environments, but did not change with experience (Table 2). However, predators differed only weakly in the variability between prey encounters that they experienced (*CV<sub>p</sub> predator ID*, Table 2). Hence, while predators did differ in the mean speed of the prey that they encountered, they all experienced similar degrees of variation among encounters (Table 2).

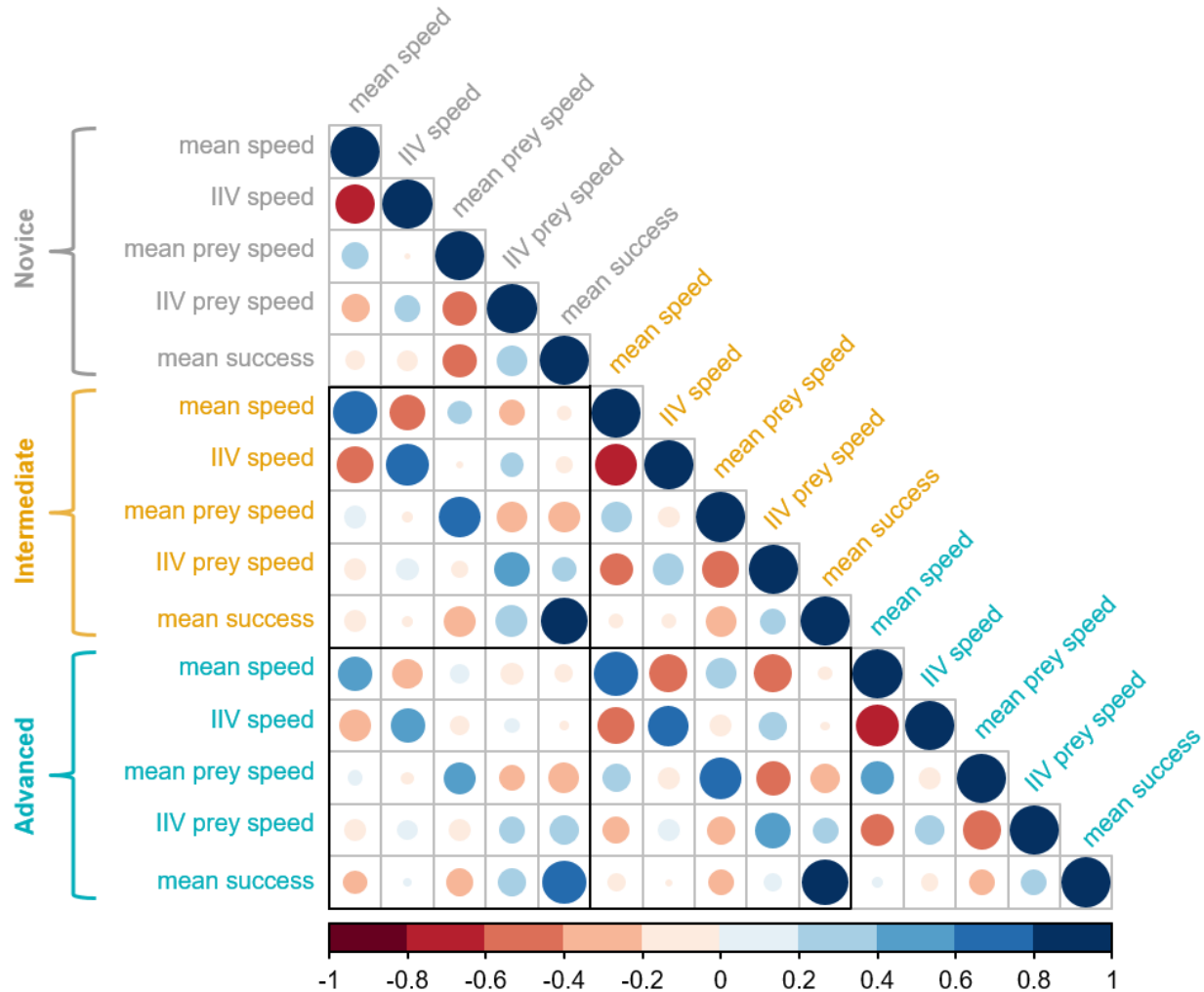


**Figure 2.** Distribution of the intra individual behavioural variation (i.e. specialization) of predators when they were (A) novices and then (B) advanced hunters. The red band displays the 95% CI of the intercept for the intra individual standard deviation in predator speed.

## Relationship between behavioural specialization and prey variability

At all experience levels, predators that were on average faster (mean) were also travelling faster in all their matches (IIV) ( $cor_{novice} = -0.618 [-0.692, -0.537]$ ,  $cor_{interm} = -0.708 [-0.765, -0.637]$ ,  $cor_{adv} = -0.721 [-0.787, -0.66]$ ) (i.e. they were more specialized at travelling fast). Thus, slower predators were also more flexible in their movement through time (Figure 3). In general, predators tended to be faster (mean) when they encountered prey that were on average faster (mean) ( $cor_{novice} = 0.27 [0.143, 0.368]$ ,  $cor_{interm} = 0.347 [0.252, 0.46]$ ,  $cor_{adv} = 0.412 [0.318, 0.516]$ ) (Figure 4). At the three experience levels, there were only weak correlations between predator IIV and mean prey speed ( $cor_{novice} = -0.007 [-0.123, 0.121]$ ,  $cor_{interm} = -0.172 [-0.286, -0.065]$ ,  $cor_{adv} = -0.18 [-0.299, -0.065]$ ) (Figure 3). Similarly, predators specialized in a faster foraging mode (IIV) when encounters with prey were more predictable (IIV) ( $cor_{novice} = 0.264 [0.088, 0.44]$ ,  $cor_{interm} = 0.377 [0.252, 0.496]$ ,  $cor_{adv} = 0.339 [0.184, 0.463]$ ), but the correlations were weak (Figure 3). In the four cases described above, the correlations became stronger as predators gained experience (Figure 3).

The foraging strategies of predators, that is, the correlations between the mean and IIV of speed, remained structurally stable among the levels of experience. For instance, novice predators that tended to be faster also kept this strategy as they gained experience (Figure 3 inside the black squares). Overall, we detected the same patterns for within-experience state correlations. The correlations between trait values were also stronger among novice-intermediate and intermediate-advanced states than between novice-advanced states, indicating that behavioural changes in predators occurred as they gained experience.



**Figure 3.** Full correlation matrix of the MDHGLM relating the mean and IIV speed of the predators, the mean and IIV in speed of the prey they encountered, and mean hunting success. Starting from the upper part of the plot are displayed the five parameters for novice predators (gray), the five for intermediate predators (yellow), and the five for advanced predators (blue). Larger dark blue circles indicate stronger positive correlations, while larger dark red circles indicate stronger negative correlations. The black squares indicate correlations between different experience levels (i.e. character states).

### Hunting success of behavioural specialists vs generalists

We did not detect strong correlations between the predators' average speed and hunting success ( $cor_{novice} = -0.135 [-0.251, -0.031]$ ,  $cor_{interm} = -0.069 [-0.183, 0.048]$ ,  $cor_{adv} = 0.028 [-0.084, 0.145]$ ), nor between the IIV in speed and hunting success ( $cor_{novice} = -0.147 [-0.245, -0.024]$ ,  $cor_{interm} = -0.065 [-0.176, 0.062]$ ,  $cor_{adv} = -0.108 [-0.233, 0.008]$ ), suggesting that both slower/flexible and faster/specialist

330 predators were both equally successful (Figure 3). However, when predators were novice, there was a  
331 strong negative correlation between the average speed of the prey that they encountered and their hunting  
332 success ( $cor_{novice} = -0.432 [-0.539, -0.024]$ ). Hence, novice individuals that encountered faster prey were  
333 less successful. This relationship was decoupled at the later experience levels, such that encounters with  
334 faster prey at intermediate and advanced stages were not as strongly correlated with hunting success  
335 anymore ( $cor_{interm} = -0.356 [-0.462, -0.256]$ ,  $cor_{adv} = -0.264 [-0.384, -0.159]$ ).

## 336 **Discussion**

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