Prey skill shapes the acquisition of predator expertise in a virtual bi-trophic system

# ABSTRACT

The acquisition of expertise is crucial for predators to be successful hunters. To achieve this, predators must hone their skills and gain knowledge through repeated and extensive practice. Prey can interfere with this process and hinder the acquisition of predator expertise by employing antipredator tactics to evade detection and pursuit. However, empirical evidence on how predators acquire expertise through repeated encounters with their prey remains limited, largely due to the challenges of monitoring direct interactions in the wild. Here, we use a virtual predator-prey system (the game *Dead by Daylight*) to investigate how experience shapes individual and population hunting success in human predators across repeated interactions with their prey. We show that predators optimized prey consumption as they gained experience, indicating that they acquired expertise through extensive practice. At the population-level, we found that more skillful prey impaired the acquisition of expertise by reducing hunting success. Prey skill was also an important mediator of this relationship at the individual level, driving differences among predators in the acquisition of expertise. More skillful prey moved faster, and predators were less successful against faster prey. Our results suggest that skilled prey use behaviours to outmanoeuver their predators, thereby mediating how predators acquire expertise at the population and individual level.

Keywords: predator-prey, experience, learning, antipredator behaviour, virtual ecology, Dead by Daylight

# INTRODUCTION

Predation is a fundamental biological process acting as an agent of evolutionary change that regulates prey populations, limits the spread of diseases, and mediates energy flow across trophic levels (Hairston Jr. and Hairston Sr. 1993; Abrams 2000; Ripple et al. 2014; Wirsing et al. 2021). These processes are driven by changes in predation risk and prey selection across landscapes as predators adjust their strategy and select suitable habitats to hunt (Quevedo, Svanbäck, and Eklöv 2009; Pettorelli et al. 2015; LaBarge et al. 2024; Schmitz 2017). Central theory suggests that predators become more efficient hunters by acquiring expertise through practicing and learning the proper skills to locate, select, and capture their prey (Woo et al. 2008; Wooster et al. 2023; LaBarge et al. 2024). Therefore, differences in hunting success between predators may be attributed to differences in the acquisition of hunting expertise. Unraveling how this expertise emerges remains a missing, but essential, link to assess how foraging behaviour shapes prey consumption during predator-prey interactions.

Expertise can be defined as the characteristics, skills, and knowledge that provide individuals with the ability to outperform novices on complex tasks (Dukas 2017). Empirical studies on human and non-human hunters show that individuals optimize foraging efficiency (e.g. search and handling times, return rates) by associative learning, by developing search images, or by exploiting cues from their prey and their environment (Edwards and Jackson 1994; Morse 2000; MacDonald 2007; Reid, Seebacher, and Ward 2010; Wilson-Rankin 2015). Through these processes, expert predators should have greater knowledge, better energy management, and acute motor skills that increase their chances of locating and capturing prey (Dukas 2019). Theory predicts that predator cognition can maintain behavioural variation, shape prey phenotypic composition, and destabilize predator-prey systems (Kondoh 2010; Skelhorn and Rowe 2016; Kikuchi and Simon 2023). Therefore, individual differences among predators in their capacity to acquire expertise over time may be important for the ecological consequences of predation.

Prey use antipredator tactics such as camouflage to avoid detection and rapid escapes to evade capture (Walker et al. 2005; Kelley and Magurran 2011; Herbert-Read et al. 2017). These strategies are hypothesized to drive differences in prey consumption among predators by disrupting the acquisition of hunting expertise (Wooster et al. 2023). Experimental studies have shown that certain camouflage tactics of prey can impair expertise acquisition in humans and birds (Stevens et al. 2012; Troscianko et al. 2013). For example, Troscianko, Skelhorn, and Stevens (2018) found that disruptive colouration interfered with human subjects’ ability to form search images, hindering improvements in detection times over repeated attempts. Antipredator behaviour may also hold the potential to hinder the acquisition of predator expertise. For instance, some predators may be limited in their capacity to develop the necessary attributes (e.g. physical, physiological, neurological) for fast-paced hunting, which could impair their acquisition of hunting expertise if they chase faster prey. Moreover, prey antipredator behaviour can improve with experience through continued exposure to predators (Turner, Turner, and Lappi 2006; Kelley and Magurran 2011; Lönnstedt et al. 2012). Indeed, animal reintroduction programs show that individuals trained to recognize predators display more antipredator behaviours and are 1.5 times more likely to survive than predator-naive individuals (Tetzlaff, Sperry, and DeGregorio 2019). To our knowledge, there is little empirical evidence showing links between prey skill, antipredator behaviour, and the acquisition of predator expertise in human and nonhuman predators, representing a significant gap in our understanding of predator-prey interactions.

A recurring challenge impeding research on predator-prey behavioural interactions is the need to collect data simultaneously on both the predator and the prey. Here we mitigate these challenges by using *Dead by Daylight* as our study system, a videogame where four prey players must forage for resources while avoiding predation by a fifth player. Similar to agent-based simulations, *Dead by Daylight* provides controlled virtual environments to test ecological hypotheses (see “Multiplayer Videogames to Analyze Behavior During Ecological Interactions” 2025 for a review), with the advantage of having real players that interact in the virtual space. In this game, the predator population comprises individuals that either ambush or hunt at high speeds (i.e., mean movement speed along an ambush-cursorial continuum of tactics), and their success is driven by the movement of the prey (Fraser Franco et al. 2022). The prey can increase their chances of survival by cooperating and moving fast to escape the predator (Céré, Montiglio, and Kelly 2021; Fraser Franco et al. 2022; Santostefano, Fraser Franco, and Montiglio 2024). The game also elicits natural reactions in players such as freezing when predation is imminent (M.F.F., personal observations), corroborating virtual ecological studies showing that predation drives individual variation in risk perception (Beauchamp 2020). These observations outline how ecological phenomena can emerge from human interactions in virtual systems with fixed rules (Brosnan and Postma 2017; Kasumovic, Blake, and Denson 2017). Videogames also generate large volumes of data on thousands of interacting players throughout their lifetime in the game under realistic, controlled, and repeatable ecological scenarios. Hence, *Dead by Daylight* allows us to tackle fundamental questions about the role of antipredator behaviour and experience in predator-prey interactions.

In this study, we assess how repeated encounters with prey shapes predator hunting success using data from players in *Dead by Daylight*. We quantify expertise acquisition as the relationship between hunting success (i.e. the probability of capturing all prey) and repeated experience (i.e. cumulated matches). First, we test the hypothesis that predator success will increase with experience up to some point at which it will stabilize (Dukas 2019). However, we hypothesize that prey skill and speed will influence predator expertise acquisition, and predict that faster and more skillful prey will reduce the gain in expertise at the population level. Prey with greater skills should move at faster speeds. Moreover, if prey skill and speed influence hunting success at the population level, then the acquisition of predator expertise should vary among individuals given these two prey features. Alternatively, if prey characteristics do not influence predator hunting success at the population level, we predict that the gain in predator expertise will be similar among individuals.

# MATERIALS AND METHODS

## Study system

*Dead by Daylight* is a survival asymmetric (i.e. gameplay mechanics differ between two groups) multiplayer online game developed by Behaviour Interactive Inc., in which players can play either as predators or prey. Every match includes only one predator and four prey. The objective of the predator is to hunt and capture the prey, and the objective of the prey is to search for resources while avoiding the predator. The resources are in the form of power generators that, once all activated, will enable the prey to escape through one of two exit doors. A skill-based matchmaking algorithm determines the composition of the predator and prey group in a match. 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.

Before the start of a match, players (predator or prey) can choose an avatar with unique 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 environments comprise 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, predators display only minimal changes in behaviour and hunting success across these environments (Fraser Franco et al. 2022). There were 35 virtual game environments available for play during the study period. Details on the basic characteristics of predator avatars are available at <https://deadbydaylight.fandom.com/wiki/Killers>. Details on the size and structure of the different virtual environments are available at <https://dbdmaps.com/> and <https://deadbydaylight.fandom.com/wiki/Realms>.

## Data collection

Behaviour Interactive Inc. provided data that spanned six months of gameplay recorded for every player from 2020-12-01 to 2021-06-01 (game build 4.4.0 to 4.7.2). We analyzed only matches where players did not know each other and were unable to communicate using voice-recording devices. We filtered any matches where players were inactive, such as when mean distances travelled per second (i.e. speed) 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 intended.

Our study population comprised 253 players that played at least 300 matches. We monitored all their matches from the first to a maximum of 500 matches, with a total record of 100 412 matches overall. The predator-players’ experience in our population sample varied between 301 and 500 matches played. These matches lasted between 3 and 70 min (mean = 11 min). We recognize that we could have introduced a bias by retaining only those individuals, as they might already be seasoned video game enthusiasts and exhibit expert-level performance in their early matches in *Dead by Daylight*. Thus, we tested sample bias by comparing a random sample of players that played either 20 to 50 matches, 51 to 100 matches, or 101 to 300 matches during the same timeframe as our population sample. We then took the first 20 matches played by these players, including those from our population sample, and compared their mean hunting success using a Bayesian hierarchical linear model. We found that all four groups had similar success as predators in their first 20 matches (Appendix 1: Table S1 and Figure S1), suggesting an absence of bias due to data sampling.

We collected the following information for every match in our population sample : the player’s anonymous ID, the predator player’s hunting success, the predator player’s cumulated experience, and the mean rank and speed of the the group of prey that the predator player encountered. We defined hunting success as the number of prey consumed during the match (min = 0, max = 4). We defined the predator’s cumulative experience as the number of matches played as the predator 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. Laslty, we measured the prey’s rank as the mean rank of the four individual prey in a match (mean = 8.74 ± 4.12), and the prey’s speed as the mean travel speed of the four individual prey in a match (mean = 2.40 ± 0.32 m/s).

We used the mean rank of the prey as a proxy of their skill. The ranking system in *Dead by Daylight* varies between 1 and 20 (1 indicating the highest skill), and was implemented by the company to pair players in a match based on their skill (<https://deadbydaylight.fandom.com/wiki/Rank>). The skill of a player increases based on their performance from match to match. While the ranking system represents an approximation of prey skill, it was the most readily available metric we could access to determine the skill of the prey group. In addition, the pairing system is subject to variation depending on factors such as player availability, which can result in predator-prey groups with unbalanced skill. This allowed us to evaluate the effect of the prey’s skill on predator success.

## Data analyses

### Model specification

We tested how predators developed their expertise by computing five Bayesian generalized additive mixed models (GAMM) with thin-plate regression splines, all of which estimated the relationship between hunting success and the predators’ cumulative experience. We parametrized the models following the method of Pedersen et al. (2019). For the first and second models (I and II), we assume that individual predators share a similar relationship between success and experience, but that this relationship can vary among them (e.g. predator 1 has a steeper curve than predator 2). This enabled us to test whether predators differed in the development of their expertise. Both models included a common global smoothing function (i.e., population effects) and random smooths for the predator ID (i.e., individual effects). Model I included the standardized match duration as a covariate, while model II included the standardized match duration and the average rank of the prey group, allowing us to test if the variation among predators in expertise acquisition was driven by prey skill. In the third model (III), we kept the individual smoothers for the predators, but removed the global smoother. This model assumes that predators do not share a common relationship between success and experience. In this model, we control for the standardized match duration and the average rank of the prey group. The fourth (IV) and fifth (V) models were expansions of the model III and model II respectively, where we included the standardized prey speed to assess its effect on the relationship between success and experience.

We computed the five models using a modified beta-binomial distribution. Hunting success was estimated as the number of prey consumed out of four, with probability of success drawn from a Beta distribution () with mean () and precision () parameters. We used a logit link function to estimate where and is the linear predictor. The precision parameter () was estimated using a log-link function. We used ten basis functions (K = 10) for the models to estimate the relationship between hunting success and experience. We assumed that the random intercepts for the predator ID () followed a Gaussian distribution with estimated standard deviation (). We compared the predictive accuracy of all five models using approximate leave-one-out cross-validation with Pareto-smoothed importance sampling (Vehtari, Gelman, and Gabry 2017; Piironen and Vehtari 2017; Vehtari et al. 2022).

We defined weakly informative Gaussian priors for the intercept () and the global trend of cumulative experience (). Following Fraser Franco et al. (2022), we defined a positive Gaussian prior () for the slope of the game duration because longer trials lead to greater success, a Gaussian prior () for the slope of the prey rank, and a negative Gaussian prior on prey speed () because encountering faster prey is associated with lower success in this system (Fraser Franco et al. 2022). We defined a positive Gaussian prior on the precision parameter (). We employed weakly informative half-Gaussian priors on all the standard deviation parameters ().

To test the hypothesis that prey speed increases with prey skill, we fitted a Bayesian linear regression estimating the relationship between prey speed and the standardized prey rank. We controlled for the game duration, using it as a linear covariate in the model, and included the predator identity as a random effect. We used a weakly informative Gaussian prior on the slope of the game duration () and a weakly informative negative Gaussian prior the slope of the prey rank () because prey of greater skill (i.e., rank 1 is the highest skill) should move faster. Lastly, we used a weakly informative Gaussian prior on the intercept () because prey should move at around two meters per second, and half-Gaussian priors on the standard deviation parameters ().

### Parameter sampling settings

We parametrized the GAMMs to run four chains of 1500 iterations each, sampling one parameter value every four iterations. We set the first 500 iterations of each model as warm-ups. Similarly, the linear model ran four chains of 1500 iterations each, sampling a parameter value at every iteration, and discarding the first 500 iterations. For GAMM model, we obtained 1000 posterior samples per parameter, and 4000 values for the linear model. We assessed the convergence of the chains using trace plots, R-hat diagnostics with a threshold of <1.01, and effective sample sizes (ESS) with a threshold of >100 (Vehtari et al. 2021). We also performed posterior predictive checks which showed an adequate fit of the models.

We fitted all models in R (version 4.1.2) using Hamiltonian Monte Carlo (HMC) sampling with the package “brms” version 2.22.0 (Bürkner 2017), an R front-end for the STAN software (Stan Development Team 2023), and “cmdstanr” version 0.8.0 (Gabry and Češnovar 2021) as the back-end for parameter estimation (cmdstan installation version 2.35.0). For further details on how to reproduce the results, please consult the GitHub repository of this project (<https://github.com/quantitative-ecologist/predator-expertise>).

### Hypothesis testing

We tested the hypothesis that prey skill and antipredator behaviour impairs the acquisition of expertise at the population level by visually comparing the global trends of model I (only controlling for game duration), model II (controlling for game duration and prey rank) and model V (controlling game duration, prey rank, and prey speed) (Figure 1). At the individual level, we tested our hypothesis that prey skill and antipredator behaviour generate differences among predators in expertise acquisition by comparing the individual-level variance parameters. Specifically, we compared the standard deviations of 1) the random intercepts (i.e. mean differences in hunting success), 2) the random slopes (i.e. linear component relating hunting success with experience), and 3) the curve wiggliness (i.e. nonlinear component relating hunting success with experience).

# RESULTS

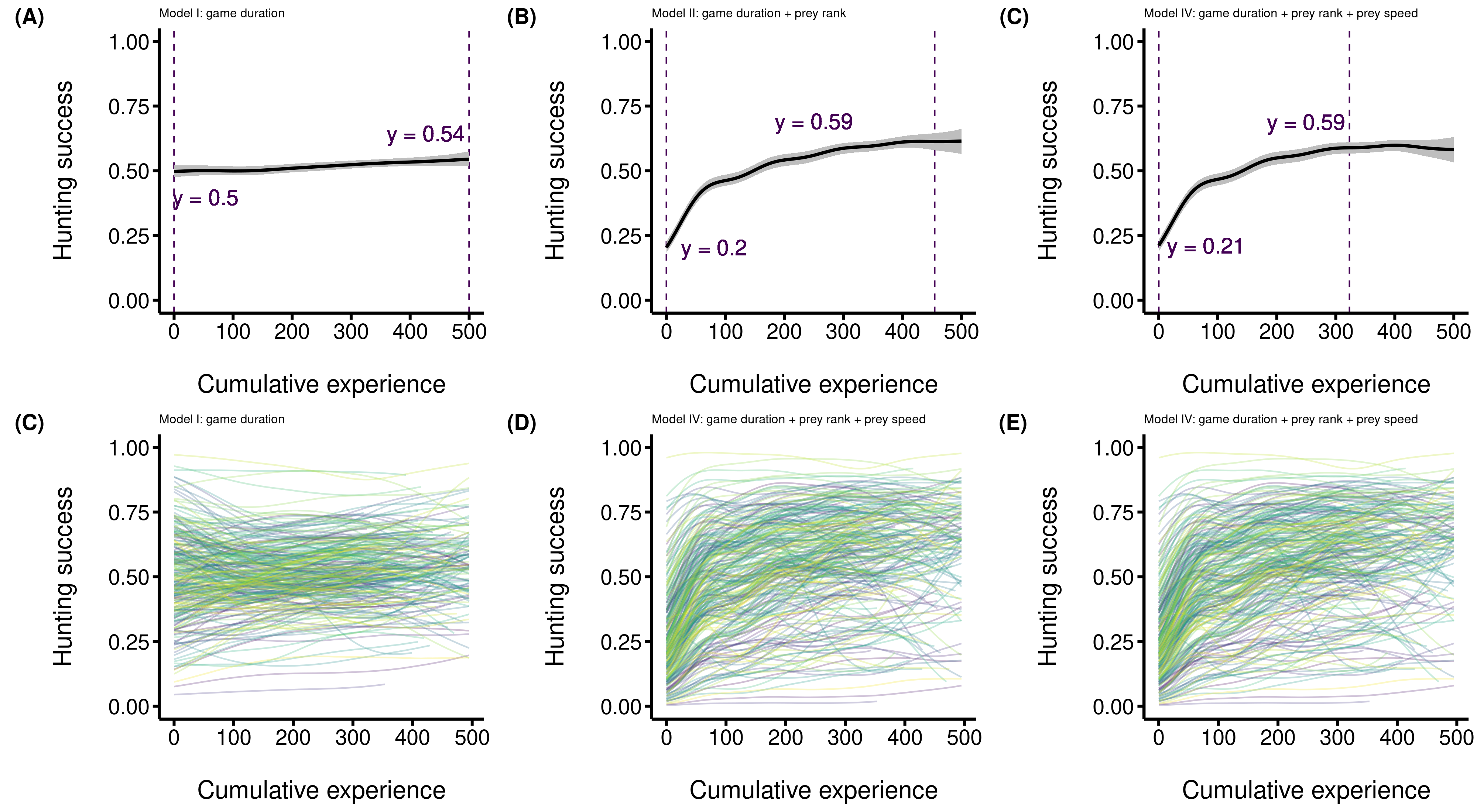
## Acquisition of expertise at the population level

Out of all five GAMM models, those that included a global smoother were better at predicting the data compared to those without a global smoother, indicating that predators shared a similar relationship between prey capture and experience (Table 1). Model V, which accounted for the prey group’s rank and speed was the best at predicting the data (Table 1).

Table 1. Leave-one-out cross-validation table of the five GAMMs relating hunting success to predator experience.

| model | elpd  difference | sd  difference | elpd loo  value | elpd loo  standard error |
| --- | --- | --- | --- | --- |
| (V) predator xp + ID smoothers + prey rank + prey speed | 0.00 | 0.00 | -136 119.95 | 201.03 |
| (IV) ID smoothers + prey rank + prey speed | -60.40 | 15.38 | -136 180.35 | 200.91 |
| (III) ID smoothers + prey rank | -5 122.15 | 104.80 | -141 242.10 | 183.12 |
| (II) predator xp + ID smoothers + prey rank | -5 184.46 | 105.86 | -141 304.41 | 182.86 |
| (I) predator xp + ID intercepts + prey rank | -10 135.30 | 136.90 | -146 255.25 | 165.41 |
| a 'elpd' refers to the expected log pointwise density and is the value chosen to select the best model. b 'xp' is an acronym for experience | | | | |

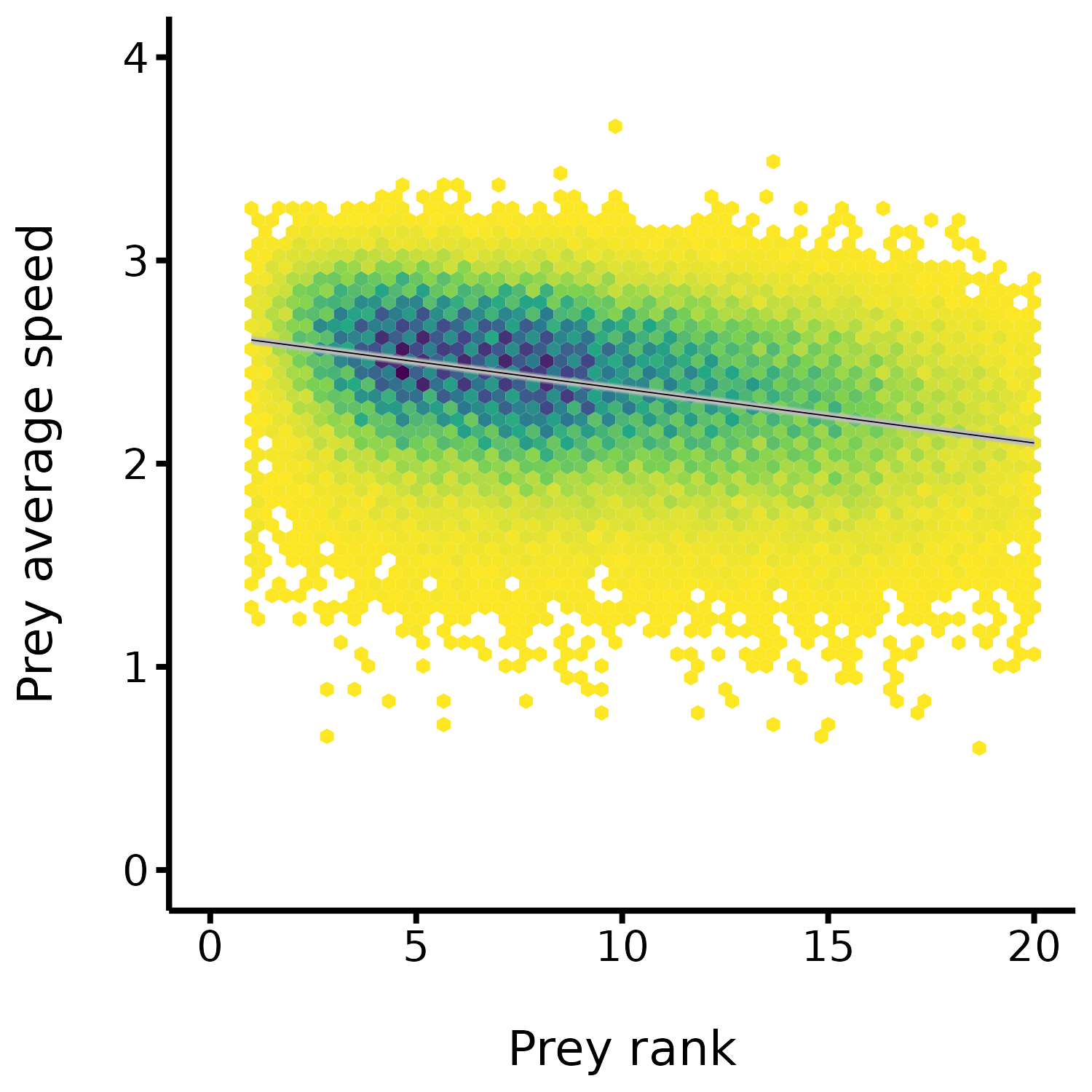
Models in which prey rank was not accounted for resulted in no change in hunting success with experience for the average individual (i.e. no gain in expertise, Figure 1A). As we predicted, accounting for the prey rank resulted in a diminishing returns curve (model II), with predators optimizing their success after playing ~400 matches (Figure 1B). The predictions indicate a 40% increase in the probability of consuming all prey for the average individual between the first and the ~400 match, where success reached a plateau (Figure 1B). Controling for prey speed did not influence the results at the population level (Figure 1C). Yet, we found strong evidence of a negative relationship between hunting success and prey speed, indicating that hunting faster prey reduced the predator’s chances of capture (Figure S2). Moreover, prey with more expertise moved at higher speeds compared to less skilled prey (Figure 2).



**Figure 1**. Median posterior predictions of the acquisition of predator hunting expertise. The predators’ hunting success (i.e. the probability of consuming the four prey) is on the y-axis, and the predators’ cumulative experience (i.e. the number of matches played before each observation) is on the x-axis. Panels A and C show the acquisition of expertise for the average individual with the vertical dashed lines on the left representing the lowest predicted values. For panel A, the right-side vertical dashed line shows the highest predicted success. For panel C, the right-side dashed line represents the point on the curve where success was optimized, which we calculated using the finite differences method to obtain the first derivative of the predicted values. Panels B and D show among individual differences in the acquisition of expertise, with each curve representing an individual predator. (A-B) model II where we control for the prey rank (C-D) model V where we control for the prey rank and the speed of the prey group.

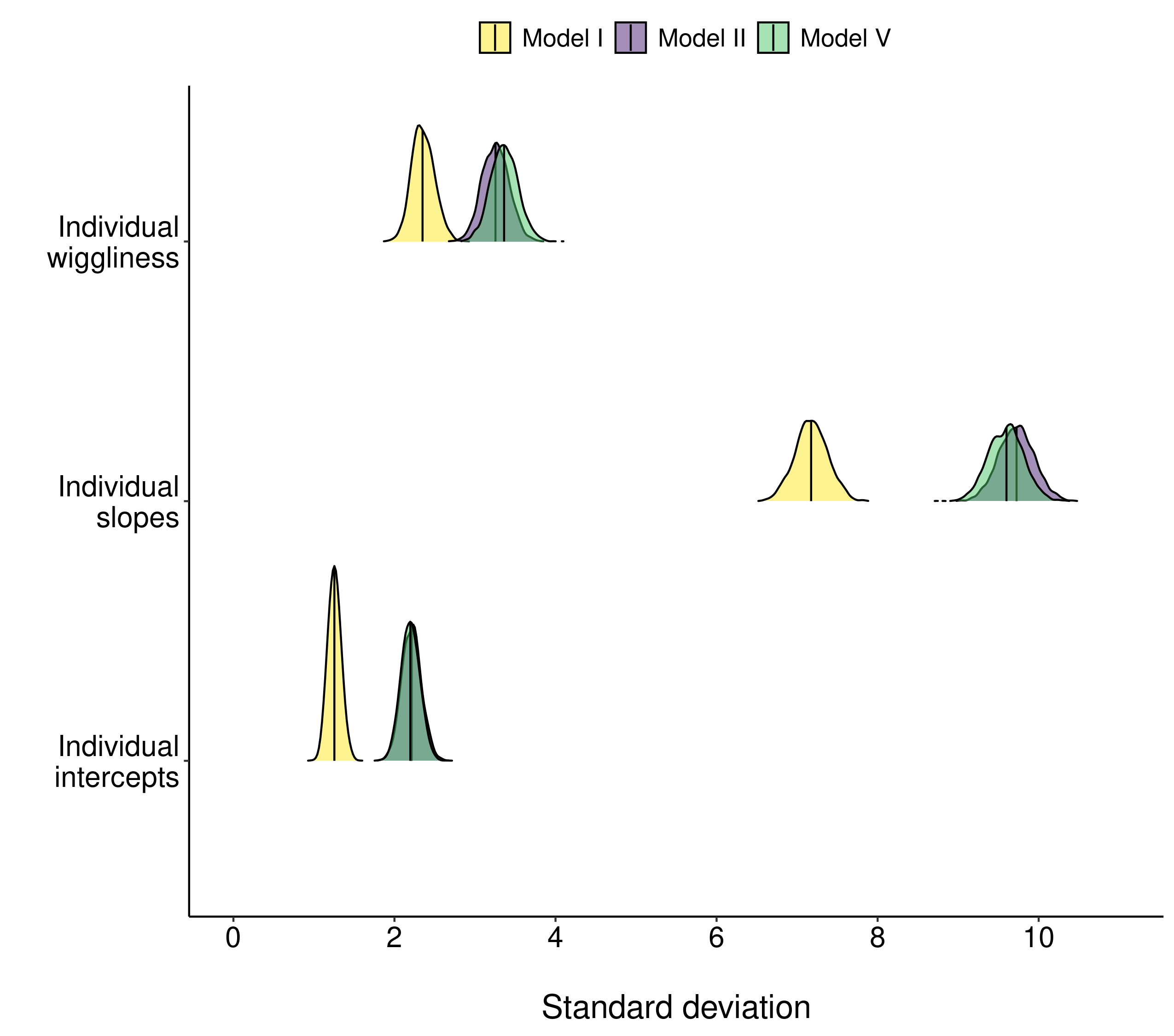
## Acquisition of expertise at the individual level

Prey speed did not influence among-individual differences in average hunting success as the posterior distributions of the standard deviations of individual intercepts were almost completely overlapping (Figure 3, median = 2.21 vs median = 2.2). However, individuals differed in the acquisition of their hunting expertise (Figure 1B-D). We found strong evidence that the speed of the prey mediated among-individual differences in the linear relationship between success and experience, as there were substantial differences in the standard deviations of the individual slopes between the two models (Figure 3, median = 9.73 vs median = 9.6). Differences among individuals in the direction of the linear relationship between success and experience were 1.01 times lower when we removed the effect of prey speed (i.e. accounting for it in the model).



**Figure 2**. Median posterior predictions of the relationship between prey speed and prey skill. The average speed of the prey group is on the y-axis, and the average rank of the prey group is on the x-axis. The colour gradient showcases the density of observations, with lighter colours indicating lower densities, and darker colours indicating higher densities of observations. Lower rank values indicate that the prey group is more skilled, while higher values indicate that the prey are less skilled

We also found strong evidence that the speed of the prey mediated the form of the relationship between hunting success and experience at the individual level. We detected large differences in the standard deviations of the wiggliness (Figure 2, median = 3.25 vs median = 3.36). The lower standard deviation for the model where we accounted for prey speed (model V) suggests that the form of the relationship between success and experience was more similar among individuals.



**Figure 3**. Posterior distributions of the standard deviation of individual-level parameters estimated by the GAMM. The parameters are displayed on the y axis, and their standard deviation are displayed on the x axis. The intercept and slope standard deviations refer to the linear components of the estimated relationship between hunting success and cumulative experience. The standard deviation of the wiggliness parameter refers to the shape of the curves (i.e. nonlinear component). The vertical lines are the medians of the posterior distributions. For each panel, the light-coloured distributions (i.e. green) are for the model with a shared trend where we did not account for prey speed (model II), and the darker-coloured distributions (i.e. purple) are for the model with a shared trend where we accounted for prey speed (model IV).

# DISCUSSION

Using a virtual predator-prey system where we monitored predator hunting success across experience, we provide rare empirical support for the hypothesis that prey antipredator behaviour can impair the acquisition of hunting expertise. We show that the predator population increased its hunting success with experience. We found, however, important differences among individuals in expertise acquisition that were related to the speed of the prey encountered.

Our results suggest that predators hone their hunting expertise through extensive practice. The predator population displayed an asymptotic relationship between experience and success, wherein initial gains in success were significant but gradually stabilized as experience accumulated. These observations are consistent with empirical studies of expertise in both humans and nonhuman animals (reviewed in Dukas 2019). However, prey speed played a crucial role in shaping this pattern at the population level as encounters with faster prey resulted in lower hunting success (Figure S2). We previously showed in *Dead by Daylight* that faster movement is effective for prey to evade predation (Fraser Franco et al. 2022), in agreement with studies in other animals (Walker et al. 2005; Kelley and Magurran 2011; Martin et al. 2022). We suspect that experienced prey may increasingly rely on this strategy, which could explain why the relationship between hunting success and experience was concave when we did not control for prey speed (model II, Figure 1A). Thus, our results suggest that predators can gain expertise and maintain success when they encounter prey that move at speeds lower than or closer to the population-average.

Prey speed also mediated differences among predator players in the acquisition of expertise, suggesting that individual predators varied in their capacity to adjust to challenging prey. Animals are expected to have limited attention spans, which restricts diet choice and the formation of search images (Dukas and Kamil 2001). Hunting faster prey demands specialized cognitive abilities and coordination that are energetically costly (Kelley and Magurran 2011). Thus, predators that failed to develop counter-strategies for detecting or chasing faster prey were likely at a disadvantage. Parallel observations have been outlined in studies of prey camouflage strategies. For example, Troscianko, Skelhorn, and Stevens (2018) showed in a computer experiment involving humans that disruptive camouflage was efficient at preventing the acquisition of expertise during search image formation. Human subjects exposed to a restricted set of strategies were also less efficient compared to those exposed to a variety of strategies. Therefore, our observations show that prey antipredator behaviour can also impair predator expertise acquisition.

Despite adjusting for the prey’s speed (i.e. model V), noticeable differences in expertise acquisition among predators persited. One possible explanation is that the predators’ hunting tactics may indirectly shape their own expertise through changes in prey behaviour. Predators tend to specialize as cursorial or ambush hunters in *Dead by Daylight* (Fraser Franco et al. 2022). Consequently, those employing a cursorial tactic may push prey to move faster, which, in turn, may hinder their own expertise acquisition due to the increased difficulty of hunting such prey. An alternative explanation is that longer time intervals between hunting events are hypothesized to hinder or delay the acquisition of expertise because individuals may forget information when delays are longer (Endler 1991; Wright et al. 2022). For example, a predator that played 300 matches in six months might forget critical information related to prey detection or escape patterns compared to one that played 300 matches in six days. While there is unequivoqual evidence that many predator species can learn quickly how to be efficient hunters, the role of the frequency of interactions remains unclear (Wooster et al. 2023). Therefore, investigating the impact of such time lags in future analyses may reveal important insights into the outcome of predator-prey interactions. Another potential reason for the persistent differences among individuals is that neither the predator nor prey players’ lives are at stake in the game. As a result, emerging patterns may be driven more by the players’ motivation to win rather than “true” survival. For example, some players could experiment with the game out of boredom, which could also contribute in shaping how expertise is honed in this particular system.

## Conclusions

We found support of our hypothesis that prey antipredator behaviour drives individual differences in expertise acquisition in a human predator population in the game *Dead by Daylight*. Future analyses should investigate how antipredator tactics developp with experience, as it may reveal important insights on the eco-evolutionary dynamics of predator-prey interactions. Our study demonstrating that prey antipredator behaviour can impair the acquisition of hunting expertise adds to a growing body of research showing how virtual systems can be used to test hypotheses on ecological interactions (Beauchamp 2020; Céré, Montiglio, and Kelly 2021; Fraser Franco et al. 2022; Lymbery, Webber, and Didham 2023; Santostefano, Fraser Franco, and Montiglio 2024). We therefore hope that our study will inspire more collaborations between scientists and the videogame industry to tackle fundamental questions in ecology.

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