Prey movement shapes the development of predator expertise in a virtual bi-trophic system

# ABSTRACT

The acquisition of expertise is crucial for predators to be successful hunters. To do so, predators need to hone their skills and acquire knowledge through repeated and extensive practice. Recent studies suggest that such acquisition of expertise may not follow expected patterns when prey use antipredator tactics to evade detection and pursuit. Such tactics may even impair the acquisition of predator expertise. Yet, there are limited empirical assessments showing how predators acquire expertise through repeated encounters with their prey 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. Prey speed was an important mediator of this relationship, driving differences among predators in the development of expertise. At the population-level, we found that faster prey could impair the acquisition of expertise by reducing hunting success. At the individual-level, our results show that prey speed shapes how individual predators acquire expertise. Therefore, our study outlines how prey antipredator behaviour can mediate the acquisition of expertise in predator populations.

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

# INTRODUCTION

The ecological consequences of predation accrue to the sum of consumptive and nonconsumptive effects (CEs and NCEs) during predator-prey interactions (Preisser, Orrock, and Schmitz 2007). Recent advances in our understanding of the mechanisms (e.g. foraging mode, reciprocal plasticity, size-dependent foraging) driving (N)CEs at the individual and population level have allowed ecologists to predict their outcome as well as their effect on prey population dynamics (Peckarsky et al. 2008; Gravel et al. 2013; Wirsing et al. 2021). For example, empirical studies show that prey tend to increase vigilance at the expense of foraging in the presence of ambush predators (NCEs) (Preisser, Orrock, and Schmitz 2007), with such hunters consuming a greater range of prey types (CEs) compared to cursorial hunters (Glaudas et al. 2019).

There are, however, internal mechanisms contributing to predator foraging success that are often overlooked when studying (N)CEs in predator-prey interactions (Wooster et al. 2023). For instance, predators need to acquire expertise by practicing and learning the proper skills to successfully locate, select, and capture their prey (Dukas 2019; Wooster et al. 2023). Empirical studies on human and non-human hunters show that individuals optimize foraging efficiency (e.g. search and handling times, return rates) by learning associative images, or by using cues from their prey and their environment (Edwards and Jackson 1994; Morse 2000; MacDonald 2007; Reid, Seebacher, and Ward 2010; Wilson-Rankin 2015). Thus, predators can integrate this information to increase their chances of locating prey, or to use the attack tactic most suited for a given context.

On the other hand, prey use antipredator tactics such as rapid escapes to evade predators (Walker et al. 2005; Kelley and Magurran 2011; Herbert-Read et al. 2017). This compels predators to develop swift motor skills to succesfully capture such prey. However, predators may be limited in their capacity to develop the necessary attributes (e.g. physical, physiological, neurological) for fast-paced hunting, which may impair the development of their hunting expertise. For example, experimental studies have shown that certain camouflage strategies, such as disruptive coloration, can impair expertise acquisition in humans and birds (Stevens et al. 2012; Troscianko et al. 2013; Troscianko, Skelhorn, and Stevens 2018). Unfortunately, while our understanding of how predation risk influences information acquisition in prey has increased over the years (reviewed in Crane et al. 2024), there is only scarce evidence showing links between prey antipredator strategies and the development of expertise in human and nonhuman predators. Therefore, our ability to accurately predict the (N)CEs of predation on prey populations remain limited.

A recurring challenge impeding research on predator-prey behavioural interactions is the need to collect data simultaneously on both the predator and the prey. Similar to agent-based simulations, online videogames can be useful systems to mitigate these challenges and test specific ecological hypotheses. They provide controlled virtual environments to test ecological hypotheses (see Lymbery, Webber, and Didham 2023) with the advantage of having real players that interact in the virtual space. For example, in the predator-prey videogame *Dead by Daylight*, four prey players need to forage for resources while avoiding predation by a fifth player. In this virtual system, the predator population is composed of individuals that either ambush or hunt at high speeds (i.e. mean movement speed along a slow-fast continuum), 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 ellicits natural reactions in players such as freezing when predation is imminent (personal observations), which corroborates with another virtual ecological study showing that predation drives individual variation in risk perception (Beauchamp 2020). These observations outline how fundamental ecological patterns 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 interacting players throughout their lifetime in the game under realistic, controlled, and repeatable ecological scenarios. Hence, virtual systems such as *Dead by Daylight* offer the opportunity to tackle fundamental questions about the role of experience on 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*. First, we investigate how the predator population develops its hunting expertise. We hypothesize that the predator population’s success will increase with experience up to a certain level where it will stabilize (Dukas 2019). However, we expect this pattern to change depending on the movement of the prey encountered. We hypothesize that prey will influence the development of expertise, and predict that faster prey will reduce the gain in expertise. Therefore, we then investigate how prey movement influences the development of expertise at the individual level. If prey speed does not influence hunting success, we predict that the gain in expertise will be similar among individuals. Alternatively, if prey speed influences hunting success, then the acquisition of expertise will vary among individuals.

# MATERIALS AND METHODS

## Study system

*DBD* is a survival asymmetric multiplayer online game (i.e. a game where the gameplay mechanics differ between two groups) developed by Behaviour Interactive Inc, in which players can play either as a predator or a 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. The composition of the predator and prey group in 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.

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 are 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, predators display only minimal changes in behaviour and hunting success across these environments, probably due to a game feature enabling them to have visual cues on the resources (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

The videogame company provided data that spanned a period of 6 months of gameplay recorded for every player from 2020-12-01 to 2021-06-01. We only analyzed matches where players did not know each other (i.e. “Online” mode). We filtered any matches where players were inactive, such as when mean distances traveled 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. We then sampled players that played 300 matches or more, and monitored all their matches from the first to a maximum of 500 matches.

Our population consists of 253 players that played strictly as the predator, 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 min (mean = 11 min). The following information is collected and reported for every match : the player’s anonymous ID, its avatar (i.e. the predator character chosen with its specific skill-gameplay mechanics), the game environment, the predator-player’s experience, the mean speed of the groups of prey that the predator player encountered, and the mean rank of the prey encountered (a proxy for prey skill). 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>), and failing to account for it would prevent us from detecting a change in the predator’s foraging success with experience.

We analyzed the mean speed of the prey group encountered by the predator. We measured the preys’ speed as the mean travel speed of the four individual prey in a match (mean = 2.40 ± 0.32 m/s). 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 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. We did not account for matches where predators played as the prey.

We recognize that we could have introduced a bias in our analyses by retaining only individuals who played for at least 300 matches. For example, these individuals might be experienced videogame players and could thus already be playing like experts in their first matches in *DBD*. To verify that our sample was not biased, we compared 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 sampled population. We then took the first 20 matches played by these players, including those from our sampled population, and compared their median hunting success using a Bayesian hierarchical linear model. We found that all four groups had similar success as predators (Appendix 1: Table S1 and Figure S1), suggesting an absence of bias due to data sampling.

## Statistical 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 (i.e. number of prey consumed) 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 and random intercepts for the predator ID. In this model, we assume that predators 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 individual smoothers for the predator ID. Here, 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. In the third model, 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. The fourth and fifth models were reproductions of the second and third models respectively, where we included the prey speed to assess its effect on the relationship between success and experience. We included the standardized match duration and prey rank as covariates in all five models.

We computed the five models using a modified version of the beta-binomial distribution implemented in “brms”. Hunting success was estimated as the probability of consuming the four prey (), drawn from a Beta distribution () with mean () and precision () parameters. We used a logit link function to estimate where and is the linear predictor, while the precision parameter () was estimated with an identity link. 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 () followed a Gaussian distribution with estimated standard deviation ().

We used 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 on the precision parameter (), a positive Gaussian prior () on the game duration because longer trials lead to greater success, and a negative Gaussian prior on prey speed () because encountering faster prey is associated with lower success in this system. We employed weakly informative half-Gaussian priors on all the standard deviation parameters (). 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).

### Markov Chain Monte Carlo settings

We parametrized the GAMMs to run four MCMC chains. We ran 2500 iterations with a thinning set to eight for the additive model with a global smoother only (see Table 1), and 1500 iterations with a thinning set to four for the remaining additive models. We set the first 500 iterations of each model as warm ups. For each model, we obtained 1000 posterior samples per parameter. We assessed the convergence of the MCMC 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.

### Software and computer specifications

All models were fitted in R (version 4.1.2) using Markov chain Monte Carlo (MCMC) sampling with the package “brms” version 2.16.3 (Bürkner 2017), an R front-end for the STAN software (Team 2023), and “cmdstanr” version 0.4.0 (Gabry and Češnovar 2021) as the back-end for parameter estimation (cmdstan installation version 2.28.2). The models were run on Cedar (Operating system: CentOS Linux 7), a computer cluster maintained by the Digital Research Alliance of Canada (<https://docs.alliancecan.ca/wiki/Cedar>). Each required 64GB of RAM with 48 cores to compile within 5 days. For details on how to reproduce our analyses, please consult the GitHub repository of this project (<https://github.com/quantitative-ecologist/predator-expertise>).

# RESULTS

## Development of expertise at the population level

Out of all five GAMM models, the two that accounted for the prey group’s rank and speed were the best at predicting the data, achieving similar expected log pointwise densities (Table 1). Models in which prey effects were not accounted for resulted in no change in hunting success with experience for the average individual (i.e. no gain in expertise). Accounting for the prey rank resulted in a concave-shaped relationship, with the highest success ranging between ~200 and ~300 matches (Figure 1A).

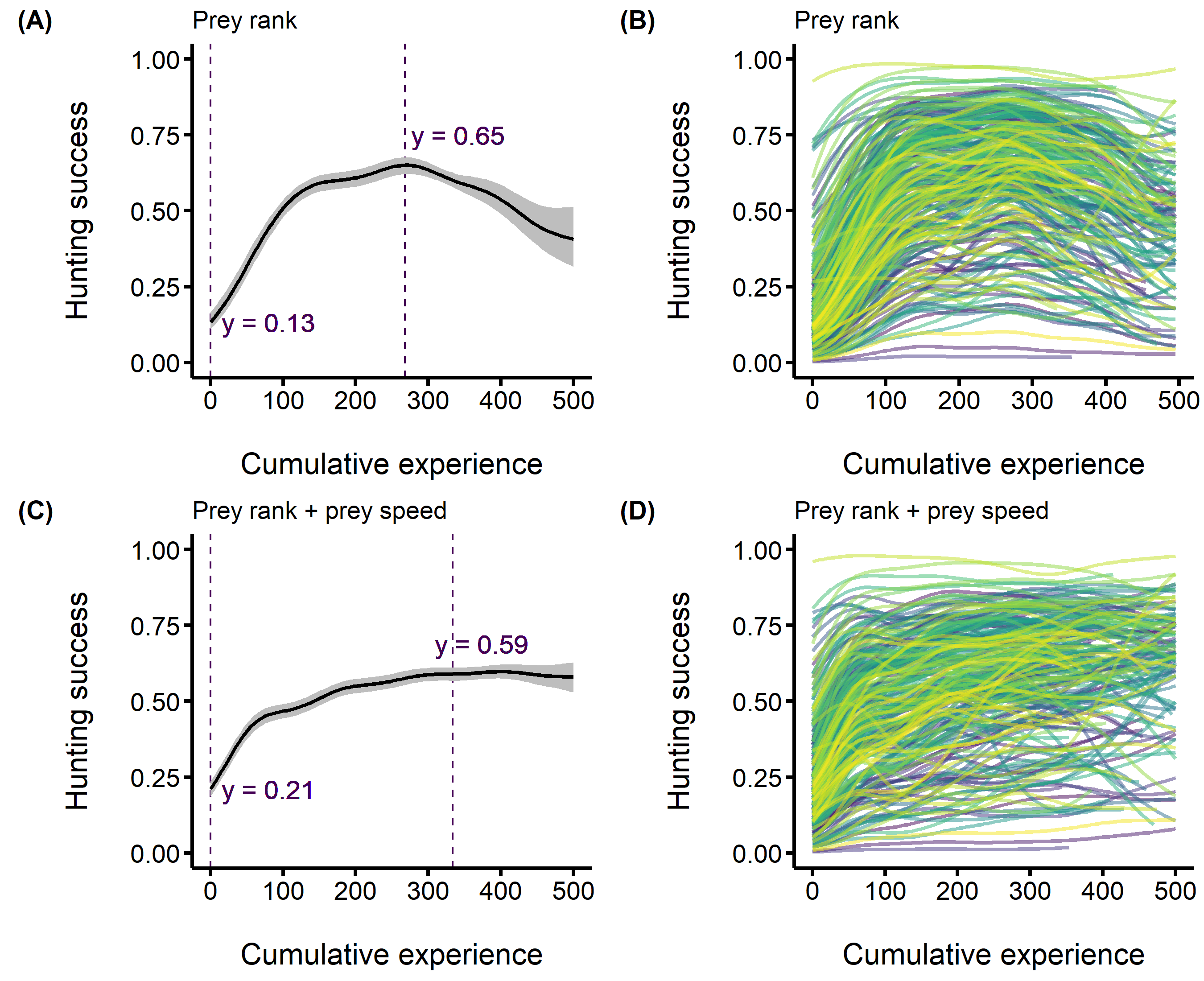
We found strong evidence of a negative relationship between hunting success and prey speed (Figure S2). In the model where we included the prey’s speed, the effect of experience on hunting success for the average individual followed a diminishing returns curve as we predicted, with predators optimizing their success after playing ~300 matches (Figure 1C). The curve shows there was a 38% increase in the probability of consuming all prey for the average individual between the first and the ~330 match, where success reached a plateau (Figure 1C).

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 |
| --- | --- | --- | --- | --- |
| predator xp + ID smoothers + prey rank + prey speed | 0.00 | 0.00 | -136 123.69 | 201.04 |
| ID smoothers + prey rank + prey speed | -562.90 | 23.59 | -136 686.59 | 202.06 |
| ID smoothers + prey rank | -5 717.54 | 107.99 | -141 841.22 | 184.27 |
| predator xp + ID smoothers + prey rank | -8 536.39 | 129.62 | -144 660.08 | 197.49 |
| predator xp + prey rank | -8 593.08 | 131.73 | -144 716.77 | 187.16 |
| 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 | | | | |

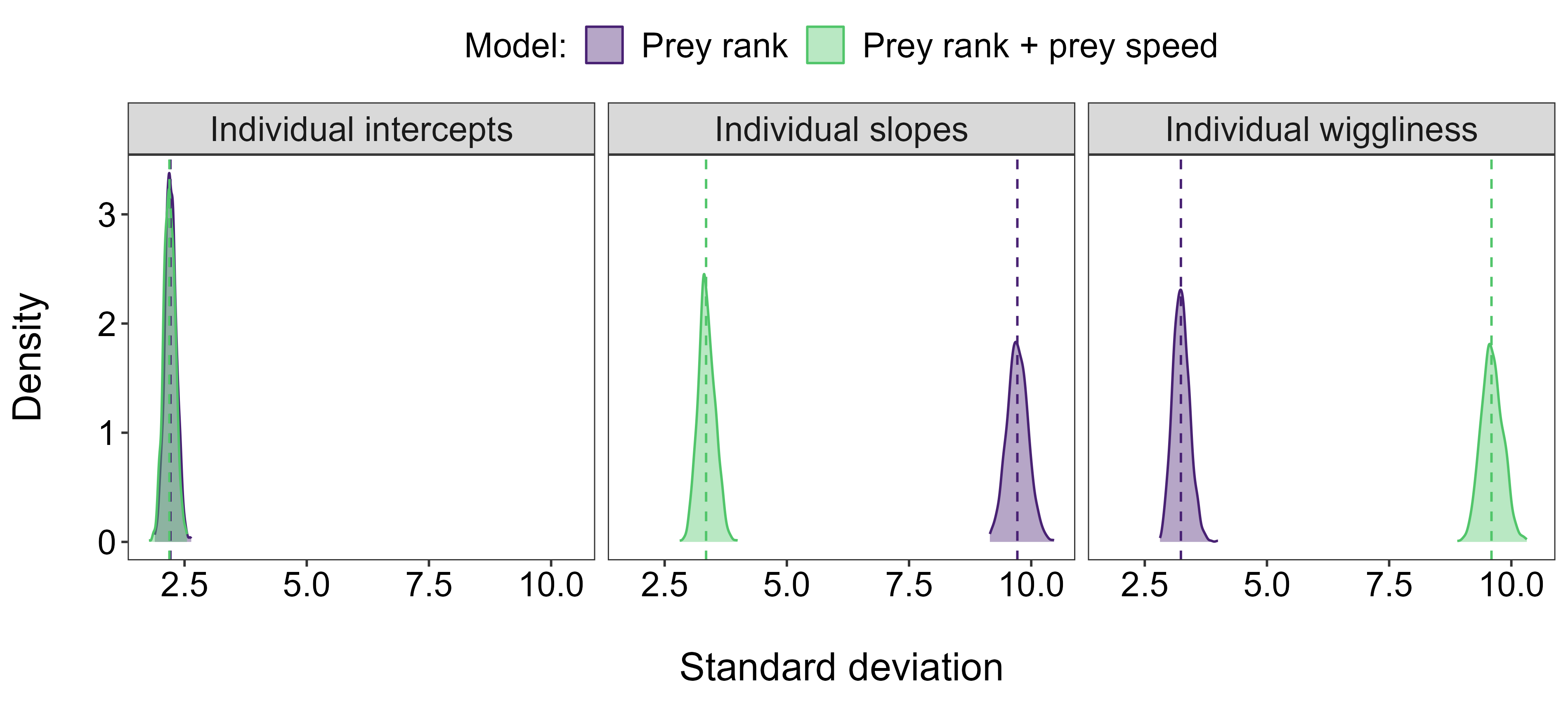
## Development of expertise at the individual level

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 2, median = 2.21 vs median = 2.19). However, individuals differed in the development 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 2, median = 9.72 vs median = 3.35). Differences among individuals in the direction of the linear relationship between success and experience were 2.9 times lower when we removed the effect of prey speed (i.e. accounting for it in the model).



**Figure 1**. Median posterior predictions of the development 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 prior to each observation) is on the x axis. Panels A and C show the development 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 development of expertise, with each curve representing an individual predator. (A-B) GAMM where we control for the prey rank (C-D) GAMM where we control for the prey rank and the speed of the prey group.

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 = 3.24 vs median = 9.59). The lower standard deviation for the model where we accounted for prey speed suggests that the form of the relationship between success and experience was more similar among individuals.



**Figure 2**. Posterior distributions of the individual-level standard deviation parameters. The first two panels represent the intercept and slope standard deviations of the linear components relating hunting success to cumulative experience, and the third panel represents the standard deviation of the wiggliness component of the curves. The vertical dashed lines are the medians of the posterior distributions. The light coloured distributions are for the model with a shared trend where we did not account for prey speed, and the darker coloured distributions are for the model with a shared trend where we accounted for prey speed (i.e. the model with the highest predictive accuracy)

# DISCUSSION

Predators usually optimize prey consumption through time by acquiring hunting expertise (Dukas 2019; Wooster et al. 2023). Yet, few studies have empirically tested how prey antipredator strategies mediate the acquisition of hunting expertise due to the challenges of investigating direct predator-prey interactions in the wild. By capitalizing on a virtual predator-prey system where interactions were directly monitored, we found that a predator-player population in *Dead by Daylight* increased their hunting success with experience. Yet, there were important differences among individuals in the development of said expertise, which we found to be in part due to the movement of the prey encountered.

Our results suggest that the acquisition of hunting expertise was honed 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. Our observations are consistent with empirical studies of expertise in both humans and nonhuman animals (reviewed in Dukas 2019). However, the prey’s speed was important in mediating this pattern at the population level. Encountering faster prey led to more difficult encounters for predators. We previously showed in *DBD* that faster movement is an effective strategy used by the prey to avoid predation (Fraser Franco et al. 2022), and other studies have found that as well (Walker et al. 2005; Kelley and Magurran 2011; Martin et al. 2022). This could explain why the relationship was concave in the model where we did not account for prey speed, because the prey were probably increasing their speed as they gained experience. Because the matchmaking algorithm pairs players based on their skill, adept predators were probably encountering prey moving at higher speeds. Thus, our results suggest that predators can gain expertise and maintain success when they encounter prey that move at speeds lower or close to the population-average.

Prey speed also mediated differences among predator players in the development of their expertise. Individual predator players probably differed in their capacity to adjust to difficult prey. Animals are expected to have limited attention that constrain diet choice and image search formation (Dukas and Kamil 2001). Moreover, hunting faster prey requires specialized cognitive abilities and coordination that are energetically costly (Kelley and Magurran 2011). Thus, predators that couldn’t develop counter-strategies to detect or chase 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 suggest that prey antipredator behaviour can also impair predator expertise acquisition, with potential implications for predator-prey dynamics.

Despite adjusting for the prey’s speed, discernible variations in expertise acquisition among predator players persisted, indicating the possible influence of other factors. It is hypothesized that longer time intervals between hunting events can hinder or delay the acquisition of expertise because individuals may forget information when delays are longer (Endler 1991; Wright et al. 2022). In *DBD*, a predator that played 300 matches in the span of six months might forget more critical information related to prey detection or escape patterns than one that played 300 matches in the span of six days. Investigating the impact of such time lags in future analyses may reveal important insights on the outcome of predator-prey interactions. Another limitation of our study is that the life of neither the predator nor the prey players are at stake in *DBD*, such that emerging patterns could be driven by their motivation to win and not “true” survival. For example, some players could experiment with the game out of boredom, which could impede ecologically realistic interpretations of our data. Lastly, the prey can be consumed in a match but carry that experience on to the next round without any penalty. Thus, interpretations of our results must be made with these caveats in mind.

## Conclusions

We found support of our hypothesis that prey antipredator behaviour was driving individual differences in expertise in a predator population. Our results suggest that predators gained expertise, as their success increased wit extensive practice, but that prey speed impaired expertise acquisition. Future analyses should investigate how efficient antipredator tactics are associated with prey experience, as this may reveal important insights on the eco-evolutionary dynamics of predator prey interactions. Lastly, virtual systems are increasingly used as systems 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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