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

# ABSTRACT

**revoir abstract pour être moins centré sur la tactique**

**revoir la phrase sur ce qu’on fait dans l’étude. Intégrer l’aspect des proies**

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. 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 with 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 individual hunting success changes with repeated encounters (i.e. how individuals develop their hunting expertise). At the population level, we hypothesize that the predators’ success will increase with experience up to a certain level where it will stabilize (Dukas 2019). However, we expect this pattern to vary among individuals due to differences in the movement of prey encountered. Therefore, we then investigate how prey movement influences the development of expertise. If predators encounter groups of prey with similar speeds, we predict that the gain in expertise will be similar among individuals. Alternatively, if predators encounter groups of prey with varying speeds, then the acquisition of expertise will vary among individuals. We predict that faster prey will impair expertise acquisition, such that predators that encountered faster prey will have lower success throughout experience.

# 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 mean hunting success using a Bayesian hierarchical linear model. We found that all four groups had similar successes as predators (Appendix 2: Table S1-S2), which suggests 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 and the MDHGLM to run four MCMC chains with 1000 posterior samples for each parameter. 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 other additive models. We set the first 500 iterations in each model as warm ups. We parametrized the MDHGLM to run 2500 iterations with a thinning set to eight, with the first 500 iterations used as warm ups. 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. We report all the posterior parameter estimates using the median of the posterior distribution with the highest posterior density (HPD) intervals at 50%, 80%, and 95%.

### 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

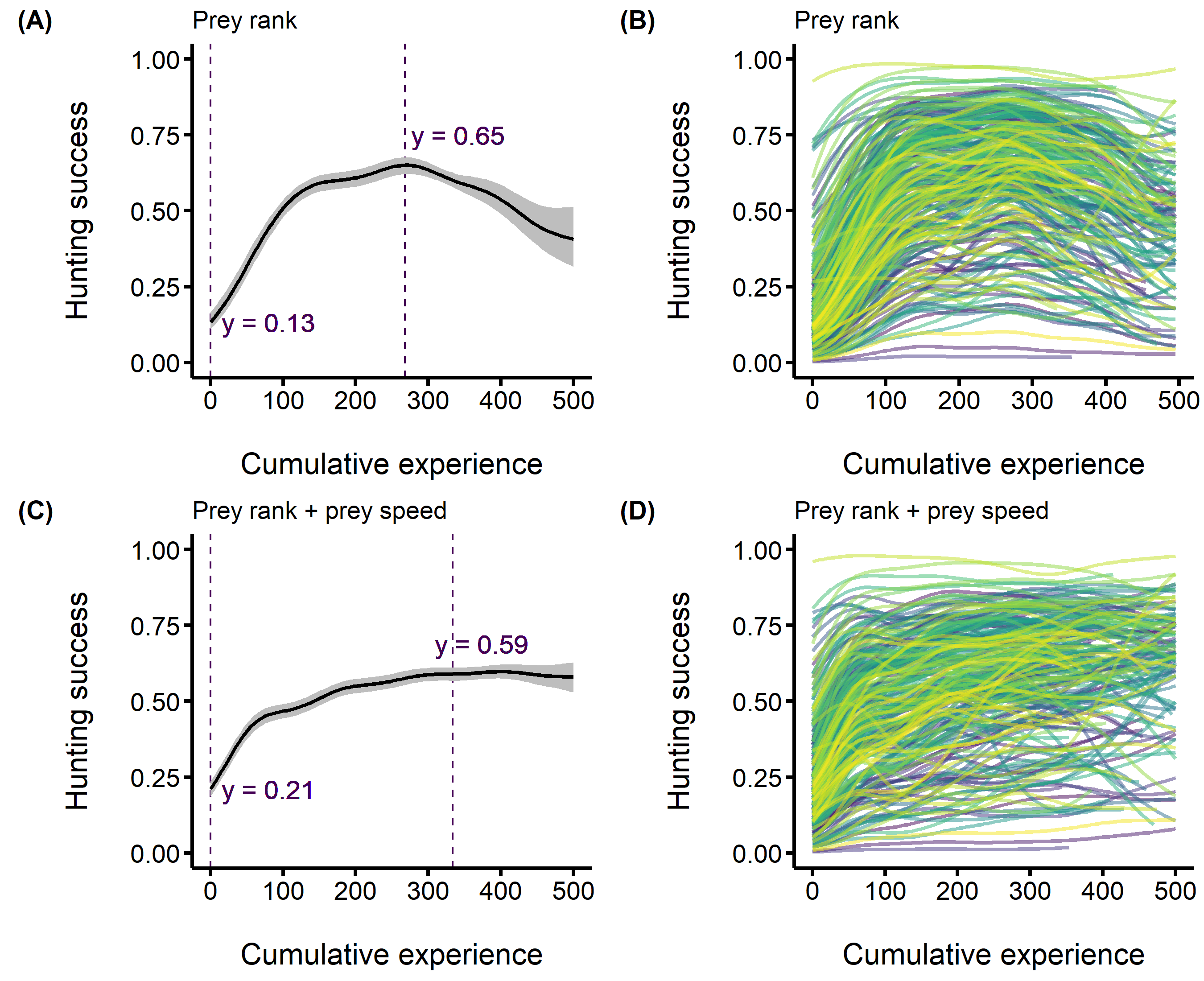
## Development of expertise

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 (i.e. expertise) for the average individual (**Appendix XX**). Accounting for the prey rank resulted in a concave-shaped relationship, with the highest success ranging between 100 and 400 matches (Figure 1A). In the model where we additionally 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).

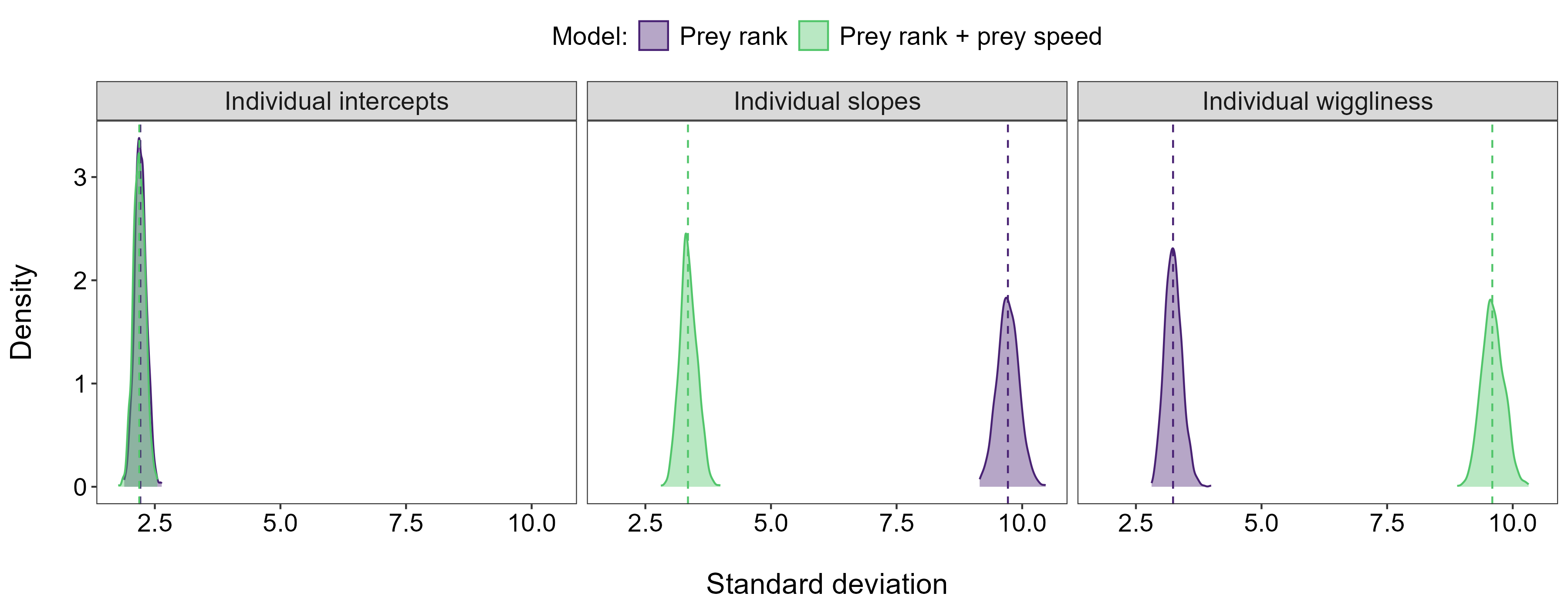
Table 1. Leave-one-out cross-validation table of the five GAMMs relating hunting success to predator experience.

| 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 | | | | |

The relationship between hunting success and cumulative experience differed among predators (Figure 1B-D). Only 28.5% of the population had an increase in success from the first match to the last in the model where we did not account for the prey’s speed and rank (Appendix S1: Figure S1A). In contrast, accounting for both effects resulted in 90.1% of the population increasing its success with experience from the first match to the last. The prey speed mediated individual differences in the relationship between success and experience. The standard deviation of the individual slopes component of the model accounting only for prey rank was equal to 9.72 (9.30, 10.15 ), while the one for the model accounting for prey rank and speed was equal to 3.36 (3.04, 3.71 ), indicating that individual differences in the development of expertise decreased when accounting for prey speed.



**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.



**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 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 power)

# DISCUSSION

It is generally assumed that predators increase prey consumption through time by acquiring hunting expertise (Dukas 2019; Wooster et al. 2023). Yet, few studies have empirically tested this hypothesis in part because of 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, suggesting that predator expertise was honed through extensive practice. Yet, there were important differences among individuals in the development of expertise, which was in part due to differences among individuals in the movement of the prey encountered.

Our results suggest that predator expertise is 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, consistent empirical observations of expertise in both humans and nonhuman animals (reviewed in Dukas 2019) The prey’s speed was important in mediating this pattern at the population level, probably because they also increased their speed as predators gained experience. 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 would explain why the relationship was concave in the model where we did not account for prey speed, because adept predators were probably encountering prey with 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 a portion of the differences among predator players in the development of their expertise, implying that prey antipredator behaviour can impair the development of an individual predator’s expertise. Individual predator players probably differed in their capacity to adjust to difficult prey. For example, 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 for faster prey were likely at a disadvantage.

**Such trade-offs may reflect limitations in learning all the skills required to successfully hunt all types of prey (Healy 1992; Bélisle and Cresswell 1997; Dukas 2019), particularly if the skills required to hunt slower prey are nontransferable to faster prey.**

However, even after we took the prey’s speed into account, there were still important differences in expertise acquisition among predator players, suggesting that other antipredator tactics were potentially involved. For example, the prey can use camouflage and hide to avoid detection (not currently measurable in *DBD*), requiring predators to learn how to exploit visual cues that facilitate cryptic prey detection, such as habitat characteristics or prey colour patterns (Ehlinger 1989; Hughes et al. 1992; Warburton 2003; Szopa-Comley, Donald, and Ioannou 2020). Furthermore, it is hypothesized that longer time intervals between hunting events could hinder or delay the acquisition of expertise as individuals may forget information with longer delays (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.

**Of course, the life of neither the predator nor the prey players are at stake, such that emerging patterns could be driven by their motivation to win and not “true” survival. Yet,** **A potential caveat is that the more flexible hunters might have experimented with various tactics out of boredom, which could impede ecologically realistic interpretations of our data. However, the consistent association between this tactic and heterogeneous prey groups gives us confidence that it emerged from their interactions. One limitation of our study was that we couldn’t monitor all the matches of the prey, which prevented us from assessing their responses to the predator through their experience.** Hence, future studies should aim at monitoring reciprocal behavioural dynamics through time, which may reveal important insights on the mechanisms driving stable equilibria in predator-prey systems.

**Comment by reviewer:**

Some characteristics to be aware of: - Predators do not compete. - Both predators and prey can fail in a round yet still carry that experience and knowledge on to the next round with no real penalty (think of the movie Groundhog Day). - Predator and prey are surely playing a game with each other, but prey may also be playing a game among themselves, which may affect their game with the predator. - This particular video game appears to have a few unusual characteristics. Prey do not appear to forage for resources. but rather they create a public good. Furthermore, handling time for the predator is extremely complicated and lengthy. - Finally, it may be rather complicated to discern all of the rules of how the different virtual environments work and what all the aptitudes of all the different predators and prey are.

## Conclusions

We found support of our prediction that prey were driving individual differences in expertise in a predator population. Our results suggest that predators learned with experience, as their success increased… Even though individuals were not all equally successful. Lastly, virtual systems are increasingly recognized as being useful to test hypotheses on ecological interactions (Beauchamp 2020; Céré, Montiglio, and Kelly 2021; Fraser Franco et al. 2022; Lymbery, Webber, and Didham 2023). We therefore hope that our study will inspire more collaborations between scientists and the videogame industry to tackle fundamental questions in ecology.

# REFERENCES

Beauchamp, Guy. 2020. “Predator Attack Patterns Influence Vigilance in a Virtual Experiment.” *Behavioral Ecology and Sociobiology* 74 (4): 49. <https://doi.org/10.1007/s00265-020-02833-0>.

Bélisle, Claude, and James Cresswell. 1997. “The Effects of a Limited Memory Capacity on Foraging Behavior.” *Theoretical Population Biology* 52 (1): 78–90. <https://doi.org/10.1006/tpbi.1997.1319>.

Brosnan, Sarah F., and Erik Postma. 2017. “Humans as a Model for Understanding Biological Fundamentals.” *Proceedings of the Royal Society B: Biological Sciences* 284 (1869): 20172146. <https://doi.org/10.1098/rspb.2017.2146>.

Bürkner, Paul-Christian. 2017. “Brms: An R Package for Bayesian Multilevel Models Using Stan.” *Journal of Statistical Software* 80 (1): 1–28. <https://doi.org/10.18637/jss.v080.i01>.

Céré, Julien, Pierre-Olivier Montiglio, and Clint D Kelly. 2021. “Indirect Effect of Familiarity on Survival: A Path Analysis on Video Game Data.” *Animal Behaviour* 181: 105–16. <https://doi.org/10.1016/j.anbehav.2021.06.010>.

Crane, Adam L., Laurence E. A. Feyten, Alexyz A. Preagola, Maud C. O. Ferrari, and Grant E. Brown. 2024. “Uncertainty about Predation Risk: A Conceptual Review.” *Biological Reviews* 99 (1): 238–52. https://doi.org/<https://doi.org/10.1111/brv.13019>.

Dukas, Reuven. 2019. “Animal Expertise: Mechanisms, Ecology and Evolution.” *Animal Behaviour* 147: 199–210. <https://doi.org/10.1016/j.anbehav.2018.05.010>.

Edwards, G. B., and Robert R. Jackson. 1994. “The Role of Experience in the Development of Predatory Behaviour in Phidippus Regius, a Jumping Spider (Araneae, Salticidae) from Florida.” *New Zealand Journal of Zoology* 21 (3): 269–77. <https://doi.org/10.1080/03014223.1994.9517994>.

Ehlinger, Timothy J. 1989. “Learning and Individual Variation in Bluegill Foraging: Habitat-Specific Techniques.” *Animal Behaviour* 38 (4): 643–58. <https://doi.org/10.1016/S0003-3472(89)80010-7>.

Endler, J. A. 1991. “Interactions Between Predators and Prey.” In *Behavioural Ecology*, edited by J. R. Krebs and N. B. Davies, Third, 169–96. Oxford: Blackwell.

Fraser Franco, Maxime, Francesca Santostefano, Clint D Kelly, and Pierre-Olivier Montiglio. 2022. “Studying Predator Foraging Mode and Hunting Success at the Individual Level with an Online Videogame.” *Behavioral Ecology* 33 (5): 967–78. <https://doi.org/10.1093/beheco/arac063>.

Gabry, Jonah, and Rok Češnovar. 2021. “Cmdstanr: R Interface to "CmdStan".”

Glaudas, Xavier, Kelsey L. Glennon, Marcio Martins, Luca Luiselli, Simon Fearn, Dane F. Trembath, Dušan Jelić, and Graham J. Alexander. 2019. “Foraging Mode, Relative Prey Size and Diet Breadth: A Phylogenetically Explicit Analysis of Snake Feeding Ecology.” *Journal of Animal Ecology* 88 (5): 757–67. <https://doi.org/10.1111/1365-2656.12972>.

Gravel, Dominique, Timothée Poisot, Camille Albouy, Laure Velez, and David Mouillot. 2013. “Inferring Food Web Structure from Predator-Prey Body Size Relationships.” *Methods in Ecology and Evolution* 4 (11): 1083–90. https://doi.org/<https://doi.org/10.1111/2041-210X.12103>.

Healy, Sue. 1992. “Optimal Memory: Toward an Evolutionary Ecology of Animal Cognition?” *Trends in Ecology & Evolution* 7 (12): 399–400. <https://doi.org/10.1016/0169-5347(92)90019-8>.

Herbert-Read, J. E., A. J. W. Ward, D. J. T. Sumpter, and R. P. Mann. 2017. “Escape Path Complexity and Its Context Dependency in Pacific Blue-Eyes (Pseudomugil Signifer).” *Journal of Experimental Biology* 220 (11): 2076–81. <https://doi.org/10.1242/jeb.154534>.

Hughes, R. N., M. J. Kaiser, P. A. Mackney, and K. Warburton. 1992. “Optimizing Foraging Behaviour Through Learning.” *Journal of Fish Biology* 41: 77–91. <https://doi.org/10.1111/j.1095-8649.1992.tb03870.x>.

Kasumovic, Michael M., Khandis Blake, and Thomas F. Denson. 2017. “Using Knowledge from Human Research to Improve Understanding of Contest Theory and Contest Dynamics.” *Proceedings of the Royal Society B: Biological Sciences* 284 (1869): 20172182. <https://doi.org/10.1098/rspb.2017.2182>.

Kelley, Jennifer L., and Anne E. Magurran. 2011. “Learned Defences and Counterdefences in Predator-Prey Interactions.” In *Fish Cognition and Behavior*, 36–58. John Wiley & Sons, Ltd. <https://doi.org/10.1002/9781444342536.ch3>.

Lymbery, Samuel J., Bruce L. Webber, and Raphael K. Didham. 2023. “Complex Battlefields Favor Strong Soldiers over Large Armies in Social Animal Warfare.” *Proceedings of the National Academy of Sciences* 120 (37): e2217973120. <https://doi.org/10.1073/pnas.2217973120>.

MacDonald, Katharine. 2007. “Cross-Cultural Comparison of Learning in Human Hunting.” *Human Nature* 18 (4): 386–402. <https://doi.org/10.1007/s12110-007-9019-8>.

Martin, Benjamin T., Michael A. Gil, Ashkaan K. Fahimipour, and Andrew M. Hein. 2022. “Informational Constraints on Predator-Prey Interactions.” *Oikos* 2022 (10): e08143. <https://doi.org/10.1111/oik.08143>.

Morse, Douglass H. 2000. “The Effect of Experience on the Hunting Success of Newly Emerged Spiderlings.” *Animal Behaviour* 60 (6): 827–35. <https://doi.org/10.1006/anbe.2000.1546>.

Peckarsky, Barbara L., Peter A. Abrams, Daniel I. Bolnick, Lawrence M. Dill, Jonathan H. Grabowski, Barney Luttbeg, John L. Orrock, et al. 2008. “Revisiting the Classics: Considering Nonconsumptive Effects in Textbook Examples of Predator-Prey Interactions.” *Ecology* 89 (9): 2416–25. https://doi.org/<https://doi.org/10.1890/07-1131.1>.

Pedersen, Eric J., David L. Miller, Gavin L. Simpson, and Noam Ross. 2019. “Hierarchical Generalized Additive Models in Ecology: An Introduction With Mgcv.” *PeerJ* 7: e6876. <https://doi.org/10.7717/peerj.6876>.

Piironen, Juho, and Aki Vehtari. 2017. “Comparison of Bayesian Predictive Methods for Model Selection.” *Statistics and Computing* 27 (3): 711–35. <https://doi.org/10.1007/s11222-016-9649-y>.

Preisser, Evan L., John L. Orrock, and Oswald J. Schmitz. 2007. “Predator Hunting Mode and Habitat Domain Alter Nonconsumptive Effects in Predator–Prey Interactions.” *Ecology* 88 (11): 2744–51. <https://doi.org/10.1890/07-0260.1>.

Reid, Amelia, Frank Seebacher, and Ashley Ward. 2010. “Learning to Hunt: The Role of Experience in Predator Success.” *Behaviour* 147 (2): 223–33. <https://doi.org/10.1163/000579509X12512871386137>.

Santostefano, Francesca, Maxime Fraser Franco, and Pierre-Olivier Montiglio. 2024. “Social interactions generate complex selection patterns in virtual worlds.” *Journal of Evolutionary Biology*, May, voae055. <https://doi.org/10.1093/jeb/voae055>.

Stevens, Martin, Kate L. A. Marshall, Jolyon Troscianko, Sive Finlay, Dan Burnand, and Sarah L. Chadwick. 2012. “Revealed by conspicuousness: distractive markings reduce camouflage.” *Behavioral Ecology* 24 (1): 213–22. <https://doi.org/10.1093/beheco/ars156>.

Szopa-Comley, Andrew W., William Gregory Donald, and Christos C. Ioannou. 2020. “Predator Personality and Prey Detection: Inter-Individual Variation in Responses to Cryptic and Conspicuous Prey.” *Behavioral Ecology and Sociobiology* 74 (6): 70. <https://doi.org/10.1007/s00265-020-02854-9>.

Team, Stan Development. 2023. *Stan Modeling Language Users Guide and Reference Manual*. 2.31 ed.

Troscianko, Jolyon, Alice E. Lown, Anna E. Hughes, and Martin Stevens. 2013. “Defeating Crypsis: Detection and Learning of Camouflage Strategies.” *PLOS ONE* 8 (9): 1–8. <https://doi.org/10.1371/journal.pone.0073733>.

Troscianko, Jolyon, John Skelhorn, and Martin Stevens. 2018. “Camouflage Strategies Interfere Differently with Observer Search Images.” *Proceedings of the Royal Society B: Biological Sciences* 285 (1886): 20181386. <https://doi.org/10.1098/rspb.2018.1386>.

Vehtari, Aki, Andrew Gelman, and Jonah Gabry. 2017. “Practical Bayesian Model Evaluation Using Leave-One-Out Cross-Validation and WAIC.” *Statistics and Computing* 27 (5): 1413–32. <https://doi.org/10.1007/s11222-016-9696-4>.

Vehtari, Aki, Andrew Gelman, Daniel Simpson, Bob Carpenter, and Paul-Christian Bürkner. 2021. “Rank-Normalization, Folding, and Localization: An Improved $\Widehat{}R{}$ for Assessing Convergence of MCMC (with Discussion).” *Bayesian Analysis* 16 (2): 667–718. <https://doi.org/10.1214/20-BA1221>.

Vehtari, Aki, Daniel Simpson, Andrew Gelman, Yuling Yao, and Jonah Gabry. 2022. “Pareto Smoothed Importance Sampling.” arXiv. <https://doi.org/10.48550/arXiv.1507.02646>.

Walker, J. A., C. K. Ghalambor, O. L. Griset, D. McKENNEY, and D. N. Reznick. 2005. “Do Faster Starts Increase the Probability of Evading Predators?” *Functional Ecology* 19 (5): 808–15. <https://doi.org/10.1111/j.1365-2435.2005.01033.x>.

Warburton, Kevin. 2003. “Learning of Foraging Skills by Fish.” *Fish and Fisheries* 4 (3): 203–15. <https://doi.org/10.1046/j.1467-2979.2003.00125.x>.

Wilson-Rankin, Erin E. 2015. “Level of Experience Modulates Individual Foraging Strategies of an Invasive Predatory Wasp.” *Behavioral Ecology and Sociobiology* 69 (3): 491–99. <https://doi.org/10.1007/s00265-014-1861-1>.

Wirsing, Aaron J., Michael R. Heithaus, Joel S. Brown, Burt P. Kotler, and Oswald J. Schmitz. 2021. “The Context Dependence of Non-Consumptive Predator Effects.” *Ecology Letters* 24 (1): 113–29. https://doi.org/<https://doi.org/10.1111/ele.13614>.

Wooster, Eamonn I. F., Kaitlyn M. Gaynor, Alexandra J. R. Carthey, Arian D. Wallach, Lauren A. Stanton, Daniel Ramp, and Erick J. Lundgren. 2023. “Animal Cognition and Culture Mediate Predatorprey Interactions.” *Trends in Ecology & Evolution*. <https://doi.org/10.1016/j.tree.2023.09.012>.

Wright, Jonathan, Thomas R. Haaland, Niels J. Dingemanse, and David F. Westneat. 2022. “A Reaction Norm Framework for the Evolution of Learning: How Cumulative Experience Shapes Phenotypic Plasticity.” *Biological Reviews* 97 (5): 1999–2021. <https://doi.org/10.1111/brv.12879>.