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

# ABSTRACT

The capacity of predators to match their hunting tactic to their prey is expected to drive the outcome of predator-prey interactions. To do so, predators need to practice their tactics extensively to develop the expertise to be successful hunters. Yet, there are limited empirical assessments showing links between experience and hunting success at the individual and population levels 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 predators across repeated interactions with their prey. We show that predators optimized prey consumption as they gained experience. Prey speed was an important mediator of this relationship, resulting in differences among predators in the development of expertise. **Décrire le reste des résultats…**

Keywords: foraging behaviour, experience, learning, antipredator behaviour, virtual ecology, Dead by Daylight

# INTRODUCTION

**Est-ce que j’intègre le time lag???**

The ecological consequences of predation are defined by the sum of consumptive and nonconsumptive effects (CEs and NCEs) when predators hunt [refs]. Recent advances in our understanding of the behavioural mechanisms (e.g. reciprocal plasticity, foraging specialization) driving prey consumption at the individual and population level have allowed ecologists to use information on predation regimes to predict the outcome of (N)CEs and their effect on prey population and community dynamics [refs]. For example, empirical studies show that prey tend to increase vigilance at the expense of foraging in the presence of ambush predators (NCEs). Because ambush predators are opportunistic hunters, they also tend to consume a greater range of prey types (CEs) compared to cursorial predators [refs].

While the foraging mode of predators is a reliable trait used to predict prey consumption, predators can only be successful if they practiced and learned the skills that makes them adept at hunting their prey, that is, hunting expertise [Dukas (2019);wooster.etal2023]. The aquisition of expertise is predicted to be paramount in many predator systems where hunting tactics are learned (e.g. orca whales). Yet, there is only fraction of evidence showing the link between experience and success in natural predators, impeding our ability to accurately predict the consequences of predation on prey populations.

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 using cues from their prey and their environment (Edwards and Jackson 1994; Morse 2000; MacDonald 2007; Reid, Seebacher, and Ward 2010; Wilson-Rankin 2015). Predators can integrate this information to use the appropriate hunting tactic (e.g. ambushing or fast movement speeds) for the type of prey that they encounter (Toscano and Griffen 2014; Patrick and Weimerskirch 2014; Toscano et al. 2016). However, prey often use antipredator tactics such as rapid or unpredictable movements which are proven to be effective to successfully escape predators (Walker et al. 2005; Jennifer L. Kelley and Magurran 2011; Herbert-Read et al. 2017; Szopa-Comley and Ioannou 2022). This results in reciprocal interactions where predators need to learn to predict the movement of their prey to capture them. Predators should thus benefit from rapidly acquiring expertise to maximise prey consumption.

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 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). We found that prey can increase their chances of survival by cooperating and moving fast when they forage (Céré, Montiglio, and Kelly 2021; Fraser Franco et al. 2022, Santostefano et al. 2024). 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, the game ellicits natural reactions in players such as fear from predation (personal observations), which corroborates with another virtual ecological study showing that predation drives individual variation in risk perception (Beauchamp 2020). In a different system, Lymbery, Webber, and Didham (2023) showed that complex environments favor strong soldiers over large armies in a virtual game as well as in the laboratory with two ant species. These observations outline how ecological patterns can emerge from interactions in virtual systems with fixed rules. 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 experience shapes predator foraging success using data from players in *Dead by Daylight*. First, we investigate how individual hunting success changes with experience (i.e. how individuals develop their hunting expertise). We hypothesize that the predators’ success will increase with experience up to a certain level where it will stagnate. We expect this pattern to vary among individuals due to differences in prey encounters.

Second, we investigate how the interaction between experience and prey encounters influence the development of expertise.

If all predators encounter similar groups of prey, we predict that individuals (and thus the population) should all specialize in similar speeds. In contrast, if all predators encounter varying groups of prey, then they should all converge towards flexible speeds. In both scenarios, differences among individuals in IIV across experience should be low (i.e. similar individual foraging specialization), whereas the population variance would either decrease (specialization) or increase (flexibility). Alternatively, differences among individuals in foraging specialization may emerge if they experience different interactions with their prey. In this case, we expect predators that encountered similar groups of prey across experience to specialize in similar speeds, while predators that encountered heterogeneous groups across matches should adopt flexible movement speeds, resulting in an increase in among individual differences in IIV with experience. If we detect such prey-dependent fine-tuning with experience, then all hunters along the flexible-specialist continuum should attain equal success.

# 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. Each player, predator or prey, can choose an avatar with abilities that encourage specific play styles (e.g. bold vs cautious prey, or ambush vs roaming predator). During our study period, the game offered 23 predator avatars. The virtual 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 the environments, probably due to a game feature enabling them to have visual cues of the generators (Fraser Franco et al. 2022). There were 35 virtual game environments available for play during the study period.

## 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 predator players with a total record of 100 412 matches. The predator-players’ experience varied between 301 and 500 matches played. These matches lasted between 3 and 70 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 the player encountered, and their mean rank (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 also categorized predators for each match based on their cumulated experience. We labeled predators as novices for matches where they had cumulated less than 100 matches, intermediate for matches where they had cumulated between 100 and 299 matches, and advanced for matches where they had cumulated more than 299 matches (max 499). Since our goal was to monitor predator players throughout their experience and that they all played at least 300 matches, they all appeared in each of the three experience categories.

We recognize that we could have biased 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 speed using a Bayesian hierarchical linear model. We found that all four groups had similar mean speeds as predators (Appendix 2: Table S1-S2), which indicates an absence of bias due to data sampling.

## Statistical analyses

### Software and computer specifications

All models were fitted under a Bayesian framework 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 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.

### Model specification

We tested how prey influenced the development of predator 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 models’ predictive accuracies 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 (for details, see <https://github.com/quantitative-ecologist/experience-hunting-tactics>). 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%.

# RESULTS

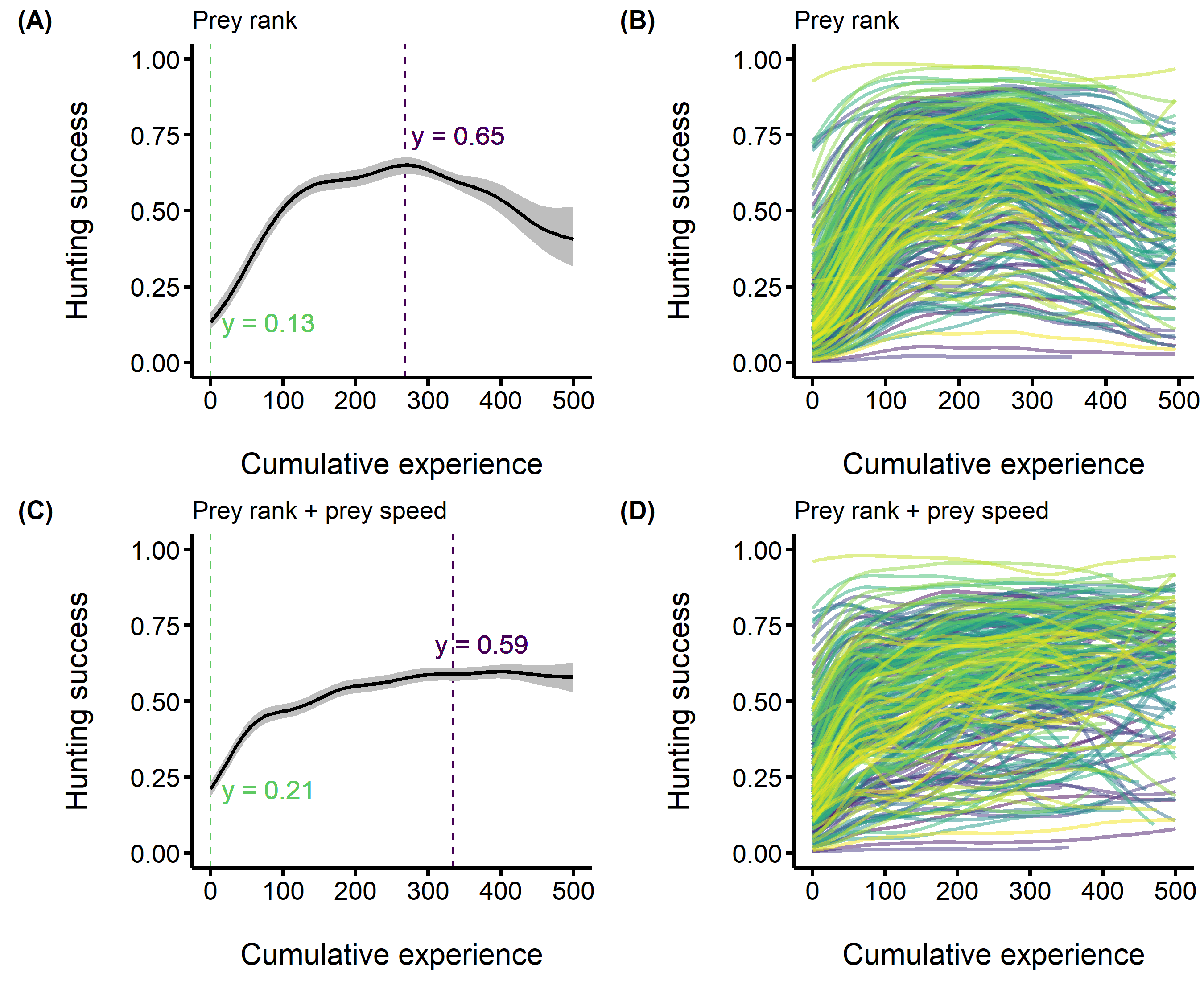
## Development of expertise

Out of all five GAMM models, two predicted the data the best and achieved similar expected log pointwise densities (elpd). Both models accounted for the prey group’s rank and speed (Table 1). Models in which these effects were not accounted for resulted in no change in hunting success with experience (i.e. expertise) for the average individual (results not shown). 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, 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 alone also 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.

# DISCUSSION

A general assumption of predator-prey studies is that predators maximize success by matching their tactic to their prey (Abrams 2000), yet, it has remained largely unknown whether this results from predators learning how to hunt their prey in part because of the challenges of investigating direct interactions in the wild. By capitalizing on a virtual predator-prey system where interactions were directly monitored, we found that predators in *Dead by Daylight* increased their hunting success with experience, suggesting that predator expertise was honed through extensive practice. **parler de l’effet des proies**

## The development of expertise

Our results suggest that predator expertise is honed through extensive practice. The predator population increased and stabilized its success with experience in a diminishing returns fashion as it is typically found in empirical studies of expertise (reviewed in Dukas 2019). The prey were important in mediating this pattern, probably because they 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; Jennifer L. Kelley and Magurran 2011; Martin et al. 2022). This resulted in discernable differences in the relationship between success and experience among predators, implying that the development of expertise depends on an individual’s capacity to adjust to difficulty. Hunting faster prey requires costly and specialized cognitive abilities and coordination (Jennifer L. Kelley and Magurran 2011), and that could explain why such prey were more difficult to capture. Thus, predators that couldn’t properly hunt at high speeds or develop counter-strategies for faster prey were likely at a disadvantage.

## The role of prey behaviour

However, even after we took the prey’s speed into account, there were still important differences in expertise acquisition among predators, suggesting that other antipredator tactics were potentially involved. For example, if the prey used camouflage or hiding to avoid being detected, then predators may have found them only if they learned how to exploit the 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).

In addition, longer time intervals between hunting events may delay or even impede learning due to forgetting important information (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.

Yet, because prey can also learn how to avoid predation (Jennifer L. Kelley and Magurran 2003; Turner, Turner, and Lappi 2006; McComb et al. 2011), we believe that the predator-prey phenotype matching more likely emerged from reciprocal adjustments in speed by predators and prey as they interacted (Kishida, Mizuta, and Nishimura 2006; Kishida, Trussell, and Nishimura 2009; Edgell and Rochette 2009; McGhee, Pintor, and Bell 2013). Hence, if the prey also learned through repeated interactions with the predators, it is possible that experience contributed in stabilizing the system as both were adjusting to each other, similar to Red Queen dynamics (Brockhurst et al. 2014).

However, there were still considerable differences in success among individuals through time, suggesting that some predators were limited in their capacity to match their tactic to their prey or to increase their success through other means. Specialist foragers were faster, and thus, probably better equipped to hunt the more difficult faster prey in *DBD*. However, if the prey responded to fast predators by also being faster, then hunting at high speeds resulted in more difficult encounters for these predators, thereby decreasing the benefits of using this tactic (Figure 4). Thus, specializing probably compensated for the difficulty of hunting prey at high speeds by helping predators to better predict the location and movement of their prey. On the other hand, flexible foragers encountered variable prey with slower speeds. Yet, because the prey increased their speed with experience, the benefits of being able to hunt multiple prey types for flexible hunters may have come at the cost of not being adept at capturing faster prey (Pintor et al. 2014). 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.

## 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. **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. 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.

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