Implications of prey skill and antipredator behaviour in the acquisition of predator expertise: a virtual ecological study

# ABSTRACT

**à compléter**

The acquisition of expertise is crucial for predators to be successful hunters. To achieve this, predators must hone their skills and gain knowledge through repeated and extensive practice. It is hypothesized that prey can interfere in this process and hinder the acquisition of predator expertise by employing antipredator tactics to evade detection and pursuit. However, empirical evidence on how predators acquire expertise through repeated encounters with their prey remains limited, largely due to the challenges of monitoring direct interactions in the wild. Here, we use the game *Dead by Daylight*, a virtual predator-prey system where a human predator chases four human prey, to investigate how experience shapes population and individual hunting success in predators across repeated interactions with their prey. We observed that predators were less successful when hunting faster and more skillful prey. As the prey gained skill, they also moved faster. Our analyses reveal that the predator population should optimize prey consumption over repeated encounters with prey of average skill, and optimize their success sooner if they consistently encounter prey moving at average speeds. However, both prey features did not mediate differences in expertise acquisition among individual predators.

Our results suggest that skilled prey use behaviours such as fast movement to outmanoeuver their predators, thereby impacting how predators acquire expertise at the population level.

impaired the acquisition of expertise by reducing hunting success

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

# INTRODUCTION

Predation is an agent of evolutionary change that regulates prey populations, limits the spread of diseases, and mediates energy flow across trophic levels (Hairston Jr. and Hairston Sr. 1993; Abrams 2000; Ripple et al. 2014; Wirsing et al. 2021). These processes are driven by changes in predation risk and prey capture across landscapes as predators select suitable habitats to hunt and adjust their strategies accordingly (Quevedo, Svanbäck, and Eklöv 2009; Pettorelli et al. 2015; LaBarge et al. 2024; Schmitz 2017). Theory suggests that predators become more efficient hunters by acquiring expertise through practicing and learning the proper skills and tactics to locate, select, and capture their prey (Woo et al. 2008; Wooster et al. 2023; LaBarge et al. 2024). This raises the hypothesis that differences in hunting success between predators may be attributed to differences in the capacity to acquire hunting expertise. Hence, unraveling how expertise emerges is essential to better assess how foraging behaviour shapes prey consumption during predator-prey interactions.

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

Prey respond to predators by using antipredator tactics such as camouflage to avoid detection and rapid escapes to evade capture (Walker et al. 2005; Kelley and Magurran 2011; Herbert-Read et al. 2017). These strategies are hypothesized to drive differences in prey consumption among predators by disrupting their capacity to acquire hunting expertise (Wooster et al. 2023). This has been supported by experimental studies showing that prey camouflage can impair expertise acquisition in humans and birds (Stevens et al. 2012; Troscianko et al. 2013). For example, using a virtual experiment, Troscianko, Skelhorn, and Stevens (2018) found in human subjects that disruptive colouration interfered with their ability to form search images, hindering improvements in detection times over repeated attempts. Beyond prey camouflage, there is limited evidence to suggest that antipredator behaviour hinders the acquisition of predator expertise. Yet, some predators may be limited in their capacity to develop the necessary attributes (e.g. physical, physiological, neurological) for fast-paced hunting, which could impair their acquisition of hunting expertise when facing faster prey. Prey antipredator behaviour can also improve through continued exposure to predators (Turner, Turner, and Lappi 2006; Kelley and Magurran 2011; Lönnstedt et al. 2012). For instance, prey alter their activity patterns under increasing predation risk (Wirsing et al. 2021). Animal reintroduction programs show that individuals trained to recognize predators display more antipredator behaviours and are 1.5 times more likely to survive than individuals that were never exposed to predators (Tetzlaff, Sperry, and DeGregorio 2019). Hence, encountering prey with greater skill or experience may also impair expertise acquisition in predators. To our knowledge, the relationships among prey skill, antipredator behaviour, and the acquisition of expertise by human and nonhuman hunters remain unclear, representing a significant gap in our understanding of predator-prey interactions.

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

In this study, we assess how predator expertise emerges over repeated encounters with prey using data from players in *Dead by Daylight*. We quantify expertise acquisition as the relationship between hunting success (i.e., prey capture) and repeated experience (i.e., cumulated matches). First, we test the hypothesis that predator success will increase with experience up to some point at which it will stabilize (Dukas 2019). However, we hypothesize that prey speed and space coverage will influence predator expertise acquisition by modulating the rate of gain in expertise at the population level. Second, we test the hypothesis that prey with more skill should have improved antipredator behaviour, and we predict that prey with greater predator-avoidance skills will move at faster speeds and cover more space in the virtual environment. Third, if prey antipredator behavior influences the hunting success of predators at the population level, then we expect that the acquisition of predator expertise will vary among individuals.

# MATERIALS AND METHODS

## Study system

*Dead by Daylight* is a survival asymmetric (i.e., gameplay mechanics differ between two groups) multiplayer online game developed by Behaviour Interactive Inc. (Montreal, Canada), in which players can play either as a predator or prey. Every match includes only one predator and four prey. The objective of the predator is to hunt and capture the prey, and the objective of the prey is to search for resources while avoiding the predator. The resources are in the form of power generators that, once all activated, will enable the prey to escape through one of two exit doors. A skill-based matchmaking algorithm determines the composition of the predator and prey group in a match. A match ends when the predator kills all the prey available (i.e., that have not escaped), or when the last remaining prey escapes the virtual environment.

Before the start of a match, players (predator or prey) can choose an avatar with unique abilities that encourage specific play styles (e.g. bold vs cautious prey, or ambush vs roaming predator). During our study period, the game offered 23 predator avatars. The virtual environments comprise fixed and procedurally generated habitat components, such as vegetation, mazes, and buildings. Some of these environments are larger than others, with varying structural complexity. However, predators display only minimal changes in behaviour and hunting success across these environments (Fraser Franco et al. 2022). There were 35 virtual game environments available for play during the study period. Details on the basic characteristics of predator avatars are available at <https://deadbydaylight.fandom.com/wiki/Killers>. Details on the size and structure of the different virtual environments are available at <https://dbdmaps.com/> and <https://deadbydaylight.fandom.com/wiki/Realms>.

## Data collection

Behaviour Interactive Inc. provided data that spanned six months of gameplay recorded for every player from 2020-12-01 to 2021-06-01 (game builds 4.4.0 to 4.7.2). We analyzed only matches where players did not know each other and were unable to communicate using voice-recording devices. We filtered any matches where players were inactive, such as when mean distances travelled per second (i.e., speed) were equal to, or very close to, zero. Moreover, we used our knowledge of the game to remove any matches where players were potentially hacking, or not playing the game as intended.

Our study population comprised 253 players who played at least 300 matches. We monitored all their matches from the first to a maximum of 500 matches, with a total record of 100,412 matches overall. The predator-players’ experience in our population sample varied between 301 and 500 matches played. These matches lasted between 3 and 70 min (mean = 11 min). We recognize that we could have introduced a bias by retaining only those individuals, as they might already be seasoned video game enthusiasts and exhibit expert-level performance in their early matches in *Dead by Daylight*. Thus, we tested sample bias by comparing the results from our dataset to those from a random sample of players who played either 20 to 50 matches, 51 to 100 matches, or 101 to 300 matches during the same timeframe. We then took the first 20 matches played by these players, including those from our population sample, and compared their mean hunting success using a Bayesian hierarchical linear model. We found that all three groups of players had very similar success as the predator in their first 20 matches among them and compared to those used as our focal sample (Appendix 1: Table S1 and Figure S1), giving us confidence that we did not introduce a significant sampling bias.

We collected the following information for every match in our population sample: the player’s anonymous ID, the predator player’s hunting success, the predator player’s cumulated experience, and the mean rank, speed, and space coverage of the group of prey that the predator player encountered. We defined hunting success as the number of prey consumed during the match (min = 0, max = 4). We defined the predator’s cumulative experience as the number of matches played as the predator prior to the match being monitored. For example, the first match of a player would have a cumulative experience value of 0, while the tenth match would have a value of 9.

We used the mean rank of the prey as a proxy of their predator-avoidance skill. Player ranks vary between 1 and 20, with a rank of 1 indicating the highest skill. The ranking system in *Dead by Daylight* was implemented by the company to pair players in a match based on their skill (<https://deadbydaylight.fandom.com/wiki/Rank>). The skill of a player increases based on their performance from match to match. While the ranking system represents an approximation of prey skill, it was the most readily available metric we could access to determine the skill of the prey group, as we did not have access to the prior matches of the prey. In addition, the pairing system is subject to variation depending on factors such as player availability, which can result in predator-prey groups with unbalanced skill, allowing us to evaluate the effect of the prey’s skill on predator success. For a given match, we measured the prey’s rank as the mean rank of the four individual prey (mean = 8.74 ± 4.12), and the prey’s speed as the mean travel speed of the four individual prey in a match (mean = 2.40 ± 0.32 m/s). Lastly, the prey space coverage represents the number of unique 16x16 tiles entered by the predator in a grid that covers the whole virtual environment (mean = 22.98 ± 5.38 tile visits).

## Data analyses

### Model specification

We tested how predators developed their expertise by computing six Bayesian generalized additive mixed models (GAMM) with thin-plate regression splines, all of which estimated the relationship between hunting success and the predators’ cumulative experience. We parametrised the models following the method of Pedersen et al. (2019). For the first and second models (I and II), we assume that individual predators share a similar relationship between success and experience, but that this relationship can vary among them (e.g. predator 1 has a steeper curve than predator 2). This enabled us to test whether predators differed in the development of their expertise. Both models included a common global smoothing function (i.e., population effects) and random smooths for the predator ID (i.e., individual effects). Model I included the standardized match duration as a covariate, while model II included the standardized match duration and the average rank of the prey group, allowing us to test if the variation among predators in expertise acquisition was driven by prey skill. The third model had the same structure as model II but without a global smoother. This model assumes that predators do not share a common relationship between success and experience. In this model, we control for the standardized match duration and the average rank of the prey group. The fourth (IV) and fifth (V) models were expansions of model II, but included the standardized prey speed to assess its effect on the relationship between success and experience. Model IV does not have a standard global smoother, while model V includes one. Lastly, model VI was an extension of model V and included all the aforementioned variables with the addition of the standardized space covered by the prey.

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

We defined weakly informative Gaussian priors for the intercept () and the global trend of cumulative experience (). Following Fraser Franco et al. (2022), we defined a positive Gaussian prior () for the slope of the game duration, a Gaussian prior () for the slope of the prey rank, and negative Gaussian priors on prey speed and space coverage (). We defined a positive Gaussian prior on the precision parameter (). We employed weakly informative half-Gaussian priors on all the standard deviation parameters ().

To test the hypothesis that prey speed and space coverage increases with prey skill, we fitted Bayesian linear regression models estimating the relationship between 1) prey speed and the standardized prey rank and 2) prey space coverage and the standardized prey rank. In both models, we controlled for the game duration, using it as a linear covariate, and included the predator identity as a random effect. We used weakly informative Gaussian priors on the slopes of the game duration () and weakly informative negative Gaussian priors on the slopes of the prey rank () because prey of greater skill (i.e., rank 1 is the highest skill) should move faster and cover more space in the environment. Lastly, we used weakly informative Gaussian priors on the intercepts of prey speed () and space coverage () as we assumed that prey should move at around two meters per second and cover at least 15 tiles in the virtual environment. Lastly, we employed half-Gaussian priors on the standard deviation parameters () in both models.

### Parameter sampling settings

We parametrised the GAMMs to run four chains of 1500 iterations each, discarding the first 500 iterations of each chain as warm-up, and sampling one parameter value per iteration thereafter. Similarly, the linear models ran four chains of 1500 iterations each, sampling a parameter value at every iteration, and discarding the first 500 iterations. We thus obtained 4000 posterior samples per parameter in each model. We assessed the convergence of the chains using trace plots, R-hat diagnostics with a threshold set between 1.00 and 1.02, and effective sample sizes (ESS) with a threshold of >100 (Vehtari et al. 2021). We also performed posterior predictive checks, which showed an adequate fit of the models.

We fitted all models on a remote computer cluster (<https://docs.alliancecan.ca/wiki/Cedar>) using R (version 4.4.0). Model fitting was performed via Hamiltonian Monte Carlo (HMC) sampling with the “brms” package version 2.22.12 (Bürkner 2017), an R front-end for the STAN software (Stan Development Team 2023). We used “cmdstanr” version 0.9.0 (Gabry and Češnovar 2021) as the computational back-end for parameter estimation, with CmdStan installation version 2.36.0. We provide a detailed workflow for reproducing our results in the following GitHub repository (<https://github.com/quantitative-ecologist/predator-expertise>).

### Hypothesis testing

We tested the hypothesis that antipredator behaviour impairs the acquisition of predator expertise at the population level by comparing the global trends of model I (only controlling for game duration), model II (controlling for game duration and prey rank), model V (controlling for game duration, prey rank, and prey speed), and model VI (controlling for game duration, prey rank, prey speed, and prey space coverage) using the finite differences method (Figure 1). This allowed us to locate the point at which hunting success was optimized. At the individual level, we tested the hypothesis that antipredator behaviour generates differences among predators in expertise acquisition by comparing the individual-level variance parameters. Specifically, we compared the posterior distributions of standard deviations for 1) the random intercepts (i.e., mean differences in hunting success), 2) the random slopes (i.e., linear component relating hunting success with experience), and 3) the curve wiggliness (i.e., nonlinear component relating hunting success with experience).

# RESULTS

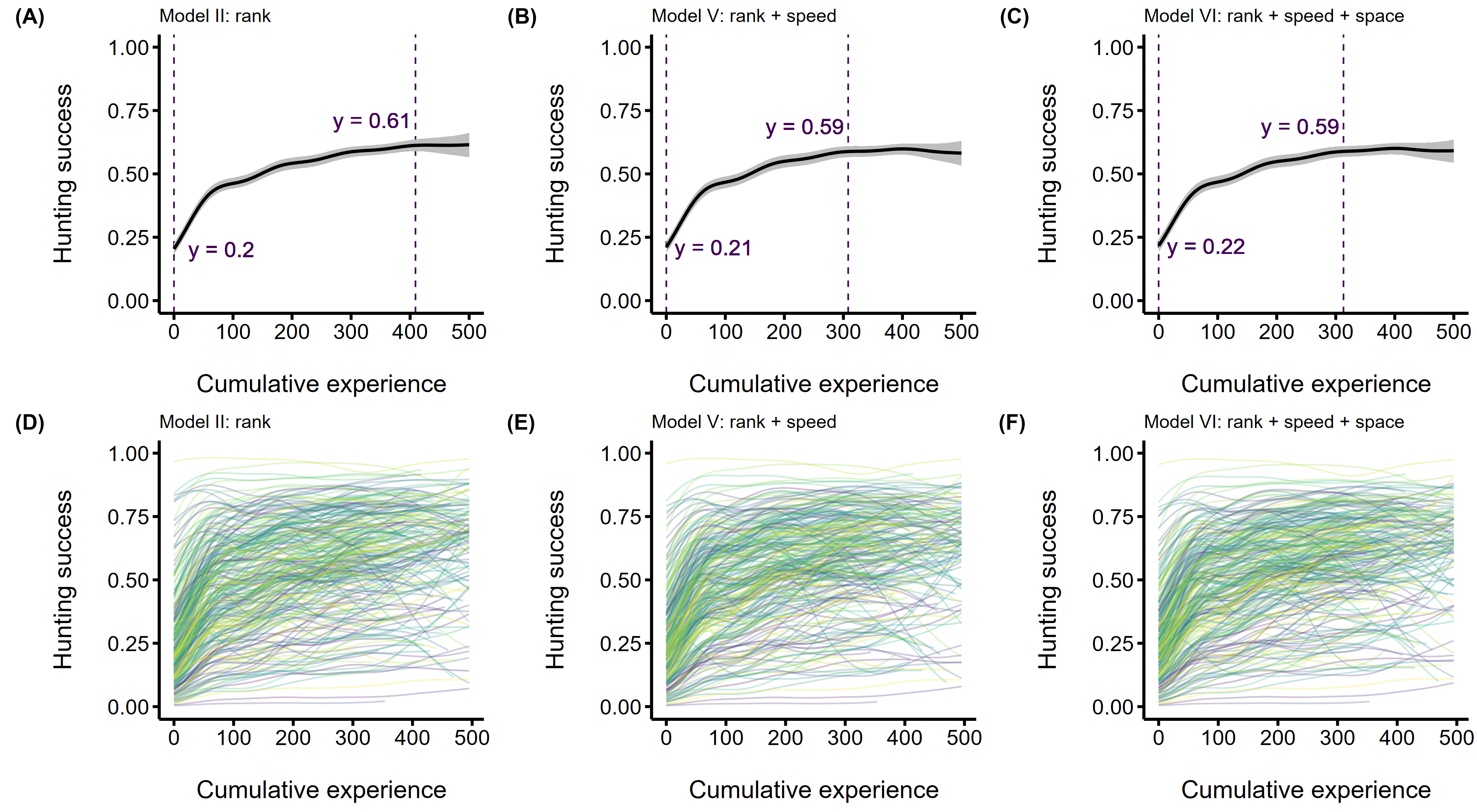
## Acquisition of expertise at the population level

When comparing models with the same covariate structure (i.e., model II and III; model IV and V), those that included a global smoother generally performed better at predicting hunting success than those without one (Table 1). This suggests that there is a common underlying structure in the relationship between success and experience across the population, despite differences among individual predators (Figure 1). Overall, model VI, which included all prey features, was the best at predicting predator hunting success (Table 1).

Table 1. Leave-one-out (loo) cross-validation results comparing the predictive performance of the five GAMMs estimating the relationship between hunting success and predator experience. All models reported include the game duration as a control. Only differences in smoothing functions and prey covariates are reported.

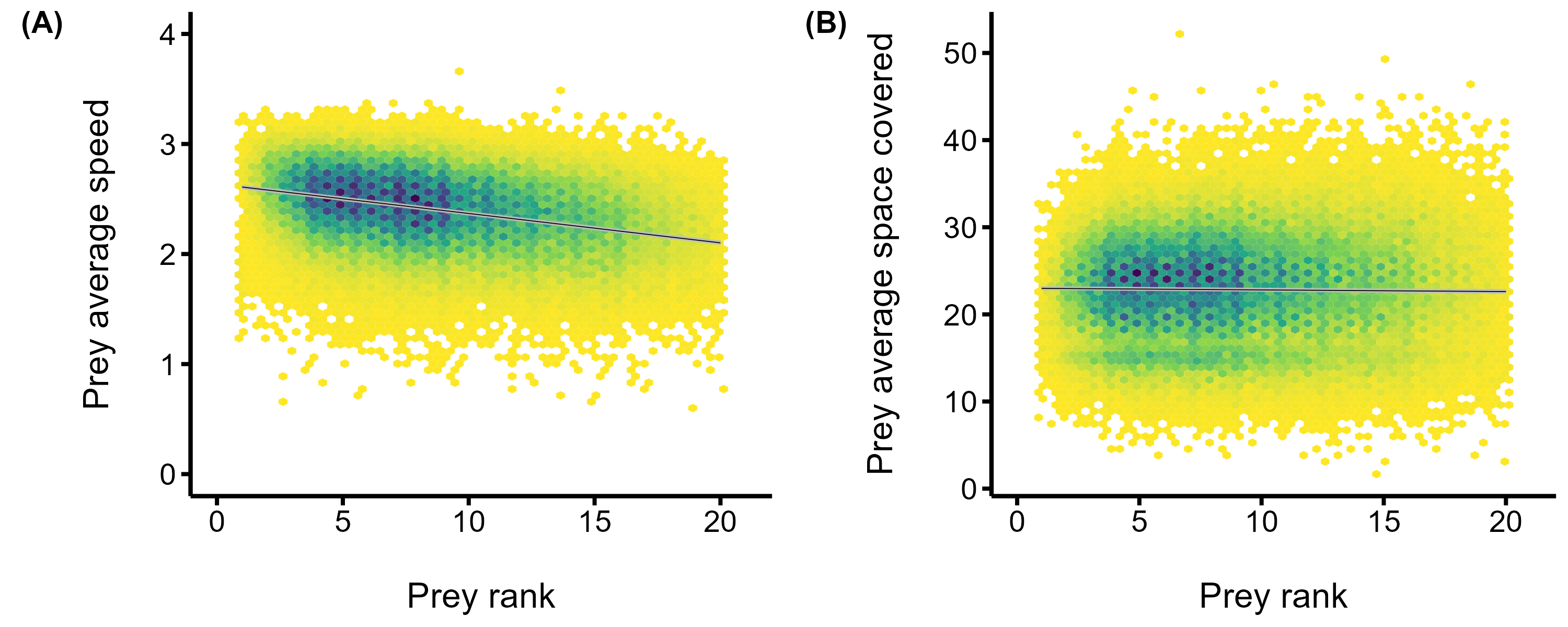
| model | elpd  differencea | sd  difference | elpd loo  value | elpd loo  standard error |
| --- | --- | --- | --- | --- |
| (VI) experience + ID smoothers + prey rank + prey speed + prey space | 0.00 | 0.00 | -135 073.46 | 204.52 |
| (V) experience + ID smoothers + prey rank + prey speed | -1 046.49 | 48.16 | -136 119.95 | 201.03 |
| (IV) ID smoothers + prey rank + prey speed | -1 106.89 | 50.45 | -136 180.35 | 200.91 |
| (II) experience + ID smoothers + prey rank | -6 168.64 | 114.86 | -141 242.10 | 183.12 |
| (III) ID smoothers + prey rank | -6 230.95 | 115.80 | -141 304.41 | 182.86 |
| (I) experience + ID smoothers | -11 181.79 | 143.63 | -146 255.25 | 165.41 |
| a 'elpd' refers to the expected log pointwise density and is the value chosen to select the best model. | | | | |

As we expected, models in which we did not account for the prey rank resulted in almost no change in hunting success with experience for the average individual (i.e., no gain in expertise, Figure S2) due to the matchmaking algorithm pairing predators and prey with similar skill levels. Accounting for the prey rank (model II) influenced the form of the relationship, revealing a diminishing returns curve with predators optimizing their success after playing 454 matches (Figure 1A). Our results indicate that the average predator improves its hunting success by ~40% from the first to the 454 match by hunting prey of average skill (Figure 1A).



**Figure 1**. Median posterior predictions of the acquisition of predator hunting expertise. The predators’ hunting success (i.e., the probability of consuming the four prey) is on the y-axis, and the predators’ cumulative experience (i.e., the number of matches played before each observation) is on the x-axis. Panels A to C show the acquisition of expertise for the average individual, with the vertical dashed lines on the left representing the lowest predicted values. For panel A, the right-side vertical dashed line shows the highest predicted success. For panels B and 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 D to F show among-individual differences in the acquisition of expertise, with each curve representing an individual predator. All models displayed include the game duration as a linear covariate. (A-D) Model II, where we control for the game duration and the prey rank exclusively. (B-E) Model V, where we control for game duration as well as the rank and speed of the prey group. (C-F) Model VI, where we control for game duration as well as the rank, speed, and space coverage of the prey group.

Controlling for prey speed and space coverage did not qualitatively alter the form of the relationship between success and experience at the population level. However, the rate of expertise acquisition shifted slightly: the predator population reached its maximal hunting success earlier, after 323 matches (Figure 1B-C). We also found strong evidence that hunting success declined when predators pursued faster prey or prey occupying more space in the virtual environment (Figure S3A-B). Moreover, prey groups composed of individuals with greater skill moved faster than those composed of individuals with lower skill (Figure 2A). In contrast, there was no change in prey space coverage with increasing skill (Figure 2B).

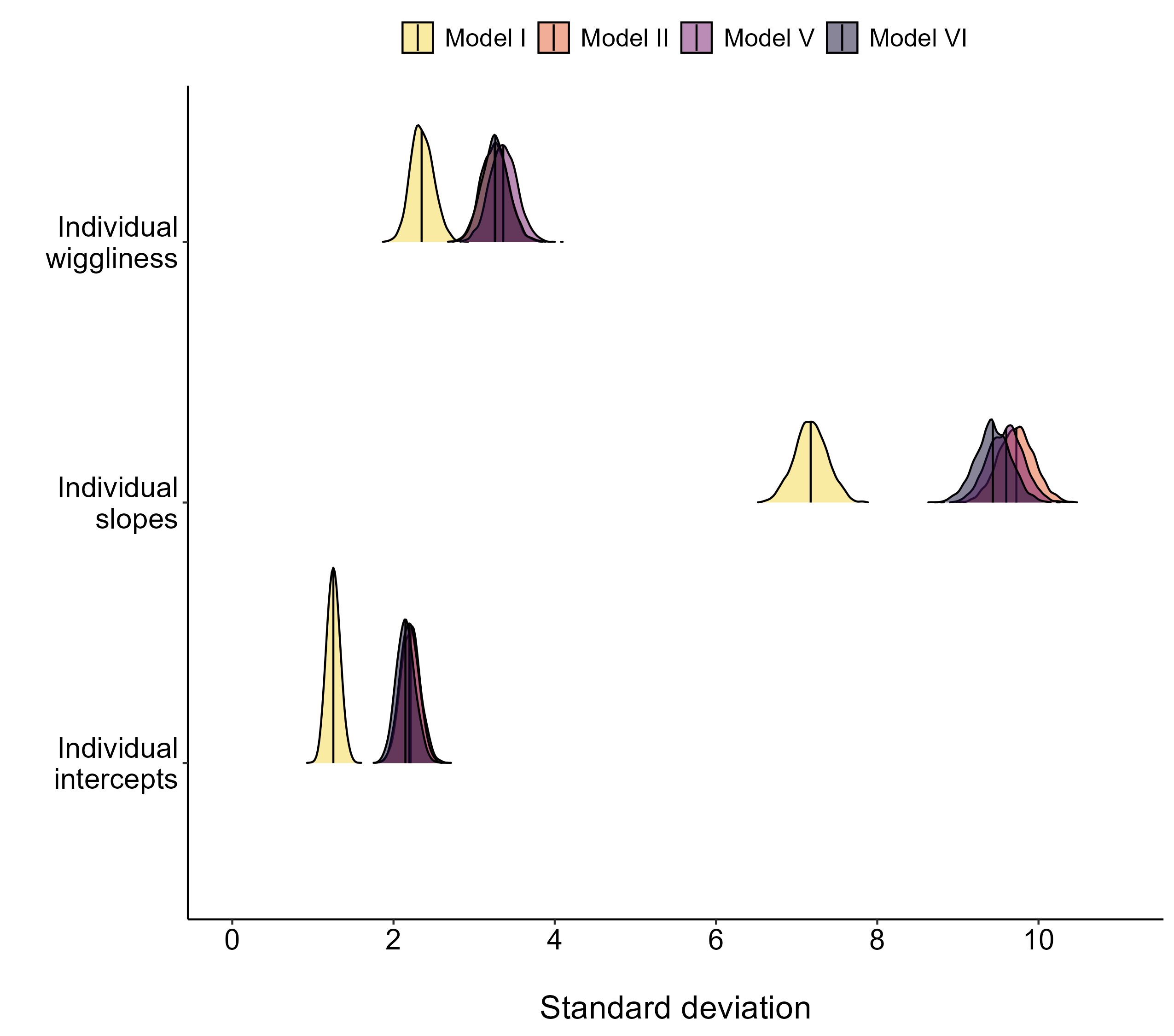


**Figure 2**. Median posterior predictions of the relationship between prey behaviour and prey skill. The average behaviour of the prey group is on the y-axis, and the average rank of the prey group is on the x-axis. The colour gradient showcases the density of observations, with lighter colours indicating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

## Acquisition of expertise at the individual level

Our results show that individual predators varied in their acquisition of expertise, regardless of whether we controlled for prey features (Figure 1 D-F and Figure 3). However, the extent of the variation in the relationship between success and experience was shaped by the prey’s skill, as shown by the posterior distributions of individual-level parameters in the model accounting for the rank of the prey (model II, Figure 2). Specifically, the standard deviations of individual intercepts (median model I = 1.25 vs median model II = 2.21), slopes (median model I = 7.17 vs median model II = 9.73), and wiggliness (median model I = 2.35 vs median model II = 3.25) were all larger in model II compared to model I. Controlling for prey rank thus reveals how predators may differ in expertise acquisition if they hunt prey that are not of the same skill level as themselves.

Among-individual differences in average hunting success remained unchanged regardless of whether we controlled for prey speed or prey space coverage (median model II = 2.21 vs median model V = 2.2 vs median model VI = 2.15). Similarly, controlling for both behaviours did not alter expertise acquisition (median model II = 9.73 vs median model V = 9.6 vs median model VI = 9.43), as the posterior distributions of the standard deviations showed nearly complete overlap (Figure 3).



**Figure 3**. Posterior distributions of the standard deviation of individual-level parameters estimated by the GAMM. The parameters are displayed on the y-axis, and their standard deviation are displayed on the x-axis. The intercept and slope standard deviations refer to the linear components of the estimated relationship between hunting success and cumulative experience. The standard deviation of the wiggliness parameter refers to the shape of the curves (i.e., nonlinear component). The vertical lines are the medians of the posterior distributions. The yellow (lightest) distributions are for the model accounting only for the game duration (model I), the pink (lighter) distributions are for the model accounting for game duration and the prey rank (model II), the purple (darker) distributions are for the model accounting for the game duration, prey rank, and prey speed (model V), and the dark purple (darkest) distributions are for the model accounting for the game duration and all prey features (model VI). The standard deviations of individual intercepts and wiggliness parameters for models II, V, and VI overlap.

# DISCUSSION

Using a virtual predator-prey system where we monitored predator hunting success across experience, we provide rare empirical support for the hypothesis that prey behaviour can modulate the acquisition of hunting expertise at the population level. We show that the predator population is expected to increase its hunting success with experience if it hunts prey were of average skill. While we could not show that prey behaviour directly impaired expertise acquisition, we found that the predator population would optimize its success sooner if the prey moved at average speeds over repeated encounters. This is most likely due to faster prey being more difficult to hunt, which predators had lower success against. We also observed that prey with greater skill moved faster. At the individual level, predators displayed important differences in expertise acquisition that were apparent only after accounting for prey skill. While this most likely due the game pairing system, it highlights how prey can shape the predator hunting success over time.

The matchmaking algorithm in *Dead by Daylight* is intended to pair players with similar skill levels within matches, and our results show that the system is effective, as the population maintained consistent hunting success across experience (Figure 1A). However, when we controlled for the prey’s skill, the gain in expertise changed at both the population and individual levels: the relationship between success and experience became asymptotic, wherein initial gains in success were significant and gradually stabilized as experience accumulated. This suggests that an increase in hunting success would emerge if predators hunted prey of average skill. This pattern of expertise acquisition is consistent with empirical studies in both humans and nonhuman animals (reviewed in Dukas 2019), but provides additional information on how it may change given the difficulty of the task. For example, the population may have had a slower gain in expertise if the skill of the prey encountered was consistently higher.

Prey behaviour also played a role in shaping expertise acquisition at the population level. First, encounters with faster prey resulted in lower hunting success (Figure S2). We previously showed in *Dead by Daylight* that faster movement is effective for prey to evade predation (Fraser Franco et al. 2022), a pattern observed in studies involving other animals (Walker et al. 2005; Kelley and Magurran 2011; Martin et al. 2022). Prey of greater skill increasingly relied on this strategy, and predators were less successful against skillful prey, suggesting that the effect of prey skill on the gain in expertise by predators was in part mediated by changes in prey behaviour following previous predator encounters(Tetzlaff, Sperry, and DeGregorio 2019). Second, we observed that predators optimized their hunting success sooner when we controlled for the prey’s speed — after 323 matches played, compared to 454 matches when prey speed was not accounted for. 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. Hence, our analyses provide evidence that prey antipredator behaviour could mediate the acquisition of hunting expertise in predators by increasing or slowing its rate at the population level.

Our analyses also revealed important differences among individual predators in the acquisition of expertise, indicating that predators varied in their capacity to improve over time. However, prey speed did not influence among-individual differences in expertise. The large indivual variation in expertise acquisition emerged when we controlled for the prey skill and persisted when we controlled for the prey’s speed, suggesting that it would be observed even if predators hunted prey of average speed. This suggests that other proximal or ecological factors may be at play. For example, predators have limited attention spans that restrict diet choice and the formation of search images when they need to focus on hunting multiple prey simultaneously (Dukas and Kamil 2001; Troscianko, Skelhorn, and Stevens 2018). Chasing prey demands specialized cognitive abilities and coordination that are energetically costly (Kelley and Magurran 2011). Hence, individuals with neurological or physical attributes allowing them to better concentrate on the hunting task may have shown greater improvement in success over time (Dukas 2019). Alternatively, predators may also shape their own expertise via their hunting tactic. For example, faster hunters may push their prey to move faster and display altruistic behaviours, which, in turn, may hinder their own expertise acquisition due to the increased difficulty of hunting such prey (Fraser Franco et al. 2022; Céré, Kelly, and Montiglio 2024). Lastly, longer time intervals between hunting events are hypothesized to hinder or delay the acquisition of expertise due to information loss (Endler 1991; Wright et al. 2022; Wooster et al. 2023). For example, a predator who played 300 matches within six months might forget critical information related to prey detection or escape patterns compared to one who played 300 matches within six weeks. Therefore, investigating the impact of the aforementioned elements may reveal important insights into the outcome of predator-prey interactions, but integrating them into a unified framework remains challenging due to computational constraints and limitations in current modeling approaches.

## Conclusions

We found support for the hypothesis that prey antipredator behaviour can drive the acquisition of hunting expertise using a human predator population in the game *Dead by Daylight*. However, the effect of antipredator behaviour was observed only at the population level. While there were important differences among individuals in expertise acquisition, we did not find evidence that they were mediated by either the prey’s skill or prey movement behaviour. Future analyses should integrate physical and behavioural antipredator tactics into a unified framework to assess their influence on the acquisition of predator expertise, which may reveal important insights on the eco-evolutionary dynamics of predator-prey interactions. One limitation and criticism of using videogames to study behaviour which may partly explain the persistence of differences among individuals in expertise is that neither the predator nor the prey players’ lives are at stake in the game. As a result, emerging patterns may be driven more by the players’ motivation to win rather than “true” survival. Indeed, some players may experiment with the game out of boredom, which could contribute in shaping how expertise is honed in this particular system. Yet, motivation and perseverance have been outlined as core components that increase the gain in expertise in human and nonhuman hunters (Dukas 2019). We believe that failing to account for motivation represents a limitation of our study more than in the use of videogames to study ecological interactions. Therefore, our demonstration of how prey antipredator behaviour can mediate the acquisition of hunting expertise adds to a growing body of research showing how virtual systems can be used to test hypotheses on ecological interactions (Beauchamp 2020; Céré, Montiglio, and Kelly 2021; Fraser Franco et al. 2022; Lymbery, Webber, and Didham 2023; Santostefano, Fraser Franco, and Montiglio 2024). We hope that this will inspire more collaborations between scientists and the videogame industry to tackle fundamental questions in ecology.

# REFERENCES

Abrams, Peter A. 2000. “The Evolution of Predator-Prey Interactions: Theory and Evidence.” *Annual Review of Ecology and Systematics* 31 (1): 79–105. <https://doi.org/10.1146/annurev.ecolsys.31.1.79>.

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>.

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, Clint D. Kelly, and Pierre-Olivier Montiglio. 2024. “Untangling the Contribution of Active and Passive Group Augmentation Benefits to the Multilevel Selection of Altruism Using a Video Game.” *Behavioral Ecology and Sociobiology* 78 (6): 66. <https://doi.org/10.1007/s00265-024-03463-6>.

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>.

Dukas, Reuven. 2017. “Cognitive Innovations and the Evolutionary Biology of Expertise.” *Philosophical Transactions of the Royal Society B: Biological Sciences* 372 (1735): 20160427. <https://doi.org/10.1098/rstb.2016.0427>.

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

Dukas, Reuven, and Alan C. Kamil. 2001. “Limited attention: the constraint underlying search image.” *Behavioral Ecology* 12 (2): 192–99. <https://doi.org/10.1093/beheco/12.2.192>.

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>.

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".”

Hairston Jr., Nelson G., and Nelson G. Hairston Sr. 1993. “Cause-Effect Relationships in Energy Flow, Trophic Structure, and Interspecific Interactions.” *The American Naturalist* 142 (3): 379–411. <https://doi.org/10.1086/285546>.

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>.

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>.

Kikuchi, David W., and Margaret W. Simon. 2023. “Social Learning of Innovations in Dynamic Predator-Prey Systems.” *The American Naturalist* 201 (6): 895–907. <https://doi.org/10.1086/724491>.

Kondoh, Michio. 2010. “Linking Learning Adaptation to Trophic Interactions: A Brain Size-Based Approach.” *Functional Ecology* 24 (1): 35–43. https://doi.org/<https://doi.org/10.1111/j.1365-2435.2009.01631.x>.

LaBarge, Laura R., Miha Krofel, Maximilian L. Allen, Russell A. Hill, Andreanna J. Welch, and Andrew T. L. Allan. 2024. “Keystone Individuals - Linking Predator Traits to Community Ecology.” *Trends in Ecology & Evolution*. https://doi.org/<https://doi.org/10.1016/j.tree.2024.07.001>.

Lönnstedt, Oona M., Mark I. McCormick, Mark G. Meekan, Maud C. O. Ferrari, and Douglas P. Chivers. 2012. “Learn and Live: Predator Experience and Feeding History Determines Prey Behaviour and Survival.” *Proceedings of the Royal Society B: Biological Sciences* 279 (1736): 2091–98. <https://doi.org/10.1098/rspb.2011.2516>.

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>.

Montiglio, Pierre-Olivier, Maxime Fraser Franco, and Francesca Santostefano. 2025. “Multiplayer Videogames to Analyze Behavior During Ecological Interactions.” *Trends in Ecology & Evolution* 40 (5): 489–501. https://doi.org/<https://doi.org/10.1016/j.tree.2025.02.003>.

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>.

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>.

Pettorelli, Nathalie, Anne Hilborn, Clare Duncan, and Sarah M. Durant. 2015. “Chapter Two - Individual Variability: The Missing Component to Our Understanding of Predator-Prey Interactions.” In *Trait-Based Ecology - from Structure to Function*, edited by Samraat Pawar, Guy Woodward, and Anthony I. Dell, 52:19–44. Advances in Ecological Research. Academic Press. https://doi.org/<https://doi.org/10.1016/bs.aecr.2015.01.001>.

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>.

Quevedo, Mario, Richard Svanbäck, and Peter Eklöv. 2009. “Intrapopulation Niche Partitioning in a Generalist Predator Limits Food Web Connectivity.” *Ecology* 90 (8): 2263–74. https://doi.org/<https://doi.org/10.1890/07-1580.1>.

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>.

Ripple, William J., James A. Estes, Robert L. Beschta, Christopher C. Wilmers, Euan G. Ritchie, Mark Hebblewhite, Joel Berger, et al. 2014. “Status and Ecological Effects of the World’s Largest Carnivores.” *Science* 343 (6167): 1241484. <https://doi.org/10.1126/science.1241484>.

Santostefano, Francesca, Maxime Fraser Franco, and Pierre-Olivier Montiglio. 2024. “Social interactions generate complex selection patterns in virtual worlds.” *Journal of Evolutionary Biology* 37 (7): 807–17. <https://doi.org/10.1093/jeb/voae055>.

Schmitz, Oswald. 2017. “Predator and Prey Functional Traits: Understanding the Adaptive Machinery Driving Predator-Prey Interactions.” *F1000Research* 6 (1767). <https://doi.org/10.12688/f1000research.11813.1>.

Skelhorn, John, and Candy Rowe. 2016. “Cognition and the Evolution of Camouflage.” *Proceedings of the Royal Society B: Biological Sciences* 283 (1825): 20152890. <https://doi.org/10.1098/rspb.2015.2890>.

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

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>.

Tetzlaff, Sasha J., Jinelle H. Sperry, and Brett A. DeGregorio. 2019. “Effects of Antipredator Training, Environmental Enrichment, and Soft Release on Wildlife Translocations: A Review and Meta-Analysis.” *Biological Conservation* 236: 324–31. https://doi.org/<https://doi.org/10.1016/j.biocon.2019.05.054>.

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>.

Turner, Andrew M., Sarah E. Turner, and Heidi M. Lappi. 2006. “Learning, Memory and Predator Avoidance by Freshwater Snails: Effects of Experience on Predator Recognition and Defensive Strategy.” *Animal Behaviour* 72 (6): 1443–50. <https://doi.org/10.1016/j.anbehav.2006.05.010>.

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>.

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>.

Woo, Kerry J., Kyle Hamish Elliott, Melissa Davidson, Anthony J. Gaston, and Gail K. Davoren. 2008. “Individual Specialization in Diet by a Generalist Marine Predator Reflects Specialization in Foraging Behaviour.” *Journal of Animal Ecology* 77 (6): 1082–91. <https://doi.org/10.1111/j.1365-2656.2008.01429.x>.

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>.