Experience shapes individual foraging specialization and success in a virtual predator-prey system

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# ABSTRACT

The capacity of predators to match their tactic to the behaviour of 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 skills and expertise to successfully hunt their prey, which may result in individual foraging specialization. Yet, there are very limited empirical assessments showing links between experience, foraging specialization, and performance at the individual level, due to the numerous challenges of monitoring direct interactions in the wild. In this study, we used a virtual predator-prey system (the online game *Dead by Daylight*) to investigate if and how hunting experience shapes individual foraging specialization and success in predators across repeated interactions with their prey. Our results show that predators optimized prey consumption as they gained experience. Prey behaviour was an important mediator of this relationship, which also drove individual differences in the development of expertise. With experience, differences among individuals in foraging specialization increased, as individual predators became either specialist or flexible foragers. Yet, many individuals remained specialists throughout the study period. Moreover, the matching between the predator’s strategies (i.e. flexible or specialized foraging) and the prey was not strong, suggesting that part of the population did not match their tactic to the prey. This individual heterogeneity coincided with differences among individuals in success through time. While flexible foragers performed slightly less than specialist foragers, both achieved similar success overall. Our observations suggest that individual differences in behavioural change with experience may drive among individual differences in hunting tactics, which may act as a stabilizing mechanism promoting behavioural diversification in predator-prey systems.

# INTRODUCTION

Individual variation in predator foraging behaviour is increasingly recognized as a major driver of trophic interactions and community dynamics (Griffen et al. 2012, Michalko and Pekár 2016, Moran et al. 2017, Michalko et al. 2021). Indeed, predator populations often comprise assemblages of individuals specializing on different foraging tactics, with consequences for habitat use, functional responses, prey choice, and foraging rate (Kobler et al. 2009, Toscano and Griffen 2014, Patrick and Weimerskirch 2014a, Matsumura and Miyatake 2022). Despite clear evidence that individual specialization is important in predator-prey interactions, its underlying mechanisms remain surprisingly unclear. One hypothesis suggests that reciprocal interactions between predators and prey could drive individual foraging specialization (Araújo et al. 2011, Toscano et al. 2016, De Lisle et al. 2022). For instance, predators often hunt using techniques that are fine-tuned to the type of prey that they encounter (Estes et al. 2003, Woo et al. 2008, Courbin et al. 2018), and their refinement is crucial for young predators to reach adulthood and survive (Phillips et al. 2017, Heithaus et al. 2018). Thus, the capacity of predators to effectively use hunting tactics should be contingent on periods of extensive practice (i.e. experience), which may result in different foraging specializations.

Theory predicts that foraging specialization may emerge via learning and expertise acquisition (Tinker et al. 2009, Dukas 2019). Dukas (2019) defines expertise as the characteristics, skills, and knowledge that allow individuals with extensive experience to outperform novices on complex tasks. It is described as the relationship between success and experience, where extensive practice optimizes success when individuals reach an advanced level of experience. Empirical studies on human and non-human hunters show that experience optimizes foraging efficiency (e.g. search and handling times, return rates) potentially via associative images or reliance on prey and environmental cues (Edwards and Jackson 1994, Morse 2000, MacDonald 2007, Reid et al. 2010, Wilson-Rankin 2015). This body of work suggests that such optimization may thus promote individual foraging specialization (e.g. repeatedly using fast attacks) if the success of a tactic is constant through time. It may also be costly to test different tactics by trial and error when prey are scarce or unpredictable. Alternatively, the costs/risks faced by hunters when switching tactics may be offset through extensive practice, as individuals gain experience and information on their prey, leading to increased individual foraging flexibility (Stephens 1993, Ishii and Shimada 2010, Mery and Burns 2010, Kelley and Magurran 2011, Snell-Rood 2013). To develop proper responses to fluctuating resources, individuals would need to sample their environment broadly during an extensive period, leading to greater performance at later stages of development (reviewed in Snell-Rood 2013). However, predators can differ in the challenges that they face during their lifetime, which could result in both processes (i.e. specialization and flexibility) operating at the same time within a predator population. For example, some individuals may hunt in habitats where prey are faster, which are often proven to be more difficult to hunt (Walker et al. 2005, Kelley and Magurran 2011, Martin et al. 2022). Thus, it should be essential for predators to learn how to adjust their tactic to their prey to optimize their success.

There is currently a lack of consensus on the fitness advantages of specialized vs flexible foraging strategies (Phillips et al. 2017). Some studies have found greater success for individuals specializing on a foraging tactic (Patrick and Weimerskirch 2014b, Pintor et al. 2014, van den Bosch et al. 2019) while others have found that individuals using flexible foraging tactics have greater success (Paull et al. 2012, Santoro et al. 2019, Manlick et al. 2021). This discrepancy may in part be due to the limited information we have on the ecological contexts favoring individual specialization over flexibility. However, many studies also show that both type of foragers can attain equal success depending on timescales, and suggest that fluctuating resources throughout a predator’s lifetime may be key in shaping individual foraging specialization (Weimerskirch 2007, Woo et al. 2008, Potier et al. 2015, Phillips et al. 2017, Courbin et al. 2018). It is hypothesized that when resources are predictable (or stable), individual specialists should have higher capture rates by reducing the energy and time required to search for and handle prey. In contrast, individual generalists should benefit from adjusting to fluctuating resources by reducing the consequences of uncertainty (Dall 2010). While it is clear that predators can match their hunting behaviour and locomotion to their prey (Bro-Jørgensen 2013, McGhee et al. 2013, Chang et al. 2017, Szopa-Comley and Ioannou 2022), the important question remaining is how. Given the dynamic nature of predator-prey interactions, it is likely that ontogenic behavioural changes in predators play an important role, because complex hunting strategies require practice to be effective (Kelley and Magurran 2011). Uncovering the role of experience in shaping direct predator-prey interactions would help to predict the behavioural decisions and the success of predators when they are hunting.

A recurring challenge impeding research on predator-prey behavioural interactions, at the individual level, is the need to collect data simultaneously on both the predator and the prey. We recently showed, using an online predator-prey videogame called *Dead by Daylight* (*DBD*), that virtual systems can overcome this challenge (Fraser Franco et al. 2022). In this dynamic virtual system, four prey players need to forage for resources while avoiding predation by a fifth player. The prey can contribute to the group’s success by healing or helping others escape from the predator, or be selfish and attempt to escape by themselves (Céré et al. 2021). The predators’ hunting tactics and success are driven by the movement of the prey (Fraser Franco et al. 2022). Predators should thus benefit from learning how the prey behave to be successful. Other virtual predator-prey studies show that predation regimes drive individual variation in risk perception (Beauchamp 2020), that familiarity between prey has a positive indirect effect on survival (Céré et al. 2021), and that prey face contrasting natural and social selection regimes (Santostefano et al., public communications and unpublished manuscript). These examples outline how virtual systems could be useful in identifying general ecological patterns, which in turn might help to advance predator-prey research. They 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, including *DBD*, offer the opportunity to tackle fundamental questions about the role of experience on predator-prey interactions.

In this study, we evaluated how hunting experience shapes predator foraging specialization and success using data from players in the online videogame *Dead by Daylight*. First, we investigate how predators develop their individual hunting expertise. We hypothesize that predators should differ in the development of their expertise if they encountered varying levels of difficulty with the prey that they pursued. For example, a predator may face greater difficulty than other individuals if it encountered elusive groups of prey more often. Second, we test the hypothesis that experience will shape individual foraging specialization. We define foraging tactics as the mean movement speed of the predator along a slow-fast continuum, and the level of individual foraging specialization as the intra-individual variance (i.e. IIV) in movement speed across matches, where low IIV translates to individual specialization (e.g. always using a fast tactic). If experience reduces the costs of switching between low and high speeds as predators encounter varying groups of prey, we predict that individuals (and thus the population) should all converge towards flexible speeds. However, if individuals encounter similar groups of prey, then the efficiency of a specific tactic should increase with experience and everyone should instead specialize in similar speeds. In both scenarios, among individual variation in IIV (i.e. individual differences in specialization) would be low across experience, whereas the population variance would either increase (flexibility) or decrease (specialization). Alternatively, both processes may operate at the same time if behavioural interactions with the prey vary among predators, such that among individual variation in IIV would increase. In this case, we expect predators that experienced more predictable encounters with their prey (i.e. similar groups across matches) to specialize in similar speeds, while predators that experienced unpredictable encounters with their prey (i.e. heterogeneous groups across matches) should adopt flexible movement speeds. If we detect such prey-dependent fine-tuning, then all hunters along the flexible-specialist continuum should attain equal success probably because they learned from experience how to adjust their hunting style to their prey.

# 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 along with its speed, 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 predator’s mean speed and the mean speed of the prey group encountered by the predator. The predator’s mean speed is measured as the mean distance traveled per second during a match (mean= 3.31 ± 0.49 m/s). 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 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 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.

### Development of expertise

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 (Piironen and Vehtari 2017, Vehtari et al. 2017, Vehtari et al. 2022).

### Foraging behaviour and predator-prey interactions across experience

We tested whether foraging behaviour changed with experience, and compared the success of predators along the flexible-specialist hunter continuum, using a multivariate double-hierarchical generalized linear model (MDHGLM) (Lee and Nelder 2006, Cleasby et al. 2015, Mitchell et al. 2016). For each experience level, we fitted the model on three traits: the predator’s speed () and the prey’s speed () using a Gaussian error distribution, and the predator’s hunting success () using a beta-binomial error distribution. Fixed and random effect structure were trait-specific and the same for all experience levels. The predator and the prey speed included a mean and a dispersion part (eqn 1.1, 1.2 and 2.1, 2.2). For both traits, we controlled for the standardized prey rank on both the mean and the dispersion parts of the model. We included game environment, predator avatar, and individual predator identity random effects on the mean part of the model. The dispersion part included individual predator identity random effects exclusively. For hunting success, we modeled the mean part only (eqn 3) and controlled for the standardized prey rank and game duration, and included an individual identity random effect.

The model simultaneously estimated five among-individual variance components with their covariances for each experience level, resulting in a 15x15 (co)variance matrix. For each experience level, the model estimated among individual variance in mean predator speed, mean prey speed, and mean hunting success. This allows to test for individual differences in tactic use (i.e. along the slow-fast continuum), in the mean speed of the prey encountered, and in mean prey consumption. The model also estimated among individual variance in intra-individual variation (IIV) for both prey and predator speed. This allows to test if predators do not experience the same degree of prey heterogeneity and if they differ in individual specialization. Finally, the model estimated all pairwise covariances at the individual level among traits, among experience, and across traits and experience. The resulting 15x15 (co)variance matrix thus provides the structure of the predator-prey trait interactions as well as the relationship between specialization and success across experience at the individual-level.

The model can be written as:

|  |  |
| --- | --- |
|  | (eqn. 1.1) |
|  | (eqn. 1.2) |
|  | (eqn. 2.1) |
|  | (eqn. 2.2) |
|  | (eqn. 3) |

where is the index of the three experience levels (i.e. novice, intermediate, advanced). The subscript indicates that a term is from the dispersion part of the model. The terms are vectors of fixed effects with their design matrices specific to each trait and experience level. The terms , , and are the vectors of random environment, random avatar, and random individual identity effects associated with their design matrices , , and specific to each trait and experience level. For all experience levels of and , we assumed that the game environment and avatar random effects followed a Gaussian distribution with estimated standard deviation ( and ). is the identity matrix, with indicating that the random effects are independently and identically distributed. In addition, we assumed that the residuals follow a Gaussian distribution with observation-specific variance . The 15 individual identity random effects across all response variables and experience levels (five for each of the three experience levels) are indexed in vector . The vector follows a multivariate Gaussian distribution where is a 15x15 (co)variance matrix of among individual variation across all response variables and experience levels, with on the diagonal and covariances off-diagonal.

We used weakly informative Gaussian priors for the prey rank (: eqn. 1.1 to 2.2) and game duration (: eqn. 3). Based on previous results showing that the mean predator speed revolves around 3 m/s (Fraser Franco et al. 2022), we applied a weakly informative Gaussian prior on the intercept for predator and prey speed (: eqn. 1.1 and 2.1). Similarly, we used a weakly informative Gaussian prior on the intercept for the dispersion part (: eqn 1.2 and 2.2). For hunting success, we applied a positive Gaussian prior on the precision parameter (: eqn. 3) and a negative Gaussian prior (: eqn 3) on the intercept because hunting success should be close to 0 at the lowest game duration. For every predicted variable, we applied a weakly informative half-Gaussian prior () on the random effects for the mean part and the dispersion part of the model. We used a regularizing prior on the correlation matrix.

After inspection of the results, we found that key parameter values for our hypotheses were in the direction of our predictions, but they were largely driven by the very slow speed of one predator. Removing this individual reduced the estimates by a significant margin. To remain conservative, we thus present the results of the model without this individual in the main text, and provide the results of the model including it in the Appendix S3.

### 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).

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.

## Changes in foraging behaviour, prey behaviour, and hunting success

The mean speed of the predator population remained stable with experience (Figure 2 and Appendix S1: Table S1). Likewise, the variation in speed did not change with experience, indicating that foraging specialization remained stable at the population level (Figure 2 and Appendix S1: Table S1). At the individual level, predators differed slightly in their mean speed across experience levels, indicating marginal differences in hunting tactics (Figure 2 and Appendix S1: Table S2). However, they displayed important differences in foraging specialization (Appendix S1: Table S2) which also increased slightly with experience as there was a 0.11 unit increase in among individual differences in IIV from novice to advanced (Figure 2). 12% of the population switched from a flexible to a specialized hunting tactic, and vice-versa, as predators gained experience (i.e. >0.2 change in standard deviation; Figure 3). In contrast, 44% displayed lower changes (i.e. >0.05 and <0.2 change in standard deviation) and 44% showed almost no change with experience (i.e. <0.05 change in standard deviation).

As the predator population gained experience, there was strong evidence that the prey increased their speed, although slightly (Figure 2 and Appendix S1: Table S1). The population also encountered groups of prey using different speeds (Appendix S1: Table S1) which did not change with experience (Figure 2). At the individual level, all predators encountered prey with similar speeds on average throughout experience (Figure 2 and Appendix S1: Table S2). Yet, even if they experienced similar average prey speeds across all groups encountered, there were important differences among predators in how (dis)similar were the groups they encountered (Appendix S1: Table S2). Thus, some predators encountered similar groups (i.e. all groups using similar speeds) while others encountered distinct groups (i.e. some slower and some faster). These differences among individuals in IIV for prey encounters increased only marginally with experience (Figure 2).

Similar to the GAMMs, the predator population’s mean hunting success increased with experience (Figure 2 and Appendix S1: Table S1), with mean prey consumption revolving around two prey. There were also important differences among individuals in mean hunting success (Appendix S1: Table S2), but they remained stable across experience (Figure 2).

## Predator-prey interactions across experience

Predators that were on average faster had lower IIV in speed (Figure 4A-B and Appendix S4: Table S1). Thus, faster predators specialized on fast movement, while slower predators were more flexible in their movement. As predators gained experience, these strategies were increasingly defined as the correlation changed by 0.16 from -0.62 (-0.91, -0.41 ) for when predators were novices to -0.78 (-1.00, -0.53 ) as they reached the advanced stage (Figure 4C). Predators that were on average faster also tended to encounter groups of prey that were on average faster and more similar (Figure 4A-B and Appendix S4: Table S1). There was however no evidence that these correlations increased with experience (Figure 4C)

There was no correlation (-0.01 (-0.17, 0.09 )) between mean prey speed and IIV in predator speed when predators were novice (Figure 4A), but the correlation increased to -0.16 (-0.33, -0.04 ) at the advanced stage (Figure 4B), such that advanced hunters that encountered faster prey tended to be more specialized (Figure 4C). The predators’ IIV in speed and IIV in prey speed were weakly positively correlated (Figure 4A-B and Appendix S4: Table S1). Hence, predators that encountered groups of prey with similar speeds tended to be more specialized in their tactic, while those that encountered groups of prey with varying speeds tended to be more flexible. We did not find evidence that this correlation increased with experience (Figure 4C).

## Success along the foraging continuum

The predator’s mean speed and IIV were only weakly negatively correlated with hunting success across experience (Figure 4 and Appendix S4: Table S1), suggesting that slower/flexible and faster/specialist predators were overall both equally successful. This is further supported in the scatterplot showing no apparent relationship between success and IIV in speed (Appendix S1: Figure S2). There was however a slight increase in the correlation between the predator’s IIV in speed and success (Figure 4C), suggesting that flexible foragers at the advanced stage were marginally less successful. There was strong evidence that individuals who encountered groups of prey with faster speeds were less successful (Figure 4A-B and Appendix S4: Table S1). Predators also had greater success across the study when encountering more variable groups of prey (Figure 4A-B and Appendix S4: Table S1). Both relationships remained structurally stable across experience (Figure 4C).

# DISCUSSION

Learning from experience is predicted to increase individual predator foraging specialization when prey distribution, behaviour, and movement is predictable through time (Estes et al. 2003, Tinker et al. 2008, 2009). However, if predators encounter varying prey with a greater behavioural range through time, then learning should increase behavioural flexibility (Stephens 1993, Ishii and Shimada 2010, Mery and Burns 2010, Snell-Rood 2013, Wright et al. 2022). We found that predators in *DBD* increased their hunting success with experience, suggesting that the development of predator expertise was honed through extensive practice. While there was no directional increase in either behavioural specialization or flexibility with experience at the population level, individual predators developed their own behavioural trajectories over successive encounters with the prey. This was characterized by a continuum of hunting styles ranging from a slower and flexible strategy to a highly specialized fast-paced strategy, with some predators switching between the two with experience. The behavioural strategies of predators and prey tended to match across experience, suggesting that both were probably adjusting to each other. Specialized cursorial hunters tended to encounter similar groups of prey, while slower and flexible hunters tended to encounter varying groups of prey. Yet, an important part of the population did not change its behaviour with experience, which probably contributed to an imperfect matching between predator and prey behaviour, resulting in among individual differences in hunting success. Overall, predators along the flexible-specialist continuum achieved similar success, although flexible hunters were slightly less successful as advanced hunters.

## 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, 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 in predators (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.

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 (Bowen et al. 2002, Carey and Wahl 2011, Nomura et al. 2011), 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 et al. 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.

## Predator-prey interactions across experience

The predator population maintained its speed and degree of specialization throughout the study period, and individuals differed only slightly in their average speeds. However, differences in specialization among individuals were important and increased slightly with experience. Predators hunting at higher speeds specialized in this tactic and tended to encounter groups of prey with similar speeds, while those hunting at slower speeds were flexible and tended to encounter varying groups of prey. On one hand, this pattern could arise if some predators adjusted their strategy to their prey, because fast-paced hunting is a specialized tactic suited for prey that use rapid evasive movements (Endler 1991, Bro-Jørgensen 2013, Wilson et al. 2018), while a slower and flexible tactic can be useful to minimize the consequences of uncertainty when prey escape unpredictably (Szopa-Comley and Ioannou 2022). However, we observed that 44% of the predator population showed close to no change in specialization with experience. Since these individuals were already specialized as novices (Fraser Franco, personal observation), there would be no point in them changing their tactic with experience if they were already successful, or there could have been costs to switch their strategy if they more often encountered faster prey. This could explain why the behavioural interactions between the predator and the prey remained stable across the predator’s experience. Yet, because prey can also learn how to avoid predation (Kelley and Magurran 2003, Turner et al. 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 et al. 2006, 2009, Edgell and Rochette 2009, McGhee et al. 2013). Indeed, 56% of the predator population altered its behaviour with experience to different degrees, including 12% that even switched between flexibility and specialization. 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). Our results appear to support this since many individuals were shifting their behavioural niche while the population niche remained stable across experience.

Classical theory predicts that individual foraging specialization should maximize prey consumption by optimizing foraging efficiency (Stephens and Krebs 1986), but other work suggests that flexibility and specialization could both be adaptive as resources fluctuate (Woo et al. 2008, Phillips et al. 2017). Our results support empirical findings indicating that flexible and specialist foragers obtained similar success (Weimerskirch 2007, Woo et al. 2008, Potier et al. 2015, Phillips et al. 2017, Courbin et al. 2018), although flexible foragers were slightly less successful. Both strategies appeared to emerge in part from individuals learning how to hunt their prey, resulting in a general increase in success in the population. 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. 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 the predator, 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. As the benefits of each hunting style changed under different scenarios, the combination of predatory styles in our virtual system reflects how resource fluctuations can maintain fitness equilibrium within populations, resulting in behavioural diversity in predator-prey systems (Woo et al. 2008, Tinker et al. 2008, Mougi and Kishida 2009).

## Conclusions

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 support of our prediction that prey were driving individual differences in expertise in a predator population. We also confirmed that experience and predator-prey encounters drove the patterns of individual foraging specialization and flexibility. Our results suggest that predators learned with experience, as their success increased and their speed remained matched to the speed of their prey. Even though individuals were not all equally successful, both specialized and flexible hunters achieved similar success. 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. 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 among ecologists as being useful to test hypotheses on consumer-resource interactions (Beauchamp 2020, Barbe et al. 2020, Céré et al. 2021, Fraser Franco et al. 2022). 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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# CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

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# TABLES

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 | | | | |

# FIGURE CAPTIONS

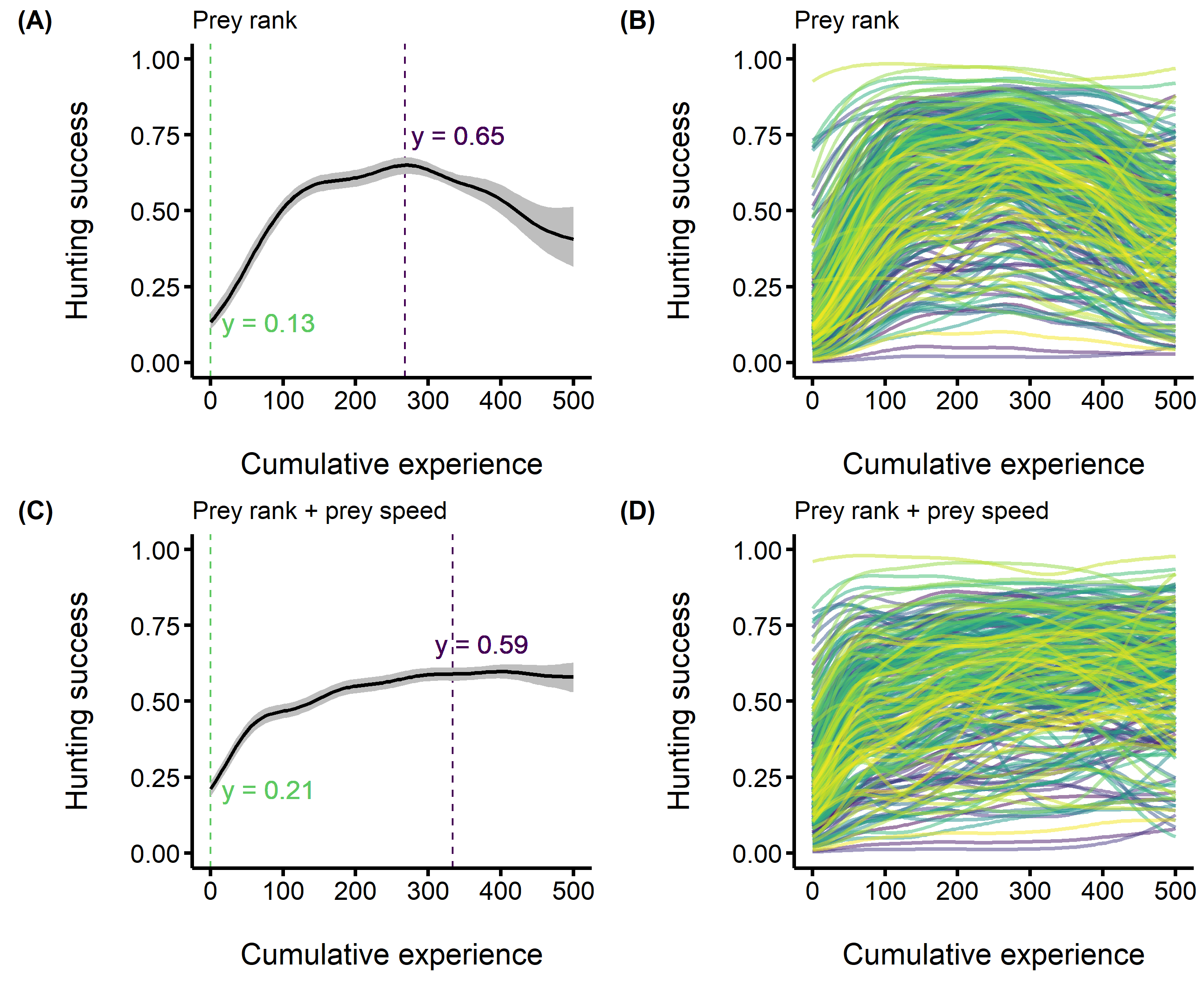
**Figure 1.** Median posterior predictions of the development of predator hunting expertise. The predators’ hunting success (i.e. the probability of consuming the four prey) is on the y axis, and the predators’ cumulative experience (i.e. the number of matches played prior to each observation) is on 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.** Median posterior differences and HPD intervals comparing predator foraging behaviour at the population and individual level across experience stages. The behavioural parameter predicted by the MDHGLM being compared is on the y axis, and the difference in parameter values between two experience stages is on the x axis. The pairwise comparisons between experience stages are displayed across the three panels A, B, and C. We compare the mean speed of the predator population, the speed of the prey it encountered, and its hunting success across experience (population mean). We also compare the population’s foraging specialization and variation in speed of the prey it encountered across experience (population variance). At the individual level, we compare among individual differences in speed, the speed of the prey encountered, and hunting success (individual variation mean). Lastly, we compare individual variation in IIV across experience, indicating whether individual differences in foraging specialization and in the variation of the groups of prey encountered changed with experience (individual variation IIV).

**Figure 3.** Individual behavioural distribution of the predators’ speed drawn from the MDHGLM estimates for individuals that had (A) the greatest increase in specialization and (B) the greatest increase in flexibility. The background (gray) distributions are for when individuals were novice hunters, and the foreground (blue) distributions with solid contour lines are for when they were advanced hunters. Both figure panels are ordered by ascending degree of increase in either specialization or flexibility. We built the figure by first subtracting the estimated standard deviation of all individuals as novices with their standard deviation as advanced hunters, and then selected those with the greatest difference using the 25% and 75% quantiles. Individuals on panel A have an increase in specialization equal or greater than 0.2 standard deviations, while those on panel B have an increase in flexibility equal to or greater than 0.2 standard deviations.

**Figure 4.** Correlation matrices of the MDHGLM relating the mean and IIV in speed of the predators, the mean and IIV in speed of the prey they encountered, and mean hunting success. Larger dark blue circles indicate stronger positive correlations (positive values on the colour legend), while larger dark red circles indicate stronger negative correlations (negative values on the colour legend). A) Correlations when predators were novice hunters. B) Correlations when predators were advanced hunters. C) Posterior median differences and HPD intervals comparing the trait correlations predicted by the MDHGLM between the advanced and novice levels. The difference is displayed on the y axis and the correlated traits being compared are displayed on the x axis. Positive values indicate an increase in correlation strength from novice to the advanced stage, while negative values indicate stronger correlations when predators were novice.

# FIGURES



**Figure 1**



**Figure 2**



**Figure 3**



**Figure 4**