Hunting experience shapes individual foraging specialization and predator-prey interactions in an online videogame

Journal name : Ecology

Manuscript type : article

Authors : Maxime Fraser Franco1, Francesca Santostefano1,2, Julien G. A. Martin3, Clint D. Kelly1, Pierre-Olivier Montiglio1

Affiliations : 1 Département des Sciences Biologiques, Université du Québec à Montréal, Montréal, QC, Canada. 2 Centre for Ecology and Conservation, Penryn Campus, University of Exeter, Cornwall, United Kingdom. 3 Department of Biology, University of Ottawa, Ottawa, ON, Canada.

Corresponding author : [fraser\_franco.maxime@courrier.uqam.ca](mailto:fraser_franco.maxime@courrier.uqam.ca)

Authorship statement : With MFF as the leader, all authors participated in conceiving the ideas behind the study. MFF prepared the data, conducted the analyses, and wrote the manuscript with input from all coauthors. All authors reviewed and accepted the final version of the manuscript.

Open research statement : The data and code used to produce the results in this manuscript are freely available on GitHub <https://github.com/quantitative-ecologist/experience-hunting-tactics>

Keywords: foraging behaviour, reciprocal behavioural plasticity, learning, antipredator behaviour, virtual ecology, Dead by Daylight

# ABSTRACT

Many predator-prey systems are driven by reciprocal interactions where one responds to changes in the behaviour of the other. However, the mechanisms driving these individual responses are only beginning to be explored, in part because of the challenges associated with monitoring direct predator-prey interactions. 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.

*à modifier pour parler plutôt de l’interaction qui devient fine tuned (i.e. predators and prey)* We found that with increasing experience, predators fine-tuned their tactics to the behaviour of their prey. Individuals that adopted a flexible tactic (i.e. generalists) encountered groups of prey with varying speeds, and those that adopted a cursorial and specialized tactic (i.e. specialists) encountered groups of prey with similar speeds throughout the study period.

Our results suggest that experience enables predators to learn how to optimize their tactics to the type of prey that they encounter (i.e. fast or slow), 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). This is reflected in the literature showing contrasting results in the links between specialization and fitness at the individual level. Some studies have found greater success for individuals that use specialized foraging tactics (Patrick and Weimerskirch 2014b, Pintor et al. 2014, van den Bosch et al. 2019) while others found that individuals using flexible foraging tactics have greater success (Paull et al. 2012, Santoro et al. 2019, Manlick et al. 2021). This disrepancy may in part be due to the limited information we have on the ecological contexts favoring individual specialization over flexibility. However, many studies have found that both type of foragers can also 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 unlikely that evolution alone could explain such behavioural adjustments by predators, because complex hunting strategies require practice to be effective (Kelley and Magurran 2011). Thus, uncovering the role of learning during 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. in prep). 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. If experience increases a tactic’s efficiency for specific types of prey assuming that all individuals encounter similar groups of prey, then they may instead specialize in their speed. In both scenarios, among individual variation in IIV (i.e. individual differences in specialization) should be low across experience because everyone is either a flexible or a specialist forager, but 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 should increase. In this case, we expect predators that experienced more predictable encounters with their prey (i.e. similar groups across matches) to specialize in their speed, 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 compiled 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 a reproduction 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). We fitted the model on both the predator () and prey () speeds using a Gaussian error distribution, and on the predator’s hunting success () using a beta-binomial error distribution.

The model simultaneously estimated three distinct individual components for each trait across experience levels. The first component, estimated on the mean part of the model, is among individual variation in mean speed and 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 second component, estimated on the dispersion part of the model by modeling the residuals, is among individual variation in intra-individual variation (IIV). This allows to test if predators do not experience the same degree of prey heterogeneity and if they differ in individual specialization . The third component consists of pairwise comparisons between the individual identity standard deviations on the mean and dispersion part of the model among traits, among experience, and across traits and experience. This results in a 15x15 (co)variance matrix, allowing to describe the structure of the predator-prey trait interactions as well as the relationship between specialization and success across experience at the individual-level.

For the predator and the prey speed, 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 and controlled for the standardized prey rank and game duration, and included an individual identity random effect.

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 experience levels. The model is fitted on the three experience levels denoted by , where ranges from 1 to 3 (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 . The terms , , and are the vectors of random environment, random avatar, and random individual identity effects associated with their design matrices , , and . For all experience levels of the predator and prey speed, 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. All the individual identity random effects (mean and dispersion) across all response variables and experience levels are indexed in vector . The vector follows a multivariate Gaussian distribution where is a 15x15 (co)variance matrix of the individual identity standard deviations across all experience levels and response variables.

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 39% increase in the probability of consuming all prey for the average individual between the first and the 400 match which has the highest predicted success (Figure 1C).

The relationship between hunting success and cumulative experience differed among predators (Figure 1B and 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 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% 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

*je suis rendu ici* Predators that were on average faster (mean speed) had a lower intra-individual variability (IIV 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 through time. As predators gained experience, these strategies were increasingly defined as there was a 0.16 unit increase in the correlation at the advanced stage (Figure 4C). Predators that were on average faster (mean speed) also encountered groups of prey that were on average faster (mean prey speed) and more similar (IIV prey speed) (Figure 4A-B and Appendix S4: Table S1). There was however only weak to no evidence that these correlations increased with experience (Figure 4C)

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

## Comparing the success of flexible and specialist foragers

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 both equally successful. This is further supported in the scatterplot showing no apparent relationship between success and IIV in speed (Appendix S1: Figure S2). However, 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 4-C)

# DISCUSSION

Learning from experience is predicted to increase foraging specialization when predators encounter prey behaving predictably through time (Estes et al. 2003, Tinker et al. 2008, 2009). However, if predators encounter prey behaving unpredictably 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). Our results show that predators substantially increased their hunting success with experience. While there was no directional increase in either behavioural specialization or flexibility with experience at the population level, we found that individual predators developed their own expertise and 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.

*parler directement du succès des tactiques ici?*

*ici parler de la covariance qui suggère un ajustement par les deux. Peut être dire que c’était fortement corrélé, mais que ça changeait pas tant avec l’expérience* Specialized cursorial hunters encountered similar groups of prey while slower and flexible hunters encountered varying groups of prey, with both achieving similar success over the study period.

*ici, changer la phrase pour parler que l”interaction a changé, comme ça c’est aveugle au feedback* With experience, predators increasingly matched their foraging specialization to the speed of the prey that they encountered,

but they did not achieve greater success, probably because the prey were also matching their speed to the predator. Our observations suggest that predators in *DBD* learn to adjust their foraging specialization, not to the variance, but to the mean behaviour of the prey that they encounter throughout their lifetime in the game.

## The development of expertise with hunting experience

Empirical research shows that task proficiency often increases nonlinearly with experience and stabilizes at an expert level (reviewed in Dukas 2019). Our analyses revealed a similar trend, with a 13% population increase in success when predators became advanced hunters. However, because the game pairs players with similar skill, the increase in expertise could have potentially been greater if predators and prey were paired randomly. Individual predators in *DBD* also displayed distinct patterns of expertise acquisition. We predicted that this would occur if, by chance, predators differed in the prey that they encountered, because some may be easier and others more difficult to capture. In nature, prey can use a variety of defenses such as physical armaments, toxins, camouflage, or antipredator behaviours to escape predation (Brodie III and Brodie Jr. 1999, Bowen et al. 2002, Brodie and Wilkinson 2010, Carey and Wahl 2011, Nomura et al. 2011). In *DBD* we previously showed 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). Our results confirm that prey speed influenced expertise acquisition at the individual level to some extent. This is not surprising because capturing faster prey requires costly and specialized cognitive abilities and coordination (Kelley and Magurran 2011).

However, there were still important differences in expertise acquisition, which suggests that other antipredator tactics may also be involved. For example, a well known antipredator tactic associated with speed that confuses human and non-human predators during the attack sequence is unpredictable escapes (Jones et al. 2011, Herbert-Read et al. 2017, Moore et al. 2017, Richardson et al. 2018). This tactic compromises the predator’s ability to anticipate prey escape routes, but they can adjust to it by using slower approaches before attacking (Szopa-Comley and Ioannou 2022). Yet, because unpredictability exploits the predator’s cognition, slow learners could struggle to optimize their success if they often encounter prey using this tactic which is also extensively used in *DBD* (personal observation).

Alternatively, it is possible that individual variation in learning rates due to time delays between hunting events drove the observed differences in expertise acquisition. For example, in *DBD*, a predator that played 300 matches in the span of six months might forget more critical information (e.g. prey escape patterns or muscle memory) than one that played 300 matches in the span of 6 days. While this has not been formally tested, a greater delay between exposure events is hypothesized to attenuate or even negate the relationship between success and experience (Endler 1991, Wright et al. 2022). Moreover, the predators could have differed in their ability to detect prey. For instance, nonhuman predators can learn visual cues such as coloration to recognize and avoid unpalatable prey (Skelhorn et al. 2016, Ward-Fear et al. 2020, McLellan et al. 2021), or habitat characteristics to locate food patches (Ehlinger 1989, Hughes et al. 1992, Warburton 2003). Szopa-Comley et al. (2020) also found consistent among individual variation in the capacity to detect cryptic and conspicuous prey in three-spined sticklebacks (*Gasterosteus aculeatus*). Thus, predators could differ in their expertise if they do not learn equally how to exploit the visual cues that facilitate prey detection.

## Changes in individual hunting specialization with experience and consequences for predator-prey interactions

There were only weak differences among predators in tactic use (i.e. mean speed), but differences in specialization were important and related to how different were the groups of prey that they encountered. Predators that encountered groups of prey with similar speeds across matches specialized in hunting at high speeds, while those that encountered varying groups of prey adopted a slower and flexible strategy. Fast-paced hunting is indeed a highly specialized tactic suited for prey that use rapid escapes (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 hunting prey that use unpredictable escapes (Szopa-Comley and Ioannou 2022). However, it remains uncertain whether this phenotypic matching enables predators with different degrees of specialization to achieve equal success within populations (Woo et al. 2008). Here, we found that all hunters along the flexible-specialist continuum achieved similar success throughout the study period (Appendix S1: Figure S2). Thus, our results provide direct evidence that predators matching their tactic to their prey may be key in maintaining behavioural diversification in predator-prey systems.

Surprisingly, the effect of experience on foraging behaviour was much more subtle than we expected. For instance, the predator population maintained their speed and degree of specialization throughout the study period, and individual differences in mean speed did not change with experience. However, differences among predators in foraging specialization did increase slightly with experience, with some individuals becoming increasingly flexible. Interestingly, the behavioural response (i.e. specialization) to experience by individual predators differed. For instance, 44% of the population did not alter their degree of specialization with experience (i.e. remaining either faster and more specialized, or slower and more flexible), while 56% of the population displayed a switch from a specialized to a flexible tactic or vice-versa with experience. These changes were accompanied by predators increasingly matching their specialization to the mean speed of the prey groups across experience, instead of the variability between encounters. This suggests that it may be easier for predators to specialize on their prey by relying on mean cues (i.e. mean behaviour) instead of relying solely on resource heterogeneity (Weimerskirch et al. 2005, Weimerskirch 2007, Woo et al. 2008, Phillips et al. 2017).

*expliquer pourquoi les généralistes ont moins bien performé ici*

It is likely that predators were also driving changes in prey behaviour because most predator-prey behavioural relationships remained stable even though half of the population switched from a specialist to a flexible strategy and vice-versa across experience. This implies that the prey were probably also learning how to avoid predation through repeated interactions. Our results concord with what Mougi et al. (2011) define as a matching response relationship, because faster-specialist and slower-flexible hunters preyed upon different prey, but they both achieved equal success. These types of reciprocal responses to interactions have been observed in other predator-prey systems (Kishida et al. 2006, 2009, Edgell and Rochette 2009, McGhee et al. 2013), but their broader consequences remain unclear. Assuming that prey also learned during the interaction, which has been shown across many taxa [refs], we can deduce that learning from reciprocal interactions may contribute in stabilizing predator-prey systems, similar to Red Queen dynamics (Brockhurst et al. 2014).

While experience did not alter most of the interaction, predators still managed to increase foraging specialization with increasing prey speed across experience, while individual differences in hunting success simultaneously decreased. When prey express defensive phenotypes such as high speeds, selection on predators should be strong because of the consequences of repeated failures. If predators improve their exploitative ability, then the consequences of hunting these prey should decrease (Brodie III and Brodie Jr. 1999). Similarly, theoretical studies predict that learning may attenuate selection (Anderson 1995, Ancel 1999, Borenstein et al. 2006, Paenke et al. 2007), but failing to account for reciprocal interactions may mask more complex outcomes. Here, learning appears to have reduced differences in success among predators, but success remained lower when predators hunted faster prey. Again, if prey learned how to avoid the predators, then this would explain why advanced hunters still struggled to achieve similar success against faster prey compared to slower prey. Thus, disentanling the consequences of learning from reciprocal interactions may reveal important insights on predator-prey interactions.

## Conclusions

Trait-mediated interactions that affect prey capture are the most important processes driving predator-prey dynamics (Abrams 2000). While most studies assume that predators maximize success by matching their tactic to their prey (Abrams 2000), it has remained largely unknown whether this results from predators learning how to hunt their prey, in part because of the challenges of investigating direct interactions in the wild. By capitalizing on a virtual predator-prey system where interactions were directly monitored, we found that individual predators displayed large differences in the development of their expertise. With experience, the population became increasingly distinct along a flexible-specialist continuum, while interactions remained largely stable. Overall, all hunters achieved similar hunting success. Our results have potential applications for predator-prey models of trait-matching. For instance, simulation studies could incorporate individual variation in experience or learning to better predict under which ecological/evolutionary contexts specialization should be favoured over flexibility. 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), but also in other fields such as citizen science and conservation (Sandbrook et al. 2015, Redpath et al. 2018, Duthie et al. 2021). We therefore hope that our study will inspire more collaborations between scientists and the videogame industry to tackle fundamental questions in ecology.

# ACKNOWLEDGEMENTS

We warmly thank Behaviour Interactive Inc. for our collaboration which helps in advancing predator-prey science. We thank Julien Céré who managed the communication between us and the company, and Marine Dupuy who helped us prepare the data used in this study. We thank Alastair J. Wilson for insightful comments on the results. We also thank all members of Pierre-Olivier Montiglio’s laboratory who provided useful feedback on earlier versions on this work. This work was supported by an NSERC postgraduate doctoral scholarship (569716-2022).

# CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest

# REFERENCES

Abrams, P. A. 2000. [The Evolution of Predator-Prey Interactions: Theory and Evidence](https://doi.org/10.1146/annurev.ecolsys.31.1.79). Annual Review of Ecology and Systematics 31:79–105.

Ancel, L. W. 1999. [A Quantitative Model of the Simpson-Baldwin Effect](https://doi.org/10.1006/jtbi.1998.0833). Journal of Theoretical Biology 196:197–209.

Anderson, R. W. 1995. [Learning and Evolution: A Quantitative Genetics Approach](https://doi.org/10.1006/jtbi.1995.0123). Journal of Theoretical Biology 175:89–101.

Araújo, M. S., D. I. Bolnick, and C. A. Layman. 2011. [The Ecological Causes of Individual Specialisation](https://doi.org/10.1111/j.1461-0248.2011.01662.x). Ecology Letters 14:948–958.

Barbe, L., C. Mony, and B. W. Abbott. 2020. [Artificial Intelligence Accidentally Learned Ecology through Video Games](https://doi.org/10.1016/j.tree.2020.04.006). Trends in Ecology & Evolution 35:557–560.

Beauchamp, G. 2020. [Predator Attack Patterns Influence Vigilance in a Virtual Experiment](https://doi.org/10.1007/s00265-020-02833-0). Behavioral Ecology and Sociobiology 74:49.

Borenstein, E., I. Meilijson, and E. Ruppin. 2006. [The Effect Of Phenotypic Plasticity on Evolution in Multipeaked Fitness Landscapes](https://doi.org/10.1111/j.1420-9101.2006.01125.x). Journal of Evolutionary Biology 19:1555–1570.

Bowen, W. D., D. Tully, D. J. Boness, B. M. Bulheier, and G. J. Marshall. 2002. [Prey-Dependent Foraging Tactics and Prey Profitability in a Marine Mammal](https://doi.org/10.3354/meps244235). Marine Ecology Progress Series 244:235–245.

Brockhurst, M. A., T. Chapman, K. C. King, J. E. Mank, S. Paterson, and G. D. D. Hurst. 2014. [Running with the Red Queen: The role of biotic conflicts in evolution](https://doi.org/10.1098/rspb.2014.1382). Proceedings of the Royal Society B: Biological Sciences 281:20141382.

Brodie, E. D., and A. Wilkinson. 2010. [Co-Evolution of Predators and Prey](https://doi.org/10.1016/B978-0-08-045337-8.00301-6). Pages 287–295 *in* M. D. Breed and J. Moore, editors. Encyclopedia of Animal Behavior. Academic Press, Oxford.

Brodie III, E. D., and E. D. Brodie Jr. 1999. [Predator-Prey Arms Races: Asymmetrical Selection on Predators and Prey May Be Reduced When Prey Are Dangerous](https://doi.org/10.2307/1313476). BioScience 49:557–568.

Bro-Jørgensen, J. 2013. [Evolution of Sprint Speed in African Savannah Herbivores in Relation to Predation](https://doi.org/10.1111/evo.12233). Evolution 67:3371–3376.

Bürkner, P.-C. 2017. [Brms: An R Package for Bayesian Multilevel Models Using Stan](https://doi.org/10.18637/jss.v080.i01). Journal of Statistical Software 80:1–28.

Carey, M. P., and D. H. Wahl. 2011. [Foraging Modes of Predators and Behaviors of Prey Determine the Outcome of Multiple Predator Interactions](https://doi.org/10.1080/00028487.2011.603983). Transactions of the American Fisheries Society 140:1015–1022.

Céré, J., P.-O. Montiglio, and C. D. Kelly. 2021. [Indirect Effect of Familiarity on Survival: A Path Analysis on Video Game Data](https://doi.org/10.1016/j.anbehav.2021.06.010). Animal Behaviour 181:105–116.

Chang, C., H. Y. Teo, Y. Norma-Rashid, and D. Li. 2017. [Predator Personality and Prey Behavioural Predictability Jointly Determine Foraging Performance](https://doi.org/10.1038/srep40734). Scientific Reports 7:40734.

Cleasby, I. R., S. Nakagawa, and H. Schielzeth. 2015. [Quantifying the Predictability of Behaviour: Statistical Approaches for the Study of Between-Individual Variation in the Within-Individual Variance](https://doi.org/10.1111/2041-210X.12281). Methods in Ecology and Evolution 6:27–37.

Courbin, N., A. Besnard, C. Péron, C. Saraux, J. Fort, S. Perret, J. Tornos, and D. Grémillet. 2018. [Short-Term Prey Field Lability Constrains Individual Specialisation in Resource Selection and Foraging Site Fidelity in a Marine Predator](https://doi.org/10.1111/ele.12970). Ecology Letters 21:1043–1054.

Dall, S. R. X. 2010. Managing Risk: The Perils of Uncertainty. Pages 194–206 *in* D. F. Westneat and C. W. Fox, editors. Evolutionary Behavioral Ecology. Oxford University Press, Oxford, New York.

De Lisle, S. P., D. I. Bolnick, E. D. Brodie III, A. J. Moore, and J. W. McGlothlin. 2022. [Interacting phenotypes and the coevolutionary process: Interspecific indirect genetic effects alter coevolutionary dynamics](https://doi.org/10.1111/evo.14427). Evolution 76:429–444.

Dukas, R. 2019. [Animal Expertise: Mechanisms, Ecology and Evolution](https://doi.org/10.1016/j.anbehav.2018.05.010). Animal Behaviour 147:199–210.

Duthie, A. B., J. Minderman, O. S. Rakotonarivo, G. Ochoa, and N. Bunnefeld. 2021. [Online Multiplayer Games as Virtual Laboratories for Collecting Data on Social-Ecological Decision Making](https://doi.org/10.1111/cobi.13633). Conservation Biology 35:1051–1053.

Edgell, T. C., and R. Rochette. 2009. [Prey-Induced Changes to a Predator’s Behaviour and Morphology: Implications for Shell in the Northwest Atlantic](https://doi.org/10.1016/j.jembe.2009.10.004). Journal of Experimental Marine Biology and Ecology 382:1–7.

Edwards, G. B., and R. R. Jackson. 1994. [The Role of Experience in the Development of Predatory Behaviour in Phidippus regius, a Jumping Spider (Araneae, Salticidae) from Florida](https://doi.org/10.1080/03014223.1994.9517994). New Zealand Journal of Zoology 21:269–277.

Ehlinger, T. J. 1989. [Learning and Individual Variation in Bluegill Foraging: Habitat-Specific Techniques](https://doi.org/10.1016/S0003-3472(89)80010-7). Animal Behaviour 38:643–658.

Endler, J. A. 1991. Interactions between predators and prey. Pages 169–196 *in* J. R. Krebs and N. B. Davies, editors. Behavioural Ecology. Third. Blackwell, Oxford.

Estes, J. A., M. L. Riedman, M. M. Staedler, M. T. Tinker, and B. E. Lyon. 2003. [Individual Variation in Prey Selection by Sea Otters: Patterns, Causes and Implications](https://doi.org/10.1046/j.1365-2656.2003.00690.x). Journal of Animal Ecology 72:144–155.

Fraser Franco, M., F. Santostefano, C. D. Kelly, and P.-O. Montiglio. 2022. [Studying Predator Foraging Mode and Hunting Success at the Individual Level with an Online Videogame](https://doi.org/10.1093/beheco/arac063). Behavioral Ecology 33:967–978.

Gabry, J., and R. Češnovar. 2021. Cmdstanr: R Interface to "CmdStan".

Griffen, B. D., B. J. Toscano, and J. Gatto. 2012. [The Role of Individual Behavior Type in Mediating Indirect Interactions](https://doi.org/10.1890/11-2153.1). Ecology 93:1935–1943.

Heithaus, M. R., L. M. Dill, and J. J. Kiszka. 2018. [Feeding Strategies and Tactics](https://doi.org/10.1016/B978-0-12-804327-1.00126-6). Pages 354–363 *in* B. Würsig, J. G. M. Thewissen, and K. M. Kovacs, editors. Encyclopedia of Marine Mammals (Third Edition). Academic Press.

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)](https://doi.org/10.1242/jeb.154534). Journal of Experimental Biology 220:2076–2081.

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

Ishii, Y., and M. Shimada. 2010. [The Effect of Learning and Search Images on Predator-Prey Interactions](https://doi.org/10.1007/s10144-009-0185-x). Population Ecology 52:27–35.

Jones, K. A., A. L. Jackson, and G. D. Ruxton. 2011. [Prey Jitters; Protean Behaviour in Grouped Prey](https://doi.org/10.1093/beheco/arr062). Behavioral Ecology 22:831–836.

Kelley, J. L., and A. E. Magurran. 2011. [Learned Defences and Counterdefences in Predator-Prey Interactions](https://doi.org/10.1002/9781444342536.ch3). Pages 36–58 Fish Cognition and Behavior. John Wiley & Sons, Ltd.

Kishida, O., Y. Mizuta, and K. Nishimura. 2006. [Reciprocal Phenotypic Plasticity in a Predator-Prey Interaction Between Larval Amphibians](https://doi.org/10.1890/0012-9658(2006)87[1599:RPPIAP]2.0.CO;2). Ecology 87:1599–1604.

Kishida, O., G. C. Trussell, and K. Nishimura. 2009. [Top-Down Effects on Antagonistic Inducible Defense and Offense](https://doi.org/10.1890/08-0238.1). Ecology 90:1217–1226.

Kobler, A., T. Klefoth, T. Mehner, and R. Arlinghaus. 2009. [Coexistence of Behavioural Types in an Aquatic Top Predator: A Response to Resource Limitation?](https://doi.org/10.1007/s00442-009-1415-9) Oecologia 161:837–847.

Lee, Y., and J. A. Nelder. 2006. [Double Hierarchical Generalized Linear Models (With Discussion)](https://doi.org/10.1111/j.1467-9876.2006.00538.x). Journal of the Royal Statistical Society: Series C (Applied Statistics) 55:139–185.

MacDonald, K. 2007. [Cross-Cultural Comparison of Learning in Human Hunting](https://doi.org/10.1007/s12110-007-9019-8). Human Nature 18:386–402.

Manlick, P. J., K. Maldonado, and S. D. Newsome. 2021. [Competition Shapes Individual Foraging and Survival in a Desert Rodent Ensemble](https://doi.org/10.1111/1365-2656.13583). Journal of Animal Ecology 90:2806–2818.

Martin, B. T., M. A. Gil, A. K. Fahimipour, and A. M. Hein. 2022. [Informational Constraints on Predator-Prey Interactions](https://doi.org/10.1111/oik.08143). Oikos 2022:e08143.

Matsumura, K., and T. Miyatake. 2022. [Effects of Individual Differences in the Locomotor Activity of Assassin Bugs on Predator-Prey Interactions](https://doi.org/10.1111/eth.13272). Ethology 128:395–401.

McGhee, K. E., L. M. Pintor, and A. M. Bell. 2013. [Reciprocal Behavioral Plasticity and Behavioral Types during Predator-Prey Interactions.](https://doi.org/10.1086/673526) The American Naturalist 182:704–717.

McLellan, C. F., N. E. Scott-Samuel, and I. C. Cuthill. 2021. [Birds Learn to Avoid Aposematic Prey by Using the Appearance of Host Plants](https://doi.org/10.1016/j.cub.2021.09.048). Current Biology 31:5364–5369.e4.

Mery, F., and J. G. Burns. 2010. [Behavioural Plasticity: An Interaction Between Evolution and Experience](https://doi.org/10.1007/s10682-009-9336-y). Evolutionary Ecology 24:571–583.

Michalko, R., A. T. Gibbons, S. L. Goodacre, and S. Pekár. 2021. [Foraging Aggressiveness Determines Trophic Niche in a Generalist Biological Control Species](https://doi.org/10.1093/beheco/araa123). Behavioral Ecology 32:257–264.

Michalko, R., and S. Pekár. 2016. [Different Hunting Strategies of Generalist Predators Result in Functional Differences](https://doi.org/10.1007/s00442-016-3631-4). Oecologia 181:1187–1197.

Mitchell, D. J., B. G. Fanson, C. Beckmann, and P. A. Biro. 2016. [Towards powerful experimental and statistical approaches to study intraindividual variability in labile traits](https://doi.org/10.1098/rsos.160352). Royal Society Open Science 3:160352.

Moore, T. Y., K. L. Cooper, A. A. Biewener, and R. Vasudevan. 2017. [Unpredictability of Escape Trajectory Explains Predator Evasion Ability and Microhabitat Preference of Desert Rodents](https://doi.org/10.1038/s41467-017-00373-2). Nature Communications 8:440.

Moran, N. P., B. B. M. Wong, and R. M. Thompson. 2017. [Weaving Animal Temperament Into Food Webs: Implications for Biodiversity](https://doi.org/10.1111/oik.03642). Oikos 126:917–930.

Morse, D. H. 2000. [The Effect of Experience on the Hunting Success of Newly Emerged Spiderlings](https://doi.org/10.1006/anbe.2000.1546). Animal Behaviour 60:827–835.

Mougi, A., O. Kishida, and Y. Iwasa. 2011. [Coevolution of Phenotypic Plasticity in Predator and Prey: Why Are Inducible Offenses Rarer Than Inducible Defenses?](https://doi.org/10.1111/j.1558-5646.2010.01187.x) Evolution 65:1079–1087.

Nomura, F., V. H. M. do Prado, F. R. da Silva, R. E. Borges, N. Y. N. Dias, and D. de C. Rossa-Feres. 2011. [Are You Experienced? Predator Type and Predator Experience Trade-Offs in Relation to Tadpole Mortality Rates](https://doi.org/10.1111/j.1469-7998.2011.00791.x). Journal of Zoology 284:144–150.

Paenke, I., B. Sendhoff, and T. J. Kawecki. 2007. [Influence of Plasticity and Learning on Evolution Under Directional Selection.](https://doi.org/10.1086/518952) The American Naturalist 170:E47–58.

Patrick, S. C., and H. Weimerskirch. 2014a. [Personality, Foraging and Fitness Consequences in a Long Lived Seabird](https://doi.org/10.1371/journal.pone.0087269). PLOS ONE 9:e87269.

Patrick, S. C., and H. Weimerskirch. 2014b. [Consistency Pays: Sex Differences and Fitness Consequences of Behavioural Specialization in a Wide-Ranging Seabird](https://doi.org/10.1098/rsbl.2014.0630). Biology Letters 10:20140630.

Paull, J. S., R. A. Martin, and D. W. Pfennig. 2012. [Increased Competition as a Cost of Specialization During the Evolution of Resource Polymorphism](https://doi.org/10.1111/j.1095-8312.2012.01982.x). Biological Journal of the Linnean Society 107:845–853.

Pedersen, E. J., D. L. Miller, G. L. Simpson, and N. Ross. 2019. [Hierarchical Generalized Additive Models in Ecology: An Introduction With mgcv](https://doi.org/10.7717/peerj.6876). PeerJ 7:e6876.

Phillips, R. A., S. Lewis, J. González-Solís, and F. Daunt. 2017. [Causes and Consequences of Individual Variability and Specialization in Foraging and Migration Strategies of Seabirds](https://doi.org/10.3354/meps12217). Marine Ecology Progress Series 578:117–150.

Piironen, J., and A. Vehtari. 2017. [Comparison of Bayesian Predictive Methods for Model Selection](https://doi.org/10.1007/s11222-016-9649-y). Statistics and Computing 27:711–735.

Pintor, L. M., K. E. McGhee, D. P. Roche, and A. M. Bell. 2014. [Individual Variation in Foraging Behavior Reveals a Trade-Off Between Flexibility and Performance of a Top Predator](https://doi.org/10.1007/s00265-014-1779-7). Behavioral Ecology and Sociobiology 68:1711–1722.

Potier, S., A. Carpentier, D. Grémillet, B. Leroy, and A. Lescroël. 2015. [Individual Repeatability of Foraging Behaviour in a Marine Predator, the Great Cormorant, Phalacrocorax carbo](https://doi.org/10.1016/j.anbehav.2015.02.008). Animal Behaviour 103:83–90.

Redpath, S. M., A. Keane, H. Andrén, Z. Baynham-Herd, N. Bunnefeld, A. B. Duthie, J. Frank, C. A. Garcia, J. Månsson, L. Nilsson, C. R. J. Pollard, O. S. Rakotonarivo, C. F. Salk, and H. Travers. 2018. [Games as Tools to Address Conservation Conflicts](https://doi.org/10.1016/j.tree.2018.03.005). Trends in Ecology & Evolution 33:415–426.

Reid, A., F. Seebacher, and A. Ward. 2010. [Learning to Hunt: The Role of Experience in Predator Success](https://doi.org/10.1163/000579509X12512871386137). Behaviour 147:223–233.

Richardson, G., P. Dickinson, O. H. P. Burman, and T. W. Pike. 2018. [Unpredictable Movement as an Anti-Predator Strategy](https://doi.org/10.1098/rspb.2018.1112). Proceedings of the Royal Society B: Biological Sciences 285:20181112.

Sandbrook, C., W. M. Adams, and B. Monteferri. 2015. [Digital Games and Biodiversity Conservation](https://doi.org/10.1111/conl.12113). Conservation Letters 8:118–124.

Santoro, D., S. Hartley, and P. J. Lester. 2019. [Behaviourally Specialized Foragers are Less Efficient and Live Shorter Lives Than Generalists in Wasp Colonies](https://doi.org/10.1038/s41598-019-41791-0). Scientific Reports 9:5366.

Skelhorn, J., C. G. Halpin, and C. Rowe. 2016. [Learning About Aposematic Prey](https://doi.org/10.1093/beheco/arw009). Behavioral Ecology 27:955–964.

Snell-Rood, E. C. 2013. [An Overview of the Evolutionary Causes and Consequences of Behavioural Plasticity](https://doi.org/10.1016/j.anbehav.2012.12.031). Animal Behaviour 85:1004–1011.

Stephens, D. W. 1993. [Learning and Behavioral Ecology: Incomplete Information and Environmental Predictability](https://doi.org/10.1007/978-1-4615-2814-2_8). Pages 195–218 *in* D. R. Papaj and A. C. Lewis, editors. Insect Learning: Ecology and Evolutionary Perspectives. Springer US, Boston, MA.

Szopa-Comley, A. W., W. G. Donald, and C. C. Ioannou. 2020. [Predator Personality and Prey Detection: Inter-Individual Variation in Responses to Cryptic and Conspicuous Prey](https://doi.org/10.1007/s00265-020-02854-9). Behavioral Ecology and Sociobiology 74:70.

Szopa-Comley, A. W., and C. C. Ioannou. 2022. [Responsive Robotic Prey Reveal How Predators Adapt to Predictability in Escape Tactics](https://doi.org/10.1073/pnas.2117858119). Proceedings of the National Academy of Sciences 119:e2117858119.

Team, S. D. 2023. Stan Modeling Language Users Guide and Reference Manual. 2.31 edition.

Tinker, M. T., G. Bentall, and J. A. Estes. 2008. [Food Limitation Leads to Behavioral Diversification and Dietary Specialization in Sea Otters](https://doi.org/10.1073/pnas.0709263105). Proceedings of the National Academy of Sciences 105:560–565.

Tinker, M. T., M. Mangel, and J. A. Estes. 2009. Learning to Be Different: Acquired Skills, Social Learning, Frequency Dependence, and Environmental Variation can Cause Behaviourally Mediated Foraging Specializations. Evolutionary Ecology Research 11:841–869.

Toscano, B. J., N. J. Gownaris, S. M. Heerhartz, and C. J. Monaco. 2016. [Personality, Foraging Behavior and Specialization: Integrating Behavioral and Food Web Ecology at the Individual Level](https://doi.org/10.1007/s00442-016-3648-8). Oecologia 182:55–69.

Toscano, B. J., and B. D. Griffen. 2014. [Trait-Mediated Functional Responses: Predator Behavioural Type Mediates Prey Consumption](https://doi.org/10.1111/1365-2656.12236). Journal of Animal Ecology 83:1469–1477.

van den Bosch, M., J. M. Baert, W. Müller, L. Lens, and E. W. M. Stienen. 2019. [Specialization Reduces Foraging Effort and Improves Breeding Performance in a Generalist Bird](https://doi.org/10.1093/beheco/arz016). Behavioral Ecology 30:792–800.

Vehtari, A., A. Gelman, and J. Gabry. 2017. [Practical Bayesian Model Evaluation Using Leave-One-Out Cross-Validation and WAIC](https://doi.org/10.1007/s11222-016-9696-4). Statistics and Computing 27:1413–1432.

Vehtari, A., A. Gelman, D. Simpson, B. Carpenter, and P.-C. Bürkner. 2021. [Rank-Normalization, Folding, and Localization: An Improved $\widehat{}R{}$ for Assessing Convergence of MCMC (with Discussion)](https://doi.org/10.1214/20-BA1221). Bayesian Analysis 16:667–718.

Vehtari, A., D. Simpson, A. Gelman, Y. Yao, and J. Gabry. 2022, August. [Pareto Smoothed Importance Sampling](https://doi.org/10.48550/arXiv.1507.02646). arXiv.

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?](https://doi.org/10.1111/j.1365-2435.2005.01033.x) Functional Ecology 19:808–815.

Warburton, K. 2003. [Learning of Foraging Skills by Fish](https://doi.org/10.1046/j.1467-2979.2003.00125.x). Fish and Fisheries 4:203–215.

Ward-Fear, G., G. P. Brown, and R. Shine. 2020. [Predators Learning to Avoid Toxic Invasive Prey: A Study on Individual Variation Among Free-Ranging Lizards](https://doi.org/10.1163/1568539X-bja10040). Behaviour 157:1153–1172.

Weimerskirch, H. 2007. [Are Seabirds Foraging for Unpredictable Resources?](https://doi.org/10.1016/j.dsr2.2006.11.013) Deep Sea Research Part II: Topical Studies in Oceanography 54:211–223.

Weimerskirch, H., A. Gault, and Y. Cherel. 2005. [Prey Distribution and Patchiness: Factors in Foraging Success and Efficiency of Wandering Albatrosses](https://doi.org/10.1890/04-1866). Ecology 86:2611–2622.

Wilson, A. M., T. Y. Hubel, S. D. Wilshin, J. C. Lowe, M. Lorenc, O. P. Dewhirst, H. L. A. Bartlam-Brooks, R. Diack, E. Bennitt, K. A. Golabek, R. C. Woledge, J. W. McNutt, N. A. Curtin, and T. G. West. 2018. [Biomechanics of Predator-Prey Arms Race in Lion, Zebra, Cheetah and Impala](https://doi.org/10.1038/nature25479). Nature 554:183–188.

Wilson-Rankin, E. E. 2015. [Level of Experience Modulates Individual Foraging Strategies of an Invasive Predatory Wasp](https://doi.org/10.1007/s00265-014-1861-1). Behavioral Ecology and Sociobiology 69:491–499.

Woo, K. J., K. H. Elliott, M. Davidson, A. J. Gaston, and G. K. Davoren. 2008. [Individual Specialization in Diet by a Generalist Marine Predator Reflects Specialization in Foraging Behaviour](https://doi.org/10.1111/j.1365-2656.2008.01429.x). Journal of Animal Ecology 77:1082–1091.

Wright, J., T. R. Haaland, N. J. Dingemanse, and D. F. Westneat. 2022. [A Reaction Norm Framework for the Evolution of Learning: How Cumulative Experience Shapes Phenotypic Plasticity](https://doi.org/10.1111/brv.12879). Biological Reviews 97:1999–2021.

# 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

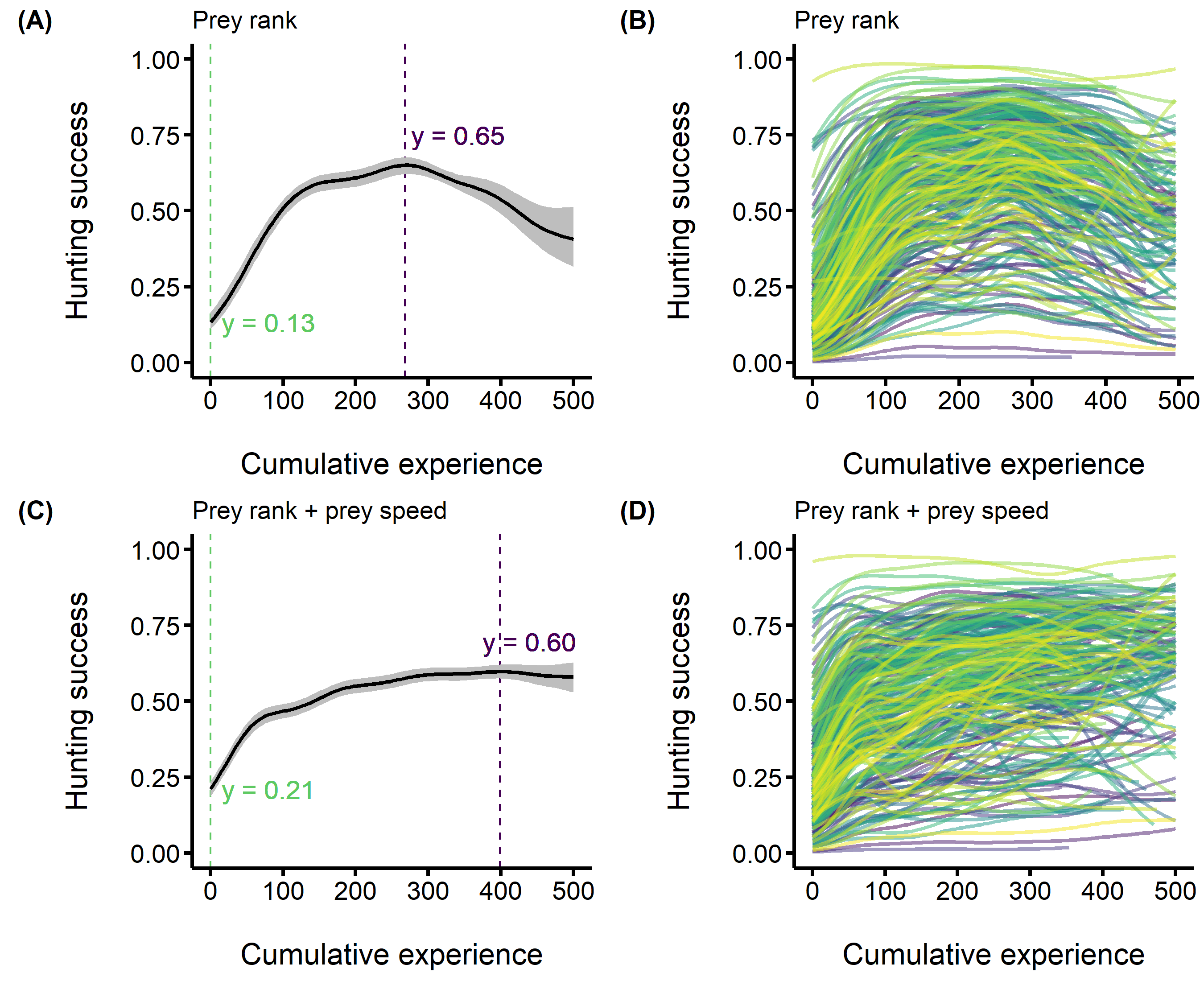
**Figure 1.** Median posterior predictions of the development of predator hunting expertise. The predators’ hunting success (i.e. the probability of consuming the four prey) is on the y axis, and the predators’ cumulative experience (i.e. the number of matches played prior to each observation) is on the x axis. Panels A and C show the development of expertise for the average individual with the vertical dashed lines representing the lowest and highest predicted values respectively. In contrast, 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 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



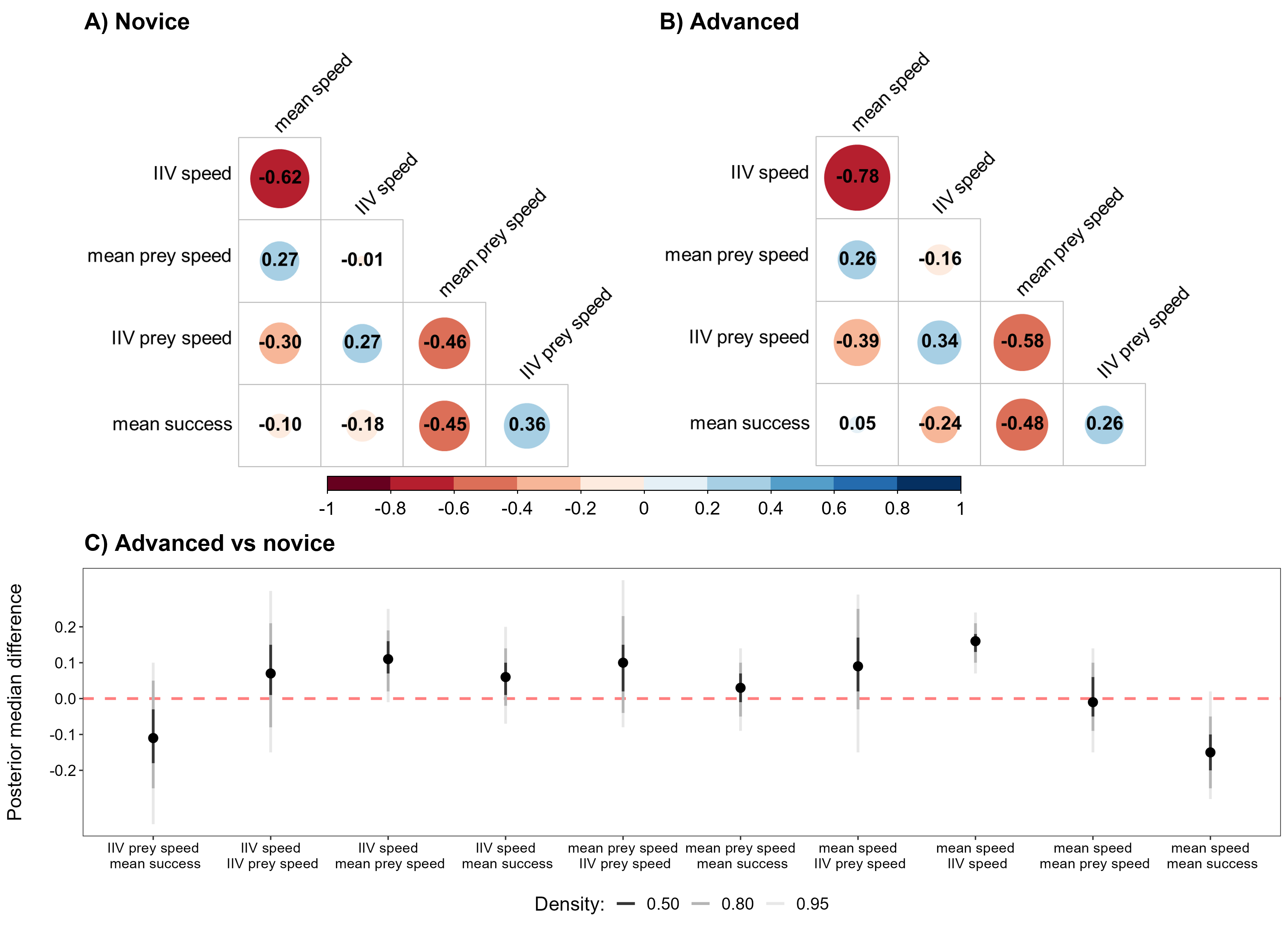
**Figure 1**



**Figure 2**



**Figure 3**



**Figure 4**