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

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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>

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# ABSTRACT

# 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 in different foraging tactics or on different resources irrespective of sexual, morphological, or age-related differences (Estes et al. 2003, Tinker et al. 2008, Kernaléguen et al. 2015, Phillips et al. 2017). A growing body of evidence suggests that ecological interactions such as predator-prey interactions can drive this individual foraging specialization (Araújo et al. 2011, Toscano et al. 2016). When they hunt, predators often use techniques that are fine-tuned to the type of prey that they encounter (Davoren et al. 2003, Estes et al. 2003, Woo et al. 2008, Courbin et al. 2018), and their capacity to use them effectively is contingent on periods of extensive practice (i.e. experience). While hunting experience may be essential to maintain or improve foraging success, we have few empirical assessments of its role in predator foraging specialization (Dukas 2019) and its consequences on predator-prey interactions.

The development of foraging tactics is crucial for young predators to reach adulthood and survive (Phillips et al. 2017, Heithaus et al. 2018). Theory predicts that foraging specialization may emerge via learning, limitations in memorizing multiple complex hunting skills, and expertise (Tinker et al. 2009, Dukas 2019). Dukas (2019) defines expertise as the characteristics, skills, and knowledge allowing individuals with extensive experience to outperform novices on complex tasks. It is described as the relationship between success and cumulative 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 the efficiency (e.g. search and handling times, return rates) of their foraging tactics 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 hunting tactic is constant each time a prey is encountered. It may also be costly to attempt different hunting tactics by trial and error when prey are scarce or highly unpredictable (Dukas 1998, Estes et al. 2003, Mery and Burns 2010). An alternative mechanism is that the costs/risks faced by hunters when switching foraging tactics may be offset through extensive practive, 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 of time, 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 mechanisms operating at the same time within a predator population. For instance, some individuals may constantly encounter faster prey, which are proven to be more difficult to hunt in simulation and empirical studies (Walker et al. 2005, Kelley and Magurran 2011, Martin et al. 2022). Thus, whether predators specialize or increase their flexibility with experience, learning to adjust their tactic to their prey should be essential to optimize their success.

There is currently a lack of consensus on the fitness advantages of specialized vs flexible foraging (Phillips et al. 2017). This is reflected in the literature showing contrasting results in the links between specialization and fitness. For instance, some studies report increasing benefits of specialization (Patrick and Weimerskirch 2014b, Pintor et al. 2014, van den Bosch et al. 2019), some report that flexible foraging has greater benefits (Paull et al. 2012, Manlick et al. 2021), and others find equal benefits depending on timescales (Woo et al. 2008, Potier et al. 2015). This may in part be due to the limited information we have on the ecological contexts favouring specialization over flexibility in nature. However, in predator-prey systems, many studies have outlined that fluctuations in the predictability of prey encounters throughout a predator’s lifetime may be a key factor shaping foraging specialization (Weimerskirch 2007, Woo et al. 2008, Chang et al. 2017, Phillips et al. 2017, Courbin et al. 2018). The resource-predictability (or resource-heterogeneity) hypothesis argues 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 when resources fluctuate, as fine adjustments to resources are key for a predator’s success and survival (Karkarey et al. 2017, Holm et al. 2019, Santoro et al. 2019). When predator-prey interactions are directly observed, empirical evidence shows that predators often match, among other types of traits (see Kishida et al. 2006, Hanifin et al. 2008, Brousseau et al. 2018, Reimche et al. 2020), their locomotor and behavioural traits to those of their prey (Bro-Jørgensen 2013, McGhee et al. 2013, Chang et al. 2017, Szopa-Comley and Ioannou 2022). Yet, a recurring question that emerges from these studies is whether and how the behavioural adjustments of predators reflect individual differences in experience/learning (Kelley and Magurran 2011). Thus, uncovering the role of learning in predator-prey systems where interactions are directly monitored would enable researchers to better predict the behavioural decisions and the success of predators when they are hunting.

The integration of individual behavioural variation in the study of predator-prey interactions has gained traction in recent years, with empirical studies revealing important 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). However, an important and 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 prey. We recently demonstrated with behavioural data from an online predator-prey videogame, called *Dead by Daylight* (*DBD*), that virtual systems can overcome this challenge and help uncover the mechanisms that shape predator-prey interactions (Fraser Franco et al. 2022). For instance, we found that some individual predators hunt at high speeds and cover space in the environment, while others prefer to stalk and ambush their prey. Individuals are also flexible in the use of these tactics by switching between them across matches. The expression of these tactics and their success is also shaped by the speed of the prey, where faster prey are more difficult to hunt. The prey need to forage for resources while paying attention to the predator to avoid being detected and chased. Some prey contribute to the group’s success by healing or helping others escape the predator, while others play alone and attempt to escape by themselves (Céré et al. 2021). Predators must learn how the prey behave and then decide how best to capture them. Thus, *DBD* simulates a highly dynamic system where both predators and prey must adjust to each other, suggesting that virtual systems could be useful in identifying general ecological patterns, which might in turn help to advance the current gaps in predator-prey research. Other studies on virtual predator-prey systems show that predation regimes can 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). Virtual predator-prey systems generate large volumes of data on interacting players throughout their lifetime in the game under realistic ecological scenarios. Hence, they offer the opportunity to tackle fundamental questions about the role of experience and prey behaviour on individual predator foraging specialization along with their potential fitness consequences.

In this study, we test how hunting experience shapes predator foraging specialization using individual behavioural data from players in the online videogame *Dead by Daylight*. *DBD* simulates a direct predator-prey interaction, where one predator player hunts four prey players in different virtual environments. The data grants a high degree of precision on the behavioural interaction, as the behaviour of both the predator and the four prey along with the predator’s success are monitored simultaneously in each trial. First, we investigate how predators develop their individual hunting expertise. We hypothesize that predators should differ in the development of their expertise, partly because they encounter varying levels of difficulty with the prey that they pursue. For example, a predator may face greater difficulty than other individuals if it more often encountered prey that were elusive. Second, we test the hypothesis that experience will shape foraging specialization. If experience reduces the costs of switching between hunting tactics, we predict that the predator population should become more flexible. Alternatively, if experience enables the refinement of the hunting tactics, then the predator population may instead specialize. Otherwise, if both mechanisms operate at the same time, then we should see no change with experience at the population level, but differences in specialization among individuals should increase. Third, we evaluate how predator foraging specialization emerges from behavioural interactions with prey. Whether predators specialize or not with experience should depend on the behaviour of their prey. We expect that predators that experienced more predictable encounters with their prey will specialize, while predators that experienced unpredictable encounters with their prey should adopt a flexible hunting strategy. If we detect such prey-dependent fine-tuning, then specialist and flexible hunters should attain equal success.

# MATERIALS AND METHODS

## Study system

*DBD* is a survival asymmetric (i.e. a game where the gameplay mechanics differ between two groups) multiplayer online game developed by Behaviour Interactive Inc, in which players can play either as a predator or a prey. The objective of the predator is to hunt and capture the four prey across a virtual environment. The objective of the four 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 for 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 environment where matches take place is 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 our study period.

## Data collection

The videogame company provided data that spanned a period of 6 months of gameplay recorded for every player. The first recorded match was played on 2020-12-01 and the last one on 2021-06-01. We cleaned and filtered the raw data to produce a dataset appropriate for our analyses. We analyzed only matches where players did not know each other (i.e. “Online” mode). We filtered any matches where players were inactive, such as when speed values 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 it is supposed to be played. We then sampled players that played 300 matches or more. To optimize the representation of gameplay experience at advanced levels, we set the maximum number of matches at 500 for these players. For instance, there could be a large difference in gameplay between 300-500 and 500-1000 matches. Players that played more than 500 matches represented ~2% of the population.

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 powers-gameplay mechanics), the game environment, the predator-player’s experience along with its speed, and the average speed of the group of prey it encountered.

We recognize that we could have introduced a bias in our analyses since we sampled individuals who stayed in the game for at least 300 matches. For instance, these players may already be used to play videogames, and thus, could differ in the way they play at early stages of their experience in the game. To ensure that our sample was not biased, the videogame company provided a random sample of players that played between 20 and 50 matches, between 51 and 100 matches, and between 101 and 300 matches from the same timeframe as our current sample. We then took the first 20 matches played by these players, including those from our sampled population, and compared their average behaviour using a Bayesian hierarchical linear model. We found that neither of the four groups differed in their average speed (Table SX), which gives us confidence that our player population was not biased.

## Variables

We analyzed the predator’s average speed and the average speed of the prey group encountered by the predator. The predator’s average speed is measured as the average distance traveled per second during a match ( = 3.31 ± 0.49 m/s). We measured the preys’ average speed as the average travel speed of the four individual prey within a match ( = 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.

## Statistical analyses

### Software and computer specifications

All our statistical analyses were executed on Cedar (<https://docs.alliancecan.ca/wiki/Cedar>), a computer cluster maintained by the Digital Research Alliance of Canada. The operating system for Cedar is CentOS Linux 7. The models were fitted in R (version 4.1.2) using Markov chain Monte Carlo (MCMC) sampling with the package “brms” version 2.16.3 (Bürkner 2017), an R front-end for the STAN software (Team 2023), and “cmdstanr” version 0.4.0 (Gabry and Češnovar 2021) as the back-end for estimation (cmdstan installation version 2.28.2).

### Effect of experience on hunting success

We tested whether predators varied in the development of their expertise using three Bayesian generalized additive mixed models (GAMM) with thin plate regression splines. These models estimate the relationship between hunting success (i.e. number of prey captured) 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 for all observations and random intercepts for the predator ID. In this model, we assume that individuals 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 group-level smoothers for the predator ID. In this model, we assume that individuals share a similar relationship between success and experience, but that this relationship can vary (e.g. individual 1 has a steeper curve than individual 2). This enabled us to test whether predators differed in the development of their expertise. In the third model, we kept the group-level smoothers for the predators, but removed the global smoother. This allows each individual to have a unique relationship between success and experience without penalization by the global smoother. Thus, this model assumes that predators do not share a common relationship between success and experience. We included match duration as a covariate in all three models.

Because a maximum of four prey can be captured in the game, and to control for overdispersion, we computed the three models using a modified version of the beta-binomial distribution implemented in “brms”. Thus, hunting success was estimated as the probability of capturing 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 for all models.

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 Gaussian priors for the game duration (), the intercept (), and the precision paremeter (). We employed the default Student t priors for the smoothing parameter (). After fitting the three models, we proceeded to select the one with the best predictive accuracy using approximate leave-one-out cross-validation with Pareto-smoothed importance sampling (Piironen and Vehtari 2017, Vehtari et al. 2017, Vehtari et al. 2022).

### Changes in foraging behaviour and predator-prey interactions with experience

We tested whether foraging behaviour changed with experience, and compared the success of generalists vs specialists, using a multivariate, double-hierarchical generalized linear model (MDHGLM) (Lee and Nelder 2006, Westneat et al. 2014, Cleasby et al. 2015, Mitchell et al. 2016, O’Dea et al. 2022). We categorized the predators by their experience based on the number of matches they played (i.e. their cumulative experience). Since we monitored all predator players throughout their experience, they appeared in all of the three following experience categories. First, we assigned predators the status of “novice” when they had a cumulative experience below 100 matches. For example, a predator player that played 500 matches in total would be labelled as a novice in its first 100 matches. Following this logic, we labelled predators as “intermediate” hunters when they had a cumulative experience between 100 and 299 and matches. Lastly, we defined predators as “advanced” hunters when they had a cumulative experience equal or above 300, with a maximum of 499 cumulated matches.

For each level of experience (i.e. novice, intermediate, advanced), the model estimated the mean speed of every individual (which we call the mean part of the model) and, by using a heterogeneous structure of the residuals, the intra-individual standard deviation of speed for every individual (which we call the dispersion part of the model). Thus, in the mean part of the model, we could estimate among individual differences in the foraging tactic used by predators (i.e. along the slow-fast continuum), while in the dispersion part of the model, we could estimate among individual differences in foraging specialization/flexibility (i.e. intra-individual variability). We followed the same structure for the preys’ speed to estimate among individual differences in the mean and standard deviation of speed of the prey groups encountered by predators. For the mean part of the model, it allows us to test whether individual predators differed in the average speed of the groups of prey encountered across the study. For the dispersion part, it allows us to test whether individual predators differed in the (dis)similarity of the groups of prey encountered across the study (i.e. if resource heterogeneity was higher for some individuals compared to others). For hunting success, we only modeled the mean part of the equation to estimate among individual differences in mean prey capture. For the predator and the prey’s speed, we controlled for the average rank of the prey that they encountered as proxy for prey skills on both the mean and dispersion part of the equation. 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>). We used the mean rank of the four prey and applied a square-root transformation. For the predator’s hunting success, we controlled for the square-root of the duration of the match.

We estimated the correlation between the individual random effect on the mean and on the dispersion within each trait (e.g. ) and among each trait (e.g. ) within a level of experience. In the first case, this allows us to assess, for example, whether predators that are on average slower/faster are more specialized or flexible. In the second case, the correlations enables us to estimate, for example, whether predators that encountered prey that were faster/slower adopted a slower/faster (or more specialized/flexible) tactic, or if slower/faster predators had lower/greater hunting success. As a complement, the model also estimated correlations among the different levels of experience (e.g. ). The latter “character-state” approach (Via and Lande 1985, Via et al. 1995), enables us to investigate whether predators express similar behaviours across each of three developmental stages. We present the character-state analyses as additional material in the Appendix S2 as they were not part of our initial objectives.

The full model has the following form, with each equation repeated three times (i.e. one for each level of experience):

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

where , , and are the vectors of random environment, random avatar, and random individual identity effects associated with their incidence matrices , , and . is the vector of fixed effects with its incidence matrix . The and subscripts indicate that an estimate is from the mean or dispersion part of the model, respectively. On the mean part of the model, 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. The residuals are assumed to follow a Gaussian distribution (). On the dispersion part of the model, the residuals vary among individuals, allowing us to estimate among individual differences in specialization. The individual identity random effects on both the mean and dispersion parts follow a multivariate Gaussian distribution where is a 15x15 variance-covariance matrix. The parameters , , and , correspond to the among environment, among avatar, and among individual standard deviations, respectively.

We parameterized equations 1.1 to 2.2 with a Gaussian distribution family (predator and prey speed) and used a beta-binomial distribution family for equation 3 (predator hunting success). We used Gaussian priors for the prey rank () and game duration () on the mean part of the model (equations 1.1, 2.1, and 3), and the default priors in “brms” for the dispersion part (equations 1.2 and 2.2). We used the default Student t priors in “brms” for the intercepts on the mean and dispersion part of the model. For hunting success, we applied a Gaussian prior on the precision parameter (). For every predicted variable, we applied a half-Gaussian prior () on the random effects for the mean part of the model (equations 1.1, 2.1, and 3), and the default “brms” Student t prior for the dispersion part of the model (equations 1.2 and 2.2).

### Markov Chain Monte Carlo settings

We parametrized every model described above 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 I), and 1500 iterations with a thinning set to four for the additive model with a global smoother and group-level smoothers as well as for the additive model with group-level smoothers only (Table I). Burn-in was set to 500 iterations in each model. We parametrized the MDHGLM to run 2500 iterations with a thinning set to 8, with the first 500 iterations used as warmups. We assessed the convergence of the MCMC chains using trace plots, R-hat diagnostics with a threshold of <1.05, and effective sample sizes (ESS) with a threshold of >100 for the bulk-ESS and tail-ESS (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>).

# RESULTS

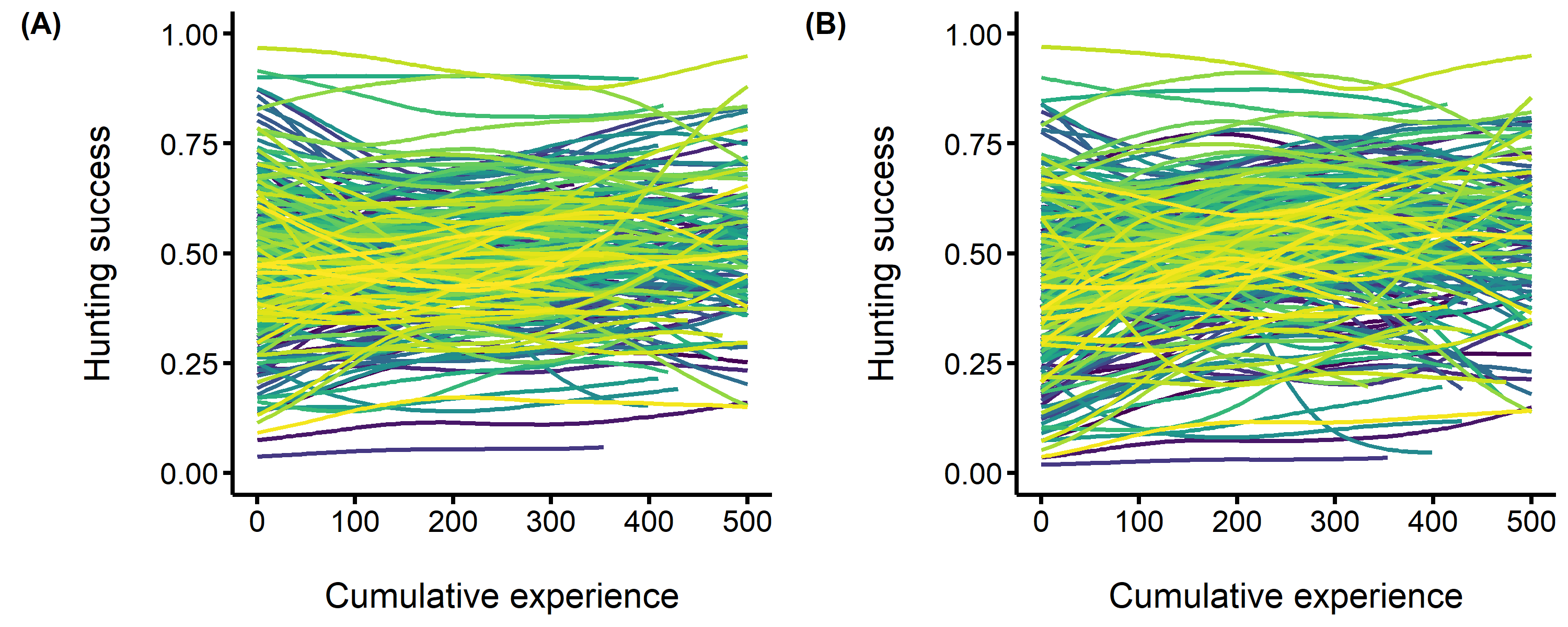
## Effect of experience on hunting success

Our results confirm that individual predators display substantial differences in the development of their expertise, as the best model included group-level smoothers exclusively (Table I). For instance, some predators steadily increased (Figure 1A, Appendix S1: Figure S1A), while others decreased (Figure 1A, Appendix S1: Figure S1B), their hunting success with greater experience, and others whose success did not change with experience (Figure 1A). Another pattern that emerged was that some individuals optimized their success at an experience level that was below what we considered “advanced” (i.e. >300 matches played).

**Table** : Leave-one-out cross-validation table of the three hierarchical GAMMs relating hunting success to player experience

| model | elpd  difference | sd  difference | elpd loo  value | elpd loo  standard error |
| --- | --- | --- | --- | --- |
| Group-level smoothers only | 0.00 | 0.00 | -146 338.37 | 166.96 |
| Global smoother + group-level smoothers | -101.47 | 6.28 | -146 439.84 | 167.21 |
| Global smoother only | -840.42 | 42.67 | -147 178.79 | 163.31 |
| \* 'elpd' refers to the 'expected log pointwise density' and is the value chosen to select the best model. | | | | |

We predicted that the relationship between hunting success and experience would vary among predators because they should differ in the type of prey that they encounter. However, after controlling for the mean speed of the prey group within a match, we did not find evidence confirming this prediction, because differences among predators remained stable (Figure 1B).



**Figure 1.** Among individual differences in the development of hunting expertise. The predators’ hunting success (i.e. the probability of capturing 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. Each fitted curve represents an individual predator. (A) A generalized additive mixed model where we do not control for prey speed (B) A generalized additive mixed model where we control for prey speed.

## Effect of experience on the development of behavioural specialization

At the population level, predators did not change their mean speed with experience (i.e. intercept of the mean predator speed; Table 2). Moreover, there was no directional increase in foraging flexibility or specialization with experience. Indeed, the observed pattern is more complex given that predators became more flexible with experience at intermediate levels of experience (i.e. intercept of sigma for predator speed is larger for intermediates than novices; Table 2 and Appendix S1: Figure S4), but then return to novice-levels of flexibility with advanced experience (i.e. intercept of sigma for predator speed is smaller for advanced players than intermediates; Table 2 and Appendix S1: Figure S4). Thus, our analyses suggest that population-level behavioural specialization changes nonlinearly (quadratic) with experience rather than linearly.

**Table** : Posterior means and 95% credible intervals of the fixed effects estimated by the MDHGLM of predator speed, prey speed, and predator hunting success.

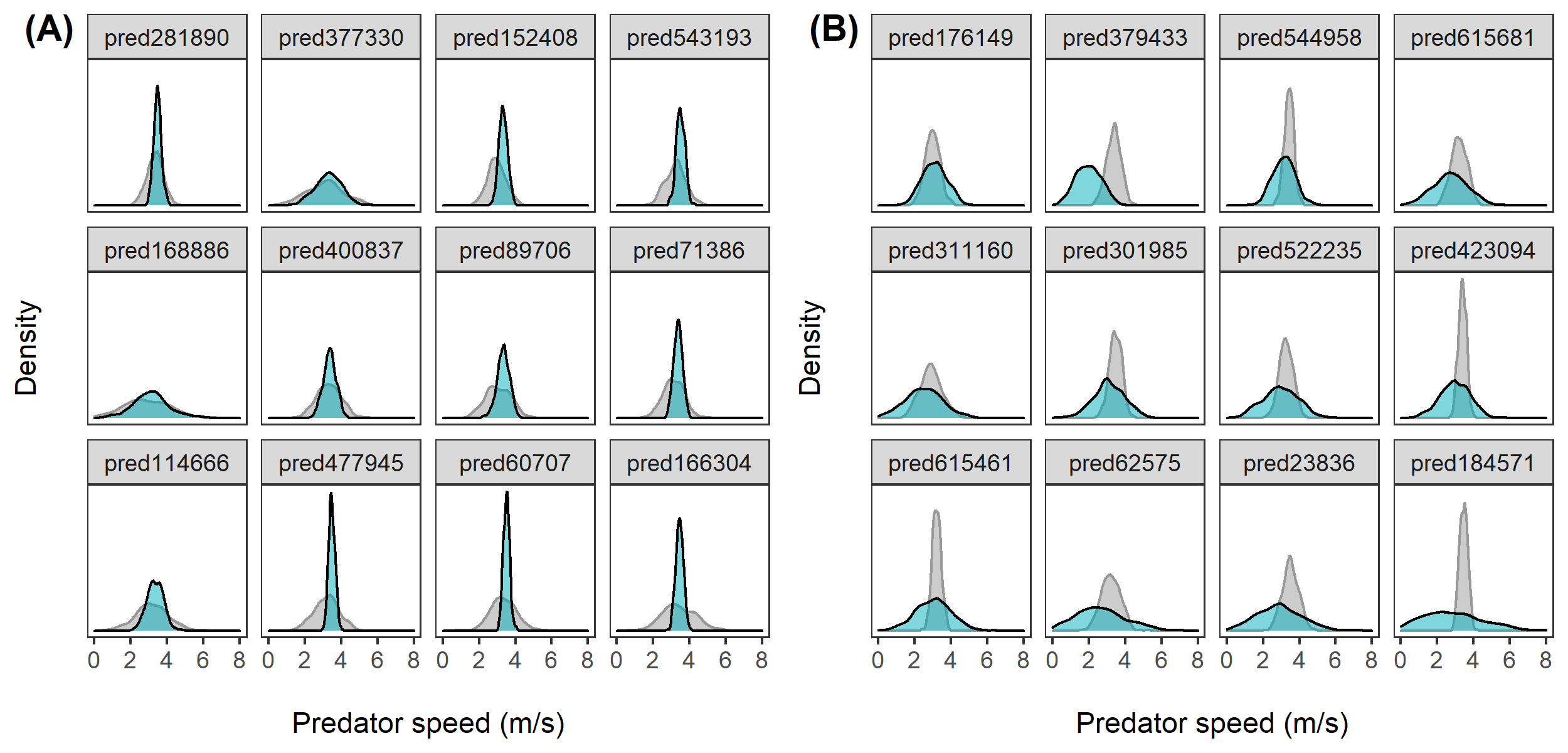
| Trait | Parameter | Novice | Intermediate | Advanced |
| --- | --- | --- | --- | --- |
| predator speed | intercept (mean) | 3.392 ( 3.283, 3.511) | 3.387 ( 3.231, 3.559) | 3.388 ( 3.242, 3.546) |
| prey rank (mean) | -0.030 (-0.036, -0.024) | -0.037 (-0.042, -0.033) | -0.045 (-0.052, -0.039) |
| intercept (sigma) | 0.292 ( 0.271, 0.315) | 0.326 ( 0.307, 0.347) | 0.289 ( 0.268, 0.311) |
| prey rank (sigma) | 0.986 ( 0.969, 1.004) | 0.967 ( 0.953, 0.980) | 0.994 ( 0.978, 1.013) |
| prey speed | intercept (mean) | 2.948 ( 2.909, 2.986) | 2.899 ( 2.864, 2.933) | 2.837 ( 2.799, 2.873) |
| prey rank (mean) | -0.181 (-0.188, -0.174) | -0.171 (-0.176, -0.166) | -0.163 (-0.169, -0.156) |
| intercept (sigma) | 0.200 ( 0.189, 0.212) | 0.201 ( 0.194, 0.209) | 0.208 ( 0.199, 0.217) |
| prey rank (sigma) | 1.116 ( 1.097, 1.134) | 1.116 ( 1.102, 1.131) | 1.107 ( 1.089, 1.124) |
| hunting success | intercept (mean) | 0.018 ( 0.015, 0.021) | 0.017 ( 0.015, 0.019) | 0.018 ( 0.016, 0.021) |
|  | match duration (mean) | 0.539 ( 0.537, 0.540) | 0.540 ( 0.539, 0.541) | 0.540 ( 0.538, 0.541) |
| a We exponentiated the dispersion parameters (i.e. sigma) which are estimated on a log scale. We back-transformed the hunting success values, estimated on a logit scale, back to a probability scale. b The intercept values on the mean part of the equation for all traits indicate mean behaviour and success at the population level. The intercept values on the dispersion (i.e. sigma) part of the equation for predator speed indicate behavioural specialization at the population level. | | | | |

At the individual level, we detected differences in the mean movement speed among predators (i.e. the intercept of the mean speed for the predator ID; Table 3). These differences remained stable from the novice to the intermediate stages, and then increased at the advanced stage to reach a level higher than when predators were novice (Table 3 and Appendix S1: Figure S4). Predators displayed considerable differences in their degree of hunting specialization, and these differences increased with experience (i.e. the intercept of sigma for the predator ID increases with experience; Table 3 and Appendix S1: Figure S4). Thus, as individual predators gain experience, the population becomes more heterogeneous, with an assemblage of both specialist and flexible hunters. Moreover, some individual predators switched from a flexible to a specialized hunting tactic, and vice-versa, as they gained experience (Figure 2). Importantly, 12.6% of the predator population displayed a large change in foraging specialization/flexibility with experience (i.e. $$0.2 change in standard deviation), 44.7% displayed lower changes (i.e. >0.05 and <0.2 change in standard deviation), while 42.7% remained relatively stable (i.e. $$0.05 change in standard deviation).

**Table** : Posterior means and 95% credible intervals of the random effects estimated by the MDHGLM of predator speed, prey speed, and predator hunting success.

| Trait | Parameter | Novice | Intermediate | Advanced |
| --- | --- | --- | --- | --- |
| predator speed | avatar (mean) | 0.307 (0.229, 0.407) | 0.366 (0.262, 0.487) | 0.370 (0.270, 0.487) |
| environment (mean) | 0.024 (0.019, 0.031) | 0.027 (0.020, 0.033) | 0.027 (0.021, 0.034) |
| predator ID (mean) | 0.158 (0.143, 0.172) | 0.154 (0.138, 0.166) | 0.194 (0.175, 0.213) |
| predator ID (sigma) | 1.486 (1.440, 1.536) | 1.521 (1.468, 1.573) | 1.587 (1.525, 1.649) |
| prey speed | avatar (mean) | 0.052 (0.036, 0.069) | 0.062 (0.044, 0.084) | 0.062 (0.045, 0.080) |
| environment (mean) | 0.057 (0.043, 0.072) | 0.055 (0.042, 0.070) | 0.054 (0.042, 0.069) |
| predator ID (mean) | 0.090 (0.081, 0.098) | 0.082 (0.075, 0.089) | 0.109 (0.098, 0.119) |
| predator ID (sigma) | 1.058 (1.044, 1.070) | 1.083 (1.073, 1.093) | 1.102 (1.088, 1.116) |
| hunting success | predator ID (mean) | 0.724 (0.660, 0.786) | 0.575 (0.528, 0.622) | 0.601 (0.547, 0.655) |
| a We exponentiated the dispersion parameters (i.e. sigma) which are estimated on a log scale. All the reported values are standard deviations. b The intercept values on the mean part of the equation for all traits indicate among individual differences in mean behaviour and success. c The intercept values on the dispersion (i.e. sigma) part of the equation for predator speed indicate among individual differences in behavioural specialization. For prey speed and hunting success, they indicate among individual differences in the variability of prey encounters and variability in hunting success, respectively. | | | | |

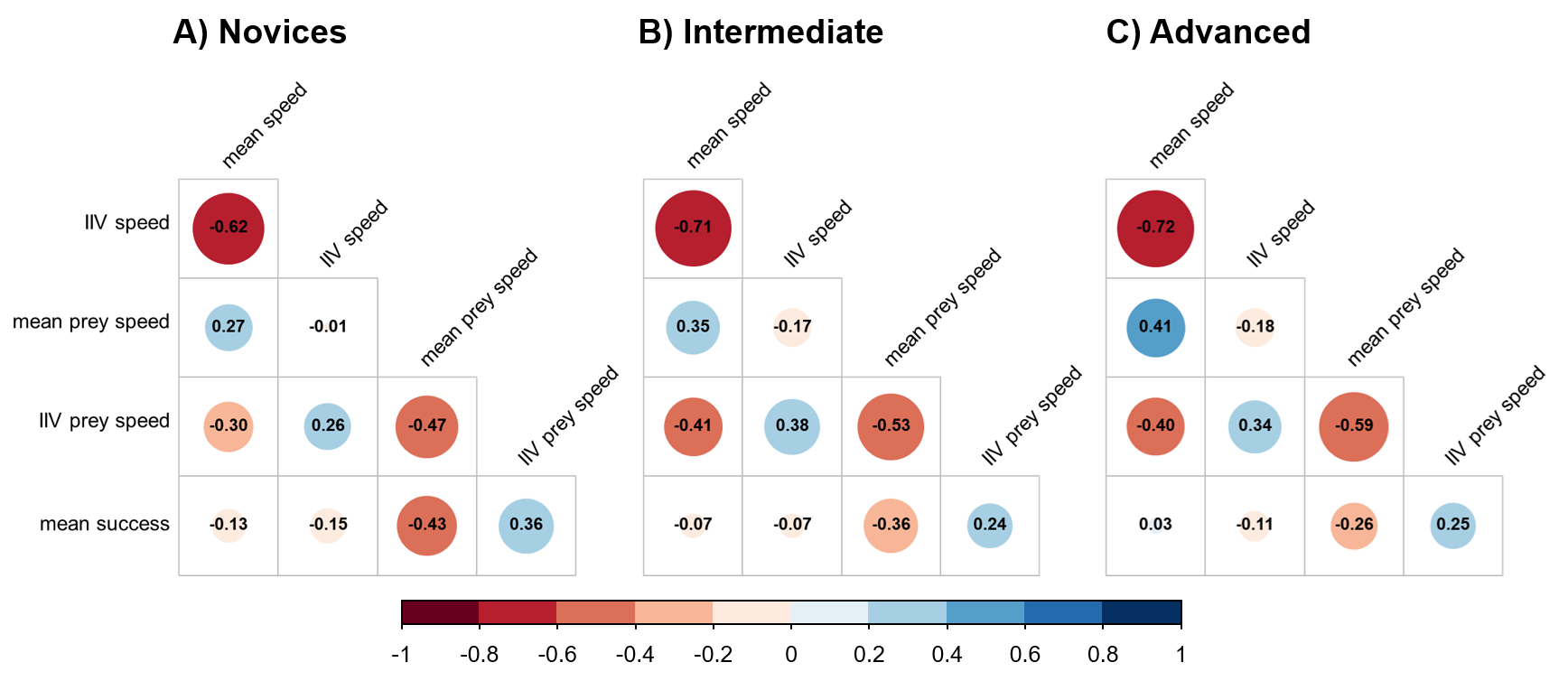
As we predicted, predators differed in the mean speed of the prey that they encountered across matches. Thus, some individuals encountered prey that were on average slower, while others encountered prey that where on average faster throughout the study period (i.e. the intercept of the mean prey speed for the predator ID; Table 3). These differences were greater when predators reached an advanced level of hunting experience (i.e. the intercept of the mean prey speed for the predator ID was higher at the advanced stage; Table 3 and Appendix S1: Figure S4). In addition, individuals differed in the heterogeneity of the groups of prey encountered across the study period. Hence, some predators encountered prey groups with similar average speeds, while others encountered prey groups with different average speeds throughout the study period (i.e. the intercept of sigma prey speed for the predator ID; Table 3).



**Figure 2.** 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 selected the individuals displayed in the figure by first substracting the estimated standard deviation of all individuals as novices with their standard deviation as advanced hunters, and then selecting 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 0.28 standard deviations.

## Relationship between behavioural specialization and prey variability

At all experience levels, predators that were on average faster (mean) also had a lower intra-individual variability (IIV; Figure 3 and Appendix S2: Table S1). Thus, faster predators specialized on fast movement, while slower predators were more flexible in their movement through time. Predators that were on average faster (mean) also encountered groups of prey that were on average faster (mean) (Figure 3 and Appendix S2: Table S1). At the three experience levels, there were only weak correlations between IIV in predator speed and mean prey speed (Figure 3 and Appendix S2: Table S1). However, predators that encountered groups of prey with similar speeds (IIV) specialized in their hunting tactic (IIV) (Figure 3 and Appendix S2: Table S1). Hence, predators that encountered groups of prey with similar average speeds were more specialized, while those that encountered groups of prey with different average speeds were more flexible. For all the results described above, the correlations strengthen as predators gain experience (Figure 3 and Appendix S2: Table S1).



**Figure 3.** Correlation matrices of the MDHGLM relating the mean and intra individual variability (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 color legend), while larger dark red circles indicate stronger negative correlations (negative values on the color legend). A) Correlations when predators were novice hunters. B) Correlations when predators were at an intermediate level of experience. C) Correlations when predators were advanced hunters.

## Hunting success of behavioural specialists vs generalists

We did not detect strong correlations between the predators’ mean speed and their hunting success (Figure 3 and Appendix S2: Table S1), nor between the predators’ IIV in speed and their hunting success (Figure 3 and Appendix S2: Table S1), suggesting that slower/flexible and faster/specialist predators were both equally successful. However, novice individuals that encountered groups of prey with faster speeds were less successful (Figure 3 and Appendix S2: Table S1). This relationship was decoupled at the later experience levels, such that encounters with faster prey at intermediate and advanced stages were not as strongly correlated with hunting success anymore (Figure 3 and Appendix S2: Table S1). Thus, the consequences of hunting faster prey were reduced at greater experience levels.

# DISCUSSION

Hunting experience is predicted to increase predator foraging specialization when resources are predictable (Estes et al. 2003, Tinker et al. 2008, 2009). However, when resources vary, others predict that learning with experience 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 there was no directional increase in either behavioural specialization or flexibility with experience at the population level. Instead, individual predators developed their own expertise and behavioural trajectory over successive encounters with prey; some specialized in fast-paced hunting, and others adopted a slower and more flexible tactic with experience. 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. With experience, predators increasingly matched their tactic to the speed of the prey that they encountered, which simultaneously relaxed the negative consequences of encountering faster prey. Together, our observations suggest that predators in *DBD* learn to adjust their hunting tactic to the behaviour of the prey that they encounter throughout their lifetime in the game. The resulting reciprocal behavioural escalation between the predators and the prey suggests that learning may be a catalyst for arms races (Agrawal 2001, Kishida et al. 2006, Mougi and Kishida 2009, Mougi et al. 2011).

## The development of expertise with hunting experience

Empirical research in humans and animals shows that task proficiency often increases nonlinearly with experience and stabilizes at an expert level (reviewed in Dukas 2019). However, we cannot derive conclusions at the individual-level from these studies either because their models assume the same increase in expertise for each individual, or because it is unclear whether their data includes repeated measures of individual success through time. Our analyses revealed that there was no population increase in expertise over time; instead, individual predators in *DBD* displayed distinct patterns of expertise acquisition (Figure 1, Appendix S1: Figure S1A-S1B). 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 speed and space coverage is an effective antipredator strategy used by the prey making them more difficult to capture (Fraser Franco et al. 2022). Other studies have also found that faster escapes are effective to escape predation [Walker et al. (2005);Kelley and Magurran (2011);Martin.etal2022]. Yet, despite that predators differed in the prey that they encountered, prey speed did not shape individual differences in expertise acquisition. It is however possible that other antipredator tactics mediated these individual responses. For example, it is well known in *DBD* that some prey groups use mobbing to confuse the predator or prevent it from capturing an injured individual. However, like natural predator-prey systems, direct predator-mobbing in *DBD* is dangerous and requires coordinated actions that are learned through experience (Graw and Manser 2007, Dutour et al. 2016, 2019, Pitman et al. 2017, Rampim et al. 2020, Szymkowiak 2021), and was thus probably not a pervasive antipredator strategy. Other antipredator tactics known to confuse human and non-human predators during the attack sequence are unpredictable escapes and turning angles (Jones et al. 2011, Briffa 2013, Herbert-Read et al. 2017, Moore et al. 2017, Richardson et al. 2018). While predators can adjust to unpredictable prey escapes (Szopa-Comley and Ioannou 2022), it could still be more arduous for a predator to learn and optimize its hunting success if it more often encountered prey using these tactics.

Alternatively, it is possible that individual variation in learning rates due to time delays between hunting events drove the observed differences in expertise acquisition, irrespective of the prey groups that predators encountered. 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 in *DBD* may have differed in their ability to detect prey. For example, it is widely demonstrated that predators 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, individual predators should differ in their expertise if they do not learn equally how to exploit the visual cues that facilitate prey detection (Dukas 2004, 2019, Wright et al. 2022).

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

The predator population displayed an increase in foraging flexibility when reaching the intermediate level of experience. As it reached an advanced level of experience, it returned to a level of flexibility that was similar to novice levels. This is commonly observed in juvenile predators across the animal kingdom, because exploring and learning different tactics at this developmental stage is crucial to become a skillful hunter (Vehanen 2003, Johnson and Wilbrecht 2011, Thiers et al. 2014, de Grissac et al. 2016). Thus, predators in *DBD* were probably exploring and refining different tactics at this stage of experience. Within the population, individuals became increasingly distinct in their tactics as well as in their specialization with experience, which was related to the degree of variability in prey encounters. 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). This is further supported by the fact that specialist and flexible hunters both achieved similar success throughout the study period. Interestingly, the behavioural response (i.e. tactic use and specialization) to experience by individual predators differed. For instance, 42.7% 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 57.3% of the population displayed a switch from a specialized to a flexible tactic or vice-versa with experience. Thus, our results provide direct evidence that the mechanism underlying the resource-predictability hypothesis may indeed involve predators learning at varying degrees how to specialize on their prey (Weimerskirch et al. 2005, Weimerskirch 2007, Woo et al. 2008, Phillips et al. 2017).

As predators gained experience, their tactic was increasingly matched to the speed of their prey. One interpretation could be that both predators and prey learned from each other in an arms-race-like reciprocal relationship (Kishida et al. 2006, 2009, Edgell and Rochette 2009, Mougi et al. 2011). For instance, predators that encountered faster prey could have learned to increase their speed to better capture them, resulting in an increase in the speed of the prey to circumvent the predator’s attacks. In this type of system, faster prey should be better at escaping both slower and faster predators (Mougi et al. 2011), which concords with what we previously observed in this sytem (Fraser Franco et al. 2022). Brodie III and Brodie Jr. (1999) argue that when prey express defensive phenotypes (e.g. physical armaments or venom), selection on predators should be strong because the consequences of being injured are greater than missing a meal. If predators improve their exploitative ability, then an arms-race should emerge, and the consequences of hunting dangerous prey should decrease (Brodie III and Brodie Jr. 1999). Similarly, we found that has the predator gained experience, the negative consequences of encountering prey groups with higher speeds were relaxed, and the variation in success among predators decreased. However, in an arms-race, faster predators would have successfully preyed upon faster and slower prey and would have obtained higher success than slower predators (Mougi et al. 2011), which was not the case in the present study. A more likely interaction scenario is that predators and prey in *DBD* were involved in a matching response relationship (Mougi et al. 2011), because faster-specialist and slower-flexible preyed upon different prey but achieved equal success. Thus predators in *DBD* appear to optimize their success by learning to match their tactic to their prey with experience, suggesting that learning through reciprocal interactions may attenuate selection exerted by prey on predators (Anderson 1995, Ancel 1999, Borenstein et al. 2006, Paenke et al. 2007).

## Conclusions

The interactions of predator and prey traits are probably the most important processes involved in population cycles and should occur when predators match their phenotype to their prey (Abrams 2000). Yet, its has remained largely unknown whether this trait-matching results from predators learning how to capture 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, half of the predator population changed their behaviour by developping either a specialized or flexible tactic that was matched to the speed of their prey. Our results could be useful to guide predator-prey models of trait-matching, which are often studied at evolutionary timescales. For instance, future studies could incorporate individual variation in experience in their models to better predict under which ecological/evolutionary contexts specialization should be favoured over flexibility. Lastly, virtual systems are increasingly recognized among ecologists as effective systems 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.

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# CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest

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