Individual foraging specialization and success change across experience in a virtual predator-prey system

ABSTRACT

The capacity of predators to match their tactic to their prey and to optimize their skills at implementing a given tactic are expected to drive the outcome of predator-prey interactions. Hence, successive interactions of predators with their prey may result in increased flexibility in tactic use or in individual foraging specialization. Yet, there are limited empirical assessments showing links between past experience, foraging specialization, and hunting success at the individual level, due to the challenges of monitoring direct interactions in the wild. Here, we used a virtual predator-prey system (the game *Dead by Daylight*) to investigate how individual predator foraging specialization and success developed across repeated interactions with their prey. We found that 68% of predators became either increasingly specialized by always moving at a fast pace, or flexible by transitioning between slow and fast speeds. The predators' strategies were partially matched to their prey's speed, suggesting that changes in hunting behaviour were driven by repeated encounters with their prey. Flexible and specialist foragers achieved similar success overall. Hence, our findings suggest that experience may promote behavioural diversification in predator-prey systems.

INTRODUCTION

Predators express a diverse array of foraging tactics to capture their prey. In natural populations, differences among individuals in tactics such as ambushing and fast movement speeds are associated with differences in prey consumption (Toscano and Griffen 2014; Patrick and Weimerskirch 2014a; Toscano et al. 2016). Prey usually respond to predation cues by reducing their activity, or use rapid or unpredictable movements to successfully escape when they are chased (Walker et al. 2005; Jennifer L. Kelley and Magurran 2011; Herbert-Read et al. 2017). This results in reciprocal interactions where predators fine-tune their tactics to their prey, suggesting that they learn and become efficient hunters through repeated encounters (Estes et al. 2003; Woo et al. 2008; Phillips et al. 2017). These behavioural adjustments with experience can shape the outcome of predator-prey interactions and may have larger implications for community and ecosystem dynamics (Wooster et al. 2023).

As predators acquire experience, theory suggests that individuals should gradually specialize in a foraging tactic (e.g. always moving fast) if it allows them to maintain successful prey captures at each attempt (Tinker, Mangel, and Estes 2009; Dukas 2019). This should occur when predators learn to hunt in environments where resources are predictable (or stable) because they require less energy and time to search for, capture, and handle prey (Weimerskirch 2007; Woo et al. 2008; Potier et al. 2015). Such conditions favor specialist hunters because there would be higher costs to switch tactics for the same type of prey. An alternative hypothesis is that learning could increase behavioural flexibility. For instance, predators can gain expertise and information on their prey through repeated hunting attempts, and may hunt optimally by learning to adjust their tactic to the type of prey that they encounter (Stephens 1993; Ishii and Shimada 2010; Jennifer L. Kelley and Magurran 2011). While there can be costs to attempt novel tactics by trial and error in

43 stable environments, predators that hunt in environments under fluctuating resources can reduce

44 the consequences of uncertainty by learning to switch hunting tactics (Dall 2010; Mathot et al.

45 2012). Nonetheless, complex feedback between ecological interactions and learning make it

46 challenging to predict under which circumstances predators should specialize with experience

47 (Stephens 1993; Ishii and Shimada 2010; Vila Pouca et al. 2021; Beyts et al. 2023).

48 There is increasing evidence suggesting that the emergence of behavioural specialization and its

49 fitness consequences are driven by resource fluctuations (Patrick and Weimerskirch 2014b; van

50 den Bosch et al. 2019; Santoro, Hartley, and Lester 2019; Manlick, Maldonado, and Newsome

51 2021). For example, Szopa-Comley and Ioannou (2022) showed that predatory blue acaras

52 (*Andinoacara pulcher*) reduce their maximum approach speed when repeatedly exposed to prey

53 that escape unpredictably, enabling them to be as successful as those exposed to predictable prey.

54 Prey using fast escapes are also more difficult to hunt (Walker et al. 2005; Jennifer L. Kelley and

55 Magurran 2011; Martin et al. 2022), and predators that encounter such prey more often should

56 benefit from specializing in fast pursuits. Therefore, if predators hunting in different

57 environments adjust their tactics to local prey fluctuations, then specialist and flexible hunters

58 can both achieve similar hunting success and coexist (Phillips et al. 2017). Empiricists should

59 thus investigate the link between foraging specialization and success across time and contexts.

60 In this study, we investigate how repeated experience shapes predator foraging specialization and

61 success using data from players in *Dead by Daylight*. In this videogame, four prey players forage

62 for resources while avoiding predation by a fifth player. The predator population is composed of

63 individuals that either move at slow speeds and ambush or hunt at high speeds (i.e. mean

64 movement speed describes an ambush-cursorial continuum of hunting tactics) (Fraser Franco et

65 al. 2022). We also observed that predators acquire expertise through extensive practice, which is

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66 driven by the movement of the prey (Fraser Franco et al. 2024). Indeed, the prey can increase

67 their chances of survival by moving faster in the virtual environment (Fraser Franco et al. 2022,

68 2024).

69 We define the level of individual foraging specialization as the intra-individual variance

70 (i.e. IIV) in movement speed across matches. Low IIV describes individual foraging

71 specialization (i.e. always using an ambush or cursorial tactic), whereas high IIV describes a

72 flexible use of foraging tactics (i.e. predators switching between an ambush and cursorial tactic).

73 Here, our objective is to assess how foraging specialization emerges throughout experience at the

74 population and individual level. If all predators encounter similar groups of prey, we predict that

75 individuals (and thus the population) should all specialize on moving at similar speeds. In

76 contrast, if all predators encounter varying groups of prey, then they should converge towards

77 flexible speeds. In both scenarios, differences among individuals in IIV across experience should

78 be low (i.e. similar individual foraging specialization), whereas the population variance would

79 either decrease (specialization) or increase (flexibility). Alternatively, differences among

80 individuals in foraging specialization may emerge if they experience different interactions with

81 their prey. In this case, we expect predators that encountered similar groups of prey across

82 experience to specialize on similar speeds, while predators that encountered heterogeneous

83 groups across matches should adopt flexible movement speeds, resulting in an increase in among

84 individual differences in IIV with experience. If we detect such prey-dependent fine-tuning with

85 experience, then all hunters along the flexible-specialist continuum should attain equal success.

MATERIALS AND METHODS

Study system

DBD is an asymmetric multiplayer survival game developed by Behaviour Interactive Inc. In this game, participants take on roles as either a predator or one of the prey, with each match consisting of one predator and four prey. A matchmaking system pairs groups of players with similar skill such that individuals should all have similar experience. The predator's primary goal is to hunt and capture the prey, while the prey aim to locate and collect resources in the form of power generators. When all generators are activated, the prey can escape through one of two exit gates and win the match. A match concludes when the predator eliminates all remaining prey that have not escaped or when the final prey successfully exits the virtual environment. Players, whether predator or prey, select avatars with distinct abilities tailored to specific playstyles (e.g. stealthy vs evasive prey, or stalking vs patrolling predators). During the study period, the game featured 23 predator avatars. The virtual environments in the game vary in size and structural complexity, combining fixed and procedurally generated elements such as vegetation, buildings, and maze-like structures. Troughout the study period, there were 35 virtual game environments available for gameplay.

Data collection

The videogame company provided six months of gameplay data, encompassing all player activity from 2020-12-01 to 2021-06-01. We focused exclusively on matches played in "Online" mode, where players were strangers to one another. We excluded matches where players were inactive, as indicated by mean movement speeds that were zero or nearly zero. Additionally, matches where players were suspected of hacking or engaging in unintended gameplay behavior

108   were also removed based on our knowledge of the game mechanics. We then selected a cohort of

109   players that played 300 matches or more, and monitored all their matches from the first to a

110   maximum of 500 matches.

111   Our dataset includes 253 unique predator players, collectively accounting for 100 412 matches.

112   The number of matches played by predator players ranged from 301 to 500. Match durations

113   varied between 3 and 70 minutes, with an average duration of 11 minutes. The following details

114   were recorded for each match: the anonymous player ID, the chosen predator avatar, the game

115   environment, the predator's level of experience, their speed, the average speed of the prey group

116   they encountered, and the average rank of those prey (used as a proxy for prey skill). The game's

117   ranking   system,   designed   to   match   players   of   similar   skill   levels

118   (https://deadbydaylight.fandom.com/wiki/Rank), was incorporated into our analysis to detect any

119   relationship between predator experience and foraging success (see Fraser Franco et al. 2024).

120   We analyzed the predator's mean speed and the mean speed of the prey group encountered by

121   the predator. The predator's mean speed is measured as the mean distance traveled per second

122   during a match (mean= 3.31 ± 0.49 m/s). We measured the preys' speed as the mean travel speed

123   of the four individual prey in a match (mean = 2.40 ± 0.32 m/s). We defined hunting success as

124   the number of prey consumed during the match (min = 0, max = 4). Lastly, we categorized

125   predators for each match based on their cumulated experience (see Fraser Franco et al. 2024).

126   We labeled predators as novices for matches where they had cumulated less than 100 matches,

127   intermediate for matches where they had cumulated between 100 and 299 matches, and advanced

128   for matches where they had cumulated more than 299 matches (max 500). Since our goal was to

129   monitor predator players throughout their experience and that they all played at least 300

130   matches, they all appeared in each of the three experience categories.

Statistical analyses

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, Nakagawa, and Schielzeth 2015; Mitchell et al. 2016). For each experience level, we fitted the model on three traits: the predator's speed (Y_1) and the prey's speed (Y_2) using a Gaussian error distribution, and the predator's hunting success (Y_3) using a beta-binomial error distribution. Fixed and random effect structure were trait-specific and the same for all experience levels. The predator and the prey speed included a mean and a dispersion part (eqn 1.1, 1.2 and 2.1, 2.2). For both traits, we controlled for the standardized prey rank on both the mean and the dispersion parts of the model. We included game environment, predator avatar, and individual predator identity random effects on the mean part of the model. The dispersion part included individual predator identity random effects exclusively. For hunting success, we modeled the mean part only (eqn 3) and controlled for the standardized prey rank and game duration, and included an individual identity random effect.

The model simultaneously estimated five among-individual variance components with their covariances for each experience level, resulting in a 15x15 (co)variance matrix. For each experience level, the model estimated among individual variance in mean predator speed, mean prey speed, and mean hunting success. This allows us to test for individual differences in tactic use (i.e. along the slow-fast continuum), in the mean speed of the prey encountered, and in mean prey consumption. The model also estimated among individual variance in intra-individual variation (IIV) for both prey and predator speed. This allows us to test if predators do not

154 experience the same degree of prey heterogeneity and if they differ in individual specialization.

155 Finally, the model estimated all pairwise covariances at the individual level among traits, among

156 experience, and across traits and experience. The resulting 15x15 (co)variance matrix thus

157 provides the structure of the predator-prey trait interactions as well as the relationship between

158 specialization and success across experience at the individual-level.

159 The model can be written as:

$$Y_{1j} = X_{1j}b_{1j} + M_{1j}en_{1j} + N_{1j}av_{1j} + Z_{1j}id_{1j} + e_{1j} \qquad \text{(eqn. 1.1)}$$

$$\log\left(\sigma_{e_{Y_{1j}}}\right) = X_{d1j}b_{d1j} + Z_{d1j}id_{d1j} \qquad \text{(eqn. 1.2)}$$

$$Y_{2j} = X_{2j}b_{2j} + M_{2j}en_{2j} + N_{2j}av_{2j} + Z_{2j}id_{2j} + e_{2j} \qquad \text{(eqn. 2.1)}$$

$$\log\left(\sigma_{e_{Y_{2j}}}\right) = X_{d2j}b_{d2j} + Z_{d2j}id_{d2j} \qquad \text{(eqn. 2.2)}$$

$$Y_{3j} = X_{3j}b_{3j} + Z_{3j}id_{3j} + e_{3j} \qquad \text{(eqn. 3)}$$

160 where j is the index of the three experience levels (i.e. novice, intermediate, advanced). The d

161 subscript indicates that a term is from the dispersion part of the model. The b terms are vectors

162 of fixed effects with their design matrices X specific to each trait and experience level. The terms

163 en, av, and id are the vectors of random environment, random avatar, and random individual

164 identity effects associated with their design matrices M, N, and Z specific to each trait and

165 experience level. For all experience levels of Y_1 and Y_2, we assumed that the game environment

166 and avatar random effects followed a Gaussian distribution with estimated standard deviation

167 $(en_{12j} \sim N\left(0,\ I\ \sigma^2_{en_{12j}}\right)$ and $av_{12j} \sim N\left(0,\ I\ \sigma^2_{av_{12j}}\right))$. I is the identity matrix, with $I\sigma^2$

168 indicating that the random effects are independently and identically distributed. In addition, we

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169 assumed that the residuals follow a Gaussian distribution with observation-specific variance

170 $e_{12j} \sim N\left(0, Diag\{\sigma^2_{e_{12j}}\}\right)$. The 15 individual identity random effects id_{ij} across all response

171 variables and experience levels (five for each of the three experience levels) are indexed in

172 vector α. The α vector follows a multivariate Gaussian distribution $\alpha \sim MVN(0, \Sigma)$ where Σ is

173 a 15x15 (co)variance matrix of among individual variation across all response variables and

174 experience levels, with $\sigma^2_{id_{ij}}$ on the diagonal and covariances off-diagonal.

175 We performed our analyses under a Bayesian framework. We used weakly informative Gaussian

176 priors for the prey rank ($N(0, 1^2)$: eqn. 1.1 to 2.2) and game duration ($N(0.5, 0.5^2)$: eqn. 3).

177 Based on previous results showing that the mean predator speed revolves around 3 m/s (Fraser

178 Franco et al. 2022), we applied a weakly informative Gaussian prior on the intercept for predator

179 and prey speed ($N(3, 0.5^2)$: eqn. 1.1 and 2.1). Similarly, we used a weakly informative Gaussian

180 prior on the intercept for the dispersion part ($N(0, 1^2)$: eqn 1.2 and 2.2). For hunting success, we

181 applied a positive Gaussian prior on the precision parameter ($N(2, 1^2)$: eqn. 3) and a negative

182 Gaussian prior ($N(-4, 1^2)$: eqn 3) on the intercept because hunting success should be close to 0

183 at the lowest game duration. For every predicted variable, we applied a weakly informative half-

184 Gaussian prior ($N(0, 1^2)$) on the random effects for the mean part and the dispersion part of the

185 model. We used a regularizing $LKJ(2)$ prior on the correlation matrix.

Model specifications

187 We fitted the model in R (version 4.1.2) using Hamiltonian Monte Carlo (HMC) sampling with

188 the package "brms" version 2.16.3 (Bürkner 2017), an R front-end for the STAN software (Team

189 2023), and "cmdstanr" version 0.4.0 (Gabry and Češnovar 2021) as the back-end for estimation

190 (cmdstan installation version 2.28.2). We ran te model on on Cedar (Operating system: CentOS

191 Linux 7), a computer cluster maintained by the Digital Research Alliance of Canada

192 (https://docs.alliancecan.ca/wiki/Cedar).

193 We parametrized the MDHGLM to run 2500 iterations with a thinning set to eight, with the first

194 500 used as warm up iterations (yielding 1000 posterior samples for each parameter). We

195 assessed the convergence of the chains using trace plots, R-hat diagnostics with a threshold of

196 <1.01, and effective sample sizes (ESS) with a threshold of >100 (Vehtari et al. 2021). We also

197 performed posterior predictive checks which showed an adequate fit of the models (for details,

198 see https://github.com/quantitative-ecologist/experience-hunting-tactics). We report all the

199 posterior parameter estimates using the median of the posterior distribution with the highest

200 posterior density (HPD) intervals at 50%, 80%, and 95%.

201 After inspection of the results, we found that key parameter values for our hypotheses were in

202 the direction of our predictions, but they were largely driven by the very slow speed of one

203 predator. Removing this individual reduced the estimates by a significant margin. To remain

204 conservative, we thus present the results of the model without this individual in the main text,

205 and provide the results of the model including it in the Appendix 2.

RESULTS

Changes in foraging behaviour, prey behaviour, and hunting success

208 The mean speed of the predator population remained stable with experience (Figure 2 and

209 Appendix 1: Table S1). Likewise, the variation in speed did not change with experience,

210 indicating that foraging specialization remained stable at the population level (Figure 2 and

211 Appendix 1: Table S1). At the individual level, predators differed slightly in their mean speed

212   across experience levels, indicating marginal differences in hunting tactics (Figure 2 and

213   Appendix 1: Table S2). However, they displayed important differences in foraging specialization

214   (Appendix 1: Table S2) which also increased slightly with experience as there was a 0.11 unit

215   increase in among individual differences in IIV from novice to advanced (Figure 1). 12% of the

216   population switched from a flexible to a specialized hunting tactic, and vice-versa, as predators

217   gained experience (i.e. >0.2 change in standard deviation; Figure 2). In contrast, 44% displayed

218   lower changes (i.e. >0.05 and <0.2 change in standard deviation) and 44% showed almost no

219   change with experience (i.e. <0.05 change in standard deviation).


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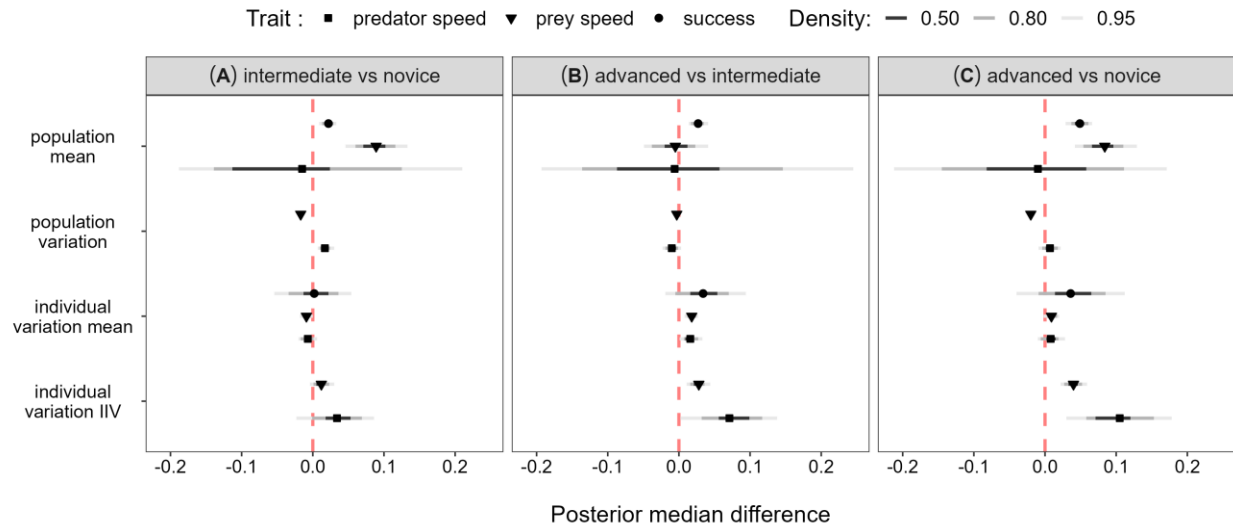
221   **Figure 1**. Median posterior differences and HPD intervals comparing predator foraging

222   behaviour at the population and individual level across experience stages. The behavioural

223   parameter predicted by the MDHGLM being compared is on the y axis, and the difference in

224   parameter values between two experience stages is on the x axis. The pairwise comparisons

225   between experience stages are displayed across the three panels A, B, and C. We compare the

226   mean speed of the predator population, the speed of the prey it encountered, and its hunting

227   success across experience (population mean). We also compare the population's foraging

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228   specialization and variation in speed of the prey it encountered across experience (population

229   variance). At the individual level, we compare among individual differences in speed, the speed

230   of the prey encountered, and hunting success (individual variation mean). Lastly, we compare

231   individual variation in IIV across experience, indicating whether individual differences in

232   foraging specialization and in the variation of the groups of prey encountered changed with

233   experience (individual variation IIV).

234   As the predator population gained experience, there was strong evidence that the prey increased

235   their speed, although slightly (Figure 1 and Appendix 1: Table S1). The population also

236   encountered groups of prey using different speeds through time (Figure 1 and Appendix 1: Table

237   S1). At the individual level, all predators encountered prey with similar average speeds

238   throughout experience (Figure 1 and Appendix 1: Table S2). Yet, even if they experienced

239   similar average prey speeds across all groups encountered, there were important differences

240   among predators in how (dis)similar were the groups they encountered (Appendix 1: Table S2).

241   Thus, some predators encountered similar groups (i.e. all groups using similar speeds) while

242   others encountered distinct groups (i.e. some slower and some faster). These differences among

243   individuals in IIV for prey encounters increased only marginally with experience (Figure 1).

244   The predator population's mean hunting success increased with experience (Figure 1 and

245   Appendix 1: Table S1), with mean prey consumption revolving around two prey. There were

246   also important differences among individuals in mean hunting success (Appendix 1: Table S2),

247   but they remained stable across experience (Figure 1).
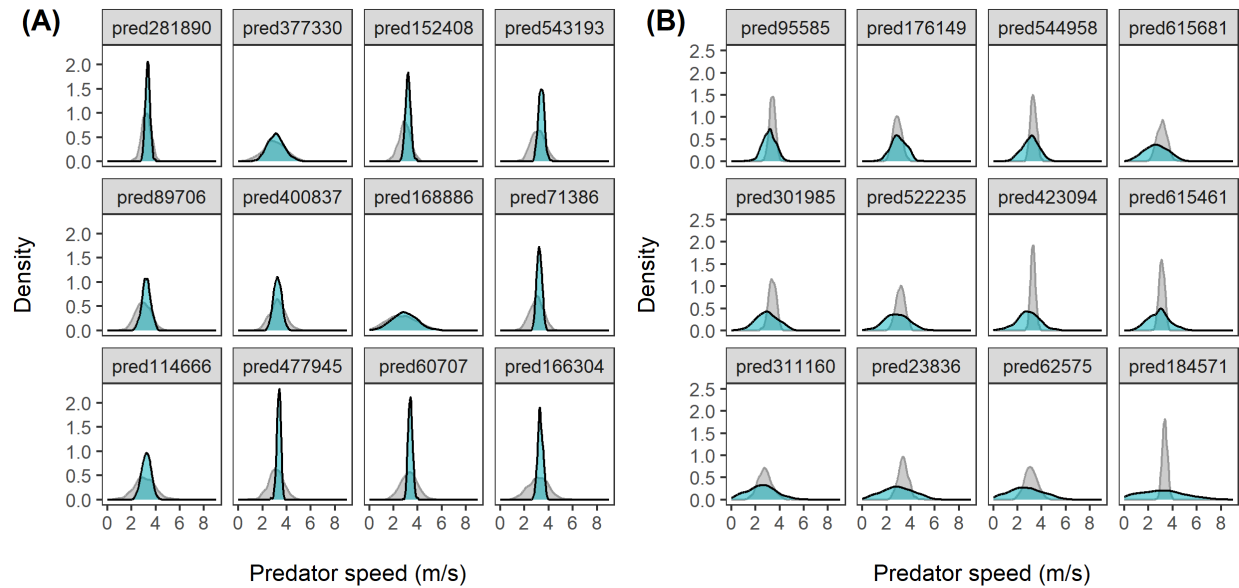
Figure 2. Individual behavioural distribution of the predators' speed drawn from the MDHGLM estimates for individuals that had (A) the greatest increase in specialization and (B) the greatest increase in flexibility. The background (gray) distributions are for when individuals were novice hunters, and 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 built the figure by first subtracting the estimated standard deviation of all individuals as novices with their standard deviation as advanced hunters, and then selected those with the greatest difference using the 25% and 75% quantiles. Individuals on panel A have an increase in specialization equal or greater than 0.2 standard deviations, while those on panel B have an increase in flexibility equal to or greater than 0.2 standard deviations.

Predator-prey interactions across experience

Predators that were on average faster had lower IIV in speed (Figure 3A-B). Thus, faster predators specialized on fast movement, while slower predators were more flexible in their movement. As predators gained experience, these strategies were increasingly defined as the

13

263 correlation changed by 0.16 units, from -0.62 (-0.91, -0.41 95% CI) for when predators were

264 novices to -0.78 (-1.00, -0.53 95% CI) as they reached the advanced stage (Figure 3C). Predators

265 that were on average faster also tended to encounter groups of prey that were on average faster

266 and more similar (Figure 3A-B). There was however no evidence that these correlations

267 increased with experience (Figure 3C)

268 There was no correlation (-0.01 (-0.17, 0.09 95% CI)) between mean prey speed and IIV in

269 predator speed when predators were novice (Figure 3A), but the correlation increased to -0.16 (-

270 0.33, -0.04 95% CI) at the advanced stage (Figure 3B), such that advanced hunters that

271 encountered faster prey tended to be more specialized (Figure 3C). The predators' IIV in speed

272 and IIV in prey speed were weakly positively correlated (Figure 3A-B). Hence, predators that

273 encountered groups of prey with similar speeds tended to be more specialized in their tactic,

274 while those that encountered groups of prey with varying speeds tended to be more flexible. We

275 did not find evidence that this correlation increased with experience (Figure 3C).
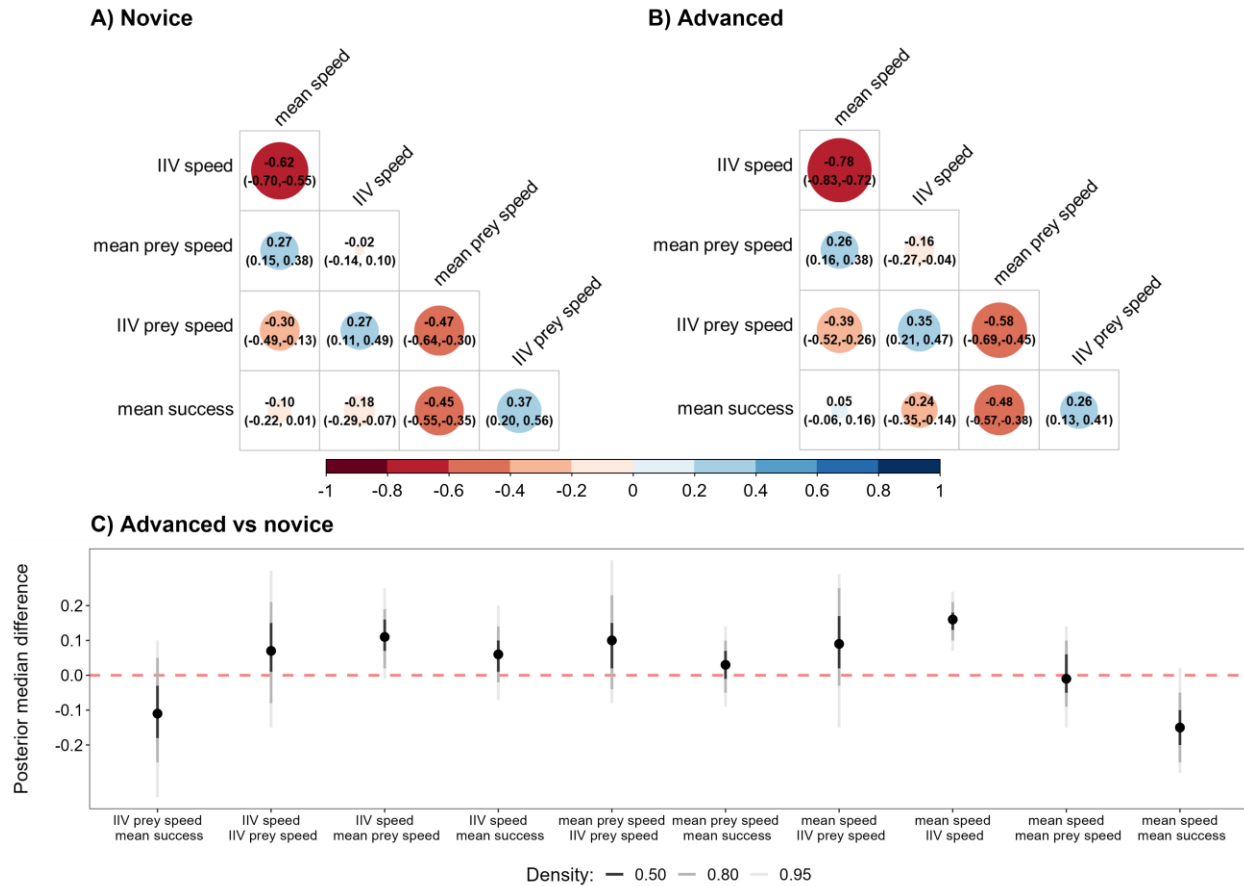
Figure 3. Correlation matrices of the MDHGLM relating the mean and IIV in speed of the predators, the mean and IIV in speed of the prey they encountered, and mean hunting success. Larger dark blue circles indicate stronger positive correlations (positive values on the colour legend), while larger dark 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.

Success along the foraging specialization continuum

The predator's mean speed and IIV were only weakly negatively correlated with hunting success across experience (Figure 3), suggesting that slower/flexible and faster/specialist predators were overall both equally successful. There was however a slight increase in the correlation between the predator's IIV in speed and success (Figure 3C), suggesting that flexible foragers at the advanced stage were marginally less successful (Appendix 1: Figure S2). We also found strong evidence that individuals who encountered groups of prey with faster speeds were less successful (Figure 3A-B). Predators also had greater success across the study when encountering more variable groups of prey (Figure 3A-B). Both relationships remained structurally stable across experience (Figure 3C).

DISCUSSION

A general assumption of predator-prey studies is that predators maximize success by matching their tactic to their prey (Abrams 2000), yet, it has remained largely unknown whether this results from predators learning how to hunt their prey in part because of the challenges of investigating direct interactions in the wild. By capitalizing on a virtual predator-prey system where interactions were directly monitored, we found that while predators in *Dead by Daylight* did not show any increase in either behavioural specialization or flexibility with experience at the population level, individual predators developed their own behavioural trajectories over successive encounters with the prey. This was characterized by a continuum of hunting styles ranging from a slower and flexible strategy to a highly specialized fast-paced strategy, with some predators switching between the two across experience. The behavioural strategies of predators and prey tended to match across experience, suggesting that both were adjusting to each other.

309   Specialized cursorial hunters encountered similar groups of prey, while slower and flexible

310   hunters encountered varying groups of prey. Overall, predators along the flexible-specialist

311   continuum achieved similar success, although flexible hunters were slightly less successful as

312   advanced hunters.

313   The predator population maintained its speed and degree of specialization throughout the study

314   period, and individuals differed only slightly in their average speeds. However, differences in

315   specialization among individuals were important and increased slightly with experience.

316   Predators hunting at higher speeds specialized in this tactic and tended to encounter groups of

317   prey with similar speeds, while those hunting at slower speeds were flexible and tended to

318   encounter varying groups of prey. On one hand, this pattern could arise if some predators

319   adjusted their strategy to their prey, because fast-paced hunting is a specialized tactic suited for

320   prey that use rapid evasive movements, while a slower and flexible tactic can be useful to

321   minimize the consequences of uncertainty when prey escape unpredictably (Endler 1991; Bro-

322   Jørgensen 2013; Wilson et al. 2018; Szopa-Comley and Ioannou 2022). However, we observed

323   that 44% of the predator population showed close to no change in specialization with experience.

324   Since these individuals were already specialized as novices (Fraser Franco, personal

325   observation), there would be no point in them changing their tactic with experience if they were

326   already successful, or there could have been costs to switch their strategy if they encountered

327   faster prey more often. This could explain why the behavioural interactions between the predator

328   and the prey remained stable across the predator's experience. Yet, because prey can also learn

329   how to avoid predation (Jennifer L. Kelley and Magurran 2003; Turner, Turner, and Lappi 2006;

330   McComb et al. 2011), we believe that the predator-prey phenotype matching more likely

331   emerged from reciprocal adjustments in speed by predators and prey as they interacted (Kishida,

332   Mizuta, and Nishimura 2006; Kishida, Trussell, and Nishimura 2009; Edgell and Rochette 2009;

333   McGhee, Pintor, and Bell 2013). Indeed, 56% of the predator population altered its behaviour

334   with experience to different degrees, including 12% that even switched between flexibility and

335   specialization. Hence, if the prey also learned through repeated interactions with the predators, it

336   is possible that experience contributed in stabilizing the system as both were adjusting to each

337   other, similar to Red Queen dynamics (Brockhurst et al. 2014).

338   Classical theory predicts that individual foraging specialization should maximize prey

339   consumption by optimizing foraging efficiency (Stephens and Krebs 1986), but other work

340   suggests that flexibility and specialization could both be adaptive as resources fluctuate (Woo et

341   al. 2008; Phillips et al. 2017). Our results support empirical findings indicating that flexible and

342   specialist foragers obtained similar success (Weimerskirch 2007; Woo et al. 2008; Potier et al.

343   2015; Phillips et al. 2017; Courbin et al. 2018), although flexible foragers were slightly less

344   successful. Both strategies appeared to emerge in part from individuals learning how to hunt

345   their prey, resulting in a general increase in success in the population. However, there were still

346   considerable differences in success among individuals through time, suggesting that some

347   predators were limited in their capacity to match their tactic to their prey or to increase their

348   success through other means.

349   Specialist foragers were faster and probably better equipped to hunt the faster and more difficult

350   prey in *DBD*. However, if the prey responded to fast predators by also being faster, then hunting

351   at high speeds resulted in challenging encounters for these predators too, thereby decreasing the

352   benefits of using this tactic (Figure 3). Thus, specializing probably compensated for the difficulty

353   of hunting prey at high speeds by helping predators to better predict the location and movement

354   of their prey. On the other hand, flexible foragers encountered a larger range of prey moving at

355 slower speeds. Yet, because the prey increased their speed with experience, the benefits of being

356 able to hunt multiple prey types for flexible hunters may have come at the cost of not being adept

357 at capturing faster prey (Pintor et al. 2014). Such trade-offs may reflect limitations in learning all

358 the skills required to successfully hunt all types of prey (Healy 1992; Bélisle and Cresswell

359 1997; Dukas 2019), particularly if the skills required to hunt slower prey are nontransferable to

360 faster prey. As the benefits of each hunting style changed under different scenarios, the

361 combination of predatory styles in this virtual system reflects how resource fluctuations can

362 maintain fitness equilibrium within populations, resulting in behavioural diversity in predator-

363 prey systems (Tinker, Bentall, and Estes 2008; Woo et al. 2008; Mougi and Kishida 2009).

364 **Conclusions**

365 We found support for our prediction that individual foraging specialization changed across

366 experience and predator-prey interactions. Our results suggest that predators learned with

367 experience, as their success increased and their speed remained matched to the speed of their

368 prey. Even though individuals were not all equally successful, both specialized and flexible

369 hunters achieved similar success overall. A potential caveat is that the more flexible hunters

370 might have experimented with various tactics out of boredom, which could impede ecologically

371 realistic interpretations of our data. However, the consistent association between this tactic and

372 heterogeneous prey groups gives us confidence that it emerged from their interactions. One

373 limitation of our study was that we couldn't monitor all the matches of the prey, which prevented

374 us from assessing their responses to the predator through their experience. Hence, future studies

375 should aim at monitoring reciprocal behavioural dynamics through time, which may reveal

376 important insights on the mechanisms driving predator-prey systems.

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