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

# ABSTRACT

The capacity of predators to match their hunting tactics to their prey and to optimize their skills at using them over successive encounters is hypothesized to promote individual foraging specialisation. Through this process, predators should be able to capture more prey. 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. In this study, 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 prey. We found that 68% of predators became either increasingly specialized by always moving at a fast pace (specialised cursorial tactic), or generalists by transitioning between slow and fast speeds (generalist ambush tactic). 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. Specialist and generalist foragers achieved similar success overall, although specialist hunters had a slight advantage. Hence, our findings suggest that experience may promote behavioural diversification in predator-prey systems.

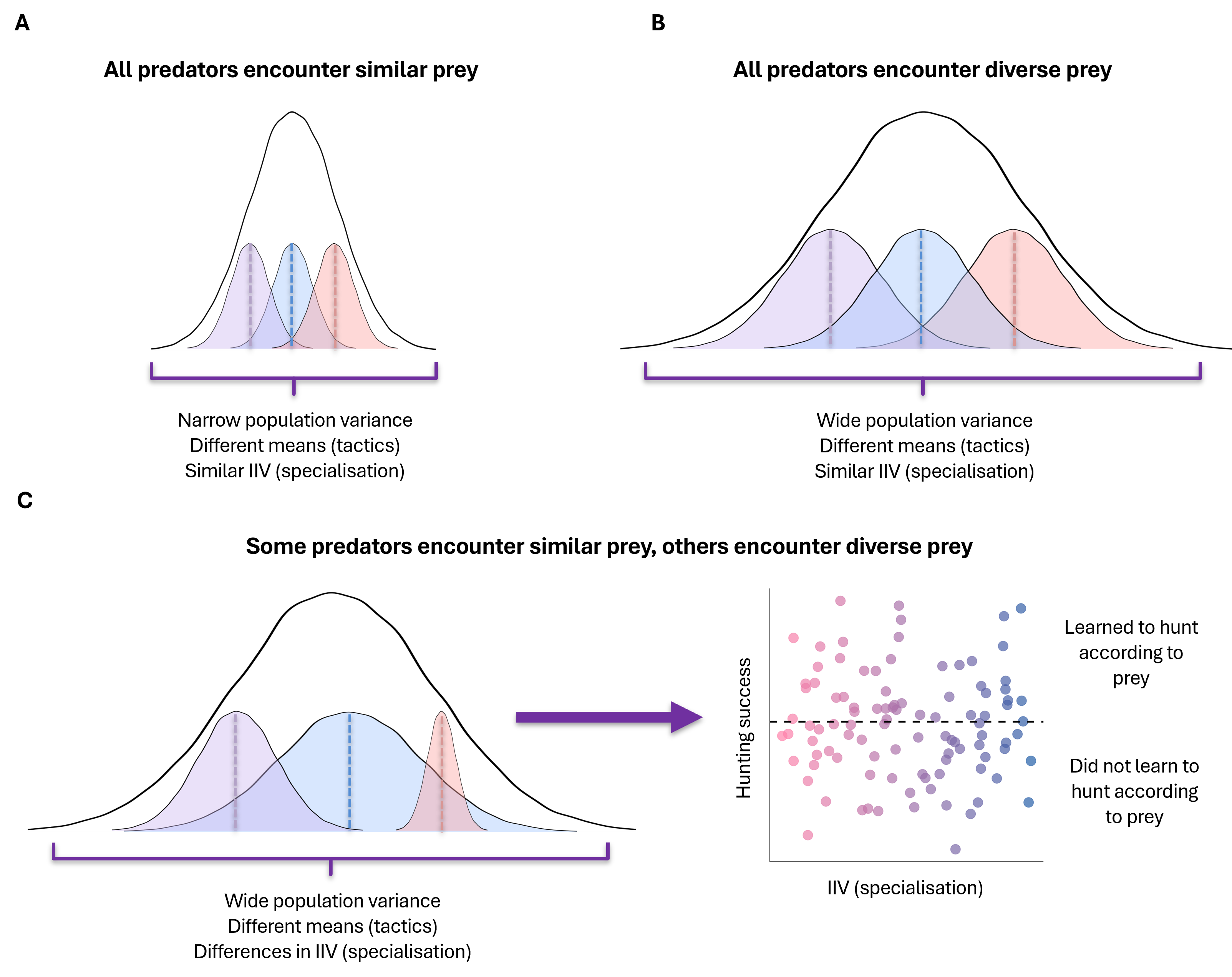
Keywords: foraging behaviour, reciprocal behavioural plasticity, learning, antipredator behaviour, virtual ecology, Dead by Daylight

# INTRODUCTION

Predators express a diverse array of foraging tactics to capture their prey. In natural populations, individuals specialise in the use of tactics such as ambushing and roaming, or switch tactics based on the prey that they encounter, often resulting in differences in prey consumption (Toscano and Griffen 2014, Patrick and Weimerskirch 2014a, Toscano et al. 2016). The success of specialist and generalist strategies depend on ecological factors: when resources are abundant, specialist hunters achieve greater success, while generalist hunters prevail under fluctuating conditions (Terraube et al. 2011, 2014, Phillips et al. 2017). While evolutionary history can partly explain how specialist and generalist species will fare under given ecological conditions, learning also plays an important part in shaping predator foraging behaviour (Wooster et al. 2023). This has prompted ecologists to hypothesize that experience may underly associations between foraging specialization and prey capture as predators learn and become efficient hunters through repeated encounters with their prey (Estes et al. 2003, Woo et al. 2008, Phillips et al. 2017). Yet, it remains challenging to monitor individual predator experience, limiting our ability to uncover how predator foraging behaviour shapes prey capture over time.

Recent evidence suggests that the resource fluctuations predators experience over time (e.g., temporal changes in prey behaviour) may be key in shaping individual behavioural specialization and its fitness consequences (Patrick and Weimerskirch 2014b, Santoro et al. 2019, van den Bosch et al. 2019, Manlick et al. 2021). Theory outlines two contrasting scenarios, with outcomes defined by the predator’s ability to learn the optimal strategy in response to resource variability. In the first scenario, individuals should gradually specialize in a foraging tactic (e.g., always moving fast) if it enables them to consistently achieve successful prey captures while learning to hunt in environments with predictable (or stable) resources (Tinker et al. 2009, Dukas 2019). Such conditions favor specialist hunters, as they require less energy and time to search for, capture, and handle prey (Weimerskirch 2007, Woo et al. 2008, Potier et al. 2015). For example, habitat specialization under stable resources is associated with reduced foraging effort and increased offspring growth rates in Herring Gulls (*Larus argentatus*) (van den Bosch et al. 2019). In the second scenario, predators are expected to be more generalist by learning to use a variety of hunting tactics when they hunt in highly variable environments. Indeed, while there can be costs to attempt novel tactics by trial and error, predators can reduce the consequences of uncertainty in environments under fluctuating resources by learning to adjust their tactic to the prey that they encounter (Stephens 1993, Dall 2010, Ishii and Shimada 2010, Kelley and Magurran 2011, Mathot et al. 2012). Szopa-Comley and Ioannou (2022) showed that predatory blue acaras (*Andinoacara pulcher*) reduce their maximum approach speed when repeatedly exposed to prey that escape unpredictably, enabling them to be as successful as those exposed to predictable prey. Under these two scenarios, if predators can learn to adjust their tactics to match the prey fluctuation regime they experience, both specialist and generalist hunters should achieve similar hunting success and coexist (Phillips et al. 2017).

In this study, we use data from players in the online videogame *Dead by Daylight* to investigate 1) how repeated interactions with prey shape predator foraging specialization and 2) how the relationship between specialization and foraging success changes over time. *Dead by Daylight* simulates a predator-prey interaction across complex virtual environments, providing a system to test ecological hypotheses on foraging behaviour, group selection, and social interactions (reviewed in Montiglio et al. 2025). In this game, four prey players forage for resources while avoiding predation by a fifth player. The predator population is composed of individuals that vary consistently in their use of hunting tactics along an ambush-cursorial continuum: at one extreme hunters move more slowly and ambush prey; at the other extreme, hunters roam the virtual environment at high velocities (Fraser Franco et al. 2022).



**Figure 1**. Hypothesis describing how prey-mediated individual foraging specialization emerges over repeated interactions. Panels A and B display two scenarios with different outcomes at the population level, but similar outcomes at the individual level. A) all predators encounter prey with similar attributes (e.g., some encountered prey that were always fast while others encountered slower prey more often) through time. They differ in their mean behaviour (tactic) which is adjusted to the prey that they encountered. Because encounters where predictable, they all display similar degrees of individual foraging specialization, resulting in the population being specialized. B) all predators encounter varying types of prey (e.g., in some encounters the prey were fast, in others the prey were slower), such that they also display similar degrees of individual foraging specialization as in panel A. However, in this case, they all become generalist hunters, resulting in the population distribution being wider. C) A scenario where predators display varying degrees of foraging specialization. In this case, some individuals consistently encountered similar prey, and thus specialized, while others encountered varying groups of prey, thus becoming generalists. Ultimately, those that learn to specialise on the proper tactic given prey encounters have greater success than those that didn’t, resulting in no differences between specialists and generalists.

To test the hypothesis that repeated interactions with prey shape predator foraging specialization, we analyze the movement speed of predators and their prey over time. To assess how foraging specialization emerges throughout experience, we define the level of individual foraging specialization as the intra-individual variance (IIV) in movement speed across matches following the definition by Cleasby et al. (2015). Low IIV describes individual foraging specialization (i.e., always using an ambush or cursorial tactic) whereas high IIV describes a flexible use of foraging tactics (i.e., generalist predators switching between ambush and cursorial tactics, see Methods for details). First, we expect predators to differ in the use of their hunting tactic (i.e., mean movement speed) which will be tuned to the mean speed of the prey that they encounter (Figure 1A-B). Second, we predict that if all predators consistently encounter prey moving at similar speeds, then the population as a whole (i.e., all individuals) should specialize on moving at similar speeds, resulting in a narrow behavioural niche (Figure 1A). In contrast, if all predators encounter groups of prey moving at varying speeds, then they should all become more flexible in their tactic use (i.e., generalists), adjusting their speed to the prey from one encounter to the other, resulting in a higher population variance in foraging behaviour (Figure 1B). In both scenarios, differences among individuals in IIV across experience should be low (i.e., similar individual foraging specialization, Figure 1A-B). Alternatively, differences among individuals in foraging specialization may emerge if they experience different interactions with their prey. In this case, predators that encountered prey moving at similar speeds across experience should specialize on moving at a more fixed speed, while predators that encountered different prey speeds across matches should adopt a generalist movement strategy, resulting in an increase in among individual differences in IIV (Figure 1C). Lastly, if we detect such prey-dependent fine-tuning with experience, then specialist and generalist hunters should attain equal success, resulting in no apparent relationship between foraging specialization and prey capture (Figure 1C).

# 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 levels such that individuals should all have similar profiency. The predator’s primary goal is to hunt and capture the prey while the prey must locate and collect resources in the form of power generators that must be activated. When all generators are activated, the prey can escape through one of two exit gates and win the match. A match ends when the predator has eliminated all remaining prey that have not escaped or when the last prey successfully exits the virtual environment. Players, whether predator or prey, select avatars with distinct abilities designed for 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 which matches are played 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 dataset comprised gameplay data from 2020-12-01 to 2021-06-01. We focused exclusively on matches played in “Online” mode, where players were strangers to one another and paired by a matchmaking algorithm. We excluded matches where players were inactive, as indicated by null or nearly null movement speeds, and matches where players were suspected of hacking or engaging in unintended gameplay behaviour based on our knowledge of the game mechanics. We then selected a cohort of players that played 300 matches or more, and monitored all their matches from the first to a maximum of 500 matches.

Our dataset includes 253 unique predator players, collectively contributing to 100 412 matches. The number of matches played by predator players ranged from 301 to 500. Match durations varied between 3 and 70 minutes, with an average duration of 11 minutes. The final dataset provided the following variables: the player ID, the chosen predator avatar, the game environment, the predator’s level of experience, the mean movement speed of the predator, the mean movement speed of the prey group, and their average rank (used as a proxy for prey skill). The game’s ranking system, designed to match players of similar skill levels (<https://deadbydaylight.fandom.com/wiki/Rank>), was incorporated into our analysis to detect any relationship between predator experience and foraging success (see Fraser Franco et al. 2024).

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 categorized predators for each match based on the experience they cumulated (see Fraser Franco et al. 2024). We labeled predators as novices when they played between 1 and 99 matches, as intermediates between 100 and 299 matches, and as advanced between 300 and 500 matches.

## Statistical analyses

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

We used a multivariate double-hierarchical generalized linear model (MDHGLM) to quantify a) changes in the average foraging tactic (i.e., the mean movement speed) and in the degree of specialization (i.e., IIV in movement speed) over successive matches for each player; and b) the relationship between the average tactic and specialization, and hunting success (Lee and Nelder 2006, Cleasby et al. 2015, Mitchell et al. 2016). For each experience level, we fitted the model on three traits: the predator’s speed () and the prey’s speed () using a Gaussian error distribution, and the predator’s hunting success () using a beta-binomial error distribution. Fixed and random effect structure was trait-specific and the same for all experience levels. For the predator and the prey speed, we modeled the mean and the residual standard deviation (eqn 1.1, 1.2 and 2.1, 2.2). For both traits, we controlled for the standardized prey rank on the mean and the residual standard deviation. We included game environment, predator avatar, and individual predator identity random effects on the mean part of the model. The residual standard deviation included individual predator identity random effects exclusively. For hunting success, we modeled the mean 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 ambush-cursorial 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 experience the same degree of prey heterogeneity and if they differ in individual specialization. Finally, the model estimated all pairwise covariances at the individual level among traits, among experience, and across traits and experience. The resulting 15x15 (co)variance matrix thus provides the structure of the predator-prey trait interactions as well as the relationship between specialization and success across experience at the individual-level.

The model can be written as:

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

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

We performed our analyses within a Bayesian framework. 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.

### Model specifications

We fitted the model in R (version 4.1.2) using Hamiltonian Monte Carlo (HMC) 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). We ran te model on on Cedar (Operating system: CentOS Linux 7), a computer cluster maintained by the Digital Research Alliance of Canada (<https://docs.alliancecan.ca/wiki/Cedar>).

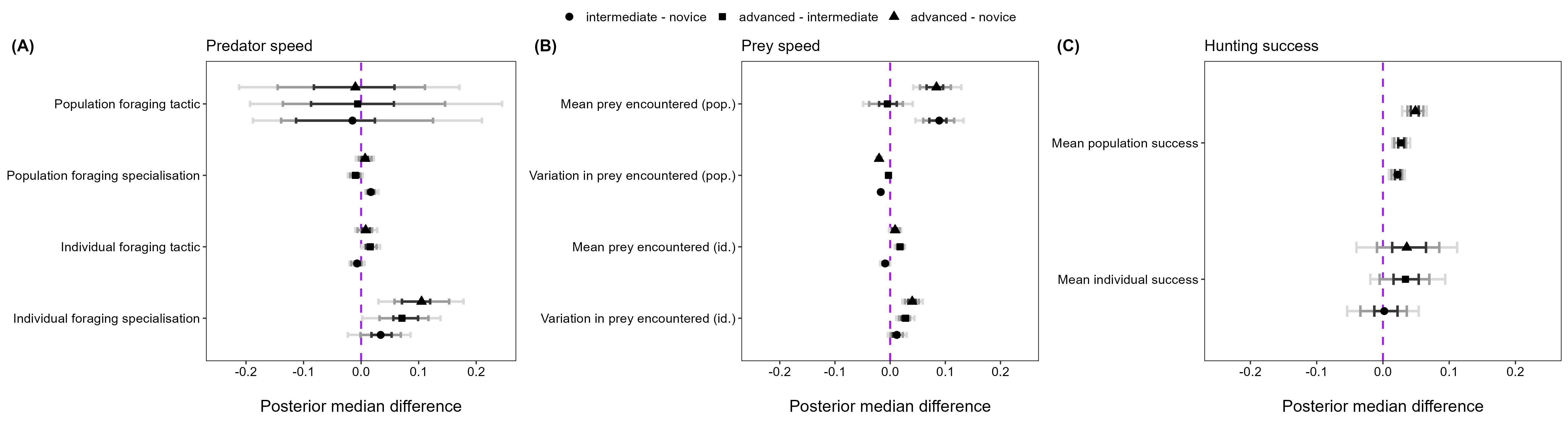
We parametrized the MDHGLM to run 2500 iterations on four chains with a thinning interval set at eight iterations, with the first 500 used as warm up iterations (yielding 1000 posterior samples for each parameter). We assessed the convergence of the chains using trace plots, R-hat diagnostics with a 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%.

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 2.

# RESULTS

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

At the population level, the mean predator speed remained stable as predators progressed from novices to advanced hunters (Figure 2A and Appendix 1: Table S1). Likewise, the variation in speed did not change with experience, indicating that foraging specialization remained stable at the population level (Figure 2A and Appendix 1: Table S1). At the individual level, differences among predators in their mean speed were weak and did not change across experience (Figure 2A and Appendix 1: Table S2). However, predators displayed minor differences in foraging specialization as novices, with differences increasing slightly as individuals gained experience (Figure 2A and Appendix 1: Table S2). 12% of the population switched from a flexible to a more specialized hunting tactic, and vice-versa, as predators gained experience (i.e., >0.2 change in standard deviation; Figure 3). In contrast, 44% displayed lower changes (i.e., >0.05 and <0.2 change in standard deviation) and 44% showed almost no change with experience (i.e., <0.05 change in standard deviation).



**Figure 2**. Median posterior differences and HPD intervals comparing predator foraging behaviour, prey behaviour, and predator hunting success at the population and individual level across experience stages. The parameters being compared are on the y axis, and the differences in parameter values between two experience stages are on the x axis. The pairwise comparisons between experience stages are displayed as different point shapes on each panel. A) For the predator speed, we compare the foraging tactic (mean) and specialisation (variance) at the population level and at the individual level between each experience stage. B) For the prey speed, we compare the mean and the variance in speed of prey encountered at the population and individual level between each experience stage. C) For the predator hunting success, we compare the mean success at the population and individual level between each experience stage.

At the population level, we found strong evidence that the prey increased their speed slightly as predators gained experience (Figure 2B and Appendix 1: Table S1). The predators also encountered a greater variation of prey speeds at later experience stages (Figure 2B and Appendix 1: Table S1). At the individual level, predators encountered prey with similar average speeds across experience stages (Figure 2B and Appendix 1: Table S2). However, predators differed in the range of prey speeds they encountered and the magnitude of these differences increased as they gained experience (Figure 2B and Appendix 1: Table S2). Thus, some predators encountered prey moving at similar speeds from one encounter to the next (i.e., all groups using similar speeds) while others encountered prey moving at different speeds (i.e., some slower and some faster).

The predator population’s mean hunting success increased with experience (Figure 2C and Appendix 1: Table S1), with mean prey consumption reaching around two prey. We did not find evidence for differences among individuals in mean hunting success at any experience stage, even though differences increased slightly (Figure 2C and Appendix 1: Table S2).



**Figure 3**. Individual behavioural distribution of the predators’ speed drawn from the MDHGLM estimates for individuals that had (A) the greatest increase and (B) the greatest decrease in specialisation. 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 change in specialization. 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 4A-B). Thus, faster predators specialized to a higher degree than slower predators. As predators gained experience, these strategies were increasingly defined as the correlation changed from -0.62 (-0.70, -0.55 ) among novices to -0.78 (-0.83, -0.72 ) among advanced hunters (Figure 4C). Faster predators tended to encounter faster prey; they also encountered groups of prey groups of prey that were more similar from match to match (Figure 4A-B), irrespective of their experience (Figure 4C).

There was no correlation (-0.02, -0.14, 0.01 ) between mean prey speed and IIV in predator speed when predators were novice (Figure 4A), but the correlation increased to -0.16 (-0.27, -0.04 ) at the advanced stage (Figure 4B), such that advanced hunters that encountered faster prey tended to be more specialized (Figure 4C). Predators with a larger IIV in speed encountered a greater range of prey speeds, but this effect was weak (Figure 4A-B). Hence, predators that encountered groups of prey with similar speeds tended to be more specialized in their tactic, while those that encountered groups of prey with varying speeds were less specialised. However, this correlation did not change with experience (Figure 4C).



**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.

## Success along the foraging specialization continuum

There were no differences in hunting success among predators in their mean speed (Figure 4). More specialised predators achieved a slightly greater foraging success, but this effect was weak (Figure 4). This relationship between the predator’s IIV in speed and success increased with experience (Figure 4C), suggesting that the success gap between generalists and specialists increased with experience (Appendix 1: Figure S2). There was strong evidence that predators that encountered faster prey and prey groups with similar speeds were less successful (Figure 4A-B), irrespective of their experience level (Figure 4C).

# 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. Specialized cursorial hunters encountered similar groups of prey, while slower and flexible hunters encountered varying groups of prey. Overall, predators along the flexible-specialist continuum achieved similar success, although flexible hunters were slightly less successful as advanced hunters.

The predator population maintained its speed and degree of specialization throughout the study period, and individuals differed only slightly in their average speeds. However, differences in specialization among individuals were important and increased slightly with experience. Predators hunting at higher speeds specialized in this tactic and tended to encounter groups of prey with similar speeds, while those hunting at slower speeds were flexible and tended to encounter varying groups of prey. On one hand, this pattern could arise if some predators adjusted their strategy to their prey, because fast-paced hunting is a specialized tactic suited for prey that use rapid evasive movements, while a slower and flexible tactic can be useful to minimize the consequences of uncertainty when prey escape unpredictably (Endler 1991, Bro-Jørgensen 2013, Wilson et al. 2018, Szopa-Comley and Ioannou 2022). However, we observed that 44% of the predator population showed close to no change in specialization with experience. Since these individuals were already specialized as novices (Fraser Franco, personal observation), there would be no point in them changing their tactic with experience if they were already successful, or there could have been costs to switch their strategy if they encountered faster prey more often. This could explain why the behavioural interactions between the predator and the prey remained stable across the predator’s experience. Yet, because prey can also learn how to avoid predation (Kelley and Magurran 2003, Turner et al. 2006, McComb et al. 2011), we believe that the predator-prey phenotype matching more likely emerged from reciprocal adjustments in speed by predators and prey as they interacted (Kishida et al. 2006, 2009, Edgell and Rochette 2009, McGhee et al. 2013). Indeed, 56% of the predator population altered its behaviour with experience to different degrees, including 12% that even switched between flexibility and specialization. Hence, if the prey also learned through repeated interactions with the predators, it is possible that experience contributed in stabilizing the system as both were adjusting to each other, similar to Red Queen dynamics (Brockhurst et al. 2014).

Classical theory predicts that individual foraging specialization should maximize prey consumption by optimizing foraging efficiency (Stephens and Krebs 1986), but other work suggests that flexibility and specialization could both be adaptive as resources fluctuate (Woo et al. 2008, Phillips et al. 2017). Our results support empirical findings indicating that flexible and specialist foragers obtained similar success (Weimerskirch 2007, Woo et al. 2008, Potier et al. 2015, Phillips et al. 2017, Courbin et al. 2018), although flexible foragers were slightly less successful. Both strategies appeared to emerge in part from individuals learning how to hunt their prey, resulting in a general increase in success in the population. However, there were still considerable differences in success among individuals through time, suggesting that some predators were limited in their capacity to match their tactic to their prey or to increase their success through other means.

Specialist foragers were faster and probably better equipped to hunt the faster and more difficult prey in *DBD*. However, if the prey responded to fast predators by also being faster, then hunting at high speeds resulted in challenging encounters for these predators too, thereby decreasing the benefits of using this tactic (Figure 3). Thus, specializing probably compensated for the difficulty of hunting prey at high speeds by helping predators to better predict the location and movement of their prey. On the other hand, flexible foragers encountered a larger range of prey moving at slower speeds. Yet, because the prey increased their speed with experience, the benefits of being able to hunt multiple prey types for flexible hunters may have come at the cost of not being adept at capturing faster prey (Pintor et al. 2014). Such trade-offs may reflect limitations in learning all the skills required to successfully hunt all types of prey (Healy 1992, Bélisle and Cresswell 1997, Dukas 2019), particularly if the skills required to hunt slower prey are nontransferable to faster prey. As the benefits of each hunting style changed under different scenarios, the combination of predatory styles in this virtual system reflects how resource fluctuations can maintain fitness equilibrium within populations, resulting in behavioural diversity in predator-prey systems (Woo et al. 2008, Tinker et al. 2008, Mougi and Kishida 2009).

## Conclusions

We found support for our prediction that individual foraging specialization changed across experience and predator-prey interactions. Our results suggest that predators learned with experience, as their success increased and their speed remained matched to the speed of their prey. Even though individuals were not all equally successful, both specialized and flexible hunters achieved similar success overall. A potential caveat is that the more flexible hunters might have experimented with various tactics out of boredom, which could impede ecologically realistic interpretations of our data. However, the consistent association between this tactic and heterogeneous prey groups gives us confidence that it emerged from their interactions. One limitation of our study was that we couldn’t monitor all the matches of the prey, which prevented us from assessing their responses to the predator through their experience. Hence, future studies should aim at monitoring reciprocal behavioural dynamics through time, which may reveal important insights on the mechanisms driving predator-prey systems.

# 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.

Bélisle, C., and J. Cresswell. 1997. [The Effects of a Limited Memory Capacity on Foraging Behavior](https://doi.org/10.1006/tpbi.1997.1319). Theoretical Population Biology 52:78–90.

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.

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.

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.

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

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.

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.

Fraser Franco, M., F. Santostefano, J. G. A. Martin, C. D. Kelly, and P.-O. Montiglio. 2024. [Prey movement shapes the acquisition of predator expertise in a virtual bi-trophic system](https://doi.org/10.1101/2024.11.15.621573). bioRxiv.

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

Healy, S. 1992. [Optimal Memory: Toward an Evolutionary Ecology of Animal Cognition?](https://doi.org/10.1016/0169-5347(92)90019-8) Trends in Ecology & Evolution 7:399–400.

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.

Kelley, J. L., and A. E. Magurran. 2003. [Learned Predator Recognition and Antipredator Responses in Fishes](https://doi.org/10.1046/j.1467-2979.2003.00126.x). Fish and Fisheries 4:216–226.

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.

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.

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.

Mathot, K. J., J. Wright, B. Kempenaers, and N. J. Dingemanse. 2012. [Adaptive strategies for managing uncertainty may explain personality-related differences in behavioural plasticity](https://doi.org/10.1111/j.1600-0706.2012.20339.x). Oikos 121:1009–1020.

McComb, K., G. Shannon, S. M. Durant, K. Sayialel, R. Slotow, J. Poole, and C. Moss. 2011. [Leadership in Elephants: The Adaptive Value of Age](https://doi.org/10.1098/rspb.2011.0168). Proceedings of the Royal Society B: Biological Sciences 278:3270–3276.

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.

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.

Montiglio, P.-O., M. Fraser Franco, and F. Santostefano. 2025. [Multiplayer videogames to analyze behavior during ecological interactions](https://doi.org/10.1016/j.tree.2025.02.003). Trends in Ecology & Evolution 0.

Mougi, A., and O. Kishida. 2009. [Reciprocal Phenotypic Plasticity Can Lead to Stable Predator](https://doi.org/10.1111/j.1365-2656.2009.01600.x). Journal of Animal Ecology 78:1172–1181.

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.

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.

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.

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.

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.

Stephens, D. W., and J. R. Krebs. 1986. [Foraging Theory](https://doi.org/10.2307/j.ctvs32s6b). Princeton University Press.

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.

Terraube, J., B. Arroyo, M. Madders, and F. Mougeot. 2011. [Diet specialization and foraging efficiency under fluctuating vole abundance: A comparison between generalist and specialist avian predators](https://doi.org/10.1111/j.1600-0706.2010.18554.x). Oikos 120:234–244.

Terraube, J., D. Guixé, and B. Arroyo. 2014. [Diet composition and foraging success in generalist predators](https://doi.org/10.1016/j.baae.2014.09.002). Basic and Applied Ecology 15:616–624.

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.

Turner, A. M., S. E. Turner, and H. M. Lappi. 2006. [Learning, Memory and Predator Avoidance by Freshwater Snails: Effects of Experience on Predator Recognition and Defensive Strategy](https://doi.org/10.1016/j.anbehav.2006.05.010). Animal Behaviour 72:1443–1450.

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, 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.

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.

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.

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.

Wooster, E. I. F., K. M. Gaynor, A. J. R. Carthey, A. D. Wallach, L. A. Stanton, D. Ramp, and E. J. Lundgren. 2023. [Animal cognition and culture mediate predatorprey interactions](https://doi.org/10.1016/j.tree.2023.09.012). Trends in Ecology & Evolution.