

UNIVERSITÉ DU QUÉBEC À MONTRÉAL

L'ÉCOLOGIE VIRTUELLE POUR L'ÉTUDE DES INTERACTIONS PRÉDATEUR-PROIE

THÈSE
PRÉSENTÉE
COMME EXIGENCE PARTIELLE
DU DOCTORAT EN BIOLOGIE

PAR
MAXIME FRASER FRANCO

JUILLET 2026

UNIVERSITÉ DU QUÉBEC À MONTRÉAL
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REMERCIEMENTS

Tout d’abord, j’aimerais remercier le Conseil de recherches en sciences naturelles et en génie du Canada (CRSNG), le programme Mitacs, ainsi que le programme de bourse de soutien universel au doctorat de l’Université du Québec à Montréal pour leur appui financier. Je remercie l’entreprise de jeux vidéo Behaviour Interactif qui m’a permis de collecter et d’analyser des données comportementales de sa population de joueur·euse·s pour faire avancer les sciences écologiques. Je tiens aussi à remercier l’Alliance de recherche numérique du Canada pour l’accès à ses serveurs afin d’effectuer mes analyses informatiques.

J’aimerais aussi remercier les personnes directement impliquées dans ce projet. Notamment, je remercie mes superviseurs Pierre-Olivier Montiglio et Clint D. Kelly qui m’ont encouragé à laisser aller mon imagination et à suivre mon intuition, me permettant de m’approprier mon projet de doctorat comme je le voulais. Je remercie également Julien Céré pour avoir géré la collaboration entre Behaviour Interactif et l’UQAM. Merci aussi à Julien G. A. Martin pour les discussions scientifiques, les rigolades et les conseils judicieux sur l’implémentation et l’interprétation de mes analyses statistiques. Je remercie également Francesca Santostefano, mon amie et collègue, pour les discussions enrichissantes sur les jeux vidéo et la science ainsi que nos nombreuses soirées à déblatérer sur tout et rien.

Plus généralement, j’aimerais remercier le corps professoral du Département des sciences biologiques de l’UQAM. Je pense entre autres au directeur du SCAE, Denis Réale, toujours à l’écoute des étudiant·e·s, ainsi qu’à Steven Kembel, Yves Mauffette, Yves Prairie, Olivier Aubry et Tanya Handa, que ce soit pour leurs conseils judicieux ou pour les précieux souvenirs des cours de terrain à Saint-Michel-des-Saints. J’aimerais aussi remercier l’ensemble de mes collègues membres du CSBQ-UQAM pour les discussions stimulantes qui m’ont grandement aidé à faire avancer mes idées durant ce doctorat.

Je n’aurais pu réaliser cette thèse sans le soutien de nombreux ami·e·s et famille que j’aimerais souligner. Tout d’abord, j’aimerais remercier mes amis Dave Mejia Samayoa, Valery Iliev-Paradis

et Éric Guimond Lanteigne pour m’avoir écouté parler de ce projet durant plusieurs années et pour les nombreux soupers où ils m’ont offert leur écoute et leur amour inconditionnel. J’aurai fini par « déposer le proposé au préposé ». J’aimerais aussi remercier mon ami et collègue Julien Beaulieu pour les excellentes discussions scientifiques et pour sa bonne humeur contagieuse. J’ai aussi surmonté les moments les plus difficiles de ce projet, incluant l’isolement dû à la pandémie de COVID-19, en partie grâce à Laurie Auclair qui a occupé une place spéciale dans ma vie durant ce parcours. Merci du fond du cœur pour ta présence et ton écoute.

Finalement, j’aimerais remercier mes parents, Jacques Fraser et Angelica Franco Gongora, pour leur soutien, leur écoute et pour avoir cru en moi jusqu’à la fin. Merci à mes frères Jean-Daniel Fraser Franco et Manuel Fraser Franco pour leur soutien également. J’aimerais conclure en remerciant ma douce Elisa Michon, que j’ai pu rencontrer deux ans avant la fin du parcours et qui a joué un rôle crucial dans les derniers moments. Merci pour ton soutien, ta bonne humeur contagieuse et d’être toi, je t’aime.

DÉDICACE

Je dédie cette thèse à mes grands-parents Guadalupe
Gongora Arispe et Elpidio Franco Jardines, qui ont toujours
été une source d'inspiration pour moi.

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LISTE DES ABRÉVIATIONS, DES SIGLES ET DES ACRONYMES

ELPD	Expected log predictive density
ESS	Effective sample sizes
HMC	Hamiltonian Monte Carlo
R-hat	The modified potential scale reduction factor, based on rank-normalizing and folding the posterior draws of a quantity sampled by Monte Carlo algorithms
CI	Credible or Compatibility interval
GLMM	Generalized linear mixed model
HPD	Highest posterior density interval
ICC	Intra-class correlation coefficient
LOO-CV	Leave-one-out cross validation
WAIC	Widely Applicable Information Criterion
MDHGLM	Multivariate double-hierarchical generalized linear model
MLGHD	Modèles linéaires généralisés hiérarchiques doubles
Player ID	Unique individual player / player identifier
SD / sd	Standard deviation
V	Variance

LISTE DES SYMBOLES ET DES UNITÉS

s	seconds / seconds
m	mètres / meters
square	tuile de 16x16 m dans une grille virtuelle / 16x16 meter tile in a virtual grid
m/s	mètres par seconde / meters per second
square/s	tuile par seconde / tile per second
min	minutes
ε	Résidus d'un modèle linéaire
env	Relatif à un environnement virtuel
ID / id	identifiant unique d'un·e joueur·euse

RÉSUMÉ

La théorie sur les interactions prédateur-proie a longtemps considéré les prédateurs comme une espèce de « boîte noire » abstraite en supposant que tout individu devrait chasser de manière identique à travers le temps et l'espace. Au fil des années, plusieurs études empiriques ont démontré que les prédateurs diffèrent dans leur comportement, notamment dans l'emploi de la stratégie pour chasser. En général, on peut classer la stratégie de chasse d'un prédateur le long d'un continuum allant de la chasse purement furtive à une stratégie de chasse mobile et de recherche active. Certains prédateurs tendent à se spécialiser dans l'une de ces stratégies, alors que d'autres sont plus flexibles et utilisent une variété de stratégies pour chasser. Ces différences de comportement de chasse entre individus peuvent déterminer le type de proie capturée ainsi que la manière dont les proies sont distribuées à travers l'espace. Ces effets ont des conséquences directes sur l'assemblage des populations de proies et la dynamique des communautés animales. Les écologistes avancent que la spécialisation dans la stratégie de chasse chez les prédateurs devrait émerger en fonction de la structure de l'habitat de chasse et selon le régime de fluctuation dans les ressources rencontrées au fil du temps. Toutefois, on comprend encore peu sur les mécanismes intrinsèques qui modulent la prise de décision chez un prédateur, ce qui limite notre capacité à prédire comment un prédateur devrait chasser en fonction des habitats et des proies qu'il a rencontré au cours de sa vie. Ce manque de connaissances est dû notamment aux nombreux défis liés à l'étude la spécialisation comportementale dans des populations naturelles. On peut entre autre penser à l'effort et aux ressources nécessaires pour mesurer le comportement de plusieurs individus à travers leur expérience, et ce, sur de nombreuses années. Tout compte fait, ces limites nous empêchent de mieux évaluer les impacts de la prédation sur les écosystèmes.

L'objectif de ma thèse est d'utiliser une nouvelle approche, l'écologie virtuelle, pour nous aider à mieux comprendre comment la spécialisation comportementale émerge et se maintient dans une population à travers le temps. Je propose comme système d'étude d'utiliser *Dead by Daylight*, un jeu vidéo multijoueur en ligne qui simule une interaction prédateur-proie, pour quantifier comment l'habitat, les interactions avec les proies et l'expérience façonnent la spécialisation comportementale et le succès de capture du prédateur. *Dead by Daylight* nous permet d'obtenir un historique de toutes les interactions entre le prédateur et ses proies à travers les parties jouées, et ce, à l'aide de mesures précises sur les comportements et le succès de capture du prédateur. Notamment, il nous permet d'obtenir ces mesures pour des milliers de joueur·euse·s.

Mes résultats indiquent que les prédateurs ajustent leur stratégie en fonction du comportement des proies qu'ils ont chassées. Contrairement à mes prédictions, les prédateurs plus mobiles avaient tendance à pourchasser des proies mobiles, alors que les prédateurs furtifs chassaient davantage de proies furtives. Cependant, les deux types de prédateurs capturaient davantage de proies sédentaires. De plus, durant la période d'étude, mes observations n'ont pas mis en évidence un effet de la structure de l'habitat sur le comportement ou le succès de capture des prédateurs. Mes résultats indiquent aussi une importante variation dans le gain en expertise chez les prédateurs au fil du temps. Toutefois, le comportement des proies avait une influence marginale sur ce gain en expertise. En effet, le comportement des proies était surtout associé au succès de capture à long terme, mais

pas à la vitesse à laquelle les prédateurs gagnaient en expertise. En général, les prédateurs avec un gain plus lent avaient tendance à atteindre un succès de capture plus élevé à long terme. Finalement, mes résultats indiquent que le développement de la spécialisation comportementale est façonné par le régime de fluctuation dans le comportement des proies rencontrées. Les prédateurs qui avaient tendance à rencontrer davantage de proies différentes sont devenus généralistes, alors que ceux qui ont rencontré des proies se déplaçant à des vitesses similaires sont devenus spécialistes. À un niveau avancé, nous avons observé que les prédateurs généralistes et spécialistes ont atteint un succès de capture similaire. Ces résultats nous aident à mieux prédire la manière dont un prédateur devrait chasser en fonction du régime de fluctuation dans les proies qu'il rencontre au cours de son expérience. En effet, mes travaux mettent en évidence comment l'expérience façonne le comportement au fil du temps : les prédateurs qui apprennent à utiliser la stratégie appropriée peuvent obtenir un succès de capture équivalent. En fin de compte, cette thèse nous permet de mieux comprendre comment les interactions et l'apprentissage façonnent le succès de capture des prédateurs et leur coexistence dans une population.

Mots-clés : interactions prédateur-proie, écologie virtuelle, jeux vidéo, stratégie de chasse, spécialisation comportementale, succès de capture.

CHAPITRE 1:

INTRODUCTION

1.1 Interactions prédateur-proie

1.1.1 Un bref historique

Les interactions prédateur-proie constituent un processus biologique fondamental au sein duquel la majorité des organismes vivants sont impliqués. Ces interactions sont au centre des théories sur la coévolution, sur la spécialisation de niche et sur l'assemblage des communautés animales (Brodie & Wilkinson, 2010; Kersch-Becker et al., 2018). Chez les animaux, les individus ajustent leur comportement afin d'éviter la prédation (Lima & Dill, 1990). En théorie, les effets de la prédation peuvent être classés en deux catégories: les effets indirects (ou non létaux) liés au risque de prédation perçu par les proies et les effets directs (ou létaux) liés à la consommation des proies par le prédateur. D'une part, les effets indirects liés au risque de prédation induisent des comportements d'évitement de la prédation (dits « antiprédateurs ») qui peuvent altérer l'acquisition d'énergie des proies en réduisant leur efficacité d'approvisionnement et, finalement, leurs chances de survie (Lima, 1998; Miller et al., 2014; Preisser et al., 2005). Les proies peuvent aussi compromettre leur reproduction afin d'allouer davantage d'énergie à éviter la prédation, ce qui peut entraîner des conséquences notables sur le recrutement annuel (Candolin, 1998; Zanette et al., 2011). Ces compromis d'allocation forment une partie intégrante des décisions prises par les proies pour éviter la prédation et agissent comme un mécanisme qui façonne leur écologie et leur évolution (Gaynor et al., 2019; Lima & Dill, 1990). D'autre part, les effets directs dus à la consommation sont étroitement liés à la sélection des proies à chasser par le prédateur. Ce processus décisionnel implique des compromis entre les besoins énergétiques du prédateur et les coûts associés à la chasse de la proie (MacArthur & Pianka, 1966; Pettorelli et al., 2015). Les prédateurs composent avec ces compromis en sélectionnant les proies selon leur espèce, leur taille, leur âge ou leur statut (Pettorelli et al., 2015). Ces choix dépendent eux-mêmes de l'habitat, du niveau d'expertise ou de l'état de satiété du prédateur (Pettorelli et al., 2015). Les conséquences des effets directs de la prédation se traduisent par la réduction des effectifs des populations de proies via le succès de capture du prédateur, un déterminant majeur de son aptitude phénotypique.

L'étude des effets directs de la prédation a permis d'établir les fondements de nos connaissances sur le fonctionnement des communautés naturelles (Abrams, 2000; Preisser et al., 2005). Notamment, les modèles de dynamique de populations de Lotka-Volterra (Lotka, 1925; Volterra, 1928) et de Nicholson-Bailey (Nicholson & Bailey, 1935) introduisent un cadre d'analyse densité-dépendant des interactions prédateur-proie qui permet de suivre les changements de densité des populations au fil du temps. Holling (1959) publie par la suite un modèle de réponse fonctionnelle du prédateur, qui établit une relation entre le taux de consommation du prédateur et la densité des proies. Plus tard, les modèles de Lotka-Volterra et de Holling seront combinés, permettant ainsi au modèle Lotka-Volterra d'assouplir la supposition irréaliste selon laquelle le taux de consommation des prédateurs est infini (Berryman, 1992). Plusieurs paramètres clés de ces modèles, tels que le taux de capture maximal et le taux de consommation per capita en fonction de la densité des proies (c.-à-d. la réponse fonctionnelle), sont modulés par les traits des prédateurs et des proies (Abrams, 2000). Ainsi, l'étude des dynamiques des populations prédateur-proie établit un cadre conceptuel pour étudier l'évolution des traits des prédateurs et des proies au fil du temps.

Historiquement, les modèles de dynamique de populations estimant l'impact de la prédation sur les proies supposaient que les prédateurs constituaient des unités abstraites exerçant des effets identiques sur les proies (Nilsen et al., 2005; Post et al., 1999; Vucetich et al., 2005). Ces suppositions s'imposaient à ce point que Lima (2002) a appelé à rompre la norme et à considérer les prédateurs comme une entité à part entière dans l'étude des interactions prédateur-proie. Lima soutient que les prédateurs ne sont pas des « boîtes noires », mais des organismes qui s'ajustent à leurs proies pour mieux les traquer, les repérer et les poursuivre. On voit dans les années qui suivent une série de publications révélant que le comportement des prédateurs, et plus précisément leur stratégie de chasse, serait un élément central de la dynamique de l'interaction (Beaupre & Montgomery, 2007; Carey & Wahl, 2011; Preisser et al., 2007; Schmitz, 2008). En effet, la stratégie de chasse des prédateurs permet de prédire leur distribution spatiale, la fréquence des rencontres avec les proies, le type de proie capturée, ou encore le succès de capture (Donihue, 2016; Gaynor et al., 2024; Glaudas et al., 2019; Scharf et al., 2006). Le comportement du prédateur est donc devenu essentiel à l'étude des interactions prédateur-proie.

1.2 Comportement de prédation

1.2.1 Les stratégies de chasse : embuscade vs déplacement soutenu

La stratégie, le mode d’approvisionnement, ou le mode de chasse sont des termes interchangeables qui décrivent la manière dont les prédateurs localisent, pourchassent et capturent leurs proies (Gerritsen & Strickler, 1977; Huey & Pianka, 1981; MacArthur & Pianka, 1966; McLaughlin, 1989). On regroupe généralement les prédateurs selon trois grands modes de chasse, caractérisés par une suite de comportements typiques exprimés de manière coordonnée (Moore & Biewener, 2015; Schmitz, 2005, 2017). Le premier mode, dit furtif, consiste à tendre des embuscades. Par exemple, plusieurs espèces de serpents furtifs ont une physiologie plus lente et des pièces buccales plus grandes qui leur permettent de capturer un éventail de proies considérable (Glaudas et al., 2019). Cette tactique aurait évolué en réponse à des pressions de sélection où les rencontres avec les proies se faisaient plus rares, et son efficacité se traduit par l’élément de surprise. Le second mode, appelé interception, implique d’attendre que la proie soit à une certaine distance avant d’initier la course (ex. *Panthera tigris*). La différence entre cette stratégie et la chasse furtive est que le prédateur doit intercepter la proie dans sa trajectoire de fuite (Moore & Biewener, 2015). Le troisième mode consiste à se déplacer de manière continue et à pourchasser les proies sur de longues distances (ex. *Canis lupus*). Les prédateurs qui emploient cette stratégie ont souvent une morphologie élancée pour courir à grande vitesse et un appareil sensori-moteur qui leur permet d’effectuer des changements soudains de trajectoire d’interception (Moore & Biewener, 2015).

La présence systématique de ces stratégies chez les espèces prédatrices soulève la question de savoir comment elles ont émergé et se maintiennent au sein des populations. Un des paradigmes pour étudier cette question repose sur l’hypothèse du syndrome d’approvisionnement, qui divise le mode de chasse en deux stratégies distinctes (c.-à-d. furtive vs active) (Cooper et al., 1999; Huey & Pianka, 1981; McLaughlin, 1989). Précisément, l’hypothèse stipule que la stratégie de chasse constitue une caractéristique invariable qui aurait évolué chez les espèces prédatrices. Celle-ci serait corrélée à la morphologie et à la physiologie de l’animal, à la manière de chercher sa nourriture, à son écologie et à son comportement. Ce syndrome de traits devrait donc contraindre l’adoption de stratégies alternatives et favoriser ainsi le maintien d’une même stratégie au fil du temps. Cependant, l’hypothèse du syndrome d’approvisionnement a été façonnée par des études comparatives, où la proximité phylogénétique confondait la comparaison des stratégies entre

espèces (Miles et al., 2007; Perry, 1999). Le partage d'un même mode d'approvisionnement chez des espèces d'une même famille s'expliquerait donc plutôt par leur proximité phylogénétique que par le partage d'un syndrome de traits.

Une hypothèse alternative avance que les stratégies de chasse auraient pu émerger par une coévolution entre les prédateurs et leurs proies (Abrams, 2000; Schmitz, 2017). Toutefois, les études empiriques sur le sujet sont rares. Un des meilleurs exemples documentés de coévolution entre prédateurs et proies est dans le système des couleuvres rayées (*Thamnophis sirtalis*) et de leur proie, une salamandre nommée triton rugueux (*Taricha granulosa*) (Brodie & Brodie, 1990). Dans ce système, les salamandres produisent une neurotoxine hautement puissante par des glandes cutanées spécialisées, et les couleuvres rayées sont les seuls prédateurs connus à pouvoir y résister. Les recherches dans ce système ont démontré que lorsqu'une proie devient dangereuse (ex. hautement toxique), la pression de sélection exercée sur la proie par le prédateur peut être renversée (c.-à-d. la proie exerce la pression de sélection sur le prédateur) (Brodie III & Brodie Jr., 1999). Avec le temps, une dynamique de course aux armements s'est développée, où l'on retrouve les couleuvres les plus résistantes dans des régions où l'on observe les salamandres les plus toxiques, et vice-versa (Reimche et al., 2020). Un autre exemple de coévolution, propre aux stratégies de prédation, est décrit dans un article fondamental publié par Huey & Pianka (1981). Les auteurs proposent que différentes stratégies de prédation pourraient coexister via un mécanisme de locomotion croisée. Selon cette hypothèse qui repose sur un principe d'économie d'énergie, les prédateurs actifs captureraient davantage de proies sédentaires, tandis que les prédateurs furtifs captureraient davantage de proies mobiles. Cette hypothèse a été vérifiée par des études empiriques chez les crabes bleus (*Callinectes sapidus*) et les poissons-crapaud d'huître (*Opsanus tau*) (Belgrad & Griffen, 2016), ainsi que chez l'araignée sauteuse *Portia labiata* (Chang et al., 2017). D'un point de vue évolutif, un processus de sélection fréquence-dépendante négative pourrait expliquer le maintien de ces stratégies par la locomotion croisée (Brodie & Wilkinson, 2010; Van Valen, 1973). Par exemple, dans le lac Tanganyika, des poissons cichlidés mangeurs d'écailles (*Perissodus microlepis*) attaquent strictement leurs proies par derrière. Chez cette espèce, il existe deux morphes qui se distinguent par l'orientation de l'ouverture de leur bouche qui se situe soit à gauche, soit à droite. L'orientation détermine le flanc par lequel le poisson attaque sa proie. L'abondance des deux morphes se situe dans un équilibre oscillatoire modulé par une sélection fréquence-

dépendante. Cette sélection est exercée par le niveau d'alerte des proies (Hori, 1993). Au début du cycle de sélection, le morphe le plus rare a un avantage sélectif, puis devient progressivement plus abondant et moins avantage, tandis que le morphe qui était plus abondant devient progressivement plus rare et plus avantage.

Dans les années 1970-80, toute source de variation entre individus était considérée comme du bruit dans les études écologiques et évolutives du comportement (Bolnick et al., 2003; Réale et al., 2010). Cette vision était partagée dans la recherche sur les interactions prédateur-proie, où on supposait que la stratégie de chasse d'un prédateur était fixe (Pettorelli et al., 2015). Cependant, au début des années 1990, on observe au sein des populations de prédateurs que les individus varient dans les stratégies de chasse qu'ils emploient (Helfman, 1990). Ces observations amèneront les écologistes à réévaluer l'hypothèse du syndrome d'approvisionnement et à démontrer que les stratégies de chasse sont plutôt caractérisées par un continuum de traits qui varie au sein d'une même espèce (Butler, 2005; Cooper, 2005; Perry, 1999).

1.2.2 Variation dans les stratégies de chasse

Plusieurs synthèses montrent que les prédateurs diffèrent dans leur utilisation des stratégies de chasse en réponse à des facteurs environnementaux et proximaux ainsi qu'aux interactions avec leurs proies (Gaynor et al., 2024; Helfman, 1990; R. A. Phillips et al., 2017; Schmitz, 2017). Cette variation est observable à différentes échelles au sein d'une même espèce : entre des groupes, entre des individus et au sein d'un même individu. Pour éclairer les mécanismes écologiques et évolutifs qui façonnent cette variation, mes réflexions s'appuieront sur la théorie sur la spécialisation de niche.

Le concept de la niche a une histoire extrêmement riche qui dépasse largement la portée de cette thèse (Elton, 1927; Grinnell, 1917; Hutchinson, 1957). Au fil du temps, la théorie de la spécialisation de niche s'est développée et recouvre maintenant plusieurs définitions, de sorte que les différentes disciplines en écologie adoptent des approches conceptuellement différentes (Devictor et al., 2010). Dans le cadre de cette thèse, j'utiliserai le concept de niche d'utilisation des ressources proposé par MacArthur et Levins (MacArthur & Levins, 1967). L'approche par utilisation des ressources est avantageuse car elle est facilement quantifiable et interprétable. Celle-

ci s'articule autour de l'étude de traits écologiques qui décrivent l'utilisation des ressources par l'organisme à l'aide de paramètres tirés de leur distribution (Schoener, 2009). MacArthur et Levins (1967) suggéraient d'utiliser la distance d entre le sommet des distributions d'un trait (qu'on peut décrire par la moyenne, le mode, ou la médiane) ainsi que la largeur w (écart-type) pour évaluer les différences de spécialisation entre espèces ou entre individus d'une même espèce à travers l'axe de variation de la niche (Figure 1.1). L'analyse des multiples axes de variation de la niche permet ainsi d'étudier comment la spécialisation émerge à travers des processus tels que la compétition, la prédation et l'évolution (Roughgarden, 1972, 1974; Van Valen, 1965). De plus, des méthodes de pointe en programmation statistique permettent aujourd'hui de quantifier aisément comment des traits varient à travers différents gradients écologiques (Bürkner, 2017, 2018; Cleasby et al., 2015).

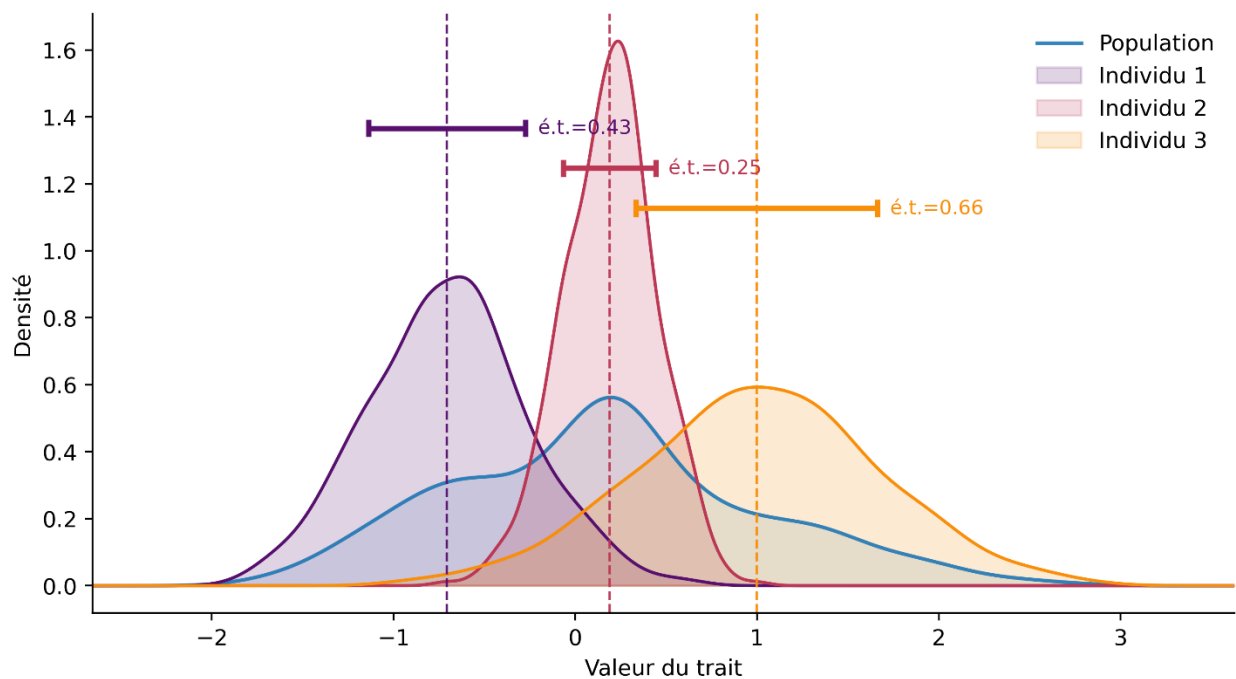


Figure 1.1 Distribution théorique d'un trait d'utilisation de ressource dans une population d'une espèce fictive. On observe que la population a une distribution globale (arrière-plan, bleu) assez large, suggérant que la population est généraliste. Lorsqu'on décompose la distribution de la population pour évaluer les individus qui la caractérisent, on observe que ceux-ci varient dans leur utilisation de la ressource, de sorte que les paramètres qui décrivent les distributions individuelles diffèrent. On observe que l'individu 1 a une moyenne (ligne pointillée) inférieure à celle des individus 2 et 3, mais la taille de sa niche (son écart-type : é.t.) est intermédiaire par rapport aux deux autres. À titre comparatif, l'individu 3 a une moyenne et une taille de niche supérieure aux deux autres.

Une des plus importantes sources de variation dans l'utilisation des stratégies de chasse chez les prédateurs est dû à la structure de l'habitat. La structure de l'habitat peut façonner les taux de rencontre avec les proies, et par conséquent, favoriser certaines stratégies par rapport à d'autres (Gaynor et al., 2019). Ceci peut entraîner des différences de comportement entre des groupes de prédateurs. Par exemple, chez des espèces où l'investissement parental est unilatéral, des différences de spécialisation de chasse peuvent émerger en raison du statut reproducteur des femelles (Thiemann et al., 2011). Dans ces systèmes, les femelles auront tendance à réduire leur utilisation de l'habitat pour protéger leurs petits et seront ainsi contraintes d'exploiter des habitats plus restreints et isolés, ce qui limite l'éventail de proies qu'elles pourront rencontrer et chasser (Nifong et al., 2015). L'habitat peut aussi façonner des différences de comportement entre individus. En général, on observe chez des individus qui chassent dans des habitats ouverts et structurellement simples qu'ils adoptent une stratégie de déplacement soutenu. Au contraire, chez une même espèce, les individus qui chassent dans des habitats plus complexes (ex. où il y a des repaires) utilisent davantage une stratégie furtive (Bolduc et al., 2026; Donihue, 2016; Wasiolka et al., 2009). Ce phénomène s'observe également au sein d'un même individu, de sorte que la configuration de l'habitat immédiat module les processus décisionnels des prédateurs d'un événement à l'autre (Gaynor et al., 2024; Greeff & Whiting, 2000). Ces observations peuvent s'expliquer en partie par le fait que l'habitat module des compromis entre les taux de rencontre et les coûts énergétiques de la stratégie. Chez le grand brochet (*Esox lucius*), les individus qui chassent en zone pélagique tendent à se spécialiser dans une stratégie active qui est plus coûteuse en énergie. Toutefois, cette tactique compense la plus faible abondance de proies dans cette zone et leur permet ainsi de capturer autant de proies que les individus qui chassent dans les zones littorales plus riches (Kobler et al., 2009).

Au fil du temps, les proies répondent aussi à leur environnement et à leurs prédateurs, ce qui module leurs déplacements et leur distribution spatiale. Les prédateurs doivent donc aussi ajuster leur comportement à celui de leurs proies pour se nourrir. La disponibilité des proies influence directement les besoins énergétiques des prédateurs et constitue un prédicteur important de la stratégie utilisée pour chasser (Barrett et al., 2015; Goundie et al., 2015). Par exemple, comme les prédateurs furtifs minimisent leurs déplacements et ont des taux de rencontres plus bas, ils sont normalement opportunistes et chasseront un plus large éventail de proies (Glaudas et al., 2019;

Huey & Pianka, 1981). Ceci peut s'expliquer par le fait que les prédateurs chassent de manière à minimiser les coûts énergétiques (Meehan et al., 2022). Cependant, plusieurs espèces de prédateurs furtifs augmentent leurs déplacements lorsque la densité des proies diminue et que leurs besoins énergétiques atteignent un seuil critique (Helfman, 1990; Inoue & Marsura, 1983). Ainsi, les prédateurs furtifs devraient être davantage généralistes. Les stratégies de déplacement et d'évasion des proies permettent aussi de prédire la stratégie qu'un prédateur utilisera pour chasser. Des mécanismes de locomotion croisée pourraient expliquer l'usage de la stratégie d'un prédateur si celui-ci cherche à minimiser les coûts énergétiques lorsqu'il chasse (Huey & Pianka, 1981). Toutefois, contrairement à ce que prédit l'hypothèse de la locomotion croisée, on observe souvent chez les proies plus mobiles et actives que leurs prédateurs chassent en déplacement soutenu. Ceci pourrait s'expliquer par le fait que les prédateurs qui emploient cette stratégie sont hautement spécialisés et dotés d'un appareil sensori-moteur qui leur permet de maintenir des poursuites à haut régime et sur de longues distances (Bro-Jørgensen, 2013; Szopa-Comley & Ioannou, 2022; Wilson et al., 2018).

En théorie, des variations spatio-temporelles dans les conditions abiotiques et les ressources devraient façonner la coexistence d'individus spécialistes et généralistes (Abrams, 2006b, 2006a; Haaland et al., 2020; Levins, 1968; Poisot et al., 2011). Plusieurs études empiriques soutiennent cette hypothèse et montrent que les prédateurs ont tendance à se spécialiser lorsque les conditions sont stables, et au contraire, qu'ils utilisent une plus grande variété de stratégies lorsque les ressources et les conditions environnementales fluctuent (Ceia & Ramos, 2015; Estes et al., 2003; Poisot et al., 2011; Woo et al., 2008). Ceci peut être expliqué par le fait qu'en conditions variables, une stratégie conservatrice (c.-à-d. généraliste) permettra au prédateur de maintenir un succès moyen constant à travers un ensemble de conditions (Haaland et al., 2020). Cependant, il demeure difficile de déterminer les facteurs à l'origine des processus décisionnels qui façonnent ces patrons.

1.3 Le rôle de l'expérience dans les interactions prédateur-proie

1.3.1 Développement de la spécialisation

Un nombre croissant d'études suggèrent que l'apprentissage et l'expérience individuelle constituent le chaînon manquant permettant de mieux comprendre l'émergence de la spécialisation comportementale (Haage et al., 2017; R. A. Phillips et al., 2017; Tinker et al., 2009; Woo et al.,

2008). Un des mécanismes clés qui modulerait le lien entre l'apprentissage et le degré de spécialisation comportementale porte sur les variations temporelles et spatiales de la disponibilité ou du comportement des proies (Manlick et al., 2021; Patrick & Weimerskirch, 2014a; Santoro et al., 2019; van den Bosch et al., 2019). Ces fluctuations constituent des opportunités d'apprentissage qui façonnent les préférences et les stratégies d'un prédateur au fil du temps. Des principes d'optimalité permettraient de prédire sous quel régime de fluctuations un organisme aurait avantage à se spécialiser (Tinker et al., 2009). En principe, un individu devrait se spécialiser graduellement dans une stratégie si son succès de capture augmente au fur et à mesure qu'il s'exerce à chasser dans un environnement où le type de proie qu'il rencontre est prévisible. La spécialisation est avantageuse dans ce scénario car elle permet au prédateur de limiter les coûts en réduisant, par exemple, l'effort de recherche, le temps avant de localiser une ressource, ou les risques de blessure (Bence, 1986; Partridge & Green, 1987; van den Bosch et al., 2019). Au contraire, lorsque les conditions fluctuent, il devient avantageux d'être flexible et d'apprendre à exploiter un éventail plus large de stratégies et de proies. Cependant, les organismes peuvent être limités dans leur capacité à apprendre et à mémoriser différentes stratégies, car il est coûteux et risqué d'apprendre à chasser de nouveaux types de proies (Healy, 1992). Malgré ces coûts, chasser de manière flexible permettrait aux prédateurs de réduire les conséquences dues à des conditions variables (Ishii & Shimada, 2010; Kelley & Magurran, 2011; Stephens, 1993). Par exemple, dans un contexte de changements climatiques, les études empiriques indiquent que la résilience accrue des prédateurs généralistes repose sur leur capacité à exploiter des stratégies et des proies alternatives, ce qui leur permet de maintenir un succès de capture plus constant que chez les prédateurs spécialistes (Patrick et al., 2021; Peers et al., 2020; White et al., 2025). À la lumière de ces observations, on peut émettre l'hypothèse qu'un prédateur devrait apprendre à utiliser la stratégie optimale (spécialiste vs généraliste) en fonction du régime de fluctuation des ressources qu'il a rencontré au cours de sa vie.

1.3.2 Acquisition d'expertise

La capacité et la vitesse à laquelle un prédateur acquiert l'expertise nécessaire pour utiliser la stratégie optimale peuvent influencer son succès de capture à long terme. Le gain en expertise consiste en l'acquisition d'attributs (ex. connaissances et compétences) permettant à un individu expérimenté de mieux performer dans une tâche complexe qu'un individu novice (Dukas, 2017;

Helton, 2003). Ce processus peut être évalué en mesurant comment le succès de capture varie en fonction de l'expérience cumulative. En général, on observe qu'un individu novice augmentera rapidement, puis graduellement, sa performance au fil de l'expérience jusqu'à un point où les rendements diminuent et atteignent un plateau (Helton, 2008). Cette courbe de gain en expertise peut être aisément décrite par une fonction asymptotique, où trois paramètres clés permettent d'évaluer la variation du gain en expertise entre individus (Figure 1.2). Mathématiquement, on peut décrire cette fonction comme suit :

$$\mu = a - (a - b)\rho^t \quad (1)$$

où b représente la performance initiale à un temps 0 hypothétique, ρ représente le taux de gain en performance et indique l'effet de l'expérience sur la performance, a représente l'asymptote qui décrit la performance optimale, puis t représente le temps ou l'expérience (Clarke & Hunt, 2025).

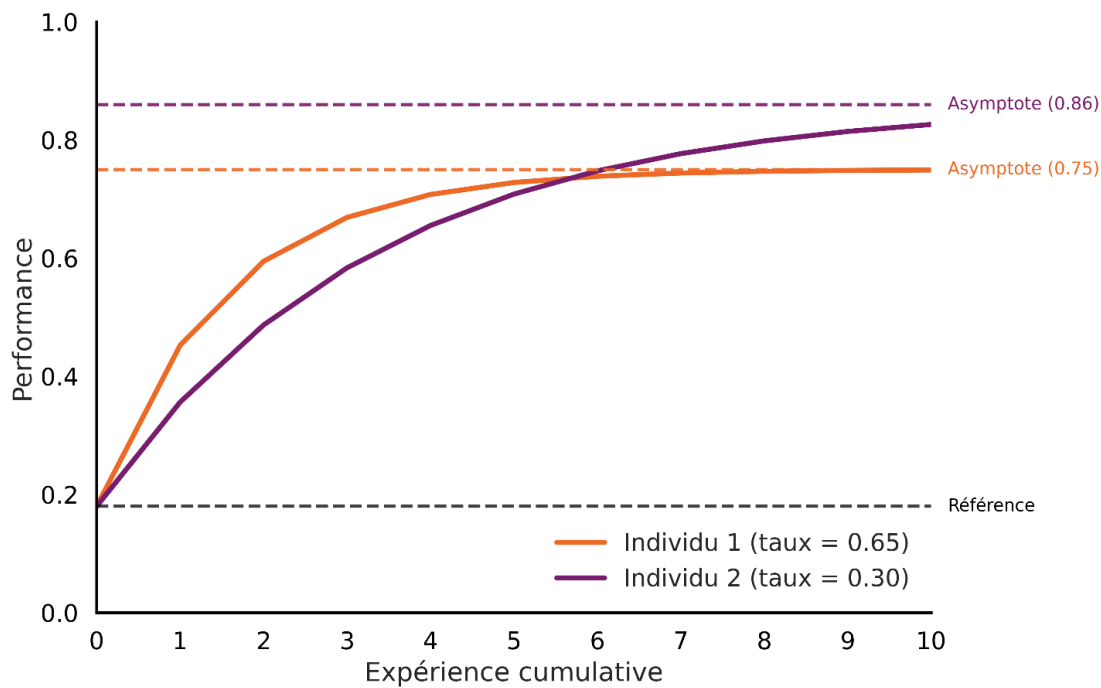


Figure 1.2 Courbe de gain en expertise de deux individus. La courbe de gain est décrite par la relation entre la performance (y) et l'expérience cumulative (x). Les deux individus ont une valeur de référence (initiale) identique. Au fil du temps, ils développent leur expertise de manière différente. L'individu 1 a une vitesse de gain plus rapide que l'individu 2, mais il atteint un succès maximal inférieur à long terme.

Chez les prédateurs, différents facteurs peuvent moduler le gain en expertise, limitant ainsi leur capacité à utiliser la stratégie optimale en fonction du régime de fluctuations des ressources. Par conséquent, des différences dans le gain en expertise entre prédateurs pourraient expliquer les différences de spécialisation comportementale au sein des populations (Dukas, 2019). Par exemple, des attributs clés tels que la mémoire à long terme, la capacité de concentration, la capacité motrice, ou la capacité d'anticipation et de perception façonnent l'acquisition d'expertise chez les humains (Dukas, 2019). Toutefois, on comprend moins bien comment l'écologie et les interactions façonnent l'acquisition d'expertise. Un des seuls exemples documentés porte sur les effets du camouflage des proies sur le gain en expertise des prédateurs lors d'une expérience où des humains devaient capturer des proies à travers un logiciel informatique (Troscianko et al., 2018). Ces travaux montrent que les stratégies de camouflage modulent la vitesse à laquelle les sujets détectent les proies au fil du temps. Notamment, la stratégie de coloration disruptive, caractérisée par des patrons de coloration à haut contraste qui dissipent la silhouette de l'organisme, empêchait les humains de s'améliorer au fil du temps. De plus, la capacité des sujets à détecter une proie avec une stratégie donnée était influencée par leur expérience avec d'autres stratégies. Les chercheurs ont observé que les participants ayant rencontré d'abord des proies avec un camouflage distrayant avaient du mal à développer une image de recherche pour les proies qui utilisaient un camouflage disruptif. Cette étude souligne la manière dont l'expérience et les stratégies antiprédatrices des proies peuvent façonner la performance à long terme. Toutefois, elle n'aborde pas la question de savoir si le régime de rencontre avec les proies modulait des différences entre individus dans le gain en expertise. À la lumière de ces observations, on peut supposer que des comportements antiprédateurs pourraient aussi façonner des différences de gain en expertise et de performance entre prédateurs. Cependant, mesurer ces changements dans des populations naturelles comporte son lot de défis, et il est extrêmement rare de pouvoir suivre un grand prédateur tout au long de son expérience de chasse.

1.4 Défis associés aux études longitudinales

Les études longitudinales sur les populations naturelles sont, sans équivoque, essentielles pour développer et tester des hypothèses dans une panoplie de disciplines en écologie. Ceci est notamment dû au fait que plusieurs processus écologiques sont observables seulement à l'échelle d'années ou de décennies (Clutton-Brock & Sheldon, 2010). D'un point de vue de l'écologie

comportementale, ces études permettent de collecter des données sur le comportement et l'aptitude des individus au travers de leur vie et des événements qu'ils traverseront. Ces mesures répétées sont extrêmement précieuses, puisqu'elles permettent aux scientifiques d'évaluer comment la sélection naturelle change au travers des stades de vie et à travers plusieurs générations (Clutton-Brock & Sheldon, 2010). Elles permettent aussi de quantifier comment l'âge et l'expérience modulent des processus populationnels et évolutifs. Malgré les avantages considérables qu'offrent les études longitudinales, de nombreux défis les rendent particulièrement difficiles à produire et à maintenir. Premièrement, des difficultés logistiques et financières rendent l'étude à long terme des populations incertaine car celles-ci nécessitent du temps avant de produire des résultats, dans un contexte où le financement de la recherche requiert que des résultats soient produits rapidement. Entre autres, ce type d'étude est souvent mené en région éloignée où l'accessibilité aux ressources et l'instabilité politique peuvent limiter la collecte des données (Clutton-Brock & Sheldon, 2010). Deuxièmement, les études à long terme reposent souvent sur la capture, le marquage et la recapture des individus. Cette méthode peut être sujette à des difficultés d'échantillonnage qui biaisent l'estimation de la survie puisque les individus les plus mobiles sont plus difficilement recapturables (Hupman et al., 2018; Sandercock, 2020). Troisièmement, des effets dus à la mesure faite par l'observateur·ice, ou simplement à sa présence, sont une source de biais qui peut influencer les résultats collectés sur le terrain. Dans le contexte des interactions prédateur-proie, la présence humaine peut altérer le comportement des proies en réduisant leur perception du risque associé aux prédateurs environnants (Nowak et al., 2014). Dans la prochaine section, je présenterai comment mon système d'étude, qui consiste en un jeu vidéo multijoueur en ligne, permet de contrecarrer plusieurs de ces défis tout en offrant des avantages additionnels pour l'étude des interactions prédateur-proie.

1.5 Système d'étude

1.5.1 Les jeux vidéo

Dans le cadre de ma thèse, je tirerai parti du jeu vidéo multijoueur en ligne *Dead by Daylight* comme système d'étude pour étudier le développement du comportement de prédation et sa variation au fil du temps. Je m'intéresserai aussi aux conséquences de cette variation sur l'issue des interactions prédateur-proie.

Plusieurs études se sont intéressées aux jeux vidéo comme systèmes pour examiner des processus écologiques. Par exemple, certaines avancent que les environnements virtuels offerts dans les jeux vidéo pourraient servir à mieux comprendre des processus socio-écologiques complexes (Duthie et al., 2021). D'autres se sont penchées sur l'utilité des jeux vidéo pour promouvoir la conservation d'espèces menacées ou en tant qu'outils éducatifs en écologie et en conservation (Coroller & Flinois, 2023; Sandbrook et al., 2015). Des études ont aussi utilisé des jeux vidéo comme systèmes expérimentaux pour tester des hypothèses dans des conditions contrôlées. Notamment, plusieurs ont examiné le comportement d'approvisionnement dans des environnements virtuels où des humains devaient accomplir des objectifs en interagissant (ou non) avec d'autres humains (Barack et al., 2024; Goldstone & Ashpole, 2004; Prpic et al., 2019; Thornton et al., 2021; Wu et al., 2025). Certaines études ont également évalué comment les stratégies de camouflage des proies interfèrent avec la détection et l'acquisition d'expertise dans des jeux virtuels où des humains doivent capturer des proies artificielles (Stevens et al., 2012; Troscianko et al., 2018).

Un point commun à ces études est que les jeux vidéo offrent l'occasion de tester des hypothèses qui seraient normalement (quasi) impossibles à vérifier dans la nature. Par exemple, les jeux permettent d'explorer comment les individus prennent des décisions stratégiques dans des situations complexes impliquant des compromis, des conflits et de l'incertitude (Duthie et al., 2021). D'autres chercheurs ont proposé d'aller plus loin et d'utiliser des jeux vidéo multijoueurs en ligne pour tester des hypothèses sur des interactions écologiques (Céré et al., 2021, 2024; Fraser Franco et al., 2022; Montiglio et al., 2025; Santostefano et al., 2024). Les jeux vidéo multijoueurs en ligne offrent des avantages supplémentaires aux environnements virtuels à un·e joueur·se. Ceux-ci donnent accès à des données comportementales riches et volumineuses qui seraient normalement impossibles à obtenir chez des espèces animales longévives. En effet, les jeux vidéo multijoueurs en ligne rassemblent souvent des communautés de millions de joueur·euse·s. Cela permet de tester des hypothèses écologiques à partir de jeux de données massifs qui documentent des centaines de milliers d'interactions en temps réel. De plus, la collecte des données s'effectue à l'aide de programmes automatisés, ce qui limite les biais d'observateur·ice tout en offrant une méthode d'échantillonnage reproductible. Ainsi, les jeux vidéo multijoueurs permettent d'étudier le comportement et la performance des individus à travers l'historique de leurs interactions.

1.5.2 Dead by Daylight

1.5.2.1 Caractéristiques générales

Dead by Daylight est un jeu vidéo multijoueur asymétrique de type horreur-survie développé par Behaviour Interactif à Montréal. D’abord paru en 2016 sur la plateforme Windows (Microsoft), le jeu a ensuite été publié sur la majorité des consoles de jeu connues dont les PlayStation 4 et 5 (Sony), les Xbox One et les Séries X/S (Microsoft), ou encore la Switch (Nintendo). Les jeux de type horreur-survie s’inspirent d’ouvrages de fiction d’horreur où le sentiment d’impuissance face à une menace est au cœur de l’expérience de jeu. Dans ces jeux, les joueur·euse·s sont souvent vulnérables et doivent faire preuve d’ingéniosité pour résoudre des énigmes et éviter les combats afin de survivre. Les jeux de survie ont aussi une importante composante de recherche, de gestion et de rationnement des ressources. En effet, les joueur·euse·s sont amené·e·s à chercher des ressources éparses et à faire des compromis quant à celles qui sont plus importantes en fonction de leur état de santé et des objectifs à accomplir.

Dead by Daylight combine le thème du jeu d’horreur-survie à une composante multijoueur asymétrique où les joueur·euse·s ont des habiletés et une expérience de jeu significativement différentes. Dans *Dead by Daylight*, une partie oppose un·e joueur·se qui incarne un meurtrier (prédateur) à quatre autres joueur·euse·s qui incarnent les survivants (proies). L’asymétrie est donc au niveau des rôles dans le jeu. L’objectif du meurtrier est de capturer et de consommer les survivants. L’expérience de jeu en tant que meurtrier se distingue de celle des survivants par sa vision à la première personne (Figure 2.1a), sa vitesse de déplacement plus rapide, ainsi que sa capacité à attaquer et blesser les survivants. Au contraire, les survivants ont une vision à la troisième personne. Leur objectif principal est de réparer cinq génératrices (Figure 2.1b). Une fois réparées, les génératrices alimenteront deux portes par lesquelles les survivants pourront s’échapper (Figure 2.1c). Le succès de cet objectif dépend de leur capacité à éviter d’être capturés par le meurtrier. Les survivants peuvent se servir de ressources distribuées dans l’environnement virtuel pour les aider à réparer les génératrices plus rapidement. L’environnement virtuel où les joueur·euse·s interagissent est constitué d’habitats réalistes tels que des forêts, des milieux urbains, ou des milieux agricoles, qui varient dans leurs composantes structurelles (ex. superficie, complexité, densité de refuges, etc.) (Figure 2.1d). D’un point de vue scientifique, on peut donc considérer *Dead by Daylight* comme un système qui simule une interaction prédateur-proie dans

un environnement virtuel où la structure de l'habitat et la distribution des ressources varient dans l'espace. À partir d'ici, j'utiliserai donc le terme prédateur pour décrire le meurtrier, et proie pour décrire les survivants.

Au moment où j'ai collecté les données, soit, avant août 2021, *Dead by Daylight* (version <5.2.0) utilisait un algorithme de jumelage basé sur un système de classement pour regrouper des joueur·euse·s avec un niveau d'expertise similaire dans une partie. Ce système de classement variait de 1 à 20, le premier rang correspondant au plus haut niveau d'expertise possible dans le jeu. Pour passer à un rang supérieur en tant que proie, les joueur·euse·s devaient progresser dans le jeu en jouant de manière altruiste, en contribuant à la réparation des génératrices, ou en accomplissant des actions téméraires tout en survivant au prédateur. Chez les prédateurs, les individus pouvaient monter dans le classement en accomplissant des actions qui contribuaient à ralentir la réparation des génératrices, à mettre de la pression sur les proies, à localiser les proies, ou encore à capturer les proies avec succès. Ce système était saisonnier, de sorte qu'après un mois, tous les rangs des joueur·euse·s étaient réinitialisés au niveau 20 et la progression mensuelle recommençait.

1.5.2.2 Déroulement d'une partie et mécaniques de jeu

Avant qu'une partie soit lancée, les joueur·euse·s doivent choisir un avatar. Dans ce système, on peut considérer les avatars comme étant des espèces distinctes avec des habiletés qui favorisent des stratégies prédatrices et antiprédatrices spécifiques. Par exemple, chez les prédateurs, l'avatar « Ghostface » est silencieux et dispose d'une habileté spéciale qui lui permet de traquer une proie spécifique et de lui tendre des embuscades. D'autres avatars, comme le « Cannibal », ont des vitesses de déplacement plus rapides et un style de jeu dynamique, avec des attaques qui couvrent de longues distances. Ces avatars sont très puissants, mais ils sont plus facilement détectés par les proies que des avatars dotés d'attributs favorisant la chasse furtive. Chez les proies, certains avatars se déplacent plus rapidement et permettent d'échapper au prédateur plus facilement lors d'une poursuite. D'autres offrent une meilleure résistance aux attaques du prédateur, favorisant un style de jeu plus téméraire. Certains possèdent aussi des habiletés qui leur permettent de soigner plus efficacement les proies, ce qui encourage un style de jeu plus altruiste.

Une fois les joueur·euse·s regroupé·e·s et prêt·e·s à jouer, la partie est lancée. Les joueur·euse·s débutent normalement en étant distribué·e·s de manière aléatoire dans l'environnement virtuel. Le prédateur commencera dès lors à se déplacer et à chercher les proies, alors que les proies pourront commencer à chercher des génératrices à réparer.

Une fois qu'une génératrice est repérée, les proies peuvent la réparer. La réparation enclenche une barre de progression et un test d'habileté qui doit être réussi à plusieurs reprises. Si le test d'habileté est échoué, une explosion se fera entendre sur la génératrice et révélera la position de la proie au prédateur. Normalement, les proies ont intérêt à s'éloigner de la génératrice lorsqu'une explosion survient car le prédateur s'y rendra dans la plupart des cas. Tant que la génératrice n'est pas complètement réparée, le prédateur peut l'endommager afin de ralentir le progrès de la réparation. Lorsqu'une génératrice est réparée, une lumière s'allume (indiquant que la réparation est complétée) et les proies pourront passer à une prochaine génératrice. Plusieurs génératrices peuvent être réparées simultanément et aucune règle ne contraint les proies à les réparer dans un ordre déterminé. Une fois les cinq génératrices réparées, celles-ci alimenteront deux portes que les proies devront localiser pour s'échapper et survivre. Ces deux portes doivent être activées à l'aide d'un interrupteur. L'activation dure 20 secondes et émet un signal d'alarme qui peut être entendu par le prédateur. Cette séquence de la partie est donc dangereuse pour la proie, mais cruciale à sa survie.

Lorsque le prédateur a localisé une proie et qu'il initie une poursuite, il devra l'attaquer et réussir à la blesser deux fois pour qu'elle s'écroule. Une fois la proie écroulée, le prédateur pourra la prendre et l'amener à un crochet où elle sera consommée. À partir d'ici, deux scénarios sont normalement possibles. Dans le premier, si le prédateur n'attrape pas la proie écroulée pour l'amener au crochet, celle-ci aura 240 secondes pour se faire soigner par un·e de ses congénères, sans quoi elle se videra de son sang et périra, mettant ainsi un terme à sa partie. Le deuxième scénario consiste en l'étape de manipulation, lorsque le prédateur attrape la proie pour l'amener au crochet. Durant cette étape, le prédateur aura 16 secondes pour transporter la proie au crochet. S'il échoue, la proie pourra s'échapper et recommencer à courir. En revanche, si le prédateur réussit à poser la proie sur un crochet, celle-ci aura 140 secondes pour se faire sauver par un·e de ses congénères, sans quoi elle périra en étant sacrifiée, mettant ainsi fin à sa partie. Au total, une proie peut être mise au crochet deux fois dans une partie et s'échapper. La troisième fois, la proie sera automatiquement sacrifiée et sa partie sera terminée.

On peut concevoir deux manières de remporter une partie en fonction des rôles dans *Dead by Daylight*. La première est de maximiser les points gagnés, même si le prédateur n'a capturé aucune proie ou que la proie n'a pas réussi à s'échapper. En ce sens, les proies pourraient se comporter de manière plus téméraire et être plus à risque d'être capturées si elles jouent pour maximiser les points. Il en va de même pour le prédateur, qui pourrait risquer de perdre des opportunités de capture en cherchant à maximiser l'apport en points, par exemple, en étendant la chasse au lieu de capturer la proie le plus rapidement possible. Toutefois, nos observations personnelles indiquent une association positive entre la survie des proies ou le nombre de proies capturées chez le prédateur et le nombre de points gagnés. La deuxième manière de remporter la partie est plus réaliste sur le plan écologique. Pour les proies, il s'agit simplement de réussir à s'échapper. Pour le prédateur, il s'agirait de consommer au moins une proie dans une partie donnée. Dans le cadre de ma thèse, je me pencherai sur le succès de capture pour évaluer la performance des prédateurs et de leur stratégie au fil du temps.

1.5.2.3 Comportements observés

Pour capturer des proies, les joueur·euse·s qui incarnent le prédateur dans *Dead by Daylight* adoptent des comportements typiques que l'on observe chez des prédateurs dans la nature. Par exemple, l'exploration de l'environnement leur permet de s'y familiariser, mais est aussi primordiale pour arriver à localiser des proies. Le prédateur peut exploiter l'environnement virtuel pour tendre des embuscades aux proies ou poser des pièges pour les attraper. On observe également des comportements caractéristiques de la stratégie de déplacement soutenu. Par exemple, certains prédateurs dans *Dead by Daylight* se déplacent continuellement et utilisent des attaques qui font du bruit et qui couvrent de longues distances. Ceux-ci entament des poursuites effrénées afin d'exercer une pression constante sur les proies. Ces stratégies sont susceptibles d'être plus avantageuses dans des environnements virtuels plus vastes que dans les environnements fermés où la mobilité est réduite et où les proies peuvent facilement se cacher.

Les proies peuvent aussi exploiter l'environnement et utiliser une variété de tactiques pour échapper au prédateur. Par exemple, elles peuvent coopérer pour réparer des génératrices, ce qui leur permet d'exploiter la ressource plus rapidement et d'augmenter leur probabilité de survie (Santostefano et al., 2024). Elles peuvent aussi sauver les proies au crochet et soigner celles qui

sont blessées, ce qui leur permet, dans certains cas, d'augmenter leur probabilité de survie (Santostefano et al., 2024). En revanche, certaines proies préfèrent jouer de manière prudente et plus individualiste, en utilisant des refuges pour se cacher et en se déplaçant de manière accroupie, ce qui leur permet aussi d'augmenter leurs chances de survie (Santostefano et al., 2024).

L'interaction entre le prédateur et les proies rend les parties hautement dynamiques. Les proies utilisent des tactiques pour s'échapper ou éviter le prédateur telles que courir à grande vitesse, créer des distractions, ou se cacher. Cependant, les proies font davantage de bruit en se déplaçant à la course, laissant des traces fraîches que le prédateur peut exploiter pour mieux les localiser. Les actions et les mouvements brusques émettent aussi des bruits susceptibles d'attirer l'attention du prédateur. Les proies doivent donc faire preuve de prudence afin de minimiser les risques d'être détectées. Le prédateur, quant à lui, doit exploiter l'environnement, les sons et les repères visuels pour traquer et pourchasser les proies. Il doit aussi tenir compte des tactiques des proies et choisir la stratégie appropriée pour assurer son succès. Son succès dépend entre autres du temps avant de localiser une proie, des caractéristiques de l'habitat virtuel, ou encore de la composition du groupe de proies (Céré et al., 2021, 2024). Il est donc possible d'observer en temps réel des compromis entre les stratégies de prédation et d'évaluer sous quelles conditions une stratégie est susceptible d'être favorisée par rapport à une autre.

1.6 Objectifs et hypothèses

L'objectif général de cette thèse est d'utiliser un jeu vidéo qui simule une interaction prédateur-proie pour évaluer comment : 1) la variation comportementale émerge chez un prédateur, 2) l'expertise et la spécialisation comportementale se développent et 3) les interactions avec les proies façonnent ces processus.

Dans le premier article de ma thèse (Chapitre 2), intitulé « Studying predator foraging mode and hunting success at the individual level with an online videogame », je m'intéresse tout d'abord à valider *Dead by Daylight* comme système pour l'étude des interactions prédateur-proie. Pour ce faire, j'ai brossé un portrait des stratégies de chasse des prédateurs à partir de plusieurs traits afin d'identifier ceux qui étaient les plus importants dans l'interaction. J'ai ensuite décomposé la variation dans ces traits en trois niveaux : à l'échelle de l'habitat, de l'individu et au sein d'un

même individu. J'é mets l'hypothèse que les prédateurs différeront dans leur stratégie de chasse, certains préférant l'embuscade et d'autres étant plus mobiles. Les comportements de chasse devraient donc être organisés en un continuum, allant d'un style de chasse furtif à un style plus mobile et actif. Une fois cette hypothèse vérifiée, je suppose que la structure de l'habitat virtuel façonnera les stratégies observées. Les prédateurs devraient employer une stratégie furtive dans les habitats plus fermés et complexes, et au contraire, une stratégie mobile dans les habitats plus vastes et homogènes. Je m'intéresse aussi à évaluer si le comportement des proies peut expliquer l'utilisation des deux stratégies en façonnant le succès de capture des prédateurs. J'é mets l'hypothèse qu'un mécanisme de locomotion croisée devrait contribuer au maintien des deux stratégies au sein de la population. Ainsi, je prédis que les prédateurs mobiles devraient capturer davantage de proies sédentaires, tandis que les prédateurs furtifs devraient capturer davantage de proies mobiles.

Dans le deuxième article de ma thèse (Chapitre 3), je présente une étude nommée « The role of prey behaviour in predator expertise acquisition: insights from a virtual ecosystem ». Ici, j'évalue comment l'expertise se développe chez les prédateurs et comment le comportement antiprédateur des proies façonne le développement de l'expertise. Pour ce faire, je quantifie la relation entre le succès de capture des prédateurs et leur expérience cumulative. J'é mets l'hypothèse que les prédateurs différeront dans leur gain en expertise. Certains prédateurs devraient augmenter leur performance plus rapidement que d'autres avec l'expérience et atteindre un succès de capture à long terme plus élevé. Je m'attends à ce que le comportement des proies façonne la vitesse à laquelle les prédateurs gagnent en expertise ainsi que leur succès de capture à long terme. Les prédateurs devraient avoir davantage de difficulté à capturer des proies plus mobiles et rapides, ce qui devrait réduire la vitesse à laquelle ils gagnent en expertise ainsi que leur succès de capture à long terme.

Finalement, je présente les résultats de mon dernier article (Chapitre 4) intitulé « Individual foraging specialization and success change with experience in a virtual predator-prey system ». Dans ce chapitre, j'ai testé l'hypothèse selon laquelle l'expérience et les interactions avec les proies devraient façonner la spécialisation comportementale des prédateurs. Pour ce faire, j'ai quantifié la niche comportementale populationnelle et les niches individuelles des prédateurs à différents stades de leur expérience. J'ai aussi mesuré comment leur succès de capture changeait au fil des

stades de l'expérience. Je m'attends à ce que le niveau de spécialisation comportementale soit associé au comportement des proies rencontrées au fil du temps. Je prédis que les prédateurs auront tendance à être plus généralistes dans leur comportement s'ils rencontrent davantage de proies différentes. Au contraire, les prédateurs plus spécialistes auront tendance à rencontrer plus souvent des proies qui se comportent de manière similaire au fil du temps. Finalement, je teste l'hypothèse selon laquelle les stratégies généralistes et spécialistes devraient coexister si elles atteignent un succès de capture similaire. Cela indiquerait que les prédateurs ont appris à utiliser la stratégie optimale en fonction du type de proie rencontrée au fil du temps.

CHAPITRE 2:

STUDYING PREDATOR FORAGING MODE AND HUNTING SUCCESS AT THE INDIVIDUAL LEVEL WITH AN ONLINE VIDEOGAME

Fraser Franco, M., Santostefano, F., Kelly, C. D., Montiglio, P.-O.

Ce chapitre a été publié : Fraser Franco, M., Santostefano, F., Kelly, C. D., Montiglio, P.-O. (2022). Studying predator foraging mode and hunting success at the individual level with an online videogame. *Behavioral Ecology*, 33(5), 967-978. <https://doi.org/10.1093/beheco/arac063>

2.1 Abstract

Predator–prey interactions are important drivers of community and ecosystem dynamics. With an online multiplayer videogame, we propose a novel system to explore within population variation in predator hunting mode, and how predator–prey behavioural interactions affect predator hunting success. We empirically examined how four predator foraging behaviours covary at three hierarchical levels (among environments, among individuals, and within individuals) to assess the structure of predator hunting mode. We also investigated how prey activity affects the foraging behaviour and hunting success of predators. Our study supports key findings on predator foraging mode and predator–prey interactions from behavioural ecology. We found that individual predators displayed a diversity of hunting tactics that were conditioned by prey behaviour. With prey movement, individual predators specialized either as cursorial or ambush hunters along a continuum of their hunting traits, but also shifted their strategy between encounters. Both types of hunters were generally better against slower moving prey, and they achieved similar prey captures over the sampling period. This suggests that virtual worlds supporting multiplayer online videogames can serve as legitimate systems to advance our knowledge on predator–prey interactions.

2.2 Introduction

Predator hunting mode plays a crucial role in structuring ecological communities and ecosystems (Huey & Pianka, 1981; Kersch-Becker et al., 2018; Preisser et al., 2007; Schmitz, 2008) and is

usually described as 1) active/cursorial when hunters search, follow, and chase prey for long distances, 2) sit-and-pursue, when hunters remain motionless and pounce on prey that is within chasing distance, and 3) sit-and-wait/ambush, when hunters wait for prey to be within immediate capture distance (McLaughlin, 1989; Schmitz, 2007). Field studies show that contrasting hunting modes (e.g., cursorial vs. ambush) found among and within predator species can lead to differences in the number of individuals or species, or in the type of prey captured (Donihue, 2016; Glaudas et al., 2019; Miller et al., 2014). As a result, predators with contrasting hunting modes can cause opposing trophic cascades and act at different trophic levels (Romero & Koricheva, 2011; Schmitz, 2008).

Predator species are often classified either as active or sit-and-wait hunters based on their average behaviour (Lima, 2002; Miles et al., 2007; Pettorelli et al., 2015; Schmitz, 2017). Whereas such categorization has proved useful to predict community and ecosystem dynamics (Wirsing et al., 2021), it ignores the complexities of predator foraging decision-making. Indeed, growing evidence suggests that behavioural variation among individual predators can have important consequences for predator–prey interactions (Pettorelli et al., 2015; Schmitz, 2017; Toscano et al., 2016). For instance, individual predator behavioural type can mediate consumptive and nonconsumptive effects during trophic interactions (Griffen et al., 2012; Smith & Blumstein, 2010; Toscano & Griffen, 2014). Yet, the extent to which predators within populations differ in their foraging mode and how these individual differences affect the outcome of predator–prey interactions remain unclear. It is, therefore, imperative that we quantify and account for individual variation in hunting mode during predator–prey interactions if we hope to understand the community consequences of predation.

Stable individual differences in hunting behaviour within populations can be driven by specialization when individuals experience temporal and/or spatial fluctuations in the distribution, availability, or behaviour of their prey (Araújo et al., 2011; Ceia & Ramos, 2015; Courbin et al., 2018; R. A. Phillips et al., 2017). For instance, individual predators can specialize in specific tactics to meet the energy/time demands required to successfully capture the type of prey generally encountered (Arthur et al., 2016; Bowen et al., 2002; Tinker et al., 2008). According to the foraging syndrome hypothesis, these tactics are characterized by a continuum of coordinated morphological, physiological, and behavioural traits that are expressed by a predator to subdue its prey (Butler,

2005; Cooper, 2005; McLaughlin, 1989; Miles et al., 2007; Perry, 1999). The activity and movement patterns of prey are major drivers of encounter rates with predators (Gerritsen & Strickler, 1977; Huey & Pianka, 1981; Scharf et al., 2006), which may therefore lead to nonrandom interactions between predator–prey behavioural types (Wolf & Weissing, 2012). For example, the locomotor crossover hypothesis (Huey & Pianka, 1981) predicts that ambush predators should be more successful when they hunt fast-moving prey, whereas cursorial predators should have greater success with sedentary prey (Belgrad & Griffen, 2016; Donihue, 2016; Scharf et al., 2006). Thus, in the presence of prey with diverse movement patterns, individual predators specializing in contrasting hunting modes might coexist within a population if they achieve similar hunting success (Araújo et al., 2011; Chang et al., 2017).

Habitat structure is a second important driver of predator foraging mode, as it shapes opportunities for prey encounter and prey capture (Donihue, 2016; James & Heck Jr., 1994; Robinson & Holmes, 1982; Sargeant, 2007; Wasiolka et al., 2009). A growing body of evidence points to predators who hunt in open and homogeneous habitats adopting a cursorial strategy, contrary to those hunting in heterogeneous and closed habitats that typically ambush their prey (Donihue, 2016; James & Heck Jr., 1994; Wasiolka et al., 2009). Hence, the habitat components of a predator's hunting grounds can shape its hunting tactic. Heterogeneous habitats are expected to favor sit-and-wait/sit-and-pursue hunters as they offer perches and cover, which are useful for ambushes (James & Heck Jr., 1994; Laurel & Brown, 2006). On the contrary, active hunters should benefit from higher encounter rates in open habitats as prey detection is easier, although, at the expense of being themselves more easily detected (Michel & Adams, 2009). This suggests that habitat structure could mediate tradeoffs between hunting strategies.

Trophic interactions are dynamic processes that can also trigger flexible behavioural adjustments by individual predators (Heithaus et al., 2018; Helfman, 1990). Predators can shift their hunting strategy in response to changes in prey density and heterogeneity (Inoue & Marsura, 1983; Woo et al., 2008), prey behavioural type (McGhee et al., 2013), prey condition (Wignall & Taylor, 2008), seasonality (Miles et al., 2007; R. A. Phillips et al., 2017), or habitat structure (Wasiolka et al., 2009). Foraging mode shifts might thus be crucial for predators to maintain capture rates when coping with prey antipredator behaviour and environmental change (Laurel & Brown, 2006).

Longitudinal studies on predator–prey interactions often involve considerable financial, technical, and ethical challenges, especially when studying larger or elusive wildlife such as apex predators (Hertel et al., 2020). For instance, a major challenge impeding empirical investigations of individual variation in hunting mode is the need for repeated behavioural measurements of numerous individuals in varying environmental settings (Dall & Griffith, 2014; Dingemanse & Wright, 2020). This also comes with the difficulty of identifying traits in predators and prey that are easily observable and ecologically relevant. Besides, numerous predator–prey studies are conducted under controlled laboratory conditions that may fail to capture the nuances and complexities of a predator’s behaviour in the wild (Carter et al., 2013; Niemelä & Dingemanse, 2014). Consequently, few studies have investigated how prey movement shapes predator foraging syndromes at multiple hierarchical levels (i.e., within and among individuals or habitats) along with the relative importance of predator and prey behaviours for predator hunting success.

Here, we propose a novel approach to circumvent these challenges by studying individual variations in predator behaviour that capitalizes on online multiplayer videogames (Ahmad et al., 2014; Balicer, 2007; Lofgren & Fefferman, 2007; Oultram, 2013; Ross et al., 2015). Online multiplayer videogames could provide numerous opportunities for ecologists to study general ecological phenomena, including the mechanisms driving individual variation in behaviour (Barbe et al., 2020; Beauchamp, 2020; Céré et al., 2021; Duthie et al., 2021). First, online videogames provide abundant repeated measurements on millions of individual players across temporal and environmental gradients. Second, the structure of the virtual environment is known and can be used to evaluate how specific components affect the behaviour of interest. Third, videogames can reproduce realistic ecological settings in which complex interactions occur among players. A classic example is the case of the “Corrupted Blood” epidemic in World of Warcraft, where transmission modes/vectors and human reactions to the disease were surprisingly similar to what would be expected in a real-world outbreak (Balicier, 2007; Lofgren & Fefferman, 2007). For these reasons, online multiplayer videogames could potentially complement traditional field studies, and thus allow us to bridge the gap between real-world ecological studies and large-scale computer simulations (Ross et al., 2015).

We used the videogame *Dead by Daylight* as our study system. *Dead by Daylight* is an asymmetrical online multiplayer horror game that pits a single player (predator) against a group of

four players (prey). The predator's main objective is to search for and consume prey (Figure 2.1a), whilst the prey's objective is to exploit resources though avoiding the predator. These resources consist of generators that need to be repaired so the prey can escape and win. Thus, analogous to real prey that moves across patches to exploit resources under predation risk, prey in *Dead by Daylight* must move around the virtual environment and locate generators to repair (Figure 2.1b). As described in classical ecological studies of patch use (Brown, 1988, 1999; Kotler & Blaustein, 1995), prey must be wary of the time they spend repairing a generator (i.e., foraging in a patch) because investing too much time can increase the risks of being captured. Prey players can use a wide range of behaviours such as cooperation or hiding (Céré et al., 2021) to successfully escape (Figure 2.1b–c), providing opportunities for the predator to express a diversity of hunting tactics. Moreover, each match in *Dead by Daylight* occurs within a specific virtual habitat such as forests, farmlands, and urban areas. These environments differ in their structure (McCoy & Bell, 1991), such as in the availability of perches and refugia, vegetation density, or surface area (Figure 2.1d). Predator players can exploit these habitat features to hunt their prey. Hence, they experience variability in the prey and habitats that they encounter, and are expected to benefit from changing their behaviour accordingly to maximize hunting success. Finally, although *Dead by Daylight* is a virtual environment, we suggest that individual players express ecologically relevant decisions in response to predation or prey behaviour, and the resulting complex interactions that are monitored can be valuable for ecological research. Therefore, an empirical approach can be adopted to study the player population (see these studies for examples on other games: Belaza et al., 2020; Fuchs & Thurner, 2014; Szell et al., 2010), with methods equivalent to those used in observational studies of natural predators.

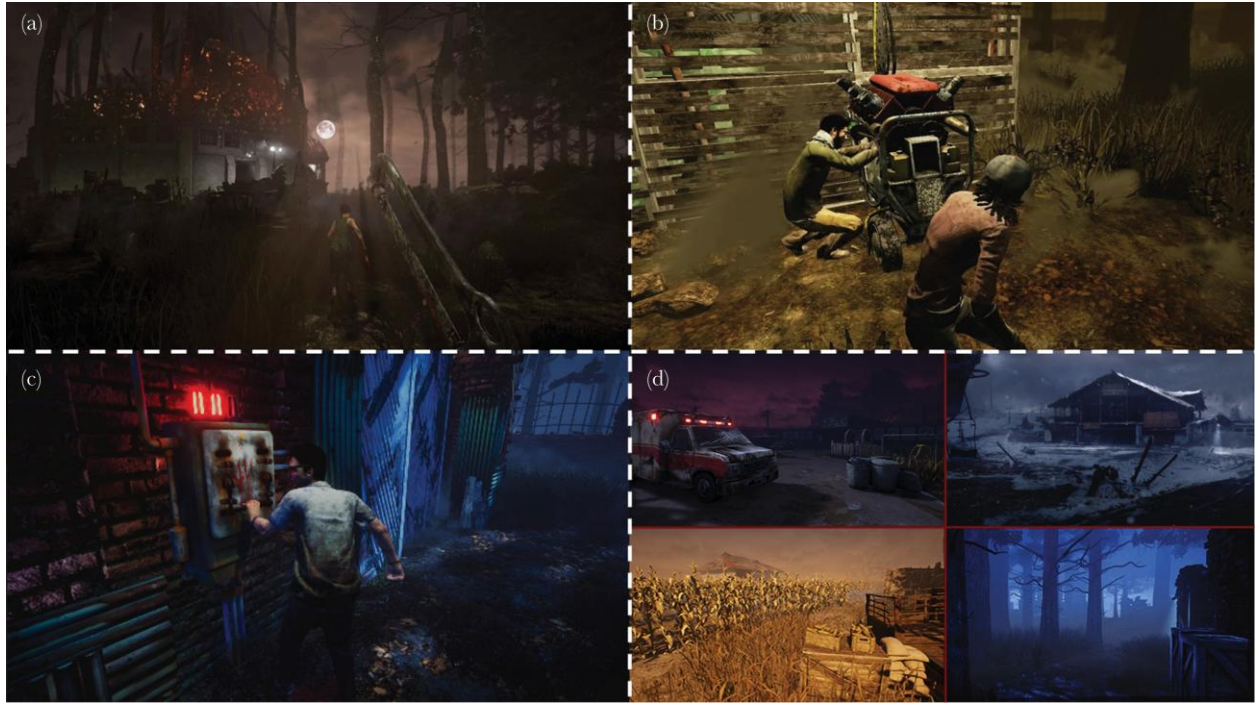


Figure 2.1 Images of the online videogame *Dead by Daylight*. (a) Image of the predator player’s first person vision. Here, we see a predator chasing a prey. (b) The prey (survivor) player’s third person vision. Prey can cooperate to repair generators. They can activate one of the two escape doors to flee and win the match when all generators are repaired. (c) Representative image of a prey player activating an escape door. (d) Representative pictures of the different game environments where matches take place. All the images were taken from the official *Dead by Daylight* wiki web page.

In this study, we use an extensive dataset on the hunting behaviour of predator players in *Dead by Daylight* to empirically investigate environmental and individual variation in hunting mode, and how predator and prey behaviour affect prey capture. We use four hunting related behaviours as proxies of hunting mode: Travel speed, the rate of space covered in the environment, the time spent guarding captured prey, and the time elapsed before the first prey capture. Predators adopting a cursorial hunting mode should travel faster and cover more space in the environment, but should spend less time guarding and have a shorter latency before the first capture. Predators with an ambush hunting mode should exhibit the opposite tendency. Thus, both strategies should represent the extremes of a continuum. We use multivariate mixed modeling to quantify variation in these behaviours and their correlations as a way to decompose the hunting mode continuum at different hierarchical levels within the predator population (Dingemanse & Dochtermann, 2013). These levels include behavioural differences among environments, consistent differences among

individuals in their average hunting behaviour, and differences arising from individuals adjusting their behaviour over time in response to temporal changes in environmental conditions or prey behaviour. First, we hypothesize that habitats shape the hunting mode employed by predators. If there are among environmental behavioural differences, we expect correlated trait values associated with an ambush mode in smaller and heterogeneous environments, and correlated trait values associated with a cursorial mode in open/wider and homogeneous environments (i.e., among environment behavioural correlations). Second, we hypothesize that individual predators will consistently differ in their hunting mode over time, with some specializing as cursorial hunters and others as ambush hunters. Thus, if predators differ in their average behaviours, we predict that their average trait values will be positioned along an ambush-cursorial continuum (i.e., among individual behavioural correlations), where the position designates their preferred hunting mode. Third, we expect that individual predators will switch from cursorial to ambush tactics between foraging bouts (i.e., between matches). If there is within-individual behavioural variation, we predict negative relationships between hunting behaviours at this level (i.e., within-individual behavioural correlations). Fourth, after the locomotor crossover hypothesis, we predict that ambush and cursorial predator types will coexist in the population because both achieve similar hunting success by performing better against prey with the opposite locomotor tendency.

2.3 Materials and methods

2.3.1 Study system

The datasets used to test our hypotheses were provided by Behaviour Interactive Inc., the owner and developer of *Dead by Daylight*. The company records the behaviour of players for every match played online. During our study period, *Dead by Daylight* offered 15 playable predator avatars. Players who adopt the predator's role choose their avatar before a match. Each predator avatar has unique abilities that may encourage different playstyles. Some have abilities that make them stealthier, whereas others can run faster, or have more powerful attacks. We thus controlled for the chosen avatar in our models because it may impact the playstyle of the predator player. In addition, the game environment where players compete is usually randomly assigned from a list of 27 maps differing in their physical components. For example, some maps have large playable surface areas with low vegetation density, which may favor the use of a cursorial strategy. Other maps have a smaller surface area with high vegetation density, which may impair visibility and alter prey

detection, favoring the use of an ambush strategy. However, an important game feature to consider is that predators have constant visual cues that display the location of the generators. This could interfere with how the virtual environment affects the predator’s behaviour or hunting success. For instance, predators might use these cues to approximate the distance/time required to travel between generators, which may relax the energy/concentration allocated to managing movement across the environmental features. For additional details on the game settings and map characteristics, refer to <https://deadbydaylight.com/en>, and https://deadbydaylight.gamepedia.com/Dead_by_Daylight_Wiki.

2.3.2 Data collection

The game developer provided us with raw datasets ranging from 20 March 2019 to 17 June 2019. Because the company records player data with automated scripts, technical issues or errors in the data compilation can occur. For instance, players hacking the game or disconnecting during a match, among other reasons, can cause errors in the data compilation. We thus had to combine these datasets and apply filtering, cleaning, and verification procedures to obtain our synthetic dataset. First, we filtered for matches that were played exclusively against a group of unknown people. Second, we retained matches that lasted more than 5 min, as short matches are usually interrupted because of disconnections or inactive players, and deleted any match where the match duration was missing or equal to zero. Third, we removed matches where predator players were obviously inactive, that is, when they had average speeds of, or very close to, zero although staying within a maximum of two squares or less during the match. Fourth, based on the best of our knowledge of the game, we deleted any matches where the observed behaviours were extreme and were most likely the result of hacking or players doing something different from how the game is intended to be played (e.g., farming for points).

Our synthetic dataset consists of a population of 2 378 new anonymous players who initiated their first match between 20 March and 22 March, with a total record of 77 047 matches (average: 34 matches per individual, range: 1–1059 matches). The average match duration was 11.13 min (range: 5–35 min). For every match, the date (date-hour-minutes), the duration (seconds), the predator player’s anonymous ID, the predator’s avatar, and the game environment were recorded along with the predator and prey behaviours.

2.3.3 Behavioural traits

We ran a principal components analysis on eight behavioural traits to identify the presence of structured hunting tactics in the predator player population (see Supplementary Figure S1 and Supplementary Table S1). We then selected four behaviours that summarized most of the variation in the observed tactics for all our analyses. We used this approach to ease the interpretation of the trait correlations in the multivariate models and allow the reuse of our variables in future analyses. In fact, any new sample of observations would yield a different ordination with different principal components, precluding any comparison between studies. The behaviours we selected were the average travel speed (m/s) (mean = 3.30, $SD = 0.45$), the rate of space covered (square/s) (mean = 0.05, $SD = 0.01$), the total amount of time spent guarding captured prey (mean = 42.91, $SD = 41.91$), and the time predators took to capture their first prey (mean = 178.67, $SD = 146.65$).

Our proxies of activity were the predator's average travel speed defined as the average number of meters per second traveled during a match, and space coverage defined as the number of 16x16 meters squares entered per second in a grid that covers the whole virtual environment (similar to measures of activity in open field tests, Montiglio et al., 2010). The grids are drawn by the game developer to build the game environments, but are invisible to the players. Based on these data, we divided the number of times a square were visited by the match duration to obtain the rate of space covered. Unfortunately, it was not possible to know which specific square was visited, so our variable is a raw estimate of the rate at which predators cover space in the environment. The time spent guarding prey describes the time a predator spent monitoring near capture sites to ambush prey players trying to rescue individuals that were captured. This trait is measured by drawing (invisible) 9-meter radius circles around all sites where the predator brings prey to be consumed (each site is at the center of a circle). Thus, whenever a predator brought prey to a capture site during a match, the time (in seconds) it spent monitoring within the site's circle area was recorded. We could then sum up all the events where predators were monitoring capture sites to obtain the total amount of time spent guarding captured prey during a match. Finally, the time before the first capture was calculated as the number of seconds elapsed before a predator captured its first prey.

To test the locomotor crossover hypothesis, we were provided datasets that contained the average travel speed (m/s) and rate of space covered (square/s) of all the prey players for each match played

by the predator. Both traits are measured using the same method described for predators. For both prey behaviours, we averaged the four individual prey player values within each match because we were interested in the average effect of prey behaviour on the predator’s hunting behaviour and success. Thus, we used one average value per prey behaviour for each match played by the predator.

2.3.4 Statistical analyses

2.3.4.1 Software and computer setup

We performed all statistical analyses using R (version 4.1.2, R Core Team, 2021) on a remote computer cluster (Cedar, Compute Canada, <https://docs.computecanada.ca/wiki/Cedar>) running on CentOS Linux 7. All models were fitted using the R package “brms” version 2.16.3 (Bürkner, 2017). To ensure a minimum of reproducibility and transparency, we made the data, all R code, most outputs, and the R sessions information publicly available (<https://github.com/quantitative-ecologist/predator-foraging-mode-videogames>).

2.3.4.2 Variation in hunting mode

We first parametrized a Bayesian multivariate mixed model (Bürkner, 2018; Dingemanse & Dochtermann, 2013; Mitchell & Houslay, 2020) (for an overview using “brms”, see https://paul-buerkner.github.io/brms/articles/brms_multivariate.html) to quantify the repeatability of hunting behaviour, and to evaluate among environment, among individual (specialization), and within-individual (flexibility) behavioural correlations. For each hunting behaviour, we controlled for the predator’s population-response to prey behaviour by adding the prey travel speed (x_1) and rate of space covered (x_2) as linear fixed effects. We also included the square-root of the match duration (x_3) as a fixed effect for the time spent guarding and the time before the first capture to control for differences in game length. We log-transformed the time spent guarding and the time before the first capture to achieve normality and then defined each behaviour (y_1 = speed, y_2 = space, y_3 = guarding time, y_4 = time 1st capture) as having a Gaussian distribution. All behaviours were then standardized to mean and unit variance (z-scores). The model is described by the following equations:

$$y1_{ghij} = \left(\beta_{0_{y1}} + env_{0_{y1,g}} + avatar_{0_{y1,h}} + id_{0_{y1,i}} \right) + \beta_{1_{y1}} x_1 + \beta_{2_{y1}} x_2 + \varepsilon_{0_{y1,ghij}} x_3 \quad (1)$$

$$y2_{ghij} = (\beta_{0_{y2}} + env_{0_{y2,g}} + avatar_{0_{y2,h}} + id_{0_{y2,i}}) + \beta_{1_{y2}}x_1 + \beta_{2_{y2}}x_2 + \varepsilon_{0_{y2,ghij}}x_3 \quad (2)$$

$$y3_{ghij} = (\beta_{0_{y3}} + env_{0_{y3,g}} + avatar_{0_{y3,h}} + id_{0_{y3,i}}) + \beta_{1_{y3}}x_1 + \beta_{2_{y3}}x_2 + \varepsilon_{0_{y3,ghij}}x_3 \quad (3)$$

$$y4_{ghij} = (\beta_{0_{y4}} + env_{0_{y4,g}} + avatar_{0_{y4,h}} + id_{0_{y4,i}}) + \beta_{1_{y4}}x_1 + \beta_{2_{y4}}x_2 + \varepsilon_{0_{y4,ghij}}x_3 \quad (4)$$

where g indexes the environment, h the predator avatar, i the individual player, and j the recorded match. The game environment ($env_{0_{y,g}}$), the predator avatar ($avatar_{0_{y,h}}$), and the player ID ($id_{0_{y,i}}$) are random intercepts (among environment, avatar, and individual variances), and ($\varepsilon_{0_{y,ghij}}$) are the residuals (within-individual variance). Random intercepts and residuals were assumed to follow a multivariate Gaussian distribution with their associated variance-covariance matrices (Ω_{env} , Ω_{avatar} , Ω_{id} , Ω_{ε}) (Annexe A: equations 1-4). For each combination of behaviours (y_n), we extracted the behavioural correlations among environments ($r_{env_{0,y_n}env_{0,y_n}}$), individuals ($r_{id_{0,y_n}id_{0,y_n}}$), as well as within-individual behavioural correlations ($r_{\varepsilon_{0,y_n}\varepsilon_{0,y_n}}$) (Dingemanse & Dochtermann, 2013). The sample size of each parameter's posterior distribution is 1000 (see section "Parametrization of the Bayesian multivariate mixed-model" in the Annexe A for details).

2.3.4.3 Effect of hunting behaviour and prey behaviour on prey capture

We first quantified the linear relationship between hunting success and predator behaviour by fitting a Bayesian generalized linear mixed model. Since predators can capture a maximum of four prey, we fitted the model using the number of prey captured per total number of prey in a match (four) as a binomial response variable ($\omega_{hij} \sim Binom(max_{hij}, P_{hij})$) with a logit link function. The model fits a linear function ($\beta_{n,pred}x_{hi}$) where we could estimate if hunting success increased or decreased with increasing hunting behaviour scores. We fitted the mean probability of capturing four prey (P_{hij}) in the environment h for individual i on its j match as a function of its travel speed, rate of space covered, time spent guarding, and latency before the first capture (Annexe A: equation 5). We computed a second model to account for variation in hunting success explained by prey behaviour ($\beta_{n,prey}x'_{hi}$). We thus added prey travel speed and their rate of space covered in the model equation (Annexe A: equation 6). Both models had random intercepts for the game

environment ($env_{0,h}$) and the predator player's ID ($id_{0,i}$) to partition the variance in hunting success explained by differences among players and the environments where matches occurred. The random intercepts for the game environment and the predator player ID were assumed to follow a Gaussian distribution with estimated variance ($env_{0,h} \sim N(0, V_{env}), id_{0,i} \sim N(0, V_{id})$). We included an observation-level random effect to account for overdispersion and compared the models to a beta-binomial model to ensure that the estimates were robust (Harrison, 2015). Trait values were standardized to mean and unit variance (z-scores). The sample size of each parameter's posterior distribution is 1000 for both models.

We built a third model with the same structure as the first model and included quadratic terms ($\frac{1}{2}\gamma_{n,pred}x_{hi}$), identified as lambda, to determine whether the relationships between hunting success and predator behaviour are concave or convex (Annexe A: equation 7). Concave gradients suggest that individuals at the extremes of the trait distribution perform poorly while the opposite is true when the gradient is convex (Brodie et al., 1995). We also added interaction terms for each combination of predator traits ($\gamma_{n,pred}$) to estimate correlated effects on hunting success. Finally, we computed a fourth model with the same structure as the third and included quadratic terms for prey behaviour ($\frac{1}{2}\gamma_{n,prey}x'_{hi}$), and interaction terms between predator and prey behaviours ($\gamma_{n,pred\ prey}$) to test if predators perform better against prey with the opposite locomotor tendency (locomotor crossover) (Annexe A: equation 8). All trait values were standardized to mean of 0 and unit variance (z-scores). The sample size of each parameter's posterior distribution is 1000 for both models. For the four models, we included the square-root of the match duration as a fixed effect to control for differences in game length. We provide a detailed description of the model parametrization in the Annexe A ("Parametrization of the Bayesian mixed-models for hunting success").

We performed approximate leave-one-out cross-validation using Pareto smoothing importance sampling (PSIS-LOO) (Vehtari et al., 2017) with the "loo" function in "brms" to select the best out of the four candidate models. This method outlines the best model by comparing their predictive accuracy based on the difference of their expected log predictive density (elpd). The model with the highest elpd value should thus be the best at predicting the data. We assumed that the relationship between hunting behaviour and hunting success reached statistical significance when

the 95% credible intervals of the fixed parameter values did not overlap zero (Nakagawa & Cuthill, 2007).

2.3.4.4 Variance decomposition

Following the method by Nakagawa & Schielzeth (2010) for Gaussian response models, we calculated each hunting trait's adjusted repeatability estimate (intra-class correlation coefficient, *ICC*) for the game environment, the predator avatar, and the predator player ID. To do so, we divided the mean variance (*V*) drawn out of the 1000 posterior samples of each specific random effect by the total behavioural variance such as:

$$ICC_{id_{yn}} = V_{id_{0,yn}} / (V_{env_{0,yn}} + V_{avatar_{0,yn}} + V_{id_{0,yn}} + V_{\varepsilon_{0,yn}}) \quad (5)$$

We computed the 95% credible intervals for each repeatability estimate using the highest posterior density intervals. We additionally calculated the *ICC* of the predator hunting success for the player ID and the game environment using the method by Nakagawa et al. (2017) for binomial models and computed their 95% credible intervals using the highest posterior density intervals.

2.4 Results

2.4.1 Variation in hunting mode: Repeatability of hunting behaviour

Contrary to our predictions, neither the average travel speed ($ICC_{env_{y1}}$ [95% CI] = 0.002 [0.001, 0.003]), nor the time spent guarding ($ICC_{env_{y3}}$ [95% CI] = 0.014 [0.008, 0.021]) differed among the game environments (Figure 2.2a, diagonal). We detected minimal differences among the game environments in the average rate of space covered ($ICC_{env_{y2}}$ [95% CI] = 0.040 [0.022, 0.061]) and latency before the first capture ($ICC_{env_{y4}}$ [95% CI] = 0.022 [0.012, 0.033]) (Figure 2.2a, diagonal).

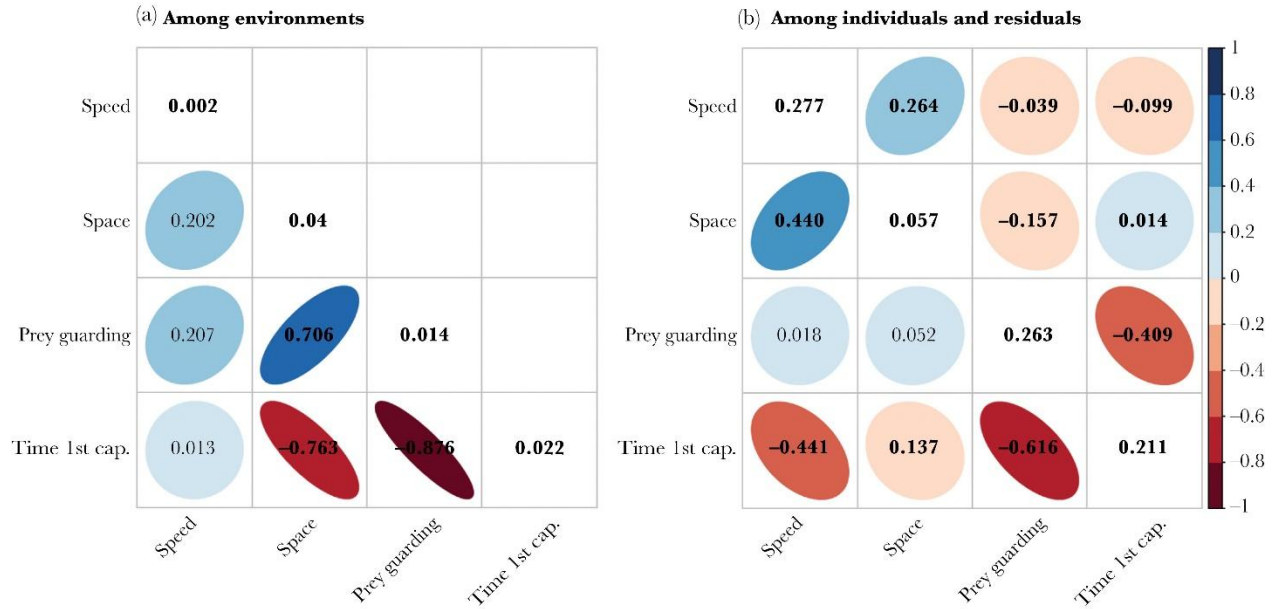


Figure 2.2 Correlations between combinations of hunting behaviours and their ICCs. For each panel, the posterior average ICC of the behaviour is displayed on the diagonal. (a) Among environment behavioural correlations on the lower off-diagonal. (b) Among individual behavioural correlations on the lower off-diagonal, and (residual) within-individual behavioural correlations on the upper off-diagonal. Behaviour names were shortened to simplify the plot.

Predator avatars differed slightly in their average travel speed ($ICC_{avatar_{y1}}$ [95% CI] = 0.081 [0.039, 0.138]). We observed weak differences among avatars for the other three hunting behaviours ($ICC_{avatar_{y2}}$ [95% CI] = 0.020 [0.008, 0.035], $ICC_{avatar_{y3}}$ [95% CI] = 0.026 [0.008, 0.049], $ICC_{avatar_{y4}}$ [95% CI] = 0.027 [0.010, 0.048]).

As predicted, we found moderate among-individual differences in the average travel speed ($ICC_{id_{y1}}$ [95% CI] = 0.277 [0.256, 0.301]), the time spent guarding ($ICC_{id_{y3}}$ [95% CI] = 0.263 [0.240, 0.282]), and the latency before the first capture ($ICC_{id_{y4}}$ [95% CI] = 0.211 [0.195, 0.228]) (Figure 2.2b, diagonal). Individual predators differed weakly in their average rate of space covered ($ICC_{id_{y2}}$ [95% CI] = 0.057 [0.049, 0.064]) (Figure 2.2b, diagonal).

2.4.2 Variation in hunting mode: Correlations between hunting behaviours

Environments where predators were faster were also those where they tended to spend more time guarding their prey ($r_{env_{0,y1}env_{0,y3}}$ [95% CI] = 0.207 [-0.124, 0.541]) (Figure 2.2a, lower off-diagonal), but the relationship was not significant. We detected a similar yet stronger and significant relationship between space coverage and time spent guarding ($r_{env_{0,y2}env_{0,y3}}$ [95% CI] = 0.706 [0.510, 0.892]). Predators took on average less time to capture their first prey in environments where they covered space at a faster rate ($r_{env_{0,y2}env_{0,y4}}$ [95% CI] = -0.763 [-0.899, -0.610]) and when they spent more time guarding their prey ($r_{env_{0,y3}env_{0,y4}}$ [95% CI] = -0.876 [-0.952, -0.781]) (Figure 2.2a, lower off-diagonal). Lastly, we did not detect significant among-environment correlations between travel speed and space coverage, or between travel speed and the latency to capture the first prey ($r_{env_{0,y1}env_{0,y2}}$ [95% CI] = 0.202 [-0.124, 0.536], ($r_{env_{0,y1}env_{0,y4}}$ [95% CI] = 0.013 [-0.316, 0.358]) (Figure 2.2a, lower off-diagonal).

Contrary to our expectations, individuals that traveled faster did not spend less time guarding prey ($r_{id_{0,y1}id_{0,y3}}$ [95% CI] = 0.018 [-0.042, 0.077]) (Figure 2.2b, lower off-diagonal). Similarly, the relationship between space covered and time spent guarding was weak and non significant ($r_{id_{0,y2}id_{0,y3}}$ [95% CI] = 0.052 [-0.035, 0.141]). Faster individuals covered space at a faster rate ($r_{id_{0,y1}id_{0,y2}}$ [95% CI] = 0.440 [0.376, 0.499]), and individuals who were faster or covered space at a faster rate took less time to capture their first prey ($r_{id_{0,y1}id_{0,y4}}$ [95% CI] = -0.441 [-0.489, -0.390], $r_{id_{0,y2}id_{0,y4}}$ [95% CI] = -0.137 [-0.221, -0.058]) (Figure 2.2b, lower off-diagonal). Another result opposing our predictions was that hunters that captured their first prey more quickly spent more time guarding prey ($r_{id_{0,y3}id_{0,y4}}$ [95% CI] = -0.616 [-0.655, -0.579]) (Figure 2.2b, lower off-diagonal).

At the within-individual level, we detected a moderate positive correlation between travel speed and the rate of space covered ($r_{\varepsilon_{0,y1}\varepsilon_{0,y2}}$ [95% CI] = 0.264 [0.257, 0.270]) so that predators covered space at a faster rate (relative to their average) in matches where they traveled faster. Players barely spent less time guarding prey in matches where they traveled faster ($r_{\varepsilon_{0,y1}\varepsilon_{0,y3}}$ [95% CI] = -0.039 [-0.046, -0.032]). However, players spent less time guarding prey in matches where they were

faster at covering space in the environment ($r_{\varepsilon_{0,y2}\varepsilon_{0,y3}}$ [95% CI] = -0.157 [-0.165, -0.148]) (Figure 2.2b, upper off-diagonal). Individuals tended to be faster at capturing their first prey in matches where they traveled faster ($r_{\varepsilon_{0,y1}\varepsilon_{0,y4}}$ [95% CI] = -0.099 [-0.106, -0.092]), but not when they covered space at a faster rate ($r_{\varepsilon_{0,y2}\varepsilon_{0,y4}}$ [95% CI] = 0.014 [0.006, 0.023]) (Figure 2.2b upper off-diagonal). In accordance with our observations at the among-individual level, predator players captured their first prey earlier in matches where they spent more time guarding their prey ($r_{\varepsilon_{0,y3}\varepsilon_{0,y4}}$ [95% CI] = -0.409 [-0.415, -0.404]) (Figure 2.2b upper off-diagonal).

2.4.3 Effect of the predator and prey behaviour on hunting success

The best model at predicting hunting success included a linear and quadratic effect of all the predator behaviours along with two-way interactions between predator behaviours and predator and prey behaviours (Annexe A: Table A.4). Predators maximized their hunting success when they traveled at population-average speed values (Figure 2.3a), suggesting that extreme speeds (either low or high) were at a disadvantage. Alternatively, predators were more successful when they covered space at a slower rate (Figure 2.3b). Spending time guarding prey was positively related to hunting success and was maximized at values above the population average (Figure 2.3c). The predators' hunting success decreased when they took more time to capture their first prey, implying that the more successful ones were those that secured captures earlier in a match. Predators optimized their hunting success when they encountered prey that were slower than the population average (Table 2.1). Matches where prey were faster at covering space in the environment were associated with significant reductions in the predators' hunting success (Table 2.1).

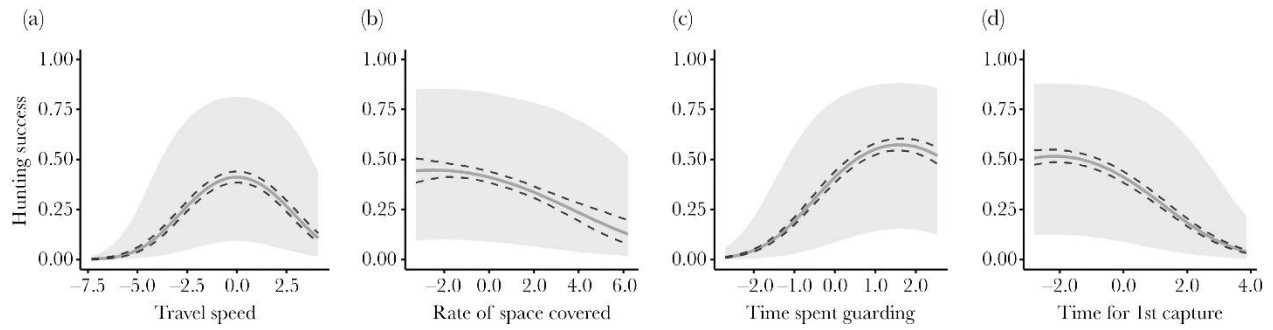


Figure 2.3 Relationships between predator hunting success and behaviour. Hunting success (i.e., the probability of capturing 4 prey) is on the y axis for all panels, and the standardized hunting behaviour is on the x axis. The solid lines illustrate the posterior predicted values, the dashed lines represent the 95% credible intervals for the predicted values, and the bands represent the 95% prediction intervals (variance in the fixed effects + variance in the random effects). (a) Relationship between hunting success and predator travel speed. (b) Relationship between hunting success and the predators' rate of space covered. (c) Relationship between hunting success and the predators' time spent guarding. (d) Relationship between hunting success and the time before predators captured their first prey.

Predator behaviours also interacted to affect hunting success. Predators were more successful when they spent more time guarding while moving at average or lower speeds (Annexe A: Figure A.2b). This suggests that prey guarding might have been used as a successful ambush strategy. Predators that were faster than the average, and that secured a first capture earlier in a match, were more successful (Annexe A: Figure A.2c). We observed a similar trend for space coverage although hunting success was optimized at higher rates and the optimum was larger (Annexe A: Figure A.2e). We also found that predators that spent more time guarding prey and captured their first prey earlier in a match were more successful (Annexe A: Figure A.2f).

Table 2.1 Posterior means and 95% credible intervals of the estimates relating predator hunting success to predator hunting behaviour, prey behaviour, and their interactions. The credible intervals are displayed between the parentheses.

Predictor	Linear	Quadratic	Predator trait interactions	Predator-prey trait interactions
travel speed	0.00 (-0.02, 0.02)	-0.10 (-0.09, -0.11)	-	-
space covered	-0.12 (-0.09, -0.15)	-0.02 (-0.01, -0.04)	-	-
time guarding	0.82 (0.80, 0.84)	-0.26 (-0.24, -0.28)	-	-
time 1st capture	-0.39 (-0.37, -0.40)	-0.09 (-0.08, -0.10)	-	-
prey travel speed	-0.25 (-0.24, -0.27)	-0.07 (-0.06, -0.08)	-	-
prey space covered	-0.68 (-0.65, -0.70)	-0.09 (-0.08, -0.11)	-	-
travel speed:space covered	-	-	0.00 (-0.02, 0.02)	-
travel speed:time guarding	-	-	-0.09 (-0.07, -0.11)	-
travel speed:time 1st capture	-	-	-0.04 (-0.03, -0.06)	-
space covered:time guarding	-	-	-0.01 (-0.04, 0.01)	-
space covered:time 1st capture	-	-	-0.11 (-0.10, -0.13)	-
time guarding:time 1st capture	-	-	-0.16 (-0.14, -0.18)	-
travel speed:prey travel speed	-	-	-	0.00 (-0.02, 0.01)
travel speed:prey space covered	-	-	-	-0.13 (-0.11, -0.15)
space covered:prey travel speed	-	-	-	-0.05 (-0.03, -0.06)
space covered:prey space covered	-	-	-	0.12 (0.09, 0.14)
time guarding:prey travel speed	-	-	-	-0.03 (-0.01, -0.05)
time guarding:prey space covered	-	-	-	-0.05 (-0.02, -0.08)

* The estimates are from the hunting success model with the highest elpd value (see Table A.4 in Annexe A)

2.4.4 Effects of the predator and prey behavioural interactions on hunting success

We did not detect a significant interaction between predator and prey travel speed (Table 2.1). Hence, predators moving at average travel speeds optimized their success against slower prey rather than locomotor opposites as we predicted (Figure 2.4a). Contrary to our expectations, predators that covered space at slower rates optimized their success against prey that covered space at slower rates (Figure 2.4d), and predators that spent more time guarding prey optimized their success against prey that were generally slower in their travel speed and rate of space covered (Figure 2.4e-f). However, faster predators were significantly more successful when they competed against prey that covered space at lower rates (Figure 2.4b), which is in line with our predictions. Lastly, predators had relatively similar hunting success irrespective of the rate of space they covered when they encountered prey that were slower or close to the population average (Figure 2.4c).

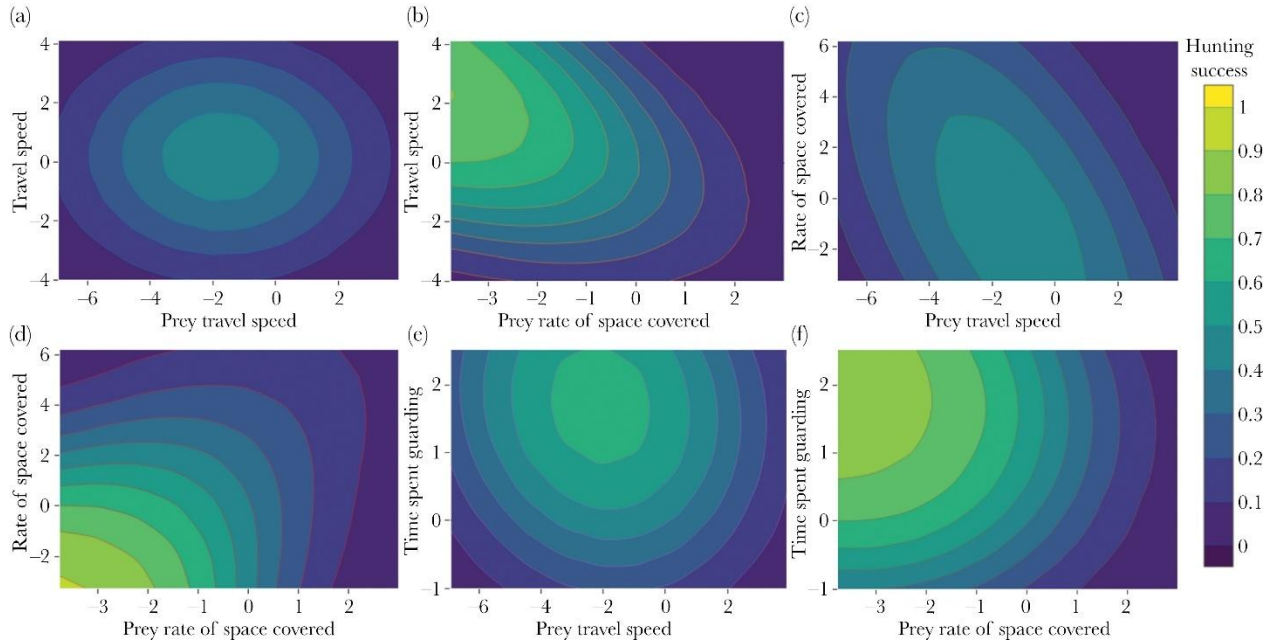


Figure 2.4 Influence of the predator and prey behavioural interactions on predator hunting success. The contour plots display the interacting influence of predator and prey behaviours on predator hunting success, represented by the color gradient. We computed the plots by predicting the mean probability of capturing four prey based on the best quadratic approximation of the predator and prey interaction terms. Here, we show interactions that enable us to assess if locomotor crossovers determine hunting success. (a) Predator and prey travel speed. (b) Predator travel speed and the prey's rate of space covered. (c) Predator space coverage and prey travel speed. (d) Predator and prey space coverage. (e) Predator time spent guarding and prey travel speed. (f) Predator time spent guarding and prey rate of space covered.

2.5 Discussion

Our study uses an online multiplayer videogame to quantify variation in predator foraging mode at multiple levels of organisation, and to investigate how predator and prey behaviour affect hunting success. We found that individual players who adopted the predator role showed consistent differences in their foraging behaviour while also displaying flexibility. The expression of some behaviours was consistent with shifts in the expression of other behaviours mostly at the within-individual level. However, the behaviours were generally not organized into foraging modes along a cursorial to sit-and-wait continuum. Contrary to our expectations, neither hunting behaviour nor prey capture varied among the game environments. At the population level, the most successful predators were those that hunted at travel speeds closer to the average, covered space at lower rates, and those that spent more time guarding prey relative to the average. Predators that took more time to capture their first prey were less successful. Prey behaviour also affected hunting success, such that predators generally captured more prey when they encountered prey that were on average less mobile. Moreover, the behavioural interactions between predators and prey revealed only partial evidence supporting the locomotor crossover hypothesis.

Our analyses show that individual predators differed in their average travel speed and in the amount of time they spent guarding prey, but did not specialize as either cursorial or guarding (ambush) hunters along a continuum when we controlled for prey behaviour. Faster players had higher rates of space use while those that guarded for longer periods were variable in their space use. In this case, fast space-covering players were efficient at capturing their first prey. However, these patterns were largely different when considering variability in prey locomotion (i.e. removing prey behaviour as controls in the models), such that individuals specialized either at covering space or at guarding prey for longer periods, revealing the presence of a space-guard continuum (see Annexe A: Table A.3). In addition, travel speed was not associated with space use anymore, and individuals specializing exclusively as prey guards were more efficient at capturing their first prey than those specializing as fast space users. The predators' preferred hunting strategies and their efficiency were thus conditioned in part by the movement of prey encountered throughout the study period.

Predator players displayed flexibility in their foraging mode as they switched between high rates of space use in some matches to a guarding strategy in others. These foraging mode switches were

accompanied by shifts in their movement as they were sometimes sedentary or otherwise highly mobile. This is most likely a consequence of pressures within a match that leave them with no choice but to guard or actively search. In nature, prey antipredator behaviour can induce dynamic shifts in a predator's searching or attack behaviours (McGhee et al., 2013; Savino & Stein, 1989). Here, prey behaviour strengthened the shift between space use and prey guarding, but did not seem to change the relationships among other behaviours at the within-individual level (Annexe A: Table A.3). Alternatively, other factors such as time constraints or reductions in prey abundance as individuals are captured could be at play. For example, starvation can force ambush hunters to adopt a cursorial mode (Inoue & Marsura, 1983), while ambush hunters often switch to a cursorial mode when prey density is lower (Helfman, 1990). Otherwise, foraging shifts may be advantageous when prey encounters are unpredictable (Ceia & Ramos, 2015; R. A. Phillips et al., 2017; Woo et al., 2008) that is, when predators can successfully adjust their strategy to varying types of prey.

Surprisingly, hunting behaviour was very similar across the different environments. This contrasts with studies showing that predators exploit habitat characteristics such as vegetation density to choose their hunting strategies (James & Heck Jr., 1994; Warfe & Barmuta, 2004; Wasiolka et al., 2009). Because hunting success was also very similar among the game environments, we cannot exclude the possibility that this may be a consequence of the game's design aiming to minimize differences in success resulting from changes between environments. In addition, the effect of the environment could be reduced because predators have visual cues on the generators and could thus simply travel between them to capture prey. While the environments do differ esthetically and in some features that affect prey escape rates (e.g. distance between generators, exit gates, surface area), we did not observe clear differences in important criteria such as heterogeneity (personal observations). Instead, habitat structure could have affected prey behaviour, for instance, by altering their perception of predation risk or their fear (Gaynor et al., 2019; Heithaus et al., 2009; Preisser et al., 2007). However, when we did not account for prey behaviour, differences among the game environments in the rate of space covered slightly increased, but differences in the other behaviours remained very low (Annexe A: Table A.2). Experiments also suggest that differences in prey antipredator responses to the environment can negate its effects on predator behaviour or success (Warfe & Barmuta, 2004). This could have occurred if, within matches, individual prey players had distinct responses to the virtual environment (e.g. some increase their activity in

heterogeneous habitats while others do the opposite). Alternatively, field observations show that predators can alter their hunting behaviour at larger scales according to prey behaviour, but at finer scales, seek for specific locations where they can easily hunt their prey (Hopcraft et al., 2005). Quantifying this would require fine-scale environmental variables that are currently not monitored by the game designer.

We hypothesized that predator-prey locomotor crossovers could maintain the diversity of hunting tactics in the population. However, we found that both cursorial and guarding (ambush) predators had greater success when they encountered sedentary prey. This could be caused by the trait itself (prey guarding) not being a proper proxy of ambush behaviour (predators need to capture a prey to guard it), or because we failed to capture other important prey strategies involved in the interaction by focusing solely on prey movement. Other studies have used taxonomic classification for predator hunting mode or prey boldness rather than the interaction between predator and prey activity to test the locomotor crossover hypothesis (Belgrad & Griffen, 2016; Chang et al., 2017; Donihue, 2016). Hence, using prey boldness could have generated different patterns. Otherwise, it is well established that predators often target juvenile/unexperienced prey (Gaynor et al., 2019; Kauffman et al., 2007; Quinn & Cresswell, 2004; Wirsing et al., 2021), and that appears like a plausible scenario assuming that slower prey were less experienced. For instance, novice prey could be more prone to inadequately respond to predator cues (e.g. exposing themselves instead of hiding or moving away), and thus, be more vulnerable to predation since prey need to move and repair generators to escape. In line with theoretical and empirical observations (Chang et al., 2017; McGhee et al., 2013; Wolf & Weissing, 2012), our results suggest that specific predator and prey behaviours may lead to non-random predator-prey encounters in this system.

While the foraging mode paradigm is useful for identifying the mechanisms driving predator-prey interactions, the ambush-cursorial dichotomy might be too simplistic since a greater diversity of modes likely exists within populations (Beaupre & Montgomery, 2007; Butler, 2005; Cooper, 2005; Miles et al., 2007). To date, the underlying causes and mechanisms of this diversity remain poorly understood. Our results suggest that prey behaviour can mediate individual specialization as either cursorial or ambush hunters rather than differences in hunting success, and predator experience might have played a role because hunting strategies are often developed by learning (Heithaus et al., 2018; Wilson-Rankin, 2015). We thus ran separate analyses on novice and experienced players

(see the ‘Methods’ section in the Annexe A) and found that both displayed distinct hunting strategies that were not apparent when they were pooled. Novice players that traveled faster spent more time guarding prey, so they probably aimed at capturing prey and securing their kill by preventing others from rescuing it. In contrast, experienced players displayed clear specialization as either cursorial or guarding (ambush) hunters (Annexe A: Table A.3). Interestingly, novice hunters were more flexible at switching between ambush and cursorial modes compared to experienced players who did not display mode switching. These notable distinctions show that considering hunting experience can reveal important insights on the dynamics of predator-prey interactions (R. A. Phillips et al., 2017; Tinker et al., 2009; Weimerskirch et al., 2005; Woo et al., 2008).

We are among the first ecologists (but see also Céré et al., 2021) to use an online multiplayer videogame to investigate how ecological mechanisms shape the dynamics of trophic interactions. As virtual worlds become increasingly present in our lives, understanding their ecology and our interactions within them will become an important topic of study (Duthie et al., 2021). We are convinced that online videogames will be valuable for testing hypotheses under realistic ecological scenarios, as they reduce several challenges associated with empirical studies, while providing rich and ecologically relevant datasets on human decision-making. Our results support this assertion as they were generally consistent with patterns reported in ecological studies of natural predators (Butler, 2005; Helfman, 1990; McGhee et al., 2013; Miles et al., 2007). However, videogames are not a panacea; they are potentially limited by player behaviour not properly reflecting behavioural decisions made by organisms in the wild, as the player can neither “die” nor be driven by hunger. Hence, individuals may take greater risks in a videogame compared to natural predators (Lofgren & Fefferman, 2007; Oultram, 2013). Moreover, while *Dead by Daylight* provides an interesting system to investigate predator-prey interactions, prey density is fixed at four players, which prevents the modelling of predator functional responses. Lastly, similar to mesocosm experiments with single predators, the game may not reflect natural systems where multiple predator species compete for the same prey. In light of these potential limitations, researchers should interpret results from online videogames with care, and aim to test specific ecological hypotheses with them.

Individual variation in predator (and prey) behaviour is increasingly recognized as a critical factor influencing the outcome of trophic interactions (Moran et al., 2017; Pettorelli et al., 2015; Toscano

et al., 2016). Our study is the first to investigate individual variation in predator foraging behaviour using an online videogame. Our results corroborate patterns observed in natural systems and highlight complex relationships between predator foraging behaviour, prey movement, and hunting success. Predator players specialized in diverse hunting strategies. These strategies varied among and within individuals along a continuum of correlated behaviours (foraging syndrome hypothesis), and were shaped by prey movement and predator experience. In addition, our results suggest that different predator behavioural types could coexist through the consumption of potentially vulnerable prey and in part by locomotor crossovers. Thus, investigating the effects of prey behaviour on predator behaviour and success at different hierarchical levels can provide a more comprehensive depiction of a predator's foraging ecology. We recommend that further studies consider these aspects when possible. To conclude, we provided support that virtual worlds can be used to identify how ecological mechanisms drive observable phenomena like individual behavioural decisions. While the potential of online multiplayer videogame data remains untapped for ecological research, we are confident that further studies employing them will provide valuable ecological insight for behavioural and community ecologists.

2.6 Acknowledgements

We thank Behaviour Interactive for generous access to their data, and members of the design team of *Dead by Daylight* for the great discussions and ideas. We are specifically thankful to members of the analytics department (Julien Céré, Guillaume Bergerot, Jean-Baptiste Le Meur, and Nicolas Robitaille) for inputs on the preliminary results. We would also like to thank all members of the CSBQ-UQAM for their insightful comments and suggestions on the whole research process. Lastly, we sincerely thank two anonymous reviewers whose comments helped us improve earlier versions of this study. This work was supported by a Mitacs Accelerate Grant (grant number IT12054) through a partnership with Behaviour Interactive and Université du Québec à Montréal.

2.7 Data and code availability

Analyses reported in this article can be reproduced by following the guidelines in this GitHub repository: <https://github.com/quantitative-ecologist/predator-foraging-mode-videogames>

CHAPITRE 3:

THE ROLE OF PREY BEHAVIOUR IN PREDATOR EXPERTISE ACQUISITION: INSIGHTS FROM A VIRTUAL ECOSYSTEM

Fraser Franco, M., Santostefano, F., Martin, J. G. A., Kelly, C. D., Montiglio, P.-O.

Une version antérieure de ce chapitre est disponible en prépublication : Fraser Franco, M., Santostefano, F., Martin, J. G. A., Kelly, C. D., Montiglio, P.-O. (2024). Prey movement shapes the acquisition of predator expertise in a virtual bi-trophic system. *BioRxiv*. <https://doi.org/10.1101/2024.11.15.621573>.

La présente version a été soumise au journal *Animal Behaviour*.

3.1 Abstract

The acquisition of expertise is crucial for predators to be successful hunters. To achieve this, predators must hone their skills and gain knowledge through repeated and extensive practice. It is hypothesized that prey can interfere in this process and hinder the acquisition of predator expertise by employing antipredator tactics to evade detection and pursuit. However, empirical evidence on how predators acquire expertise through repeated encounters with their prey remains limited, largely due to the challenges of monitoring direct interactions in the wild. Here, we use the game *Dead by Daylight*, a virtual predator-prey system where a human predator chases four human prey, to investigate how cumulated experience shapes hunting success in predators across repeated interactions with their prey. Our results show that prey of greater skill at avoiding predation relied on faster movement to outmanoeuvre predators, which limited the maximum hunting success of predators in the long term. Yet strong variation in expertise acquisition remained among predators, even after accounting for prey movement behaviour. We also observed that predators with a lower initial hunting success showed poor improvements over time, while those with the highest initial success remained successful. Moreover, individuals with a lower rate of gain in expertise achieved the greatest long term hunting success. These observations suggest cognitive styles in predators that may explain long term differences in hunting success. We further discuss the potential mechanisms underlying these patterns.

3.2 Introduction

Predation is an agent of evolutionary change that regulates prey populations, limits the spread of diseases, and mediates energy flow across trophic levels (Abrams, 2000; Hairston & Hairston, 1993; Ripple et al., 2014; Wirsing et al., 2021). These processes are driven by spatial and temporal changes in predation risk and prey capture, as predators select suitable habitats to hunt and adjust their strategies accordingly (LaBarge et al., 2024; Pettoirelli et al., 2015; Quevedo et al., 2009; Schmitz, 2017). Theory suggests that predators become proficient hunters by acquiring expertise through learning key skills and practicing the tactics required to locate, select, and capture their prey (LaBarge et al., 2024; Woo et al., 2008; Wooster et al., 2023). This raises the question of whether differences in hunting success between predators can be attributed to differences in the capacity to acquire hunting expertise. Unraveling how this expertise emerges during predator-prey interactions would allow for a better assessment of the direct effects of predation on prey.

Expertise can be defined as the characteristics, skills, and knowledge that enable individuals to outperform novices on complex tasks (Dukas, 2017; Helton, 2005). The acquisition of expertise is measured by quantifying how the success of a skill, such as hunting, varies as a function of time or repeated attempts (Dukas, 2019). This process is usually characterised by a gradual improvement in performance over time (De Resende et al., 2008; Dukas, 2008; Rutz, 2012). Different mechanisms can be involved in the acquisition of expertise. For example, in human and non-human hunters, individuals optimize foraging efficiency over time by associative learning, by developing search images, or by exploiting cues from their prey and their environment (Edwards & Jackson, 1994; MacDonald, 2007; Morse, 2000; Reid et al., 2010; Wilson-Rankin, 2015). To achieve this, predators require increased long-term memory, a superior ability to focus, acute perception and anticipation, as well as fast and coordinated motricity (Dukas, 2019). Ultimately, expert predators should have greater knowledge, better energy management, and acute motor skills that increase their chances of locating and capturing prey. Any limitations in these attributes could impair the rate at which predators acquire expertise, with potential long-term consequences for their hunting success. Therefore, differences among predators in these attributes may alter the dynamics of predator-prey systems (Kikuchi & Simon, 2023; Kondoh, 2010; Skelhorn & Rowe, 2016).

Prey respond to predators by using tactics such as camouflage to avoid detection and rapid escapes to evade capture (Herbert-Read et al., 2017; Kelley & Magurran, 2011; Walker et al., 2005). These antipredator strategies are hypothesized to disrupt a predator's capacity to acquire hunting expertise, thus driving differences in prey consumption among predators (Wooster et al., 2023). This has been supported by experimental studies showing that prey camouflage can impair the acquisition of expertise in humans and birds (Stevens et al., 2012; Troscianko et al., 2018). For example, using a virtual experiment, Troscianko, Skelhorn, and Stevens (2018) found in human subjects that disruptive colouration interfered with their ability to form search images, hindering improvements in detection times over repeated attempts. Beyond prey camouflage, there is limited evidence to suggest that antipredator behaviour hinders the acquisition of predator expertise. Yet, many prey employ strategies such as fast-paced movements and rapid turning angles to avoid capture. When predators' capacities do not match these antipredator tactics, individuals with limited ability to develop the attributes needed for fast-paced hunting may struggle to improve over time. Prey can also improve their antipredator strategies through continued exposure to predators, thus gaining skill at avoiding predation (Kelley & Magurran, 2011; Lönnstedt et al., 2012; Turner et al., 2006). For instance, prey alter their activity patterns when predation risk increases (Wirsing et al., 2021). Animal reintroduction programs show that individuals trained to recognize predators display more antipredator behaviours and are 1.5 times more likely to survive than individuals that were never exposed to predators (Tetzlaff et al., 2019). Hence, encountering prey with greater skill at using antipredator tactics and avoiding predation may impair expertise acquisition in predators. To our knowledge, the relationship between prey antipredator behaviour and the acquisition of expertise in human and nonhuman predators is poorly studied, representing a significant gap in our understanding of predator-prey interactions.

A recurring challenge impeding research on predator-prey behavioural interactions is the need to collect simultaneous data on both predator and prey across successive interactions. Here we mitigate these challenges by using *Dead by Daylight* as our study system, a videogame where four prey players must forage for resources while avoiding predation by a fifth player. *Dead by Daylight* allows us to test ecological hypotheses by providing controlled virtual environments where interactions among thousands of individuals are captured in real time (see Montiglio, Fraser Franco, and Santostefano (2025) for a review). In this game, the predator population comprises individuals

that either ambush or hunt at high speeds (i.e., mean movement speed along an ambush-cursorial continuum of tactics), and their success is driven by the movement of the prey (Fraser Franco et al., 2022). Prey can increase their chances of survival by cooperating and moving quickly to escape predators (Céré et al., 2021; Fraser Franco et al., 2022; Santostefano et al., 2024). Moreover, individuals in *Dead by Daylight* and other virtual systems display realistic behaviours in response to the fear of predation, such as freezing (M.F.F., personal observations), hiding (Santostefano et al., 2024), or increased vigilance (Beauchamp, 2020). These observations outline how ecological phenomena can emerge from human interactions in virtual systems with fixed rules (Brosnan & Postma, 2017; Kasumovic et al., 2017). Video games also generate large volumes of data on thousands of interacting players throughout their lifetime in the game under realistic, controlled, and repeatable ecological scenarios. Hence, *Dead by Daylight* allows us to tackle fundamental questions about the role of antipredator behaviour and experience during predator-prey interactions.

In this study, we assess how predator expertise emerges over repeated encounters with prey using data from players in *Dead by Daylight*. We quantify expertise acquisition as the relationship between hunting success (i.e., prey capture) and repeated experience (i.e., cumulated matches). Predators should display a monotonic increase in hunting success over time up to some point at which it will stabilize (Dukas, 2019). In *Dead by Daylight*, a ranking system indicates whether prey are skilled at repeatedly avoiding detection, collecting resources, and escaping predators from one match to the next (see Methods for details). Hence, prey with more skill should display improved antipredator behaviour, and we expect that prey with greater predator-avoidance skills will move at faster speeds and cover more space in the virtual environment. We hypothesize that prey movement behaviour will influence predator expertise acquisition. This should result in differences among individuals in the rate at which they acquire expertise as well as in their maximum hunting success. We predict that predators that encounter faster prey will have a lower rate of acquisition and a reduced maximum hunting success.

3.3 Materials and methods

3.3.1 Study system

Dead by Daylight is a survival asymmetric (i.e., gameplay mechanics differ between two groups) multiplayer online game developed by Behaviour Interactive Inc. (Montreal, Canada), in which

players can play either as a predator or prey. Every match includes only one predator and four prey. The predator's objective is to hunt and capture the prey, and the prey's objective 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. A skill-based matchmaking algorithm determines the composition of the predator and prey group in a match. 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.

Before the start of a match, players (predator or prey) can choose an avatar with unique abilities that encourage specific play styles (e.g. bold vs cautious prey, or ambush vs roaming predator). During our study period, the game offered 23 predator avatars. The virtual environments comprise 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 these environments (Fraser Franco et al., 2022). There were 35 virtual game environments available for play during the study period. Details on the basic characteristics of predator avatars are available at <https://deadbydaylight.fandom.com/wiki/Killers>. Details on the size and structure of the different virtual environments are available at <https://deadbydaylight.fandom.com/wiki/Realms>. We provide a safe copy of those webpages for consultation on our GitHub repository (<https://github.com/quantitative-ecologist/predator-expertise>).

3.3.2 Data collection

Behaviour Interactive Inc. provided data that spanned six months of gameplay recorded for every player from 2020-12-01 to 2021-06-01 (game builds 4.4.0 to 4.7.2). We analyzed only matches where players did not know each other and were unable to communicate using voice-recording devices. We filtered any matches where players were inactive, such as when mean distances travelled per second (i.e., speed) were equal to, or very close to, zero. Moreover, we used our knowledge of the game to remove any matches where players were potentially hacking, or not playing the game as intended.

Our study population comprised 253 players who played at least 300 matches. We monitored all their matches from the first to a maximum of 500 matches, with a total record of 100,412 matches

overall. The predator-players' experience in our population sample varied between 301 and 500 matches played. These matches lasted between 3 and 70 min (mean = 11 min). We recognize that we could have introduced a bias by retaining only those individuals, as they might already be seasoned video game enthusiasts and exhibit expert-level performance in their early matches in *Dead by Daylight*. Thus, we tested sample bias by comparing the results from our dataset to those from a random sample of players who played either 20 to 50 matches, 51 to 100 matches, or 101 to 300 matches during the same timeframe. We then took the first 20 matches played by these players, including those from our population sample, and compared their mean hunting success using a Bayesian hierarchical linear model. We found that all three groups of players had very similar success as the predator in their first 20 matches, compared with those used as our focal sample (Annexe B: Table B.1 and Figure B.1), giving us confidence that we did not introduce a significant sampling bias.

We collected the following information for every match in our population sample: the player's anonymous ID, the predator player's hunting success, the predator player's cumulated experience, and the mean rank, speed, and space coverage of the group of prey that the predator player encountered. We defined hunting success as the number of prey consumed during the match (min = 0, max = 4). We defined the predator's cumulative experience as the number of matches played as the predator prior to the match being monitored. For example, the first match of a player would have a cumulative experience value of 0, while the tenth match would have a value of 9.

We used the mean rank of the prey as a proxy of their predator-avoidance skill. Player ranks vary between 1 and 20, with a rank of 1 indicating the highest skill. The ranking system in *Dead by Daylight* was implemented by the company to pair players in a match based on their skill. The skill of a player increases based on their performance from match to match. While the ranking system approximates prey skill, it was the most readily available metric we could use to determine the prey group's skill, as we did not have access to the prey's prior matches. In addition, the pairing system is subject to variation depending on factors such as player availability, which can result in predator-prey groups with unbalanced skill, allowing us to evaluate the effect of the prey's skill on predator success. All the relevant information on ranks is available on this webpage <https://deadbydaylight.fandom.com/wiki/Rank>, of which we keep a persistent copy on our GitHub repository (<https://github.com/quantitative-ecologist/predator-expertise>). In each match, we

measured the prey's rank as the mean rank of the four individual prey (mean = 8.74 ± 4.12), and the prey's speed as the mean travel speed of the four individual prey in a match (mean = 2.40 ± 0.32 m/s). Lastly, the prey space coverage represents the number of unique 16x16 tiles entered per second by the predator in a grid that covers the whole virtual environment (mean = 0.04 ± 0.01 tile visits).

3.3.3 Data analyses

3.3.3.1 Model specification : predator expertise

We quantified how predators developed their expertise using Bayesian generalized asymptotic mixed models (for reference, see Clarke & Hunt, 2025). Asymptotic regression models allow one to model how a measure of performance or a behaviour changes over time, as both tend to follow a monotonic increase or decrease towards an asymptote (Clarke & Hunt, 2025). Here, we modeled changes in hunting success, which we defined as:

$$y_i | n_i \sim \text{BetaBinomial}(n_i, \mu_i, \phi)$$

where y_i is the number of prey captured out of n_i prey available (four), μ_i is the expected probability of hunting success for observation i , and ϕ is the precision parameter controlling overdispersion.

We fitted three different models (Table 3.1) that predicted the expected probability of capturing the four prey μ_i as a function of experience. All models followed the same basic structure defined as:

$$\text{logit}(\mu_i) = a_j - (a_j - b_j) \times \exp(-\exp(c_j) \times x_i) + \mathbf{Z}_i^T \boldsymbol{\beta}$$

where x_i is the cumulative experience of the predator and j indexes the predator player identity. The asymptotic parameters a , b , and c , represent the asymptote (maximum hunting success), the initial value (initial success), and the rate of gain in expertise (on the log scale), respectively. The term $\mathbf{Z}_i \boldsymbol{\beta}$ represents covariates used as controls, which were the game duration and the prey group's average rank.

We allowed the asymptotic paramaters to vary among predator players in all models. To test if prey behaviour shaped the acquisition of predator expertise, asymptotic parameters also vary as a function of prey behaviour in models II and III (Table 3.1). We defined each parameter as:

$$\begin{aligned} a_j &= \alpha_a + \mathbf{W}_{a,i}^T \boldsymbol{\gamma}_a + u_{a,j} \\ b_j &= \alpha_b + u_{b,j} \\ c_j &= \alpha_c + \mathbf{W}_{c,i}^T \boldsymbol{\gamma}_c + u_{c,j} \end{aligned}$$

where α_k is the population-level intercept for parameter $k \in \{a, b, c\}$, $\mathbf{W}_{k,i}$ is a vector of prey behaviour covariates affecting asymptotic parameter k with corresponding coefficients $\boldsymbol{\gamma}_k$, and $u_{k,j}$ is a predator-specific random intercept. The prey behaviours included in $\mathbf{W}$ for models II and III are described in Table 3.1.

We assumed that the random intercepts for the predator identity followed a multivariate Gaussian distribution:

$$\begin{pmatrix} u_{a,j} \\ u_{b,j} \\ u_{c,j} \end{pmatrix} \sim \text{MVN}(\mathbf{0}, \Sigma)$$

where Σ is a 3x3 variance-covariance matrix of the predator identity random effects for the asymptotic model parameters. This covariance structure allowed us to estimate correlations among individual differences in initial success, rate of gain, and maximum hunting success. With this, we can test if predators that were initially successful also had higher rates of gain in expertise and higher maximum hunting success.

Table 3.1 Summary of the three generalized asymptotic mixed models fitted to test how prey behaviour shapes predator expertise acquisition. All models fit a population-level expertise trend and include a predator identity random effect on the asymptotic parameters (a , b , c). We included prey behaviours as covariates only on parameters a and c .

Model	Covariates y	Covariates parameter a	Covariates parameter c	Hypothesis
I	game duration, prey rank	—	—	The predator population acquires expertise up to an optimum
II	game duration, prey rank	prey speed	prey speed	Prey speed affects population and individual-level expertise acquisition
III	game duration, prey rank	prey speed, prey space covered	prey speed, prey space covered	Prey speed and space coverage affects population and individual-level expertise acquisition

We defined informative priors for the asymptotic parameter's intercepts to reflect biologically meaningful expectations. We centered the upper asymptote (a) at 1.39 (logit scale, corresponding to 80% hunting success) with $SD = 0.7$, while the initial value (b) was centered at -1.10 (logit scale, 25% hunting success) with $SD = 0.7$. We set a $Normal(-5.5, 1)$ prior on the rate parameter (c), constraining it to plausible rates of improvement over the observed experience range. We used mildly informative priors for most effect sizes and variance components. The effects of prey speed and space use on parameters a and c received $Normal(-0.3, 0.3)$ priors, reflecting a weak expectation of negative effects. Similarly, we applied a $Normal(1, 0.5)$ prior on the game duration and a $Normal(0.5, 0.5)$ prior on the prey rank. Lastly, we applied a $Normal(0, 1)$ prior truncated at zero (half-normal) on the random effect standard deviation parameters, an $LKJ(2)$ prior on the correlation matrix, and a $Normal(\log(2), 0.5)$ prior on the shape parameter.

We tested the hypothesis that antipredator behaviour impairs the acquisition of predator expertise at the population level by comparing the mean asymptotic parameter values describing the global trends of each model (Figure 3.1). This allowed us evaluate if prey behaviour affected the acquisition of expertise at the population level. We tested the hypothesis that antipredator behaviour generates differences among predators in expertise acquisition by 1) assessing the relationship between the parameter values of a , b , and c , and prey behaviour, and 2) by comparing

the individual-level standard deviation parameters of a , b , and c . Specifically, we compared the posterior distributions of standard deviations for the random intercepts (i.e., mean differences among predators) among the three models for parameters a , b , and c (Figure 3.4). Lastly, we computed the widely applicable information criterion (WAIC) to obtain the expected pointwise density of each model, a measure of predictive accuracy allowing us to determine which model was best at predicting the data (Pironen & Vehtari, 2017; Vehtari et al., 2017; Watanabe, 2010).

3.3.3.2 Model specification : prey antipredator behaviour

To test the hypothesis that prey speed and space coverage increases with prey skill, we fitted Bayesian mixed-effects regression models estimating the relationship between 1) prey speed and the standardized prey rank and 2) prey space coverage and the standardized prey rank. In both models, we controlled for the game duration, using it as a linear covariate, and included the predator identity as a random effect.

We used weakly informative Gaussian priors on the slopes of the game duration ($Normal(0, 0.5)$) and weakly informative negative Gaussian priors on the slopes of the prey rank ($Normal(-0.3, 1)$) because prey of greater skill (i.e., rank 1 is the highest skill) should move faster and cover more space in the environment. We used weakly informative Gaussian priors on the intercepts of prey speed ($Normal(2, 0.5)$) and rate of space coverage ($Normal(\log(0.05), 0.5)$) as we assumed that prey should move at around two meters per second and cover at least 0.05 tiles per second in the virtual environment. Lastly, we employed Gaussian priors truncated at 0 ($Normal(0, 0.5)$) on the standard deviation and sigma parameters in both models.

3.3.3.3 Parameter sampling settings

We parameterised asymptotic model I to run four chains of 7,500 iterations each, discarding the first 1,500 iterations of each chain as warm-up, and sampling one parameter value per two iterations thereafter. We applied the same procedure for models II and III, but using 10,500 iterations and discarding the first 2,500 iterations of each chain as warm-up. All three models yielded 16,000 posterior samples per parameter. Similarly, the linear models ran four chains of 1500 iterations each, sampling a parameter value at every iteration, and discarding the first 500 iterations. We thus obtained 4000 posterior samples per parameter in each model. We assessed the convergence of the

chains using trace plots, R-hat diagnostics with a threshold set between 1.00 and 1.02, 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.

We fitted all models on Fir, a remote computer cluster (<https://docs.alliancecan.ca/wiki/Fir>) hosted by the Digital Research Alliance of Canada, using R (version 4.4.0). Model fitting was performed via Hamiltonian Monte Carlo (HMC) sampling with the “brms” package version 2.22.12 (Bürkner, 2017), an R front-end for the STAN software (Stan Development Team 2023). We used “cmdstanr” version 0.9.0 (Gabry & Češnovar, 2021) as the computational back-end for parameter estimation, with CmdStan installation version 2.36.0. We provide a detailed workflow for reproducing our results in the following GitHub repository (<https://github.com/quantitative-ecologist/predator-expertise>).

3.4 Results

3.4.1 Acquisition of expertise at the population level

As expected, the predator population’s expertise increased steadily before reaching a plateau. (Figure 3.1). Without accounting for any prey behaviour (model I), the population’s initial hunting success was at 0.21 (89% CI: [0.19, 0.23]), indicating a 20% chance of capturing the four prey. The rate of gain in expertise was of 0.01 (89% CI: [0.01, 0.01]) per match. Predators acquired expertise rapidly in the first 150 matches, reaching 75% of the population’s maximum hunting success. The population’s maximum hunting success was of 0.68 (89% CI: [0.65, 0.71]) probability of capturing the four prey.

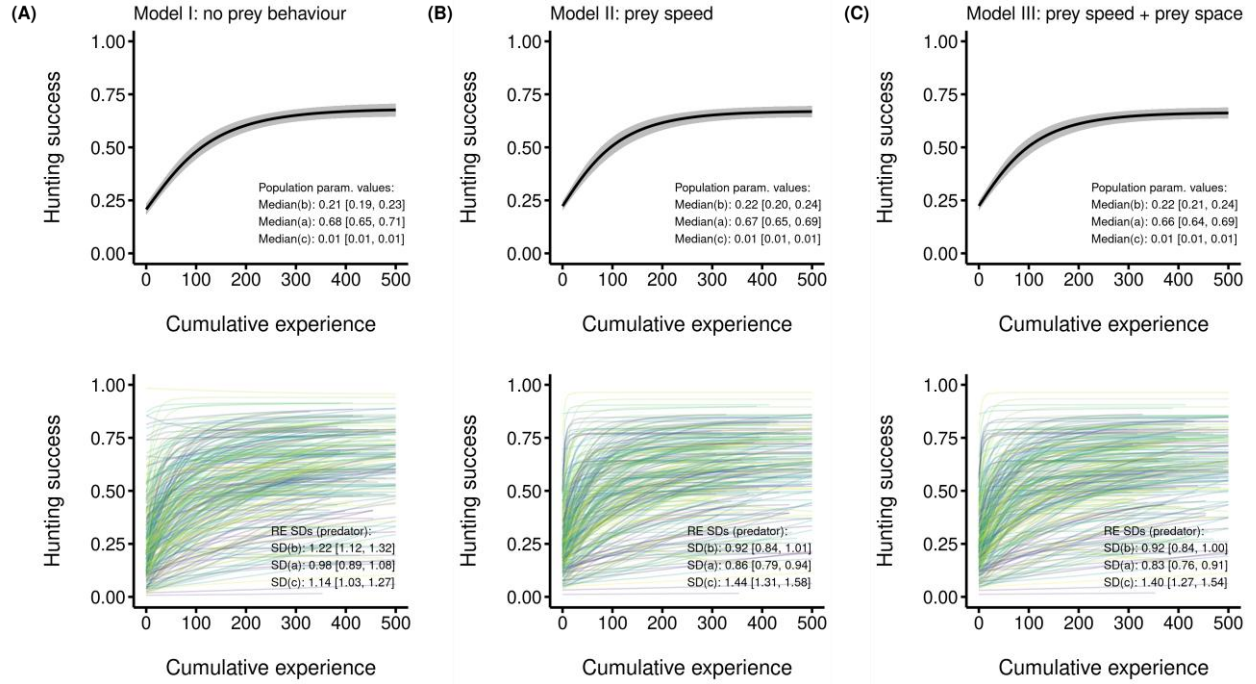


Figure 3.1 Median posterior predictions of the acquisition of predator hunting expertise. The predators' hunting success (i.e., the probability of consuming the four prey) is on the y-axis, and the predators' cumulative experience (i.e., the number of matches played before each observation) is on the x-axis. The results of model I (no control for prey behaviour), model II (control for prey speed), and model III (control for prey speed and space covered) are presented in panels, A, B, and C respectively. Panels on the upper row show the predicted acquisition of expertise for the average individual alongside the median posterior values of the asymptotic model parameters. Panels on the lower row show among-individual differences in the acquisition of expertise, with each curve representing an individual predator. The median posterior standard deviations of the individual predator random effect are shown. All models displayed include the game duration and the prey rank as covariates, which are held constant at their mean values.

We did not find evidence that prey behaviour affected the predator population's gain in expertise. Controlling for prey speed and space coverage did not qualitatively alter the form of the relationship between success and experience at the population level (Figure 3.1). Yet, model III, which included all prey features, was the best at predicting the acquisition of predator expertise (Table 3.2).

Table 3.2 WAIC comparison results for the three asymptotic mixed models estimating the relationship between hunting success (y) and predator experience (x). All models include game duration and prey rank as covariates. Models differ in the prey behavioural covariates included on asymptotic parameters. The metric 'elpd' refers to the expected log pointwise predictive density, which is the expected log probability of observing new data. Higher values indicate greater predictive accuracy.

Model	elpd WAIC (SE)	elpd difference (SE)
Model III: prey speed and prey space covered	-136632.9 (202.4)	0.0 (0.0)
Model II: prey speed	-136722.4 (201.9)	-89.5 (18.7)
Model I: no prey features	-141847.9 (183.4)	-5215.0 (109.9)

3.4.2 Prey skill and antipredator behaviour

Prey groups composed of individuals with greater skill moved faster than those composed of individuals with lower skill (Figure 3.2 a). In contrast, there was no change in prey space coverage with increasing skill (Figure 3.2 b). We found strong evidence that hunting success declined when predators pursued faster prey (Annexe B: Figure B.2 a). However, predators were slightly more successful when hunting prey that covered space at a faster rate (Annexe B: Figure B.2 b). Predators were also less successful when hunting prey of greater skill (i.e. lower rank values, Annexe B: Figure B.2 c).

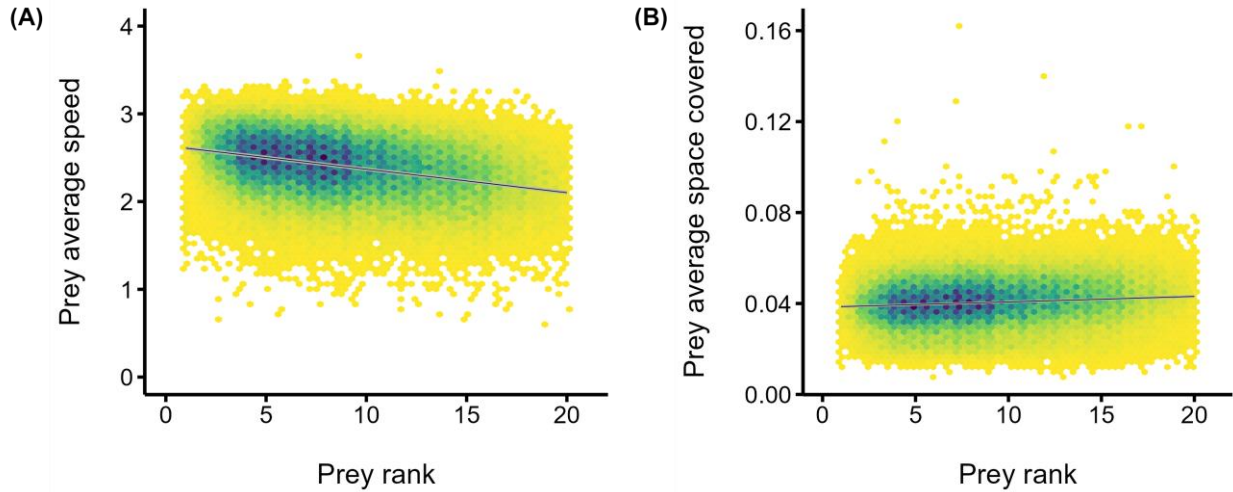


Figure 3.2 Median posterior predictions of the relationship between prey behaviour and prey skill. The average behaviour of the prey group is on the y-axis, and the average rank of the prey group is on the x-axis. The colour gradient showcases the density of observations, with lighter colours indicating lower densities, and darker colours indicating higher densities of observations. The black line represents the median posterior predictions, and the gray bands are the 89% compatibility intervals. Lower rank values indicate that the prey group is more skilled, while higher values indicate that the prey are less skilled. Panel A is for the linear model of prey speed, and panel B is for the linear model of prey space coverage.

3.4.3 Acquisition of expertise at the individual level

Our results show that individual predators displayed substantial differences in their acquisition of expertise (Figure 3.1 a-c). However, we did not detect an effect of prey behaviour on individual rates of gain in expertise (Figure 3.3). There was also no effect of prey space coverage on the predator's maximum hunting success (Figure 3.3). Yet, there was a marginal negative effect of prey speed on the maximum hunting success, suggesting that predators that encountered faster prey over time had a lower maximum hunting success (Figure 3.3).

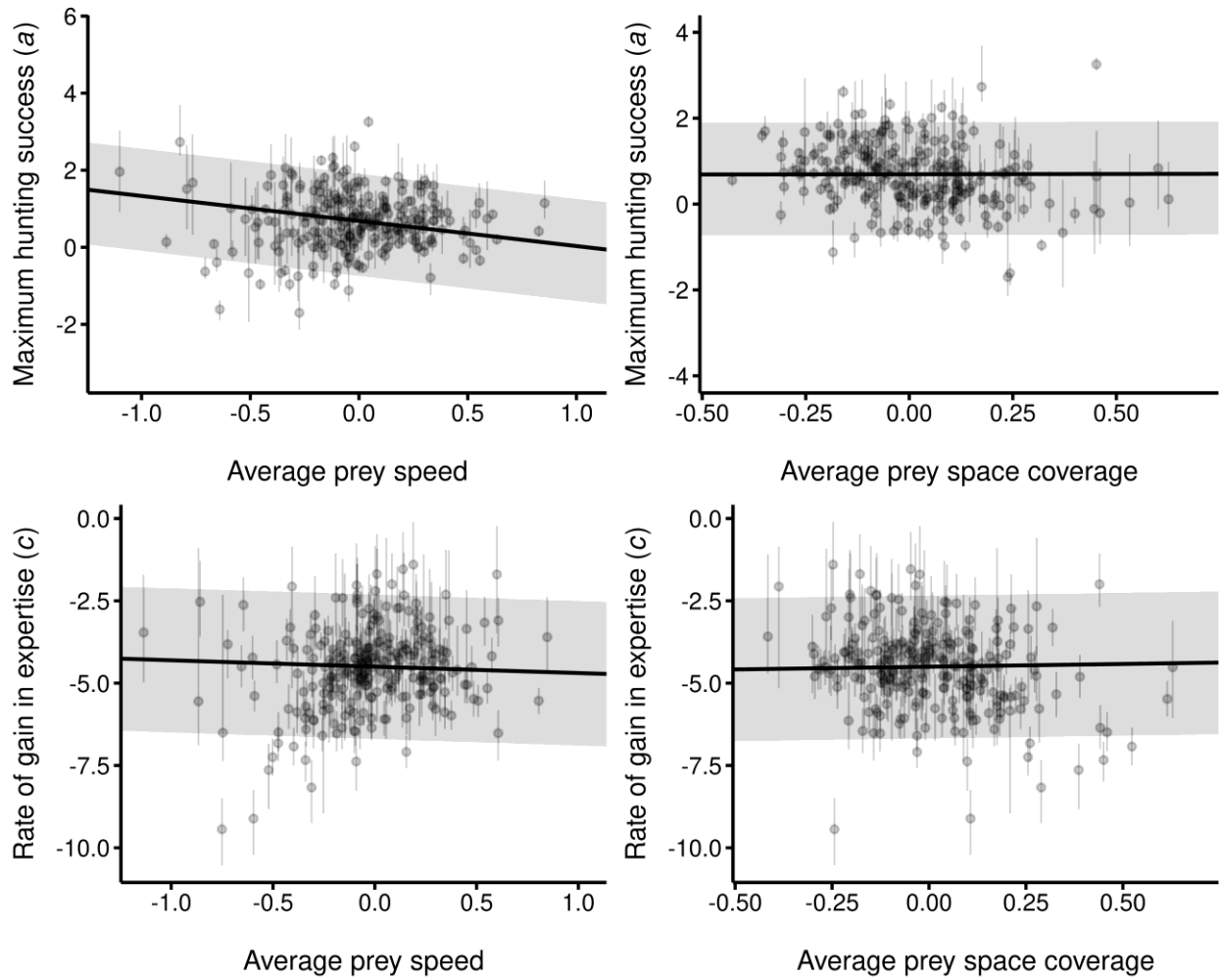


Figure 3.3 Predicted relationships between the asymptotic model parameters describing expertise acquisition and prey behaviour. Individual observations are the posterior median parameter values for each predator. The black line represents the median posterior predictions, and the gray band the 89% compatibility intervals. (Upper left) Maximum hunting success (a) as a function of the average speed of the prey group. (Upper right) Maximum hunting success (a) as a function of the average space coverage of the prey group. (Lower left) Rate of gain in expertise (c) as a function of the average speed of the prey group. (Lower right) Rate of gain in expertise (c) as a function of the average space coverage of the prey group. The predictions are from model III.

The standard deviation of the rate of gain in expertise in model I (median model I = 1.14, 89% CI: [1.03, 1.27]) was smaller than those of model II and model III (Figure 3.4). Differences in the rate of expertise acquisition among predators were similar in model II and model III (median model II = 1.44, 89% CI: [1.31, 1.58] vs median model III = 1.40, 89% CI: [1.27, 1.54]), with the posterior distributions of the standard deviations showing nearly complete overlap (Figure 3.4). Hence,

including prey space coverage did not explain additional variation in the rate of expertise acquisition among predators.

We found weak evidence that the standard deviation of the maximum hunting success of model I (median model I = 0.98, 89% CI: [0.89, 1.08]) was slightly greater than that of model II and model III (Figure 3.4). Compared to model II, among-individual differences in maximum hunting success remained unchanged after accounting for prey space coverage (median model II = 0.86, 89% CI: [0.79, 0.94] vs median model III = 0.83, 89% CI: [0.76, 0.91]).

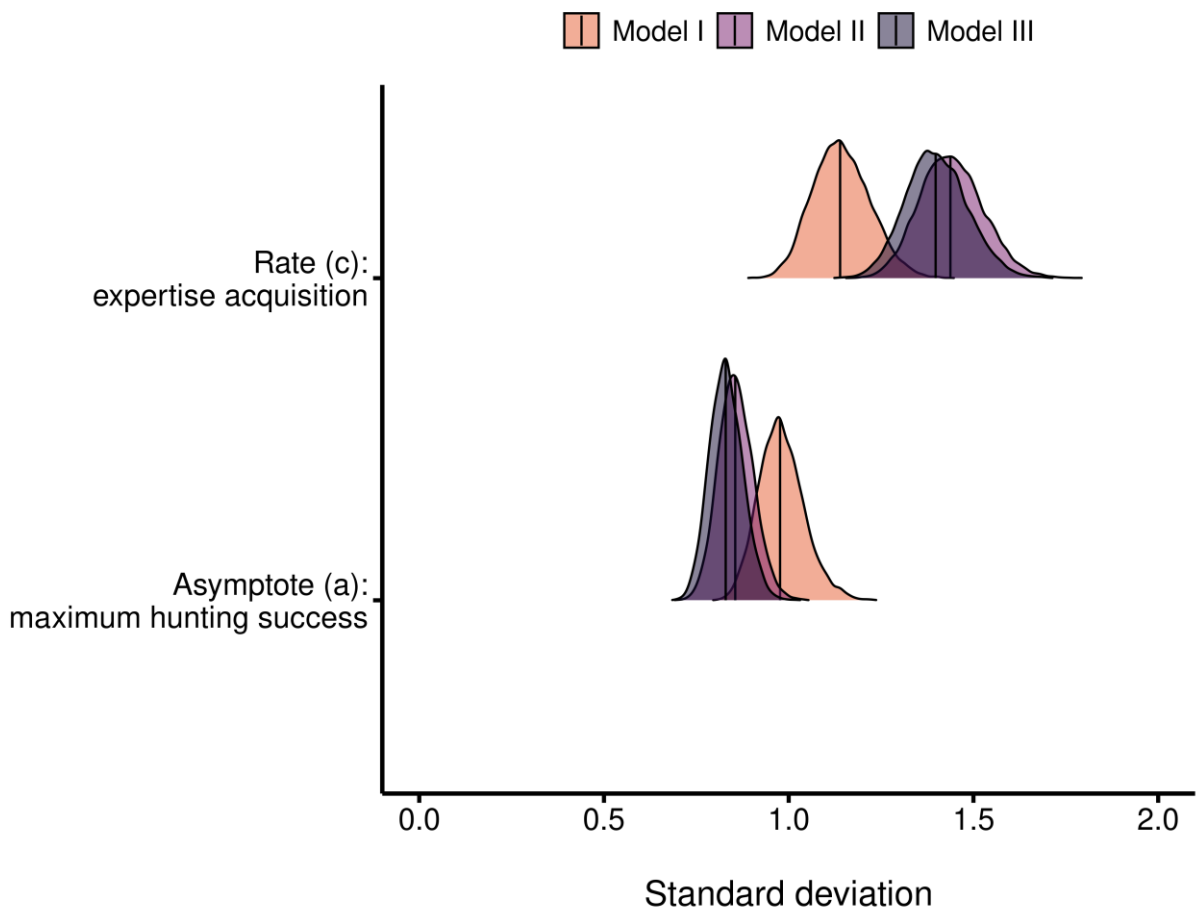


Figure 3.4 Posterior distributions of individual random effect standard deviations for asymptotic parameters. The asymptotic parameters are displayed on the y-axis, and their standard deviation values are displayed on the x-axis. The vertical lines are the medians of the posterior distributions. The light pink (lightest) distributions are for the model accounting only for the game duration and prey rank (model I), the light purple (lighter) distributions are for the model accounting for game duration and the prey rank and prey speed on asymptotic parameters (model II), and the dark purple (darker) distributions are for the model accounting for the game duration, the prey rank and all prey behaviours on asymptotic parameters (model III).

Individuals that had a low initial hunting success ended up with a lower maximum hunting success (Figure 3.5). In addition, individuals with the greatest maximum hunting success were those with a lower rate of gain in expertise (Figure 3.5). However, this relationship was decoupled when we accounted for prey behaviour in the model (cor: -.002, 89% CI: [-0.16, 0.12]), indicating that prey behaviour influenced the relationship between the maximum hunting success and the rate of gain in expertise. Lastly, there was no apparent relationship between the individual rates of gain in expertise and the maximum hunting success (Figure 3.5).

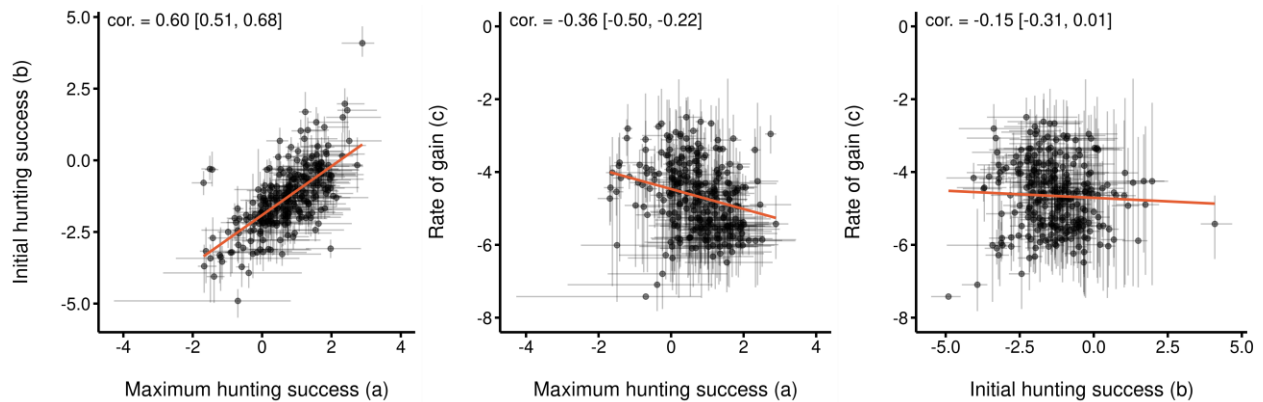


Figure 3.5 Among-individual correlations between the asymptotic model parameters. The correlation values reported are the median posterior correlations with their 89% interval. Each point represents the median posterior parameter value with the 89% credible interval for a single predator player. The left panel shows the relationship between the initial hunting success (b) and the maximum hunting success (a). The center panel shows the relationship between the rate of gain in expertise (c) and the maximum hunting success (a). The left panel shows the relationship between the rate of gain in expertise (c) and the initial hunting success (b). The correlations reported in this figure come from the model that does not account for prey behaviour (Model I).

3.5 Discussion

Using a virtual predator-prey system in which we monitored interactions across repeated encounters, we tested the hypothesis that prey behaviour modulates the acquisition of predator hunting expertise. We show that, on average, predators are expected to increase their hunting success with experience when hunting prey of average skill. Overall, prey behaviour did not influence the rate of expertise acquisition. However, predators that encountered slower prey during their experience achieved greater maximum hunting success, most likely because faster prey are more difficult to capture. This is supported by our analysis, which shows that prey with greater skill moved faster. The extent of the variation in expertise acquisition among individuals was

shaped by the prey's skill and the game pairing system, as observed by comparing the posterior distributions of individual-level parameters among models with and without the prey behaviour (Figure 4). Predators displayed important differences in expertise acquisition that were apparent only after accounting for prey skill. Accounting for prey behaviour further revealed variation in expertise acquisition that was masked by the pairing system. While we cannot establish whether prey behaviour causally influenced expertise acquisition due to this game feature, our observations suggest that prey behaviour may play a role in shaping individual differences in expertise acquisition by limiting the maximum hunting success achievable.

The matchmaking algorithm in *Dead by Daylight* is intended to pair players with similar skill levels within matches: failing to account for it results in predators maintaining a near constant hunting success over repeated encounters. Controlling for the prey's skill (i.e., prey rank) in our models reveals an asymptotic relationship between hunting success and experience, wherein initial gains in success were significant (expertise increased rapidly from the first match up to 150 matches) and gradually stabilized as experience accumulated. This pattern of expertise acquisition is consistent with empirical studies in both humans and nonhuman animals (reviewed in Dukas, 2019), and could be explained by improvements in foraging performance. For example, predators may have improved at locating prey, learned how to navigate the environment, or developed increased dexterity at handling prey (Dukas, 2008; Reid et al., 2010). Our observations also provide clues on how expertise acquisition may change given the difficulty of the task. We observed that experienced predators could achieve greater long term success if they were not matched to highly skilled prey, or have a slower gain in expertise if the skill of the prey encountered was consistently higher (Annexe B: Figure B.3). This is further supported by our results showing lower average hunting success against prey of greater skill (Annexe B: Figure B.2). Whether this is due to the prey interfering with cognitive processes that limit improvements in foraging performance remains to be tested.

Our findings suggest a marginal effect of prey behaviour in shaping expertise acquisition in predators. We found that the maximum hunting success was slightly lower in predators that mostly encountered faster prey. We previously showed in *Dead by Daylight* that faster movement is effective for prey to evade predation (Fraser Franco et al., 2022), a pattern observed in studies involving other animals (Kelley & Magurran, 2011; Martin et al., 2022; Walker et al., 2005). Prey

of greater skill increasingly relied on faster movement, and predators were less successful against skillful prey, suggesting that the effect of prey skill on the gain in expertise by predators was in part mediated by changes in prey behaviour following previous encounters (Tetzlaff et al., 2019). Different mechanisms may explain why faster prey were more difficult to hunt. For example, predators have limited attention spans that influence prey choice and the formation of search images when they need to focus on hunting multiple prey simultaneously (Dukas & Kamil, 2001; Troscianko et al., 2018). If the prey group was consistently moving faster in a coordinated fashion, then it would be difficult for predators to focus on a single prey while others rapidly progress on collecting resources (Ioannou et al., 2012). Rapid prey movements are often accompanied by unpredictability, which has been shown to hinder pursuit and increase the likelihood of predators abandoning the chase (Herbert-Read et al., 2017; Jones et al., 2011; Richardson et al., 2018). Moreover, chasing faster prey demands specialized cognitive abilities and coordination that are energetically costly (Kelley & Magurran, 2011). Hence, there may be neurological constraints that limit a predator's ability to hunt multiple fast-moving prey simultaneously. Parallel observations have been outlined in studies of prey camouflage strategies. Troscianko, Skelhorn, and Stevens (2018) showed in a human computer experiment that disruptive camouflage was effective at preventing the acquisition of expertise by interfering with search image formation. Hence, our analyses provide evidence that prey movement behaviour could mediate the acquisition of hunting expertise by limiting long-term hunting success in predators. It is worth noting that our models only capture linear effects on expertise acquisition; however, the distribution of individual rates of expertise acquisition suggests potential nonlinear dynamics that warrant further investigation, such as predators improving optimally at certain prey speed levels (Figure 3.3).

After accounting for prey behaviour, individual predators still displayed important differences in the acquisition of expertise, indicating that they varied in their capacity to improve over time. This implies that other proximal or ecological mechanisms may be at play. For example, longer time intervals between hunting events are hypothesized to hinder or delay the acquisition of expertise due to information loss (Endler, 1991; Wooster et al., 2023; Wright et al., 2022). A predator that played 300 matches within six months might forget critical information related to prey detection or escape patterns compared to one that played 300 matches within six weeks. Alternatively, predators may also shape their own expertise via their hunting tactic. Faster hunters may push their

prey to move faster or to display altruistic behaviours, which, in turn, may hinder their own expertise acquisition due to the increased difficulty of hunting such prey (Céré et al., 2024; Fraser Franco et al., 2022). However, integrating the effects of proximal mechanisms, the predator's tactics, and the prey's behaviour into a unified framework to investigate expertise acquisition remains challenging, due to computational constraints and limitations in current modeling approaches.

Interestingly, individuals who had a lower initial hunting success ended up with a lower maximum hunting success, and those with a lower rate of gain achieved greater maximum hunting success. One possible explanation is that a “slow and steady” learning strategy was beneficial in the long term. Slow learners are expected to be more sensitive to their environment in early learning phases, allowing them to gather more information and be less prone to errors in decision-making over time (Sih & Del Giudice, 2012). Empirical studies show that slow learners tend to be more explorative and flexible when their environment changes, while fast learners tend to be more rigid to changes in their environment and more prone to taking risks (Coppens et al., 2010; Mazza et al., 2019; Moreira et al., 2004). As a result, predators that gained expertise at a slower rate may have explored with different strategies before finding the optimal tactic to hunt their prey, which ultimately paid off. However, an alternative explanation is that the nature of our hunting success variable (i.e., a maximum of four prey captures per game) may have produced a ceiling effect that reinforced the observed negative correlation between rates of gain and the maximum hunting success. Indeed, we can see in Figure 3.1 that a portion of predators with a greater baseline hunting success maintained an elevated hunting success across their experience, which would necessarily result in their rate being lower. However, this appears to be the case only for a small subset of individuals. In addition, we can see that individuals who started at a lower hunting success did not end up with higher maximum hunting success, suggesting that the ecological and cognitive mechanisms discussed above, such as encountering faster prey, are more likely to explain these patterns.

One criticism of using videogames to study behaviour is that neither the predator's nor the prey player's life is at stake in the game. This may partly explain the observed persistence of differences among individuals in expertise acquisition. Hence, the gain in expertise may have been driven by the players' motivation to win rather than a “real” need to survive. For instance, some players may experiment with the game out of boredom, which could also influence how expertise is honed in

this particular system. Yet, motivation and perseverance have been outlined as core components that increase the gain in expertise in human and nonhuman hunters (Dukas, 2019). Thus, we believe that failing to account for motivation is a limitation of our study rather than the use of videogames to study ecological interactions.

We provide partial evidence supporting the hypothesis that prey antipredator behaviour can drive the acquisition of hunting expertise using a human predator population in the game *Dead by Daylight*. The effect of prey movement behaviour on expertise acquisition was observed only on the maximum hunting success. While there were important differences among individuals in expertise acquisition, we did not find conclusive evidence that they were mediated by the prey's movement behaviour. Future analyses should incorporate cognitive, physical and behavioural attributes of the prey to assess their influence on the acquisition of predator expertise, which may reveal important insights into the eco-evolutionary dynamics of predator-prey interactions. Our demonstration of how prey antipredator behaviour can mediate the acquisition of hunting expertise adds to a growing body of research showing how virtual systems can be used to test hypotheses on ecological interactions (Beauchamp, 2020; Céré et al., 2021; Fraser Franco et al., 2022; Lymbery et al., 2023; Santostefano et al., 2024). We hope that this will inspire more collaborations between scientists and the videogame industry to tackle fundamental questions in ecology.

3.6 Acknowledgements

We would like to thank Behaviour Interactive Inc. for our collaboration and for their contribution in providing their data to advance ecological sciences. We would also like to thank members of the CSBQ-UQAM and Julien Martin's laboratory at UOttawa for their comments on earlier versions of this study. This work was supported by an NSERC doctoral scholarship (569716) awarded to Maxime Fraser Franco. We declare no conflict of interest.

3.7 Data and code availability

The data and code are fully available on this GitHub repository: <https://github.com/quantitative-ecologist/predator-expertise>.

CHAPITRE 4:

INDIVIDUAL FORAGING SPECIALISATION AND SUCCESS CHANGE ACROSS EXPERIENCE IN A VIRTUAL PREDATOR-PREY SYSTEM

Fraser Franco, M., Santostefano, F., Martin, J. G. A., Kelly, C. D., Montiglio, P.-O.

Ce chapitre est disponible en prépublication : Fraser Franco, M., Santostefano, F., Martin, J. G. A., Kelly, C. D., Montiglio, P.-O. (2024). Individual foraging specialisation and success change across experience in a virtual predator-prey system. *EcoEvoRxiv*. <https://doi.org/10.32942/X27H0Z>

4.1 Abstract

The capacity of predators to match their hunting tactics to their prey and to optimise their use of these tactics over successive encounters is hypothesised to promote individual foraging specialisation. Through this process, predators should be able to capture more prey. Yet, there are few empirical assessments linking past experience, foraging specialisation, 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 specialisation and success developed across repeated interactions with prey. We found that 68% of predators became either increasingly specialised 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.

4.2 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 (Patrick & Weimerskirch, 2014b; Toscano et al., 2016; Toscano & Griffen, 2014). The success of specialist

and generalist strategies depends on ecological factors: when resources are abundant, specialist hunters achieve greater success, while generalist hunters prevail under fluctuating conditions (R. A. Phillips et al., 2017; Terraube et al., 2011, 2014). 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 hypothesise that experience may underly associations between foraging specialisation and prey capture as predators learn and become efficient hunters through repeated encounters with their prey (Estes et al., 2003; R. A. Phillips et al., 2017; Woo et al., 2008). Yet, it remains challenging to monitor individual predators' experiences, limiting our ability to uncover how predators' 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 specialisation and its fitness consequences (Manlick et al., 2021; Patrick & Weimerskirch, 2014a; Santoro et al., 2019; van den Bosch et al., 2019). 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 specialise in a foraging tactic (e.g., always moving fast) if it enables them to consistently capture prey while learning to hunt in environments with predictable (or stable) resources (Dukas, 2019; Tinker et al., 2009). Such conditions favor specialist hunters, as they require less energy and time to search for, capture, and handle prey (Potier et al., 2015; Weimerskirch, 2007; Woo et al., 2008). For example, habitat specialisation 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 where resources fluctuate by learning to adjust their tactic to the prey that they encounter (Dall, 2010; Ishii & Shimada, 2010; Kelley & Magurran, 2011; Mathot et al., 2012; Stephens, 1993). Szopa-Comley and Ioannou (2022) showed that predatory blue acarids (*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 tactic to match the prey fluctuation regime they experience, both specialist and generalist hunters should achieve similar hunting success and coexist (R. A. 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 specialisation and 2) how the relationship between specialisation and foraging success changes over time. *Dead by Daylight* simulates predator-prey interactions across complex virtual environments, providing a system for testing ecological hypotheses about 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).

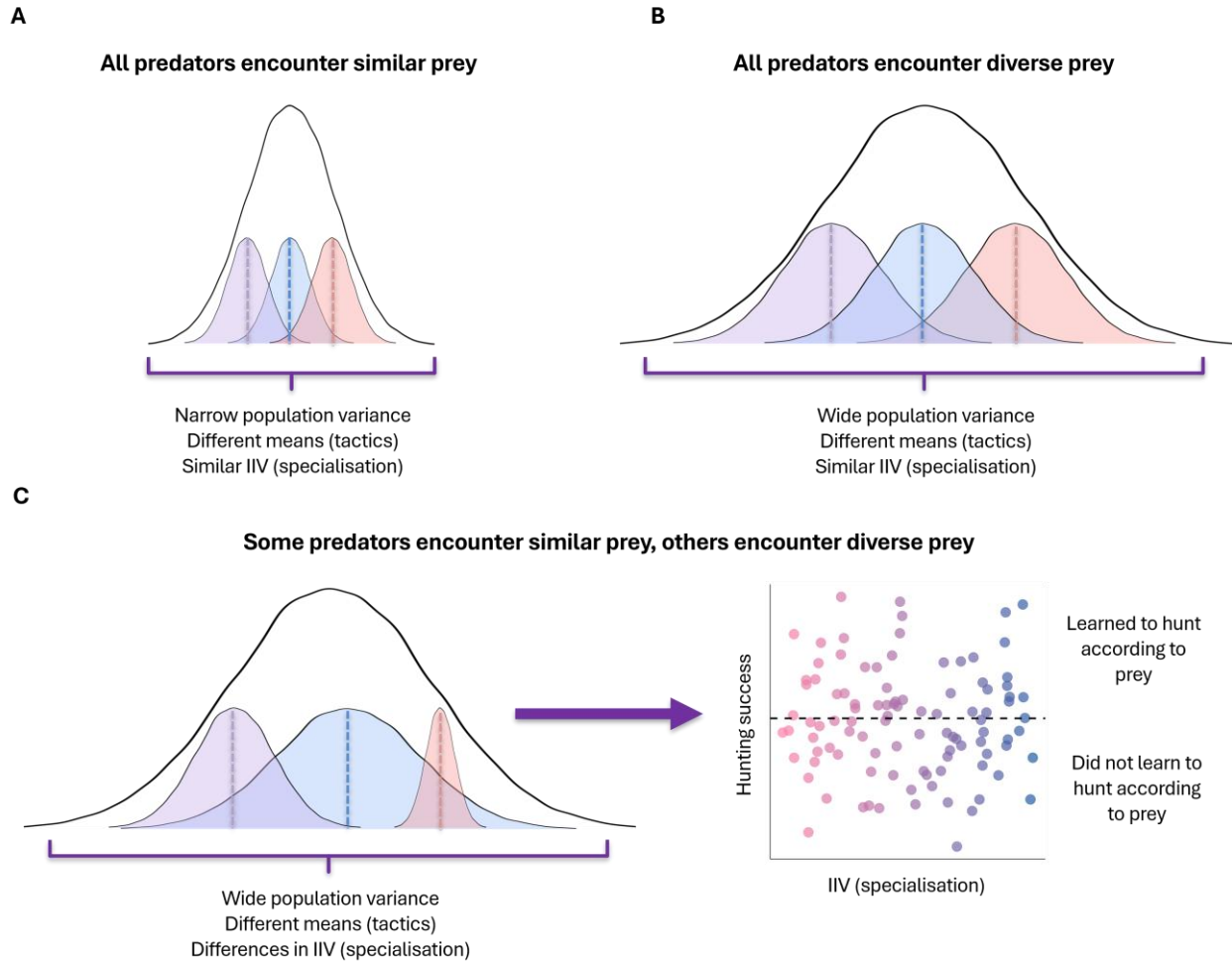


Figure 4.1 Hypothesis describing how prey-mediated individual foraging specialisation emerges over repeated interactions. Panels A and B display two scenarios with different outcomes at the population level, but similar outcomes at the individual level. A) all predators encounter prey with similar attributes (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 were predictable, they all display similar degrees of individual foraging specialisation, resulting in the population being specialised. 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 specialisation 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 specialisation. In this case, some individuals consistently encountered similar prey, and thus specialised, 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 did not, resulting in no differences between specialists and generalists.

To test the hypothesis that repeated interactions with prey can shape predator foraging specialisation, we analyze the movement speed of predators and their prey over time. To assess how foraging specialisation emerges throughout experience, we define the level of individual

foraging specialisation as the intra-individual variance (IIV) in movement speed across matches following the definition by Cleasby et al. (2015). Low IIV describes individual foraging specialisation (i.e., always using an ambush or cursorial tactic), whereas high IIV describes a general and flexible use of foraging tactics (i.e., plastic/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., individual-mean movement speed), which should be tuned to the mean speed of the prey that they encounter (Figure 4.1 a-b). Second, we predict that if most predators consistently encounter prey moving at similar speeds, then the population as a whole (i.e., all individuals) should specialise in moving at similar speeds, resulting in a narrow behavioural niche (Figure 4.1 a). In contrast, if most predators encounter groups of prey moving at varying speeds, they should become more flexible in their tactic use (i.e., generalists), adjusting their speed to the prey from one encounter to the next, resulting in a wider population variance in foraging behaviour (Figure 4.1 b). In both scenarios, differences among individuals in IIV across experience should be low (i.e., a similar degree of individual foraging specialisation, Figure 4.1 a-b). Alternatively, differences among individuals in foraging specialisation may emerge if they experience different interactions with their prey. In this case, predators that encountered prey moving at similar speeds across experiences should specialise in 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 individual differences in IIV (Figure 4.1 c). If we detect such prey-dependent fine-tuning with experience, then specialist and generalist hunters should achieve similar hunting success, resulting in no apparent relationship between foraging specialisation and prey capture (Figure 4.1 c).

4.3 Materials and methods

4.3.1 Study system

Dead by Daylight is an asymmetric multiplayer survival game developed by Behaviour Interactive Inc (Céré et al., 2021, 2024; Fraser Franco et al., 2022; Montiglio et al., 2025; Santostefano et al., 2024). In this game, participants take on roles as either a predator or 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 proficiency. 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. Throughout the study period, 35 virtual game environments were available for gameplay.

4.3.2 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 who 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 accumulated (see Fraser Franco et al., 2024). We labelled 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.

4.3.3 Statistical analyses

4.3.3.1 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 specialisation (i.e., IIV in movement speed) over successive matches for each player; and b) the relationship between the average tactic and specialisation, and hunting success (Cleasby et al., 2015; Lee & Nelder, 2006; 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 was trait-specific and the same for all experience levels. For the speeds of the predator and the prey, we modelled the mean and the residual standard deviation (equations 1.1, 1.2, 2.1, and 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 specialisation. 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 specialisation and success across experience at the individual-level.

The model can be written as:

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

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

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

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

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

where j is the index of the three experience levels (i.e., novice, intermediate, advanced). The d subscript indicates that a term is from the dispersion part of the model. The b terms are vectors of fixed effects with their design matrices X specific to each trait and experience level. The terms en , av , and id are the vectors of random environment, random avatar, and random individual identity effects associated with their design matrices M , N , and Z specific to each trait and experience level. For all experience levels of Y_1 and Y_2 , we assumed that the game environment and avatar random effects followed a Gaussian distribution with estimated standard deviation ($en_{12j} \sim N(0, I \sigma_{en_{12j}}^2)$ and $av_{12j} \sim N(0, I \sigma_{av_{12j}}^2)$). I is the identity matrix, with $I\sigma^2$ 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 $e_{12j} \sim N(0, \text{Diag}\{\sigma_{e_{12j}}^2\})$. The 15 individual identity random effects id_{ij} across all response variables and experience levels (five for each of the three experience levels) are indexed in vector α . The α

vector follows a multivariate Gaussian distribution $\alpha \sim MVN(0, \Sigma)$ where Σ is a 15x15 (co)variance matrix of among individual variation across all response variables and experience levels, with $\sigma_{id_{ij}}^2$ on the diagonal and covariances off-diagonal.

We performed our analyses within a Bayesian framework. We used weakly informative Gaussian priors on the slopes of the prey rank ($N(0, 1^2)$: eqn. 1.1 to 2.2) for both the mean and dispersion. We used a weakly informative Gaussian prior on the slope of the game duration ($N(1, 0.5^2)$: eqn. 3) for the mean hunting success. Based on previous results showing that the mean predator speed is approximately three m/s (Fraser Franco et al., 2022), we applied a weakly informative Gaussian prior on the intercept for predator and prey speed ($N(3, 0.5^2)$: eqn. 1.1 and 2.1) on the mean part. Similarly, we used a weakly informative Gaussian prior on the intercept for the dispersion part ($N(0, 1^2)$: eqn 1.2 and 2.2). For hunting success, we applied a positive Gaussian prior on the precision parameter ($N(2, 1^2)$: eqn. 3) and a negative Gaussian prior ($N(-4, 1^2)$: 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 ($N(0, 1^2)$) on the random effects for the mean part and the dispersion part of the model. We used a regularizing $LKJ(2)$ prior on the correlation matrix.

4.3.3.2 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 (Stan Development Team, 2023), and “cmdstanr” version 0.4.0 (Gabry & Češnovar, 2021) as the back-end for estimation (cmdstan installation version 2.28.2). We ran the model 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 driven by the very slow speed of one predator. Although the results are mostly similar, removing this individual reduced the variance estimates at the individual level. 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 Annexe C.

4.4 Results

4.4.1 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 4.2a and Annexe C : Table C.1). Likewise, the variation in speed did not change with experience, indicating that foraging specialisation remained stable at the population level (Figure 4.2a and Annexe C: Table C.1). At the individual level, differences among predators in their mean speed were weak and did not change across experience (Figure 4.2a and Annexe C: Table C.2). However, predators displayed minor differences in foraging specialisation as novices, with differences increasing slightly as individuals gained experience (Figure 4.2a and Annexe C: Table C.2). 12% of the population switched from a flexible to a specialised hunting tactic, and vice-versa, as predators gained experience (i.e., >0.2 change in standard deviation; Figure 4.3). 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).

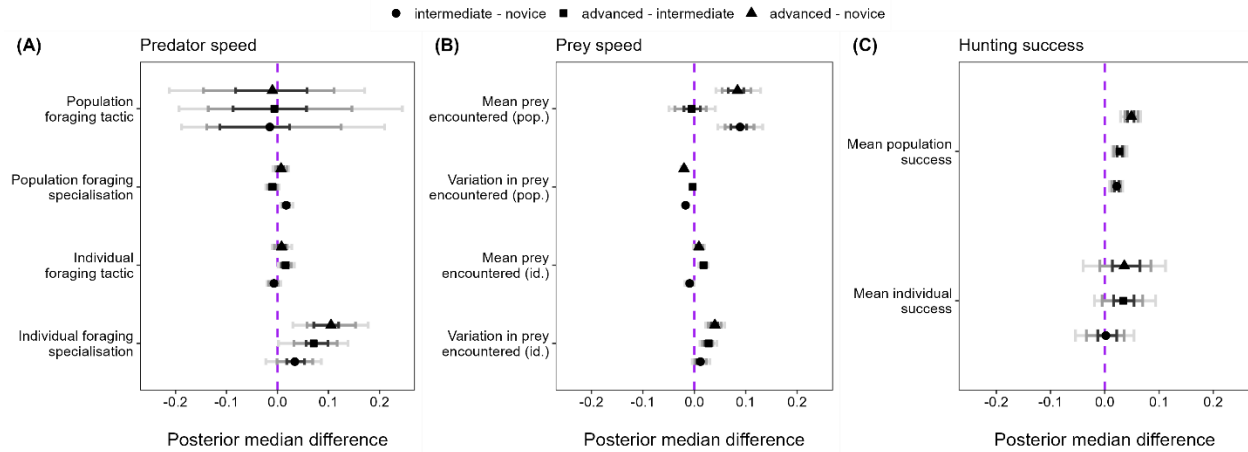


Figure 4.2 Median posterior differences and HPD intervals comparing predator foraging behaviour, prey behaviour, and predator hunting success at the population and individual level across experience stages. The parameters being compared are on the y axis, and the differences in parameter values between two experience stages are on the x axis. The pairwise comparisons between experience stages are displayed as different point shapes on each panel. The compatibility intervals are of 50%, 80%, and 95%. 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 4.2b and Annexe C: Table C.1). The predators also encountered a greater variation of prey speeds at later experience stages (Figure 4.2b and Annexe C: Table C.1). At the individual level, predators encountered prey with similar average speeds across experience stages (Figure 4.2b and Annexe C: Table C.2). However, predators differed in the range of prey speeds they encountered and the magnitude of these differences increased as they gained experience (Figure 4.2b and Annexe C: Table C.2). 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 4.2c and Annexe C: Table C.1), with mean prey consumption reaching around two prey. Individuals differed in their mean hunting success, however, the magnitude of these differences increased only marginally at more advanced levels of experience (Figure 4.2c and Annexe C: Table C.2).

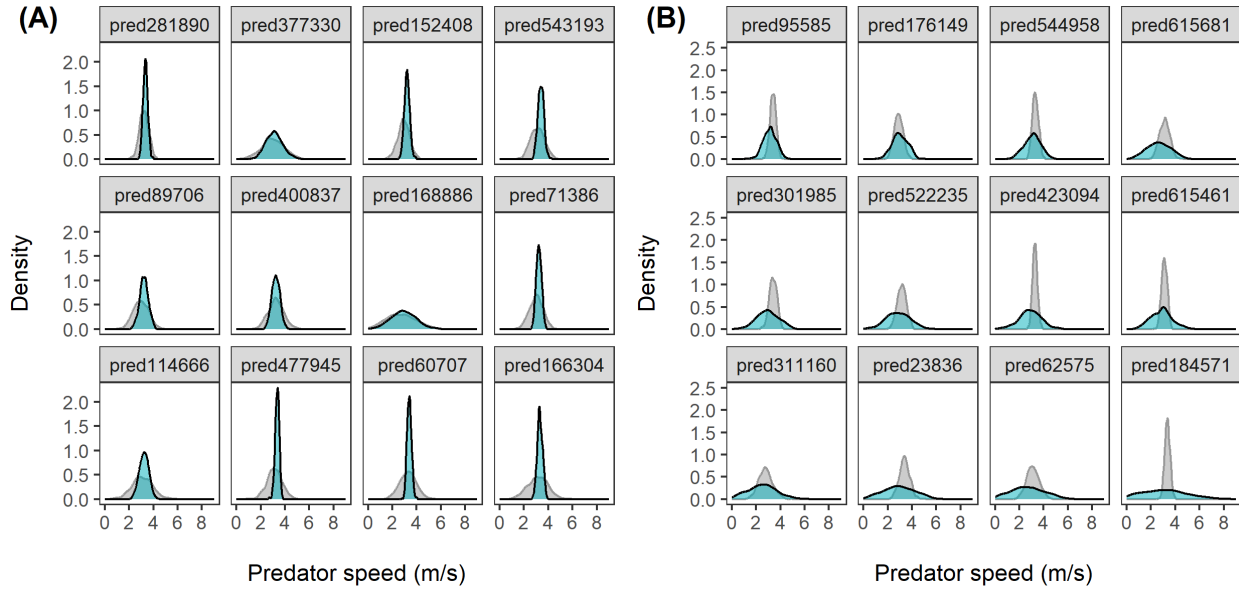


Figure 4.3 Individual behavioural distribution of the predators' speed drawn from the MDHGLM estimates for individuals that had (A) the greatest increase and (B) the greatest decrease in specialisation. The background (gray) distributions are for when individuals were novice hunters, and the foreground (blue) distributions with solid contour lines are for when they were advanced hunters. Both figure panels are ordered by ascending degree of change in specialisation. We built the figure by first subtracting the estimated standard deviation of all individuals as novices from 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 specialisation 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.

4.4.2 Predator-prey interactions across experience

Predators that were on average faster had lower IIV in speed (Figure 4.4a-b). Thus, faster predators specialised 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 95% *CI*) among novices to -0.78 (-0.83, -0.72 95% *CI*) among advanced hunters (Figure 4.4c). Faster predators tended to encounter faster prey; they also encountered groups of prey that were more similar from match to match (Figure 4.4a-b), irrespective of their experience (Figure 4c).

There was no correlation (-0.02, -0.14, 0.01 95% *CI*) between mean prey speed and IIV in predator speed when predators were novice (Figure 4.4a), but the correlation increased to -0.16 (-0.27, -0.04 95% *CI*) at the advanced stage (Figure 4.4b), such that advanced hunters that encountered faster prey tended to be more specialised (Figure 4.4c). Predators with a larger IIV in speed encountered a greater range of prey speeds, but this effect was weak (Figure 4.4a-b). Hence, predators that

encountered groups of prey with similar speeds tended to be more specialised 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 4.4c).

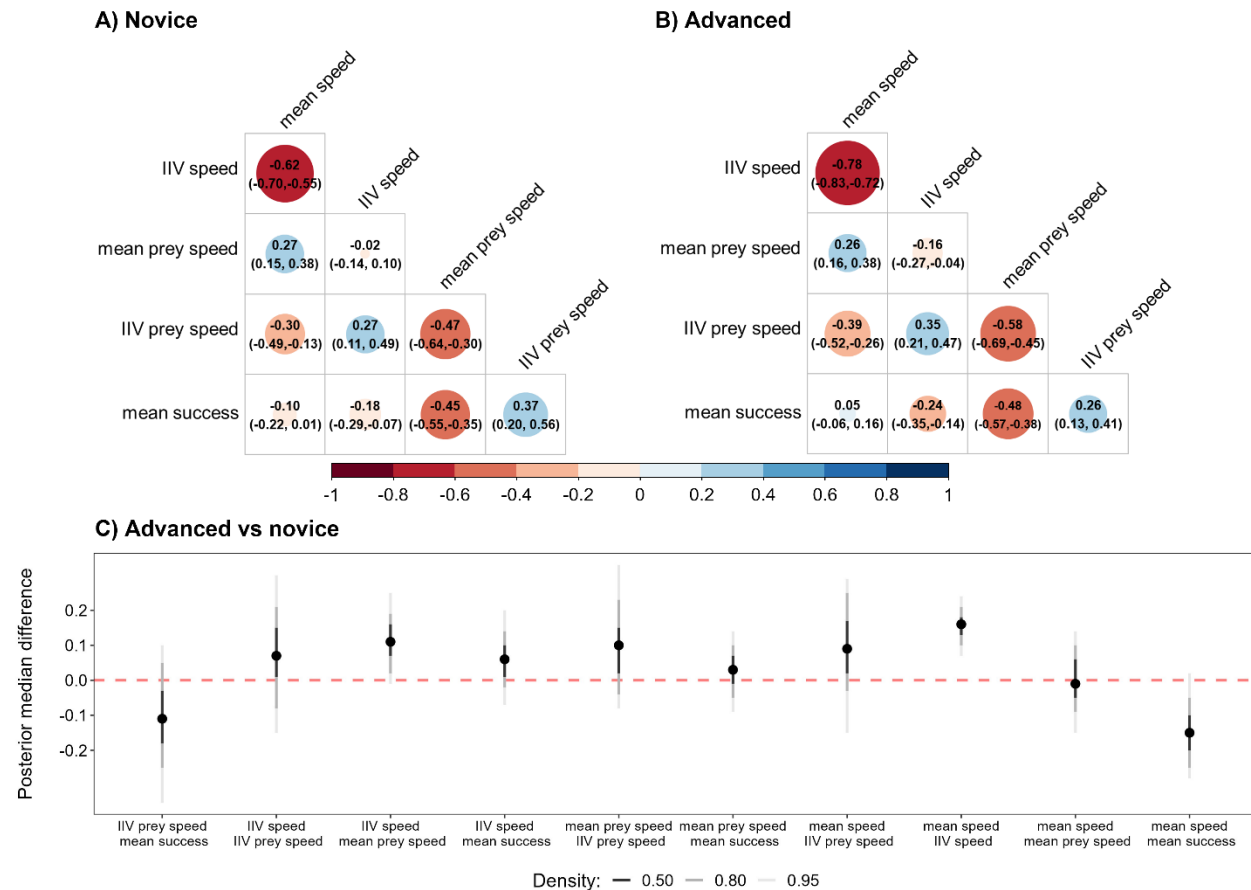


Figure 4.4 Correlation matrices of the MDHGLM relating the mean and IIV in speed of the predators, the mean and IIV in speed of the prey they encountered, and mean hunting success. Larger dark blue circles indicate stronger positive correlations (positive values on the colour legend), while larger dark 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.

4.4.3 Success along the foraging specialisation continuum

There were no differences in hunting success among predators in their mean speed (Figure 4.4). More specialised predators achieved a slightly greater foraging success, but this effect was weak (Figure 4.4). This relationship between the predator's IIV in speed and success increased with

experience (Figure 4.4c), suggesting that the success gap between generalists and specialists increased with experience (Annexe C: Figure C.1). There was strong evidence that predators that encountered faster prey and prey groups with similar speeds were less successful (Figure 4.4a-b), irrespective of their experience level (Figure 4.4c).

4.5 Discussion

A general assumption in predator-prey studies is that predators maximize their success by matching their tactics to their prey (Abrams, 2000). Yet ecologists have historically struggled to determine whether this results from predators learning to hunt their prey, in part because of the challenges of studying direct interactions in the wild. By capitalizing on a virtual predator-prey system where interactions were directly monitored, we found that individual predators in *Dead by Daylight* developed behavioural strategies that were associated with prey behaviour over successive encounters. The strategies formed a continuum of hunting styles, ranging from a slower, generalist strategy to a highly specialised, fast-paced strategy. We also found that some predators switched strategies as they gained experience. Specialized cursorial hunters encountered groups of prey moving at similar speeds, while the slower and generalist hunters encountered groups of prey moving at varying speeds. Overall, predators across the generalist-specialist continuum achieved similar success, although generalist hunters were slightly less successful at higher experience levels.

The predator population maintained its speed and degree of specialisation throughout the study period, and individuals differed only slightly in their average speeds. However, individuals differed in foraging specialisation, and these differences increased slightly as they gained experience. Predators that hunted at higher speeds specialised in this tactic and tended to encounter groups of prey with similar speeds (low variance between encounters), while those that hunted at slower speeds tended to switch tactics and be more generalist because they encountered groups of prey moving at different speeds (high variance between encounters). On the one hand, this pattern could arise if predators adjusted their strategy to their prey, because fast-paced hunting is a specialised tactic suited for prey that use rapid evasive movements, while a slower and generalist strategy can be useful to minimize the consequences of uncertainty when prey escape unpredictably (Bro-Jørgensen, 2013; Endler, 1991; Szopa-Comley & Ioannou, 2022; Wilson et al., 2018). However, we observed that 44% of the predator population showed close to no change in specialisation with

experience. Since these individuals were already specialised 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 predator and prey remained stable across the predator's experience. Yet, because prey can also learn how to avoid predation (Kelley & Magurran, 2003; McComb et al., 2011; Turner et al., 2006), we believe that the predator-prey phenotype matching more likely emerged from reciprocal adjustments in speed by predators and prey as they interacted (Edgell & Rochette, 2009; Kishida et al., 2006, 2009; McGhee et al., 2013). Indeed, 56% of the predator population altered its behaviour with experience, including 12% that even switched from a specialist to a generalist strategy and vice versa. Hence, if the prey also learned through repeated interactions with the predators, it is possible that reciprocal interactions contributed to 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 specialisation should maximise prey consumption by optimising foraging efficiency (Stephens & Krebs, 1986), but other work suggests that both generalist and specialist strategies could be adaptive as resources fluctuate (R. A. Phillips et al., 2017; Woo et al., 2008). Our results support empirical findings indicating that flexible and specialist foragers obtained similar success given prey behaviour (Courbin et al., 2018; R. A. Phillips et al., 2017; Potier et al., 2015; Weimerskirch, 2007; Woo et al., 2008), although generalist hunters were slightly less successful at more advanced stages. Both strategies appeared to emerge in part from individuals learning to hunt their prey, resulting in a general increase population success. 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 *Dead by Daylight* (Fraser Franco et al., 2022, 2024). However, if prey responded to fast predators by moving faster, then hunting at high speeds made encounters more challenging for these predators as well, thereby diminishing the benefits of this tactic (Figure 4.4). Thus, specialising probably compensated for the difficulty of hunting prey at high speeds by helping predators better predict their prey's location and movement. On the other hand, generalist hunters

encountered a larger range of prey moving at slower speeds on average. Yet, because prey increased their speed with experience, the benefits to generalist predators of hunting multiple prey types may have come at the cost of reduced ability to capture 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 (Bélisle & Cresswell, 1997; Dukas, 2019; Healy, 1992), particularly if the skills required to hunt slower prey are nontransferable to faster prey. As the benefits of each hunting style varied across 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 (Mougi & Kishida, 2009; Tinker et al., 2008; Woo et al., 2008).

We found support for our prediction that individual foraging specialisation 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 equally successful, both specialised and generalist hunters achieved similar overall success. A potential caveat is that generalist hunters might have experimented with various tactics out of boredom, which could impede the ecological realism of our interpretations. 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 into the mechanisms driving predator-prey systems.

4.6 Acknowledgements

We thank Behaviour Interactive Inc. for providing access to their data to produce this work and for allowing us to make it freely available. We would also like to thank members of the CSBQ-UQAM for their comments on earlier versions of this study and Mathieu Videlier for a thoughtful review of this manuscript. This work was supported by an NSERC doctoral scholarship (569716) awarded to Maxime Fraser Franco. The authors declare no conflict of interest.

4.7 Data and code availability

The data and code used for the analyses presented in this work are fully available on this GitHub repository: <https://github.com/quantitative-ecologist/experience-hunting-tactics>.

CONCLUSION

Contributions

L'objectif premier de cette thèse était de valider l'usage d'un jeu vidéo simulant des interactions prédateur-proie comme système modèle pour l'étude de l'écologie du comportement de prédation. Dans un deuxième temps, je me suis intéressé à la manière dont les interactions avec les proies et l'expérience au fil du temps modulent le comportement de chasse afin de mieux comprendre les mécanismes à l'origine de différences comportementales chez des prédateurs. Pour ce faire, j'ai décomposé le comportement de prédation à différentes échelles afin d'identifier les principaux axes de variation comportementale : l'habitat virtuel, la variation entre individus et la variation intra-individuelle. Dans un troisième temps, j'ai évalué sous quelles conditions une stratégie de chasse conférait un avantage par rapport aux autres en analysant comment le succès de capture variait au fil du temps selon le comportement adopté et le type de proie rencontrée. Ces éléments font l'objet de recherches intensives depuis l'âge d'or des sciences écologiques dans les années 1960-1970, mais ils demeurent difficiles à tester empiriquement en raison des défis associés à la mesure du comportement individuel. Mes travaux apportent une contribution empirique à la théorie de la spécialisation de niche dans un contexte d'interaction prédateur-proie. Notamment, ils mettent en évidence les conséquences de l'expérience antérieure sur le développement de la niche individuelle et sur la performance des stratégies de chasse d'un prédateur. Plus largement, mes travaux mettent en évidence les avantages et les limites des jeux vidéo pour l'étude écologique du comportement et démontrent que les humains adoptent les mêmes stratégies que les prédateurs non humains lorsqu'ils interagissent dans un contexte prédateur-proie.

Dans mon premier chapitre de thèse, j'ai tout d'abord fait des analyses préliminaires pour évaluer la structure du comportement de chasse à l'échelle de la population. Mes observations indiquent que les humains qui interagissent dans un monde virtuel adoptent des stratégies analogues à celles employées par des chasseurs humains en milieu naturel, et plus largement, à celles observées chez les animaux non humains (Gaynor et al., 2024; Montgomery et al., 2022). En effet, les prédateurs dans *Dead by Daylight* utilisent des tactiques le long d'un continuum allant de l'embuscade pure à la chasse en déplacement soutenu. La stratégie furtive était caractérisée par une vitesse de

déplacement plus lente et par davantage de temps passé en position d’embuscade, alors que la stratégie en déplacement soutenu montrait le patron inverse (Annexe A : Figure A.1). J’ai observé que les prédateurs ne semblent pas ajuster ces comportements en fonction des habitats virtuels dans lesquels ils chassent. Toutefois, l’effet de l’habitat sur le comportement de prédation était en partie modulé par le comportement des proies : en réagissant elles-mêmes à l’habitat, celles-ci pourraient indirectement influencer la réponse des prédateurs à leur environnement. Plusieurs études montrent que les proies réduisent ou modifient leur activité dans les habitats où le risque de prédation perçu est élevé, comme les habitats hétérogènes et complexes où elles ne peuvent pas voir directement le prédateur (Gaynor et al., 2019; Heithaus et al., 2009; Preisser et al., 2007). L’absence d’effet de l’habitat sur le comportement des prédateurs pourraient aussi être dû à l’échelle fine dans laquelle les interactions se produisent dans *Dead by Daylight*. Par exemple, des études montrent que les caractéristiques de l’habitat influencent la stratégie de recherche des prédateurs à des échelles spatiales plus larges, alors que la présence de proies et de compétiteurs l’influence davantage à des échelles plus fines (Bassing et al., 2025; Říha et al., 2021). Une explication alternative est qu’une des mécaniques de jeu dans *Dead by Daylight* permet aux prédateurs de voir constamment la localisation des ressources (c.-à-d. les génératrices) où les proies vont s’approvisionner, et ainsi, ils tendent à se déplacer d’une ressource à une autre pour localiser les proies. Ceci s’apparente en quelque sorte aux prédateurs qui rôdent autour des points de ressources où les proies vont s’approvisionner dans la nature (Hopcraft et al., 2005). Ainsi, cette mécanique de jeu amènerait les prédateurs à se déplacer entre les points de ressources sans égard à l’environnement immédiat, limitant par conséquent l’influence de l’habitat sur le comportement de chasse dans *Dead by Daylight*. J’ai aussi identifié que les tactiques de chasse des prédateurs étaient structurées à l’échelle de l’individu le long d’un continuum allant de l’embuscade à la chasse en déplacement soutenu. Cette structure était en grande partie modulée par le comportement des proies. Une des hypothèses classiques pour expliquer le maintien de ces stratégies dans une population est celle de la locomotion croisée, qui avance que les prédateurs furtifs et plus actifs devraient coexister parce qu’ils capturent des proies différentes (Huey & Pianka, 1981). Dans *Dead by Daylight*, les prédateurs capturaient davantage de proies sédentaires peu importe leur stratégie, mais leur succès variait en fonction du comportement de chasse employé. Les études qui confirment l’hypothèse de locomotion croisée sont peu nombreuses (Belgrad & Griffen, 2016; Chang et al., 2017), et certaines l’ont infirmée au niveau des prédateurs furtifs en soulignant des dynamiques plus complexes telles

que dans mes observations (Donihue, 2016; Matsumura & Miyatake, 2022). Cette complexité pourrait être en partie due au fait que la structure des tactiques de chasse variait en fonction de l'échelle considérée (c.-à-d. population, entre individus, au sein des individus). En perspective, les résultats de ce premier chapitre m'ont permis de valider que *Dead by Daylight* se prête bien à l'étude des interactions prédateur-proie. De plus, ils soulèvent des questions fondamentales sur les dynamiques que nous avons observées, notamment quant au rôle de l'expérience sur le développement du succès de capture des prédateurs que j'aborde dans les chapitres subséquents.

Mon deuxième chapitre de thèse portait sur le développement de l'expertise chez les prédateurs. L'objectif de ce chapitre était d'évaluer comment les interactions avec les proies modulent le gain en expertise des prédateurs. Dans ce chapitre, j'ai fait le postulat que les prédateurs devraient varier dans leur capacité à acquérir de l'expertise. J'ai émis l'hypothèse que cette variation devrait être due en partie au niveau de difficulté des proies chassées au fil des rencontres. En effet, le comportement antiprédateur des proies ainsi que leur niveau d'expertise sont deux composantes qui peuvent influencer le succès de capture des prédateurs (Kelley & Magurran, 2003, 2011; Rawat et al., 2025; Sansom et al., 2009), mais aucune étude n'a été en mesure de démontrer qu'elles peuvent influencer le gain en expertise. Mes observations indiquent que la population a gagné en expertise au fil des rencontres avec les proies. Le développement de l'expertise était caractérisé par une courbe d'accumulation de gain, où les prédateurs ont en moyenne optimisé leur succès de capture après avoir joué 300 parties. Ce patron concorde avec des études sur le gain en expertise chez des grands prédateurs tels le loup (*Canis lupus*) et la hyène tachetée (*Crocuta crocuta*) (Holekamp et al., 1997; Sand et al., 2006). Toutefois, puisque le jeu utilise un système de jumelage basé sur l'habileté des joueur·euse·s, cette accumulation d'expertise n'était observable qu'en contrôlant l'habileté des proies dans mes analyses. Ce système de jumelage nous empêchait de départager avec certitude les effets du comportement des proies et de leur habileté sur le gain en expertise chez les prédateurs. Effectivement, plusieurs jeux vidéo multijoueurs en ligne utilisent des systèmes de jumelage afin d'équilibrer le jeu et permettre aux joueur·euse·s de jouir d'une expérience de jeu agréable peu importe leur niveau d'expertise. Malgré tout, certains patrons biologiques ont pu être mis en évidence dans ce chapitre. Qualitativement, en tenant compte du comportement des proies, la courbe de gain en expertise conservait une forme semblable et les paramètres qui la décrivent demeuraient stables, ce qui suggère que le comportement des proies

n'expliquait pas de variation au niveau populationnel. Cependant, mes résultats soulignent un effet du comportement de déplacement des proies sur les différences entre les individus dans le gain en expertise. Les prédateurs qui ont rencontré des proies plus rapides avaient tendance à avoir un succès de capture maximal moins élevé. Cela suggère que le comportement antiprédateur des proies peut influencer la capacité des prédateurs à acquérir de l'expertise, résultant en des différences de succès de capture à long terme qui sont façonnées par les rencontres au fil du temps.

Différents mécanismes pourraient expliquer la manière dont les proies influencent le gain en expertise des prédateurs. Ces effets pourraient être dus aux changements dans le comportement des proies au fur et à mesure qu'elles gagnent elles-mêmes en expertise. Par exemple, les proies expérimentées auraient pu limiter la capacité des prédateurs à les détecter ou à les pourchasser en se camouflant plus efficacement ou en utilisant l'environnement pour entraver le prédateur. Dans *Dead by Daylight*, mes résultats indiquent que les proies augmentent leur vitesse de déplacement avec l'expertise et que les prédateurs ont un succès de capture moins élevé lorsqu'ils rencontrent des proies plus rapides. La chasse de proies rapides requiert une motricité et une énergie accrues, pouvant ainsi limiter la capacité de certains prédateurs à former des images pour mieux les repérer et à se concentrer pour mieux les pourchasser (Bro-Jørgensen, 2013; Dukas & Kamil, 2001; Troscianko et al., 2018; Wilson et al., 2018). Ces proies rendraient la chasse plus difficile, ce qui pourrait aussi diminuer la motivation du prédateur, et finalement, ses opportunités d'apprentissage (Dukas, 2019). Ces effets sur la motivation ont été démontrés dans des études empiriques où les proies rapides avaient tendance à être plus imprévisibles, augmentant ainsi les chances que les prédateurs abandonnent la poursuite (Herbert-Read et al., 2017; Jones et al., 2011; Richardson et al., 2018).

Dans mon troisième chapitre, je me suis intéressé au développement de la spécialisation comportementale des prédateurs en fonction de leur expérience et des interactions avec les proies. J'ai fait le postulat que la population de prédateurs devrait être composée de chasseurs spécialistes et de généralistes. J'ai testé l'hypothèse que ceux-ci devraient obtenir un succès de capture équivalent s'ils s'ajustent au type de proie qu'ils rencontrent au fil du temps. Mes résultats montrent que la population de prédateurs maintenait une taille de niche essentiellement stable au fil du temps. Toutefois, des différences de plus en plus apparentes entre individus émergeaient à mesure que les prédateurs gagnaient en expérience. Les prédateurs plus rapides tendaient à se spécialiser dans cette

tactique, alors que les prédateurs furtifs utilisaient un éventail de stratégies au fil du temps. Nous pouvons faire deux constats principaux quant à l'émergence de ces différences de niche comportementale individuelle. Premièrement, la niche comportementale variait selon la vitesse moyenne des proies rencontrées et selon la variation de la vitesse des proies rencontrées. En effet, une structure comportementale entre les prédateurs et leurs proies émergeait et se renforçait à mesure que ceux-ci gagnaient en expertise. Deuxièmement, les différences de niche entre prédateurs étaient associées à des différences de plus en plus marquées dans le succès de capture au fil du temps. En effet, à un niveau d'expérience avancé, les prédateurs spécialistes tendaient à avoir un peu plus de chances de capturer des proies que les prédateurs généralistes. Ces résultats suggèrent la présence d'une boucle de rétroaction positive : les prédateurs s'ajusteraient à leurs proies qui ajusteraient elles-mêmes leur comportement au cours de chaque partie. Cette rétroaction permettrait aux prédateurs spécialistes de mieux maîtriser leur stratégie et donc d'atteindre un succès plus élevé que les prédateurs généralistes qui ne peuvent développer une expertise aussi aiguisée compte tenu de l'éventail de tactiques qu'ils emploient (Bélisle & Cresswell, 1997; Healy, 1992; Pintor et al., 2014). Il est toutefois intéressant de constater que certains prédateurs hautement spécialistes sont devenus généralistes avec le temps, alors que d'autres ont exprimé le patron inverse. Ceci suggère qu'un individu initialement spécialiste aurait la capacité de devenir plus flexible dans son comportement en réponse aux interactions avec ses proies. Ces changements comportementaux pourraient aussi être dus aux différences de gain en expertise observées au chapitre précédent. En effet, les prédateurs généralistes qui peinaient à maximiser leur succès auraient pu être ceux qui étaient plus lents à développer leur expertise, probablement en ayant davantage de difficulté à apprendre comment pourchasser leur proie lorsqu'ils étaient novices. Somme toute, ce chapitre nous a permis de démontrer que l'apprentissage peut moduler la spécialisation comportementale et pourrait favoriser les prédateurs qui se spécialisent sur une tactique précise si les proies qu'ils rencontrent utilisent elles-mêmes des stratégies prévisibles au fil du temps.

À la lumière de mes résultats, je juge que ma contribution la plus pertinente a été de démontrer que les jeux vidéo multijoueurs constituent un système valide et intéressant pour étudier l'écologie comportementale des interactions prédateur-proie. Cette démonstration s'appuie sur trois arguments principaux. Premièrement, les jeux vidéo multijoueurs en ligne produisent d'immenses

et riches jeux de données sur des interactions comportementales à travers le temps dans des habitats virtuels complexes (Montiglio et al., 2025). L'acquisition de jeux de données pour tester des hypothèses écologiques sur le comportement animal demeure un défi de taille pour les études empiriques. L'augmentation du nombre de systèmes naturels menacés ainsi que leur dégradation pourrait exacerber ce défi dans les années à venir. Ainsi, les systèmes virtuels, avec leurs mondes persistants, nous permettraient de tester des hypothèses écologiques sans avoir à perturber des systèmes naturels sensibles. Deuxièmement, la collecte de données dans les mondes virtuels se fait à l'échelle de l'individu, ce qui constitue un avantage considérable pour l'étude du comportement et de sa variation qui est en grande partie caractérisée par des différences entre les individus (A. M. Bell et al., 2009; Laskowski et al., 2022). Ceci permet d'avoir un historique des interactions de chaque individu à travers le temps et de tester des hypothèses écologiques à propos des facteurs qui modulent le comportement individuel lors des interactions. À ce jour, il est encore très difficile d'évaluer comment l'expérience module le comportement et le succès de capture chez des grands prédateurs. Plusieurs études utilisent des mesures approximatives de l'expérience, comme l'âge, pour tester des hypothèses sur le rôle de l'expérience sur l'écologie des prédateurs (Aikens et al., 2024; G. A. Breed et al., 2011), mais l'âge n'est pas toujours corrélé à l'expérience des prédateurs. Ce manque de connaissances limite donc notre capacité à anticiper les impacts des prédateurs dans les communautés naturelles, particulièrement sur de courtes échelles de temps. Troisièmement, les jeux vidéo permettent, dans une certaine mesure, de manipuler l'environnement de manière expérimentale afin d'identifier des mécanismes de cause à effet (Céré et al., 2024). Malgré l'accessibilité croissante de méthodes de plus en plus sophistiquées pour faire de l'inférence causale à partir de données longitudinales (Fan et al., 2016; Hernan & Robins, 2025; Karimi et al., 2020; Koller & Friedman, 2009; Pearl, 1995), la capacité de tester une hypothèse de manière expérimentale dans un système complexe constitue un net avantage des jeux vidéo que l'on retrouve rarement dans des systèmes naturels.

Limites

Malgré les nombreux avantages offerts par les jeux vidéo, il est important de souligner que plusieurs facteurs entourant l'écosystème virtuel imposent des limites importantes quant à leur utilisation. La limite la plus importante porte sur la perception du risque dans les jeux vidéo (Lofgren & Fefferman, 2007; Oultram, 2013). Dans un monde virtuel, la vie des individus n'est

pas en jeu et ceux-ci tendent donc à exprimer des comportements hautement risqués pour la survie de leur avatar, quelque chose qu'on observerait plus rarement chez un animal dans la nature. Par exemple, les prédateurs s'attaquent généralement à des proies plus fragiles ou accessibles, ce qui minimise le risque de blessure lors de l'attaque (Brandell et al., 2022; Hayward & Kerley, 2005; Hopcraft et al., 2005; Krumm et al., 2009). Un prédateur dans la nature ne devrait adopter des comportements plus risqués que lorsque sa survie est en jeu, par exemple, lorsque les proies sont rares et que ses réserves d'énergie sont faibles (Moran et al., 2021; Mukherjee & Heithaus, 2013). Ce point nous amène au concept de la mort, qui est essentiellement absent dans les jeux vidéo. Il est selon moi difficile de tester des hypothèses sur l'évolution du comportement dans des jeux où les individus peuvent mourir et rejouer sans réelle conséquence dans le jeu ou dans la vraie vie. Ceci est particulièrement avéré pour les proies dans *Dead by Daylight* qui une fois capturées puis consommées, peuvent ensuite rejouer immédiatement et transférer leur expérience à la prochaine partie. Certains jeux simulent le concept de la mort de manière plus réaliste (ex. « roguelikes »), mais il n'existe à ma connaissance aucun jeu (du moins, populaire) où la personne n'a qu'une seule vie et où il est impossible de rejouer si l'avatar périt. Une manière de contrecarrer ces effets d'expérience post-mortem serait d'élaborer une expérience où les joueur·euse·s peuvent rejouer tant qu'ils ou elles restent en vie. Dans le contexte de ma thèse, ceci aurait pu modifier l'équilibre apparent dans le succès des prédateurs spécialistes et généralistes car les généralistes avaient moins de succès contre les proies plus rapides. Ces proies seraient devenues plus fréquentes dans la population car les proies sédentaires auraient été progressivement éliminées. Malgré tout, même si je suis d'avis que les jeux vidéo ne nous permettent pas de mesurer l'évolution (au sens biologique), ils permettent tout de même d'observer des patrons de sélection complexes qui pourraient nous aider à mieux comprendre notre histoire évolutive (Montiglio et al., 2025; Santostefano et al., 2024).

Un autre concept inhérent aux jeux vidéo multijoueurs est « l'équilibrage », qui a pour objectif de maintenir la personne qui joue engagée en rendant l'expérience juste et plaisante (Becker & Görlich, 2020; Pfau & Seif El-Nasr, 2024; Schreiber & Romero, 2021). Dans *Dead by Daylight*, ce concept se traduit par un principe de jumelage entre individus avec un niveau d'habileté semblable qui leur permet d'apprendre à jouer de manière progressive. Cette mécanique introduit un niveau d'irréalisme qui différencie *Dead by Daylight* des systèmes naturels puisque les prédateurs non humains s'attaquent normalement à des proies juvéniles ou moins expérimentées. En raison de ce

mécanisme de jeu, nous avons pu observer dans mon second chapitre que le succès de capture des prédateurs n'augmentait pas avec l'expérience si on ne tenait pas compte de l'habileté des proies.

D'un point de vue méthodologique, nous n'avons pu tirer parti de l'option de faire une expérience pour tester directement l'effet de l'habitat ou du comportement des proies sur les prédateurs dans *Dead by Daylight* (bien qu'il demeure possible de le faire, voir Céré et al., 2024). En ce sens, une des limites générales de mon doctorat est que les patrons observés demeurent de nature observationnelle : on ne peut tirer des conclusions de cause à effet. Par exemple, dans mon premier chapitre, nous avons pu mettre en lumière des relations complexes entre le comportement de prédation, le comportement des proies et le succès de capture. Ceci nous a permis de mieux comprendre dans quel contexte les prédateurs devraient maximiser leur succès. Toutefois, ces analyses nous empêchent de déterminer comment la dynamique émerge entre les prédateurs et les proies, limitant ainsi ma capacité à tirer des conclusions sur le potentiel du comportement des proies à agir comme agent de sélection sur le comportement des prédateurs (Caruso et al., 2017; Kelly, 2008; MacColl, 2011; Wade & Kalisz, 1990). Il est reconnu que les prédateurs sont des agents de sélection sur le comportement des proies et que leurs interactions mutuelles sont source de coévolution (Abrams, 1986, 2000; Brodie & Wilkinson, 2010). Toutefois, il s'avère plus difficile de démontrer que les proies agissent comme agents de sélection sur le comportement des prédateurs. La plupart des études s'étant penchées sur cette question montrent que les adaptations des prédateurs en réponse aux proies sont souvent morphologiques (B. L. Phillips & Shine, 2006; Reimche et al., 2020), alors que les modifications de leur comportement sont plutôt dues à l'apprentissage (Greenlees et al., 2010; Llewelyn et al., 2010; Nelson et al., 2011). De plus, des études récentes avancent que les prédateurs auraient en général une capacité d'adaptation moindre que leurs proies en raison de leur taille de population plus réduite et de leur temps de génération plus long (Yamamichi & Miner, 2015). Compte tenu de mes résultats et de la littérature, il semble plus probable que l'effet des interactions entre les prédateurs et les proies sur le succès de capture soit modulé par l'apprentissage chez les prédateurs plutôt que par une réponse à la sélection.

La limite majeure quant à l'interprétation des résultats de mon second et troisième chapitre porte sur le système de jumelage entre individus avec des niveaux d'habileté similaires. En temps normal, on devrait s'attendre à ce qu'un prédateur s'exerce à maintes reprises à chasser divers types de proies avec des niveaux d'expérience différents, ce qui générerait une variation naturelle dans les

courbes de gain en expertise dans une population de prédateurs. Dans mon cas, le système de jumelage faisait en sorte que l'on n'observait pas de gain en expertise chez les joueur·euse·s puisque le succès de capture demeurait stable au fil du temps. En effet, une variation n'était observée que lorsqu'on contrôlait pour le « rang » des proies dans nos modèles, une mesure définie par la compagnie de jeu qui a développé *Dead by Daylight*. Ceci rend l'interprétation plus difficile, car la courbe de gain dans la population ainsi que la variation entre les joueur·euse·s est observée lorsque les prédateurs chassent des proies avec un niveau d'expérience moyen, ce qui serait peu probable dans la nature. Ainsi, si quelqu'un voulait reproduire ces analyses, il serait pertinent de tirer parti de la facilité qu'offrent les mondes virtuels de faire une expérience contrôlée pour tester l'hypothèse que les proies influencent le gain en expertise chez les prédateurs ou que la spécialisation comportementale émerge en fonction des interactions au fil du temps.

Perspectives et recommandations

À l'aide d'un monde virtuel, cette thèse a mis en lumière comment les interactions entre des prédateurs et leurs proies peuvent influencer leur trajectoire comportementale et leur succès de capture au fil du temps. Mon approche et mes observations pourraient avoir des retombées autant de nature scientifique que pour l'industrie du jeu vidéo et ouvrir la porte à l'approfondissement d'une discipline que j'aime appeler « l'écologie virtuelle ».

D'un point de vue méthodologique, ma thèse offre un cadre d'analyse reproductible issu de méthodes existantes qui n'avaient, jusqu'à maintenant, pas ou peu été appliquées à des données empiriques en écologie comportementale. Par exemple, la théorie sur les modèles linéaires généralisés hiérarchiques doubles (MLGHD) appliqués à l'écologie a été mise en place seulement au cours des dix dernières années (Cleasby et al., 2015; Westneat et al., 2014). À ce jour, seule une poignée d'études empiriques l'exploitait pour étudier la spécialisation comportementale dans le mouvement chez des animaux non humains (Hertel et al., 2020, 2021; Kelly, 2025; Patrick et al., 2021). À ma connaissance, aucune étude n'a combiné les MLGHD à une approche multivariée en associant directement les paramètres de spécialisation à une mesure de succès comme je l'ai fait dans ma thèse. De plus, j'ai pu tirer parti de la flexibilité des modèles de régression asymptotique avec effets aléatoires afin de décortiquer les composantes du gain en expertise en plus d'en estimer les variations entre individus. Les études qui se penchent sur l'apprentissage ou le gain en expertise

vont typiquement employer des méthodes linéaires classiques (Commins et al., 2024; Lazure & Weladji, 2024), mais il a été démontré que le gain finit par atteindre un plateau (Clarke & Hunt, 2025; Dukas, 2019), alors que ces approches supposent une augmentation infinie du gain. Il est souvent difficile d'appliquer un cadre théorique à des données empiriques en raison des méthodes numériques non existantes ou non disponibles. Ainsi, mon approche entièrement disponible en ligne et reproductible pourrait être utile à la communauté.

Compte tenu de la littérature existante en écologie comportementale, il apparaît évident que les modèles linéaires dominant l'approche analytique depuis plusieurs décennies (Damgaard et al., 2018). À mon sens, cette vision nous empêche d'innover et de pousser nos réflexions plus loin en nous gardant pris dans un cadre qui fait des suppositions strictes sur la manière dont notre monde fonctionne (Damgaard et al., 2018; Heit et al., 2024). Pour progresser, il serait intéressant d'intégrer des approches novatrices et de s'ouvrir aux contributions de disciplines en dehors de l'écologie comportementale. En effet, les systèmes naturels sont complexes, de sorte que l'écologie en tant que science l'est aussi. Ainsi, il pourrait être profitable d'adopter une vision qui tire partie des systèmes complexes pour mieux comprendre les causes et les conséquences du comportement dans les écosystèmes (Riva et al., 2023). Ceci nous permettrait d'explorer des approches alternatives aux paradigmes conventionnels tels que le déterminisme et le réductionnisme, qui caractérisent une grande partie de l'approche utilisée en sciences écologiques (Riva et al., 2023). Je pense entre autres à des approches plus probabilistes, comme celle proposée par l'écologiste et philosophe Robert Ulanowicz (1997).

Mes observations pourraient avoir des implications en conservation et en gestion des populations animales. Par exemple, en ayant démontré que la spécialisation comportementale peut émerger au fil de l'expérience, considérer l'âge et l'expertise permettrait une meilleure gestion du contrôle d'espèces invasives à l'aide de prédateurs locaux, et pourrait contribuer au succès des programmes de réintroduction de prédateurs dans des milieux perturbés. En effet, des synthèses montrent que l'expérience est fortement associée au succès de réintroduction des grands carnivores et autres prédateurs en milieu naturel (Jule et al., 2008; Reading et al., 2013; Thomas et al., 2023). De plus, l'utilisation de mondes virtuels comme terrain de jeu expérimental pourrait contribuer au développement des théories sur l'écologie des interactions entre organismes. Par exemple, plusieurs modèles théoriques font le postulat que les patrons de spécialisation comportementale

sont des adaptations. En considérant le rôle du développement dans ces modèles, nous serions en mesure de mieux prédire la taille de niche au sein des populations animales. Tester ces modèles requiert d'avoir accès à des données longitudinales issues de longues campagnes d'échantillonnage dans des populations naturelles. Ainsi, les mondes virtuels offriraient un excellent compromis entre volume de données et réalisme pour tester les modèles théoriques.

Pour conclure, je crois que l'écologie virtuelle prendra de plus en plus de place dans la recherche théorique et empirique en écologie au cours des prochaines décennies. Toutefois, le développement de cette discipline n'est pas sans enjeux et défis. Des partenariats solides devront être développés où l'expertise des étudiant·e·s en écologie pourra être appliquée rigoureusement dans le contexte du développement de jeux. Ces partenariats devront être bidirectionnels, de sorte que les étudiant·e·s pourront aussi bénéficier d'apprendre à appliquer les modèles dans des environnements informatiques de pointe pour mieux se préparer au marché du travail au sein et hors du milieu universitaire. Il sera aussi nécessaire que les incitatifs liés à la recherche en écologie s'accordent avec ceux qui mènent l'industrie du jeu vidéo, ce qui peut être difficile pour des écologistes qui ont une vision plus centrée sur les organismes non humains. Somme toute, l'écologie virtuelle n'en est qu'à ses débuts, mais elle ouvre la voie à des perspectives de recherche susceptibles de changer notre manière d'étudier le monde du vivant.

ANNEXE A

SUPPORTING INFORMATION FOR: STUDYING PREDATOR FORAGING MODE AND HUNTING SUCCESS AT THE INDIVIDUAL LEVEL WITH AN ONLINE VIDEOGAME

Materials and methods

Principal components analysis

We computed a principal component analysis (PCA) using the packages ‘FactoMineR’ version 2.4 (Lê et al., 2008) and ‘factoextra’ version 1.0.7 (Kassambara & Mundt, 2020) in the R software version 4.0.4 (R Core Team, 2021), under a Windows 10 Home computer OS (version 21H2, OS build 19044.1466). The ‘PCA()’ function in ‘FactoMineR’ uses singular value decomposition. Before running the PCA, we divided each variable (except travel speed) by the match duration (seconds) to account for differences in game length among matches. We applied a square-root transformation to all the variables. They were then standardized to mean and unit variance (Z scores) before running the PCA. We then ranked the variables based on their relative contribution (in %) to a given principal component axis. To do so, for each variable, we used the ratio between their $\cos^2$ multiplied by 100 and the $\cos^2$ of the principal component.

Parameterization of the Bayesian multivariate mixed-model

We used a half-normal prior with mean of 0 and standard deviation of 1 for all the variance parameters, and applied a weakly informative LKJ prior with a shape parameter (n) set to 2 for the random effects variance-covariance matrices. We applied a Gaussian prior with mean of 0 and standard deviation of 2 for the fixed effects (i.e. prey travel speed x_1 and rate of space covered x_2) of all the submodels (i.e. for each response variable). We set the model to run 4 chains with 2500

iterations where samples were drawn at every 8 intervals (thinning), and to use the first 500 iterations as warmups. We visually inspected the trace plots, effective sample sizes, and residuals to assess convergence and stability. We also evaluated the model's prediction accuracy using posterior predictive checks. The rhat values of all the model's main parameters (intercept, slopes, interactions, variances, correlations) were lower than 1.05, while the ratio of effective samples sizes to total sample size was greater than 0.5 for all the parameters. The model computed a variance-covariance matrix (Ω_k) for each random effect (k). We extracted the among-environment, among-individual, and within-individual variance components and behavioural correlations using the function 'as_draws_df()' in the 'brms' package (for details, consult the code files on the GitHub repository: <https://github.com/quantitative-ecologist/predator-foraging-mode-videogames>). We could thus compute the mean of the variance and correlation sample values, and the HDP intervals to obtain their 95% credibl intervals. The variance-covariance matrices were parametrized as:

$$\begin{bmatrix} en_{0y1,g} \\ en_{0y2,g} \\ en_{0y3,g} \\ en_{0y4,g} \end{bmatrix} = MVN(0, \Omega_{en}): \text{where } \Omega_{en} = \begin{bmatrix} V_{en_{0y1}} & \cdots & Cov_{en_{0yn}en_{0y1}} \\ \vdots & \ddots & \vdots \\ Cov_{en_{0yn}en_{0y1}} & \cdots & V_{en_{0yn}} \end{bmatrix} \quad (\text{eq.1})$$

$$\begin{bmatrix} av_{0y1,h} \\ av_{0y2,h} \\ av_{0y3,h} \\ av_{0y4,h} \end{bmatrix} = MVN(0, \Omega_{av}): \text{where } \Omega_{av} = \begin{bmatrix} V_{av_{0y1}} & \cdots & Cov_{av_{0yn}av_{0y1}} \\ \vdots & \ddots & \vdots \\ Cov_{av_{0yn}av_{0y1}} & \cdots & V_{av_{0yn}} \end{bmatrix} \quad (\text{eq.2})$$

$$\begin{bmatrix} id_{0y1,i} \\ id_{0y2,i} \\ id_{0y3,i} \\ id_{0y4,i} \end{bmatrix} = MVN(0, \Omega_{id}): \text{where } \Omega_{id} = \begin{bmatrix} V_{id_{0y1}} & \cdots & Cov_{id_{0yn}id_{0y1}} \\ \vdots & \ddots & \vdots \\ Cov_{id_{0yn}id_{0y1}} & \cdots & V_{id_{0yn}} \end{bmatrix} \quad (\text{eq.3})$$

$$\begin{bmatrix} \varepsilon_{0y1,ghij} \\ \varepsilon_{0y2,ghij} \\ \varepsilon_{0y3,ghij} \\ \varepsilon_{0y4,ghij} \end{bmatrix} = MVN(0, \Omega_{\varepsilon}): \text{where } \Omega_{\varepsilon} = \begin{bmatrix} V_{\varepsilon_{0y1}} & \cdots & Cov_{\varepsilon_{0yn}\varepsilon_{0y1}} \\ \vdots & \ddots & \vdots \\ Cov_{\varepsilon_{0yn}\varepsilon_{0y1}} & \cdots & V_{\varepsilon_{0yn}} \end{bmatrix} \quad (\text{eq.4})$$

where the diagonals represent the random effect (k) variance ($V_{k_{0yn}}$) for each hunting trait (y_n), and the lower off-diagonals the covariance between the random effect intercepts for each

combination of hunting traits (travel speed (y_1), the rate of space covered (y_2), the time spent guarding (y_3), and the time before first capture (y_4)).

We ran three additional multivariate mixed-models:

1. Different structure: without prey behaviour as fixed effects
2. Same structure: only on novice players
3. Same structure: only on experienced players

For the first model, we investigated if accounting for prey behaviour in the predator behavioural variation (i.e. removing prey as a control) had an effect on the variance parameters and the behavioural correlations. We used this approach to test the assertion that behavioural changes in prey behaviour could modulate the tactics used by individual predators, as well as the effect of the game environments on predator behaviour. We thus computed the same multivariate model and excluded prey travel speed and rate of space covered as the linear fixed effects. For the second and third models, we investigated if the relationships between the predator behaviours (i.e. their correlations) changed with player experience. To do so, we applied the same model procedure on two distinct datasets based on player experience by splitting the total experience of individual players from the main dataset into quartiles. This resulted in 75% of the players having played up to 31 matches, which represented ~five hours of gameplay. Based on their cumulative number of matches, we then assigned novice players as those who played between one and 31 matches, and players with experience as those having above 31 cumulative matches played. Individuals who played above 31 matches could thus be found in both the novice and experienced players' datasets. We split our data this way because if we separated players based on their total number of matches, we would have had matches for experienced players where they were still novices.

Parameterization of the Bayesian mixed-models for hunting success

We computed four different models to investigate the relationship between predator behaviour, prey behaviour, and their interactions with hunting success. For all models, we used a half-normal prior for the variance parameters with a mean of 0 and a standard deviation of 1, and a Gaussian prior with a mean of 0 and a standard deviation of 2 for the fixed effects. We set up the four models

to run four chains using 2500 iterations, where samples were drawn at every eight intervals (thinning), and used the first 500 iterations for warmup. We visually inspected trace plots, effective sample sizes, and residuals to assess convergence and stability. We also evaluated the models' prediction accuracies using posterior predictive checks. The rhat values of the models' main parameters (intercept, slopes, interactions, variances) were lower than 1.05, while the ratio of effective samples sizes to total sample size was greater than 0.5 for all except the general intercept (0.43). We calculated the ICC estimate for each random effect (k) using the function `as_draws_df()` in the 'brms' package. To do so, we divided each random effect variance sample value by the total variance (following Nakagawa et al. 2017). We used the mean of the posterior variance parameters to compute the ICC_k values, and used the HDP intervals to obtain their corresponding 95% credible intervals.

For the first model, we aimed at investigating the linear relationship between hunting success and predator behaviour exclusively. The model was parametrized as:

$$\begin{aligned}
 \text{logit}(P_{hij}) = & (\beta_0 + env_{0,h} + id_{0,i} + \varepsilon_{0,hij}) \\
 & + \beta_{1,pred} speed_{hi} \\
 & + \beta_{2,pred} space_{hi} \\
 & + \beta_{3,pred} guarding\ time_{hi} \\
 & + \beta_{4,pred} time\ 1^{st}\ capture_{hi}
 \end{aligned}
 \tag{eq.5}$$

We included prey behaviour in the second model and kept the same structure as equation 5. The model was parametrized as:

$$\begin{aligned}
 \text{logit}(P_{hij}) = & (\beta_0 + env_{0,h} + id_{0,i} + \varepsilon_{0,hij}) \\
 & + \beta_{1,pred} speed_{hi} \\
 & + \beta_{2,pred} space_{hi} \\
 & + \beta_{3,pred} guarding\ time_{hi} \\
 & + \beta_{4,pred} time\ 1^{st} capture_{hi} \\
 & + \beta_{5,prey} speed'_{hi} \\
 & + \beta_{6,prey} space'_{hi}
 \end{aligned}
 \tag{eq.6}$$

In the third model, we were interested in investigating nonlinear relationships between hunting success and predator behaviour exclusively. We thus added quadratic effects for each hunting trait. We also investigated how predator behaviours interact to affect hunting success. This model was computed as:

$$\begin{aligned}
 \text{logit}(P_{hij}) = & (\beta_0 + env_{0,h} + id_{0,i} + \varepsilon_{0,hij}) \\
 & + \beta_{1,pred} speed_{hi} + \beta_{2,pred} space_{hi} \\
 & + \beta_{3,pred} guarding\ time_{hi} + \beta_{4,pred} time\ 1^{st} capture_{hi} \\
 & + \frac{1}{2} \gamma_{1,pred} speed_{hi}^2 + \frac{1}{2} \gamma_{2,pred} space_{hi}^2 \\
 & + \frac{1}{2} \gamma_{3,pred} guarding\ time_{hi}^2 + \frac{1}{2} \gamma_{4,pred} time\ 1^{st} capture_{hi}^2 \\
 & + \gamma_{1,pred} (speed_{hi} \cdot space_{hi}) \\
 & + \gamma_{2,pred} (speed_{hi} \cdot guarding\ time_{hi}) \\
 & + \gamma_{3,pred} (speed_{hi} \cdot time\ 1^{st} capture_{hi}) \\
 & + \gamma_{4,pred} (space_{hi} \cdot guarding\ time_{hi}) \\
 & + \gamma_{5,pred} (space_{hi} \cdot time\ 1^{st} capture_{hi}) \\
 & + \gamma_{6,pred} (guarding\ time_{hi} \cdot time\ 1^{st} capture_{hi})
 \end{aligned} \tag{eq.7}$$

The fourth and final model included prey behaviours with their quadratic effects as well as their interactions with predator behaviour to investigate how they jointly affect hunting success. The model is described as:

$$\begin{aligned}
 \text{logit}(P_{hij}) = & (\beta_0 + env_{0,h} + id_{0,i} + \varepsilon_{0,hij}) \\
 & + \beta_{1,pred} speed_{hi} + \beta_{2,pred} space_{hi} \\
 & + \beta_{3,pred} guarding\ time_{hi} + \beta_{4,pred} time\ 1^{st} capture_{hi} \\
 & + \beta_{5,prey} speed'_{hi} + \beta_{6,prey} space'_{hi} \\
 & + \frac{1}{2} \gamma_{1,pred} speed_{hi}^2 + \frac{1}{2} \gamma_{2,pred} space_{hi}^2 \\
 & + \frac{1}{2} \gamma_{3,pred} guarding\ time_{hi}^2 + \frac{1}{2} \gamma_{4,pred} time\ 1^{st} capture_{hi}^2 \\
 & + \frac{1}{2} \gamma_{5,prey} speed'_{hi}^2 + \frac{1}{2} \gamma_{6,prey} space'_{hi}^2 \\
 & + \gamma_{1,pred} (speed_{hi} \cdot space_{hi}) \\
 & + \gamma_{2,pred} (speed_{hi} \cdot guarding\ time_{hi}) \\
 & + \gamma_{3,pred} (speed_{hi} \cdot time\ 1^{st} capture_{hi}) \\
 & + \gamma_{4,pred} (space_{hi} \cdot guarding\ time_{hi}) \\
 & + \gamma_{5,pred} (space_{hi} \cdot time\ 1^{st} capture_{hi}) \\
 & + \gamma_{6,pred} (guarding\ time_{hi} \cdot time\ 1^{st} capture_{hi}) \\
 & + \gamma_{7,pred\ prey} (speed_{hi} \cdot speed'_{hi}) \\
 & + \gamma_{8,pred\ prey} (speed_{hi} \cdot space'_{hi}) \\
 & + \gamma_{9,pred\ prey} (space_{hi} \cdot speed'_{hi}) \\
 & + \gamma_{10,pred\ prey} (space_{hi} \cdot space'_{hi}) \\
 & + \gamma_{11,pred\ prey} (guarding\ time_{hi} \cdot speed'_{hi}) \\
 & + \gamma_{12,pred\ prey} (guarding\ time_{hi} \cdot space'_{hi}) \\
 & + \gamma_{13,pred\ prey} (time\ 1^{st} capture_{hi} \cdot speed'_{hi}) \\
 & + \gamma_{14,pred\ prey} (time\ 1^{st} capture_{hi} \cdot space'_{hi})
 \end{aligned} \tag{eq.8}$$

Results

Principal components analysis

The first principal component (PC1) explained 20.9% of the total variation, and the second principal component (PC2) explained 19.6% of the total variation in the data (Figure A.1). We found that the time before the first capture, the rate of space covered, and the time spent guarding had the highest contributions (36.71%, 27.04%, and 23.38% respectively) to the first principal component (Table A.1), while the travel speed had the highest contribution (33.29%) to the second principal component (Table A.1). Although the amount of times the predator damaged a generator explained almost an equivalent portion of the variation of the second principal component, we only kept travel speed because its contribution was higher and more ecologically meaningful.

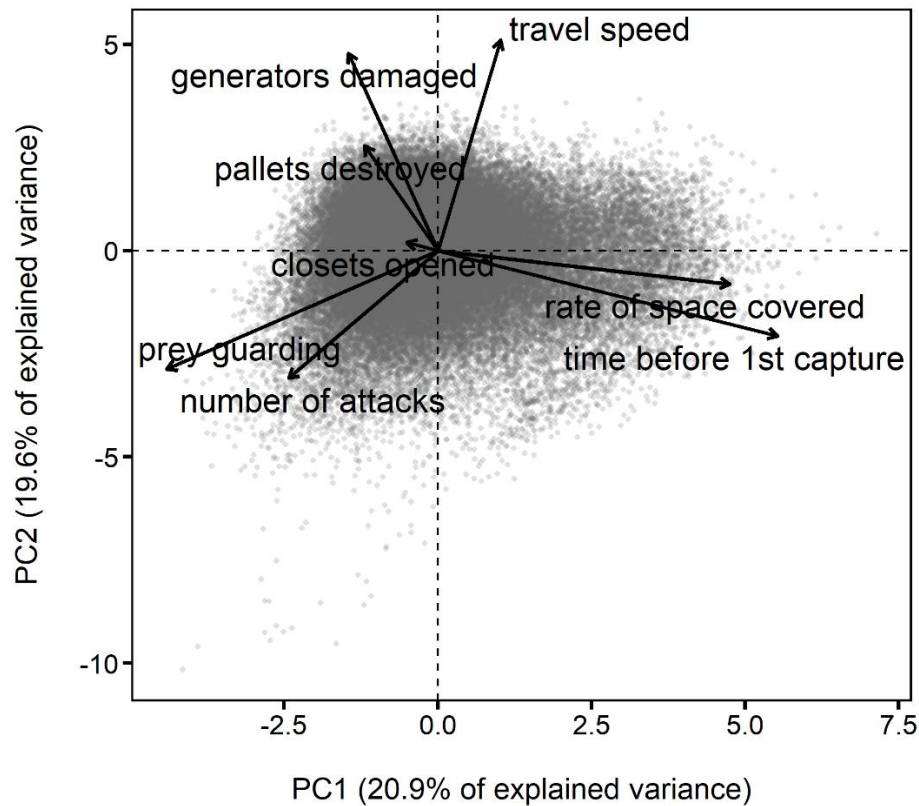


Figure A.1 Biplot of the principal components analysis on predator hunting behaviours. The variables presented in the main text were selected based on their relative contribution (%) to the first and second principal components.

Table A.1 Principal component loadings for all the predator behavioural traits

	PC1 (% variance = 20.9)		PC2 (% variance = 19.6)	
	Correlation	% variance	Correlation	% variance
travel speed	0.14	1.25	0.72	33.29
rate of space covered	0.67	27.04	-0.12	0.85
prey guarding	-0.62	23.38	-0.41	10.54
closets opened	-0.07	0.30	0.03	0.05
pallets destroyed	-0.17	1.70	0.36	8.26
generators damaged	-0.21	2.54	0.68	29.31
time before 1st capture	0.78	36.71	-0.29	5.47
number of attacks	-0.34	7.09	-0.44	12.22

Intra-class correlation coefficients of the predator behaviours for the three additional multivariate mixed-models

After removing prey behaviour as linear fixed effects (model 2), the relative contribution (%) of the game environments to the variation in travel speed, the time spent guarding, and the time required to capture the first prey was comparable to the first model (Table A.2). Thus, the expression of these behaviours was similar among the game environments. However, among environmental differences in the rate of space covered increased (Table A.2). Results show that novice and experienced players obtained similar ICCs for several of their random effects. However, experienced players were more similar in their average behaviour than novice players.

Table A.2 Posterior means of the ICC estimates for the three additional multivariate mixed-models.

Behaviour	Random effect	ICC (95% CI) Without prey	ICC (95% CI) Novices	ICC (95% CI) Experienced
travel speed	player ID	0.28 (0.26, 0.30)	0.35 (0.32, 0.38)	0.19 (0.16, 0.22)
	game environment	0.00 (0.00, 0.00)	0.00 (0.00, 0.00)	0.00 (0.00, 0.00)
	avatar	0.09 (0.04, 0.14)	0.09 (0.04, 0.15)	0.10 (0.05, 0.17)
	residuals	0.63 (0.59, 0.67)	0.56 (0.51, 0.59)	0.71 (0.65, 0.76)
space covered	player ID	0.08 (0.06, 0.09)	0.06 (0.05, 0.07)	0.06 (0.05, 0.07)
	game environment	0.19 (0.12, 0.29)	0.04 (0.02, 0.06)	0.19 (0.12, 0.28)
	avatar	0.01 (0.01, 0.03)	0.02 (0.01, 0.03)	0.02 (0.01, 0.03)
	residuals	0.72 (0.64, 0.79)	0.88 (0.86, 0.91)	0.73 (0.65, 0.80)
guard time	player ID	0.31 (0.28, 0.33)	0.23 (0.21, 0.25)	0.15 (0.13, 0.18)
	game environment	0.00 (0.00, 0.00)	0.02 (0.01, 0.02)	0.00 (0.00, 0.00)
	avatar	0.03 (0.01, 0.05)	0.02 (0.01, 0.04)	0.04 (0.01, 0.07)
	residuals	0.67 (0.64, 0.69)	0.73 (0.71, 0.75)	0.81 (0.77, 0.84)
time 1st capture	player ID	0.26 (0.24, 0.28)	0.21 (0.20, 0.23)	0.15 (0.13, 0.17)
	game environment	0.01 (0.00, 0.01)	0.03 (0.02, 0.04)	0.01 (0.00, 0.01)
	avatar	0.03 (0.01, 0.05)	0.02 (0.01, 0.04)	0.03 (0.01, 0.06)
	residuals	0.70 (0.68, 0.73)	0.74 (0.71, 0.76)	0.81 (0.78, 0.84)

Table A.3 Among-individual and within-individual behavioural correlations for the three additional multivariate mixed-models. The among-individual correlations are on the lower off-diagonal and the residual within-individual correlations on the upper off-diagonal.

	speed	space	prey guarding	time 1st cap.
Model: without prey				
speed	-	0.21 (0.21, 0.22)	-0.05 (-0.05,-0.06)	-0.07 (-0.06,-0.07)
space	-0.03 (-0.09, 0.04)	-	-0.25 (-0.24,-0.26)	0.09 (0.08, 0.10)
prey guarding	0.06 (0.00, 0.13)	-0.48 (-0.42,-0.54)	-	-0.43 (-0.43,-0.44)
time 1st cap.	-0.41 (-0.35,-0.46)	0.59 (0.53, 0.64)	-0.73 (-0.70,-0.76)	-
Model: novice players				
speed	-	0.22 (0.21, 0.23)	-0.13 (-0.12,-0.14)	-0.02 (-0.01,-0.03)
space	0.50 (0.44, 0.57)	-	-0.19 (-0.18,-0.21)	0.07 (0.05, 0.08)
prey guarding	0.08 (0.02, 0.14)	0.05 (-0.04, 0.14)	-	-0.45 (-0.44,-0.46)
time 1st cap.	-0.49 (-0.45,-0.55)	-0.21 (-0.13,-0.29)	-0.62 (-0.58,-0.66)	-
Model: experienced players				
speed	-	0.22 (0.21, 0.23)	0.00 (-0.01, 0.01)	-0.11 (-0.10,-0.12)
space	-0.03 (-0.15, 0.09)	-	-0.23 (-0.21,-0.24)	0.04 (0.02, 0.06)
prey guarding	-0.21 (-0.10,-0.32)	-0.04 (-0.16, 0.09)	-	-0.39 (-0.38,-0.40)
time 1st cap.	-0.29 (-0.19,-0.39)	0.38 (0.27, 0.48)	-0.41 (-0.32,-0.50)	-

Selection of the best hunting success model

The model with the lowest expected log predictive density was chosen as the best model for our interpretations of the relationship between behaviour and hunting success.

Table A.4 Summary table comparing the hunting success models based on approximate leave-one-out cross-validation.

model	elpd difference	sd difference	elpd loo value	elpd loo standard error
quadratic model pred-prey	0.00	0.00	-96 276.18	239.14
linear model pred-prey	-2 356.80	94.08	-98 632.99	239.65
quadratic model pred	-7 243.63	138.56	-103 519.82	250.09
linear model pred	-8 905.85	156.73	-105 182.03	248.13

Interaction effects of predator behavioural traits on hunting success

Figure A.2 shows the interacting effects of all the combinations of predator behaviours on predator hunting success drawn from the parameters presented in Table 1 in the main text.

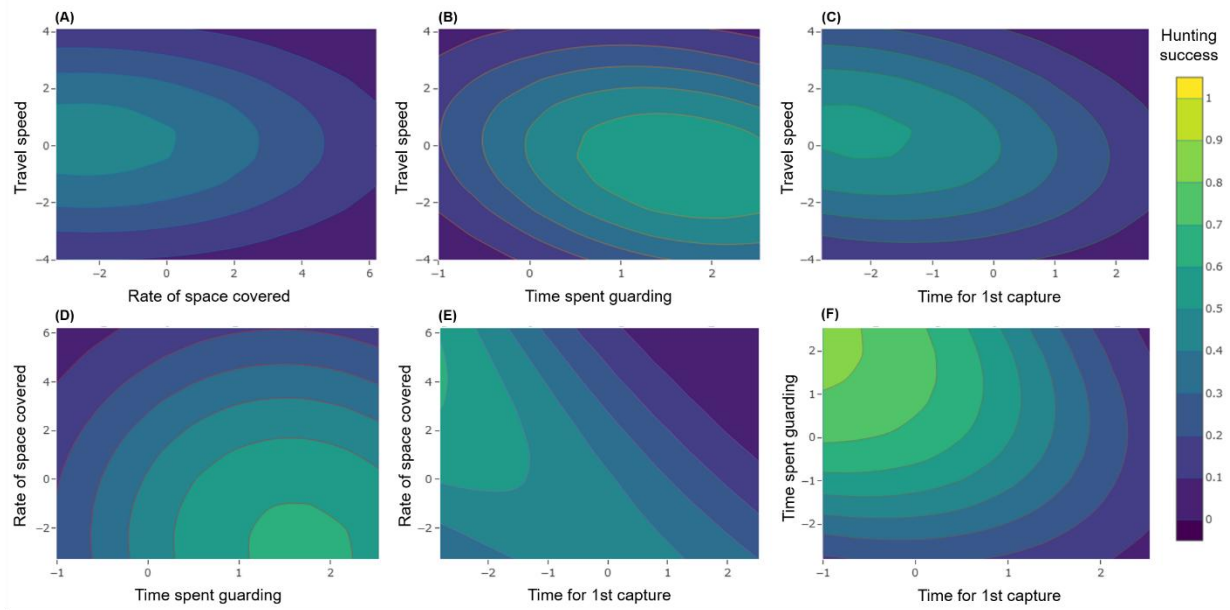


Figure A.2 Interacting effects of the predator behaviours on hunting success. Hunting success is represented by the color gradient. We computed the plots by predicting the mean probability of capturing four prey based on the best quadratic approximation of the predator behaviour interaction terms. (A) Travel speed and the rate of space covered. (B) Travel speed and the time spent guarding prey. (C) Time before the first capture and travel speed. (D) The rate of space covered and the time spent guarding. (E) The rate of space covered and the time before the first capture. (F) The time spent guarding prey and the time before the first capture.

ANNEXE B

SUPPORTING INFORMATION FOR:

THE ROLE OF PREY BEHAVIOUR IN PREDATOR EXPERTISE ACQUISITION: INSIGHTS FROM A VIRTUAL ECOSYSTEM

Table B.1 Fixed effects table comparing the success of random groups of players with different amounts of matches played to the group presented in the main text. Group 1: <50 matches, Group 2: between 50 and 99 matches, Group 3: between 100 and 299 matches, Group 4: > 299 (i.e. group in the main text).

Parameter	Estimate	lower 89% CI	upper 89% CI
game duration	0.55	0.53	0.56
cumulative experience	0.30	0.29	0.31
prey rank	0.64	0.62	0.66
group 1	0.03	-0.06	0.11
group 2	-0.01	-0.12	0.10
group 3	0.10	0.00	0.21
group 4	0.01	-0.16	0.16

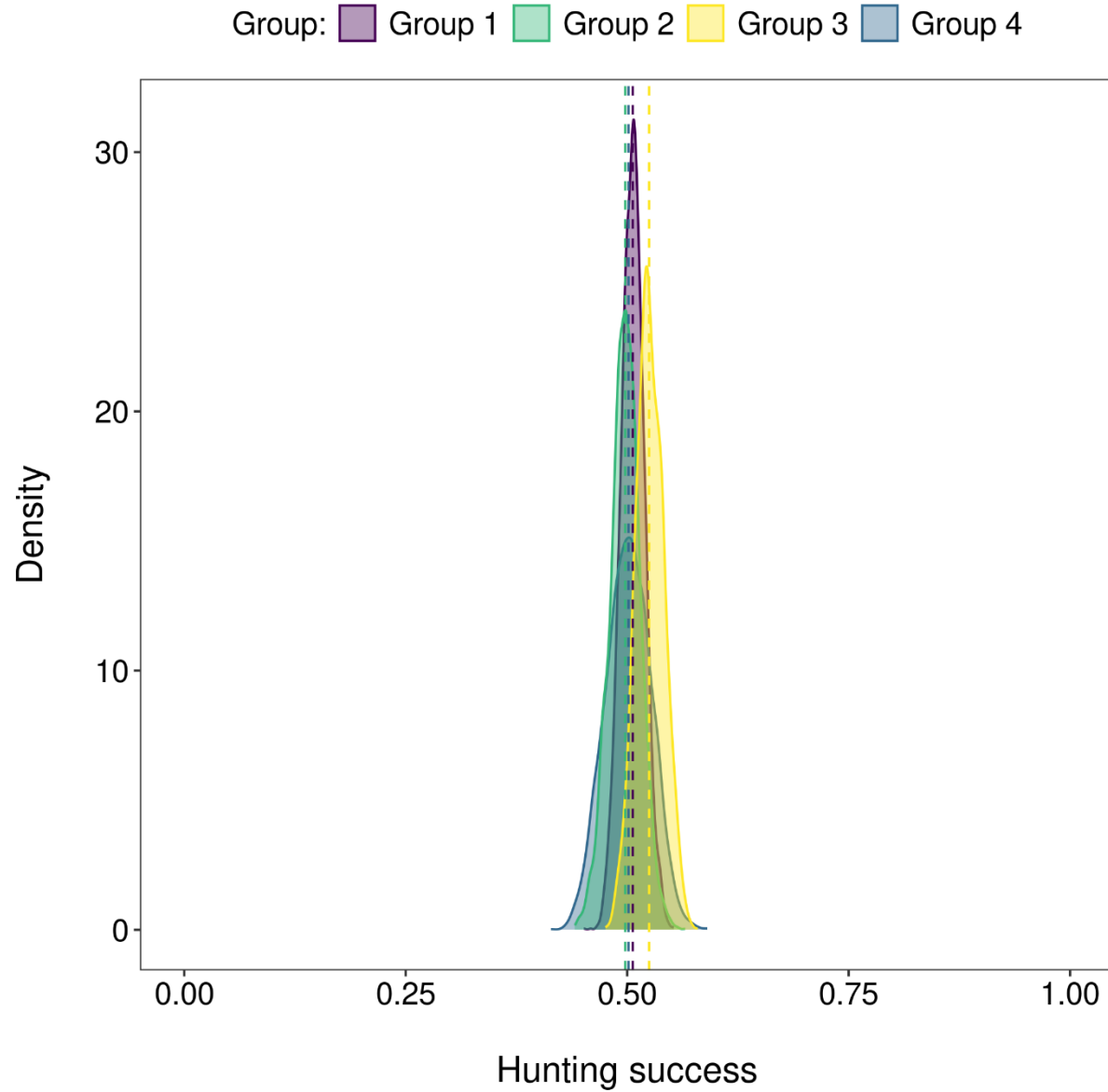


Figure B.1 Posterior distributions of the median hunting success per group of players. The values were back-transformed to probability scale and can be interpreted as the probability of capturing the four prey. Group 1: <50 matches, Group 2: between 50 and 99 matches, Group 3: between 100 and 299 matches, Group 4: > 299 (i.e. group in the main text).

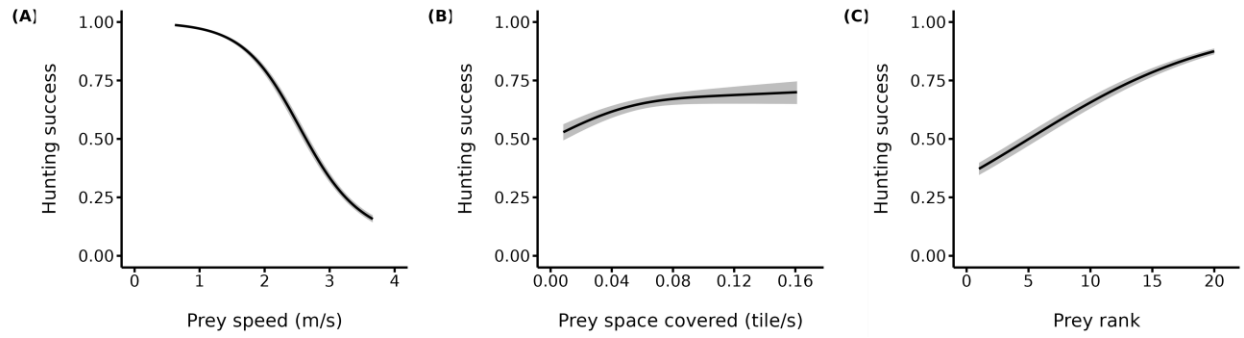


Figure B.2 Median posterior predictions of the effects of prey features on the predator's hunting success. The predators' hunting success (i.e., the probability of consuming the four prey) is on the y-axis, and the prey's features are on the x-axis. Panel A shows the effect of prey speed on the predator's hunting success. Panel B shows the effect of the prey's space coverage on hunting success. Panel C shows the effect of the prey's rank. The predictions are from Model III.

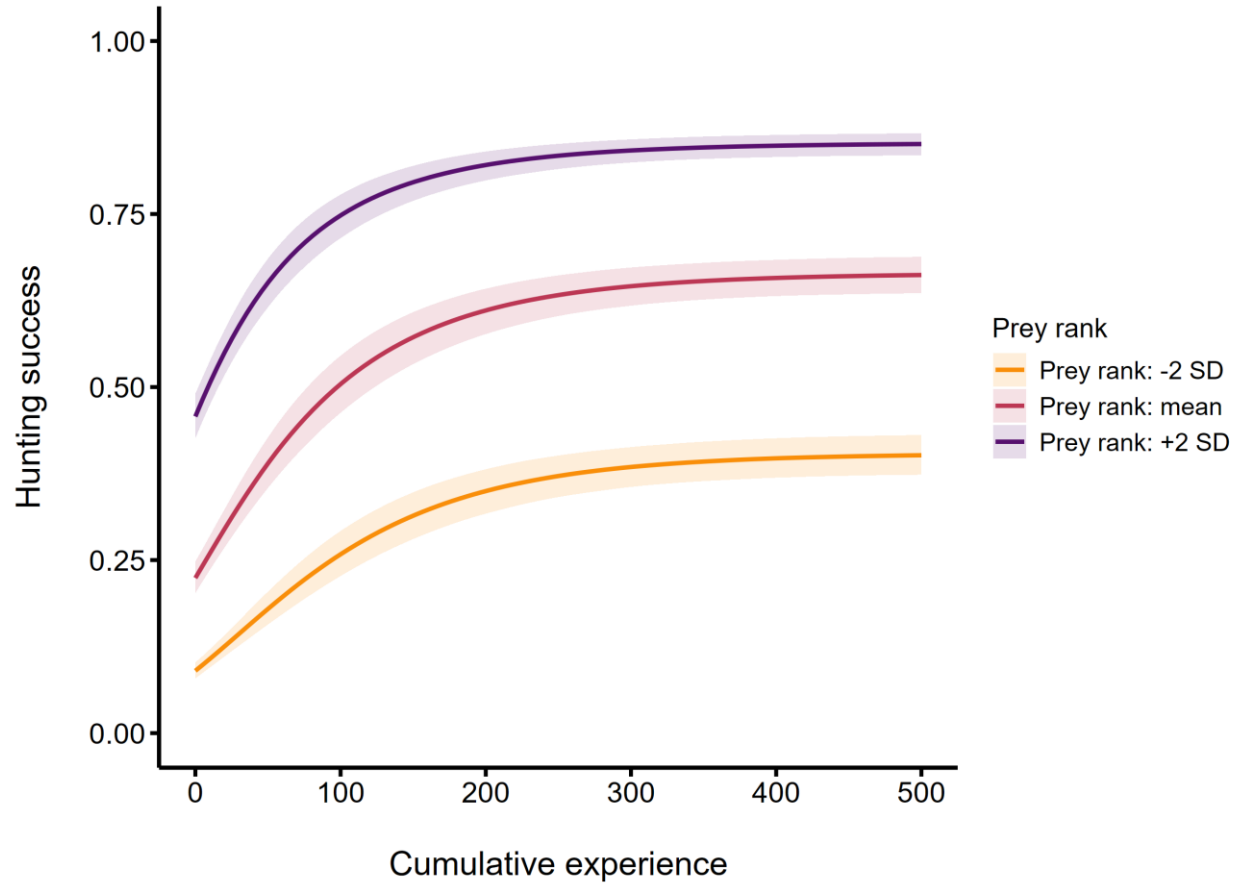


Figure B.3 Median posterior predictions of the development of predator expertise, holding the mean rank of the prey group at different fixed values ($\text{mean} \pm 2 \text{ SD}$). The predators' hunting success (i.e., the probability of consuming the four prey) is on the y-axis, and the cumulated experience is on the x-axis. Lower rank values indicate higher skill (rank 1 being the best rank). The predictions are from Model III.

ANNEXE C

SUPPORTING INFORMATION FOR:

INDIVIDUAL FORAGING SPECIALISATION AND SUCCESS CHANGE ACROSS EXPERIENCE IN A VIRTUAL PREDATOR-PREY SYSTEM

Table C.1 Posterior medians and 95% HPD intervals of the fixed effects estimated by the MDHGLM of predator speed, prey speed, and predator hunting success. 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. 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.

Trait	Parameter	Novice	Intermediate	Advanced
predator speed	intercept (mean)	3.29 (3.15, 3.41)	3.27 (3.10, 3.42)	3.27 (3.12, 3.43)
	prey rank (mean)	-0.02 (-0.02, -0.01)	-0.02 (-0.03, -0.02)	-0.03 (-0.03, -0.03)
	intercept (sigma)	0.28 (0.27, 0.29)	0.30 (0.28, 0.31)	0.29 (0.27, 0.30)
	prey rank (sigma)	0.99 (0.98, 1.00)	0.98 (0.97, 0.99)	0.99 (0.98, 1.00)
prey speed	intercept (mean)	2.34 (2.31, 2.36)	2.42 (2.39, 2.46)	2.42 (2.39, 2.46)
	prey rank (mean)	-0.11 (-0.12, -0.11)	-0.11 (-0.12, -0.11)	-0.11 (-0.12, -0.11)
	intercept (sigma)	0.29 (0.29, 0.29)	0.27 (0.27, 0.28)	0.27 (0.27, 0.27)
	prey rank (sigma)	1.07 (1.05, 1.08)	1.07 (1.06, 1.08)	1.07 (1.05, 1.08)
hunting success	intercept (mean)	0.49 (0.46, 0.52)	0.51 (0.48, 0.54)	0.54 (0.51, 0.57)
	match duration (mean)	0.64 (0.64, 0.65)	0.64 (0.64, 0.65)	0.64 (0.64, 0.65)
	prey rank (mean)	0.60 (0.60, 0.61)	0.65 (0.64, 0.65)	0.65 (0.65, 0.66)

Table C.2 Posterior medians and 95% HPD intervals of the random effect standard deviations estimated by the MDHGLM of predator speed, prey speed, and predator hunting success. We exponentiated the dispersion parameters (i.e. sigma) which are estimated on a log scale. The standard deviation values on the mean part of the equation indicate, for all traits, among individual differences in mean behaviour, prey encountered, and success. The standard deviation values on the dispersion part of the equation (i.e. sigma) for predator speed indicate among individual differences in behavioural specialization. For prey speed, they indicate among individual differences in the variability of prey encounters.

Trait	Parameter	Novice	Intermediate	Advanced
predator speed	avatar (mean)	0.31 (0.22, 0.41)	0.36 (0.25, 0.48)	0.36 (0.26, 0.49)
	environment (mean)	0.02 (0.02, 0.03)	0.03 (0.02, 0.03)	0.03 (0.02, 0.03)
	predator ID (mean)	0.16 (0.14, 0.17)	0.15 (0.14, 0.17)	0.17 (0.15, 0.18)
	predator ID (sigma)	1.48 (1.44, 1.54)	1.52 (1.47, 1.57)	1.59 (1.53, 1.65)
prey speed	avatar (mean)	0.05 (0.04, 0.07)	0.06 (0.04, 0.08)	0.06 (0.04, 0.08)
	environment (mean)	0.06 (0.04, 0.07)	0.05 (0.04, 0.07)	0.05 (0.04, 0.07)
	predator ID (mean)	0.09 (0.08, 0.10)	0.08 (0.07, 0.09)	0.10 (0.09, 0.11)
	predator ID (sigma)	1.06 (1.04, 1.07)	1.07 (1.06, 1.08)	1.10 (1.09, 1.11)
hunting success	predator ID (mean)	0.90 (0.83, 0.98)	0.90 (0.82, 0.97)	0.93 (0.85, 1.01)

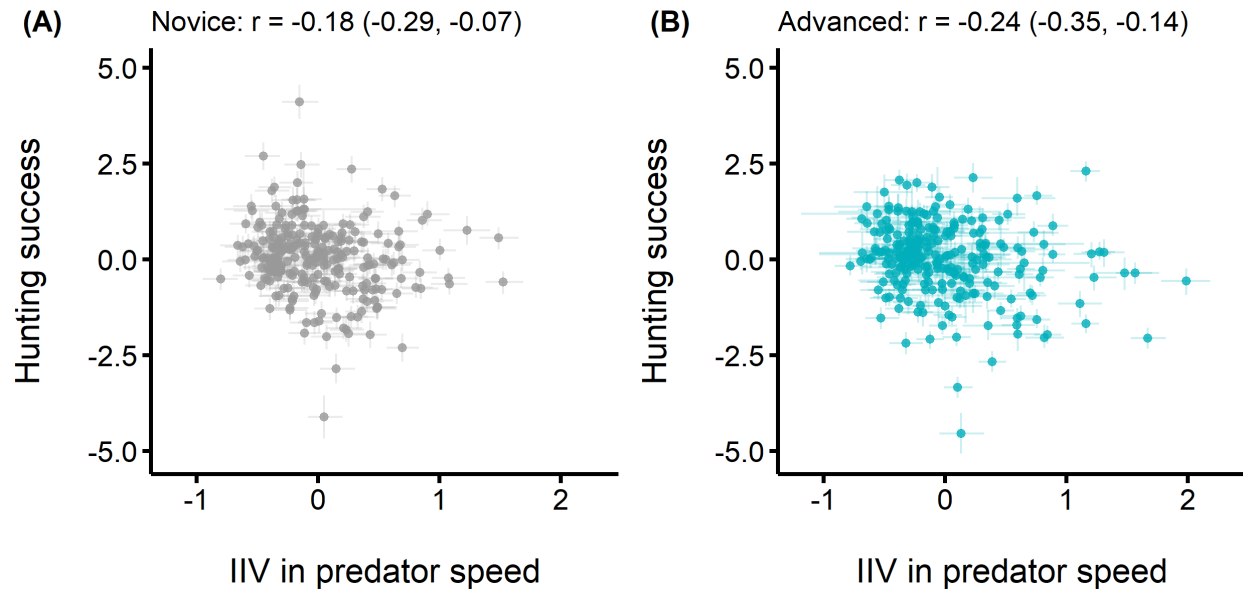


Figure C.1 Correlations between the predators' mean hunting success (y axis) and the intra-individual variance in speed (x axis) to test for differences in success between individuals along the flexible-specialist hunter continuum. Each point represents the posterior median predicted value of an individual predator along with its 95% HPD interval. Individuals with lower IIV are specialist hunters, while individuals with higher IIV are flexible hunters. (A) Correlation when predators were novice (B) Correlation when predators were advanced.

Table C.3 Posterior medians and 95% HPD intervals of the fixed effects estimated by the MDHGLM of predator speed, prey speed, and predator hunting success. The coefficients are from the model that includes the outlier. 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. 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.

Trait	Parameter	Novice	Intermediate	Advanced
predator speed	intercept (mean)	3.28 (3.17, 3.42)	3.28 (3.11, 3.41)	3.26 (3.12, 3.41)
	prey rank (mean)	-0.02 (-0.02, -0.02)	-0.02 (-0.03, -0.02)	-0.03 (-0.03, -0.03)
	intercept (sigma)	0.28 (0.27, 0.29)	0.30 (0.28, 0.32)	0.29 (0.27, 0.31)
	prey rank (sigma)	0.99 (0.98, 1.00)	0.98 (0.97, 0.99)	1.00 (0.98, 1.01)
prey speed	intercept (mean)	2.34 (2.30, 2.37)	2.42 (2.39, 2.45)	2.42 (2.39, 2.45)
	prey rank (mean)	-0.11 (-0.12, -0.11)	-0.11 (-0.12, -0.11)	-0.11 (-0.12, -0.11)
	intercept (sigma)	0.29 (0.29, 0.29)	0.27 (0.27, 0.28)	0.27 (0.27, 0.27)
	prey rank (sigma)	1.07 (1.06, 1.08)	1.07 (1.06, 1.08)	1.07 (1.06, 1.08)
hunting success	intercept (mean)	0.49 (0.46, 0.52)	0.51 (0.48, 0.54)	0.54 (0.51, 0.57)
	match duration (mean)	0.64 (0.64, 0.65)	0.64 (0.64, 0.65)	0.64 (0.64, 0.65)
	prey rank (mean)	0.60 (0.60, 0.61)	0.65 (0.64, 0.65)	0.65 (0.65, 0.66)

Table C.4 Posterior medians and 95% HPD intervals of the random effect standard deviations estimated by the MDHGLM of predator speed, prey speed, and predator hunting success. The coefficients are from the model that includes the outlier. We exponentiated the dispersion parameters (i.e. sigma) which are estimated on a log scale. The standard deviation values on the mean part of the equation indicate, for all traits, among individual differences in mean behaviour, prey encountered, and success. The standard deviation values on the dispersion part of the equation (i.e. sigma) for predator speed indicate among individual differences in behavioural specialization. For prey speed, they indicate among individual differences in the variability of prey encounters.

Trait	Parameter	Novice	Intermediate	Advanced
predator speed	avatar (mean)	0.30 (0.22, 0.39)	0.36 (0.26, 0.49)	0.37 (0.27, 0.49)
	environment (mean)	0.02 (0.02, 0.03)	0.03 (0.02, 0.03)	0.03 (0.02, 0.03)
	predator ID (mean)	0.16 (0.15, 0.17)	0.15 (0.14, 0.17)	0.20 (0.18, 0.22)
	predator ID (sigma)	1.48 (1.43, 1.53)	1.52 (1.47, 1.58)	1.59 (1.53, 1.65)
prey speed	avatar (mean)	0.05 (0.04, 0.07)	0.06 (0.05, 0.08)	0.06 (0.04, 0.08)
	environment (mean)	0.06 (0.04, 0.07)	0.05 (0.04, 0.07)	0.05 (0.04, 0.07)
	predator ID (mean)	0.09 (0.08, 0.10)	0.08 (0.07, 0.09)	0.11 (0.10, 0.12)
	predator ID (sigma)	1.06 (1.04, 1.07)	1.08 (1.07, 1.09)	1.10 (1.09, 1.11)
hunting success	predator ID (mean)	0.89 (0.82, 0.98)	0.90 (0.83, 0.97)	0.93 (0.86, 1.02)

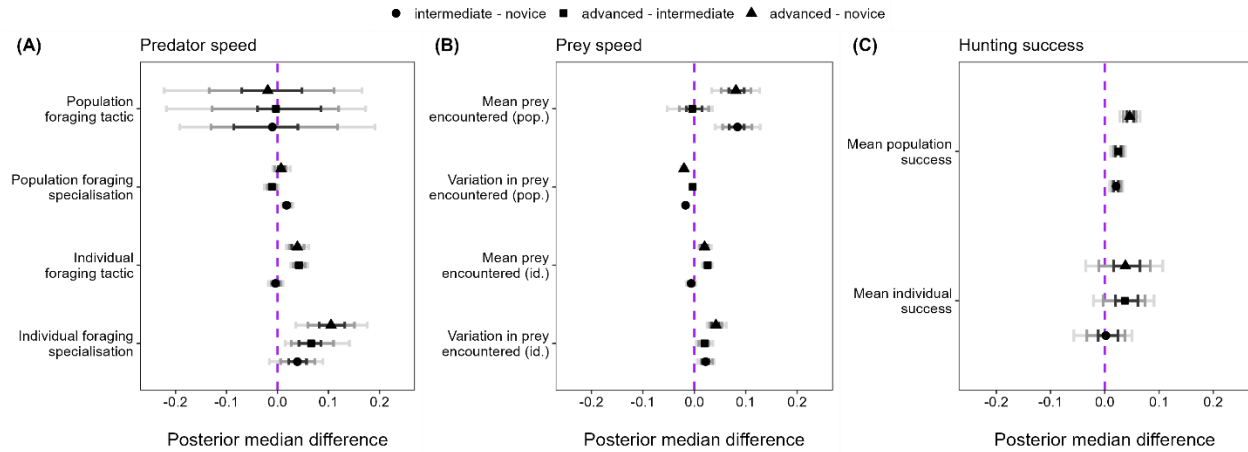


Figure C.2 Median posterior differences and HPD intervals comparing predator foraging behaviour, prey behaviour, and predator hunting success at the population and individual level across experience stages. The parameters being compared are on the y axis, and the differences in parameter values between 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. The results are from the model that includes the outlier.

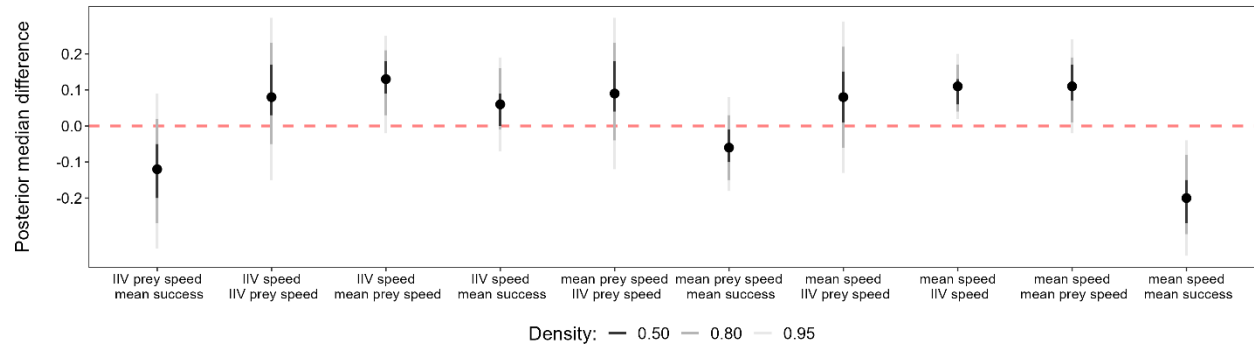


Figure C.3 Posterior median differences and HPD intervals comparing the trait correlations predicted by the MDHGLM between the advanced and novice levels. The difference is displayed on the y axis and the correlated parameters are displayed on the x axis. Positive values indicate that the correlation was greater when predators were advanced, while negative values indicate that the correlation was greater when predators were novices. The results are from the MDHGLM that includes the outlier.

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