Hunting experience and prey variability jointly shape individual foraging specialisation in a predator-prey videogame

# Abstract

Keywords: foraging behaviour, individual specialization, experience, learning, prey predictability, online videogames

# Introduction

Individual variation in predator foraging behaviour is increasingly recognized as a major driver of trophic interactions and community dynamics (Lima 2002; Schreiber *et al.* 2011; Pettorelli *et al.* 2015; Michalko & Pekár 2016). Indeed, predator populations are often composed of assemblages of individuals specializing in different foraging strategies or resources irrespective of sexual, morphological, or age-related differences (Estes *et al.* 2003; Tinker *et al.* 2008; Kernaléguen *et al.* 2015; Phillips *et al.* 2017) (FIND SOME TERRESTRIAL ANIMAL REFS). A growing body of evidence suggests that ecological interactions, such as predator-prey interactions, can be major drivers of such individual foraging specialization (Araújo *et al.* 2011; Toscano *et al.* 2016). When hunting, predators often use hunting techniques that are fine-tuned to the type of prey that they encounter (Davoren *et al.* 2003; Estes *et al.* 2003; Woo *et al.* 2008; Courbin *et al.* 2018), and their capacity to use them effectively is contingent on periods of extensive practice (i.e. expertise). While the development of hunting expertise may be essential to maintain foraging success, we have have limited evidence for its role in predator foraging specialization, and the ecological/fitness consequences of such among individual behavioural differences for predator-prey interactions.

The integration of individual behavioral variation into studies of predator-prey interactions has gained traction in recent years, with a series of empirical papers revealing important consequences for functional responses, habitat use, and prey choice (REFS). However, an important and recurring challenge impeding empirical studies of predator-prey behavioral interactions, at the individual level, is the need of collecting data simultaneously on both the predator and prey. We have recently demonstrated with behavioural data from an online predator-prey videogame that virtual systems can uncover subtle details on the mechanisms shaping these interactions (Fraser Franco *et al.* 2022). For instance, we tested the classical locomotor crossover hypothesis championed by Huey & Pianka (1981), and found support of its predictions only for active hunters, which concords with a recent experiment involving assassin bugs (Matsumura & Miyatake 2022). Thus, general ecological patterns can potentially be derived from these virtual systems and may help in advacing the current gaps in predator-prey research. Other examples of virtual ecological studies show that predation regimes can drive individual variation in risk perception (Beauchamp 2020), that familiarity with prey partners has a positive indirect effect on survival (Céré *et al.* 2021), and that prey face contrasting natural and social selection regimes [Santostefano et al. in prep]. Because these systems generate large volumes of data on prey and predators simultaneously throughout their lifetime in the game, they offer the opportunity of uncovering how expertise and prey behavior shape individual predator foraging specialization and its potential fitness consequences.

The development of foraging strategies is crucial for young predators to reach adulthood and survive (Phillips *et al.* 2017; Heithaus *et al.* 2018). Theory predicts that foraging specialization may emerge via learning, limitations in memorizing multiple complex hunting skills, and expertise (Tinker *et al.* 2009; Dukas 2019). Dukas (2019) defines expertise as the characteristics, skills, and knowledge allowing individuals with extensive experience to outperform novices on complex tasks. This body of work suggests that the development of expertise is an optimizing process that promotes foraging specialization. Empirical studies show that expertise allows predators to optimize the efficiency (e.g. search and handling times, return rates) of their foraging tactics potentially via associative images or reliance on prey and environmental cues (Edwards & Jackson 1994; Morse 2000; Reid *et al.* 2010; Wilson-Rankin 2015). Such optimization may thus reinforce the use of the same tactic (i.e. specialization) if its success is constant each time a prey is encountered. It may also be costly to attempt different hunting tactics when prey are scarce or highly unpredictable (Estes *et al.* 2003; Mery & Burns 2010). An alternative mechanism is that expertise may offset the costs/risks of switching foraging tactics as individuals gain experience and information on their prey or their environment, leading to increased individual foraging flexibility (Ishii & Shimada 2010; Mery & Burns 2010; Snell-Rood 2013). In this case, switching between foraging tactics would be advantageous when resources are variable, as behavioural flexibility is often key for survival in novel environments (reviewed in Snell-Rood 2013) (FIND OTHER REFS TO SUPPORT THIS MAYBE DAN SOL?).

*ou juste dire que pour comprendre le role de l’expertise, il faut s’attarder à l’étudier avec la specialisation et voir les consequences pour la fitness ou issue des interactions predateur proie. ca introduit mieux je crois. dire genre que une théorie prédit que spécialisation est avantage quand proies peu variable, et ensuite ça lie bien l’hypothèse de variabilité que je décris en bas. faire ressortir qu’il n’y a pas de consencus. There is right now no concencus as to whether blabla, (examples)* Some long-term studies show that generalist and specialist individuals can achieve similar fitness [sources: à partir de Woo]. An emerging explanation is that temporal fluctuations in the predictability of resources (abundance, availability, behaviour) may favor one or the other strategy depending on time scales [sources : Woo, Phillips, Ceia, etc, Courbin, Chang]. The resource-predictability hypothesis advances that when resources are predictable, particularly on short time-scales, individual specialists should benefit from higher fitness returns. The rationale is that individuals should have higher prey delivery rates when they repeatedly employ the same foraging technique, as it is easier to assess prey predictability over shorter time-scales. In contrast, individual generalists should be advantaged over longer time scales, as resource parameters are expected to fluctuate. [revoir ceia et ramos pour les sources] *ce qu’il manque, c’est qu’on a aucune idée comment des différences individuelles de variabilité environnementale se traduisent par des différences de stratégies* sources générales sur heterogeneité(Weimerskirch 2007; Ceia & Ramos 2015; Phillips *et al.* 2017; Patrick *et al.* 2021).

Here, we analyze individual behavioural data provided by a videogame company from players in *Dead by Daylight* to test how hunting expertise and prey behaviour shape predator foraging specialization. *Dead by Daylight* is an online videogame simulating a predator-prey interaction, where one predator player hunts four prey players in different virtual environments. The data grants a high degree of precision on the behavioural interaction as both the predator and the four prey were measured simultaneously in each trial. First, we investigate how predators developped their individual hunting expertise. We hypothesize that predators should differ in the development of their expertise because they encounter varying levels of difficulty with the prey that they hunt. Second, we test the hypothesis that individual variation in foraging behaviour will change with expertise. If expertise reduces the costs of switching between hunting tactics, we predict that individual predators should become more flexible with time. Alternatively, if expertise enables the refinement of the hunting tactics, then individuals may instead specialize. Third, we evaluate how predator foraging specialization interacts with variation in prey behaviour. Whether predators specialize or not with expertise may depend on the behaviour of their prey, for instance, as it may be harder to specialize when encounters are less predictable. Lastly, if individuals differ in their degree of foraging specialization, then we expect that the success of specialists and generalists will be equal. Specialist hunters should fare better when prey variability is lower, while flexible hunters should fare better when prey variability is higher.

# Litterature cited

Araújo, M.S., Bolnick, D.I. & Layman, C.A. (2011). [The ecological causes of individual specialisation](https://doi.org/10.1111/j.1461-0248.2011.01662.x). *Ecol. Lett.*, 14, 948–958.

Beauchamp, G. (2020). [Predator attack patterns influence vigilance in a virtual experiment](https://doi.org/10.1007/s00265-020-02833-0). *Behav Ecol Sociobiol*, 74, 49.

Ceia, F.R. & Ramos, J.A. (2015). [Individual specialization in the foraging and feeding strategies of seabirds: A review](https://doi.org/10.1007/s00227-015-2735-4). *Mar Biol*, 162, 1923–1938.

Céré, J., Montiglio, P.-O. & Kelly, C.D. (2021). [Indirect effect of familiarity on survival: A path analysis on video game data](https://doi.org/10.1016/j.anbehav.2021.06.010). *Animal Behaviour*, 181, 105–116.

Courbin, N., Besnard, A., Péron, C., Saraux, C., Fort, J., Perret, S., *et al.* (2018). [Short-term prey field lability constrains individual specialisation in resource selection and foraging site fidelity in a marine predator](https://doi.org/10.1111/ele.12970). *Ecol. Lett.*, 21, 1043–1054.

Davoren, G.K., Montevecchi, W.A. & Anderson, J.T. (2003). [Search Strategies of a Pursuit-Diving Marine Bird and the Persistence of Prey Patches](https://doi.org/10.1890/02-0208). *Ecol. Monogr.*, 73, 463–481.

Dukas, R. (2019). [Animal expertise: Mechanisms, ecology and evolution](https://doi.org/10.1016/j.anbehav.2018.05.010). *Animal Behaviour*, 147, 199–210.

Edwards, G.B. & Jackson, R.R. (1994). [The role of experience in the development of predatory behaviour in Phidippus regius, a jumping spider (Araneae, Salticidae) from Florida](https://doi.org/10.1080/03014223.1994.9517994). *N. Z. J. Zool.*, 21, 269–277.

Estes, J.A., Riedman, M.L., Staedler, M.M., Tinker, M.T. & Lyon, B.E. (2003). [Individual variation in prey selection by sea otters: Patterns, causes and implications](https://doi.org/10.1046/j.1365-2656.2003.00690.x). *J. Anim. Ecol.*, 72, 144–155.

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](https://doi.org/10.1093/beheco/arac063). *Behavioral Ecology*, arac063.

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

Huey, R.B. & Pianka, E.R. (1981). [Ecological consequences of foraging mode](https://doi.org/10.2307/1936998). *Ecology*, 62, 991–999.

Ishii, Y. & Shimada, M. (2010). [The effect of learning and search images on predatorprey interactions](https://doi.org/10.1007/s10144-009-0185-x). *Popul. Ecol.*, 52, 27.

Kernaléguen, L., Arnould, J.P.Y., Guinet, C. & Cherel, Y. (2015). [Determinants of individual foraging specialization in large marine vertebrates, the Antarctic and subantarctic fur seals](https://doi.org/10.1111/1365-2656.12347). *J. Anim. Ecol.*, 84, 1081–1091.

Lima, S.L. (2002). [Putting predators back into behavioral predatorprey interactions](https://doi.org/10.1016/S0169-5347(01)02393-X). *Trends in Ecology & Evolution*, 17, 70–75.

Matsumura, K. & Miyatake, T. (2022). [Effects of individual differences in the locomotor activity of assassin bugs on predatorprey interactions](https://doi.org/10.1111/eth.13272). *Ethology*, 128, 395–401.

Mery, F. & Burns, J.G. (2010). [Behavioural plasticity: An interaction between evolution and experience](https://doi.org/10.1007/s10682-009-9336-y). *Evol. Ecol.*, 24, 571–583.

Michalko, R. & Pekár, S. (2016). [Different hunting strategies of generalist predators result in functional differences](https://doi.org/10.1007/s00442-016-3631-4). *Oecologia*, 181, 1187–1197.

Morse, D.H. (2000). [The effect of experience on the hunting success of newly emerged spiderlings](https://doi.org/10.1006/anbe.2000.1546). *Animal Behaviour*, 60, 827–835.

Patrick, S.C., Martin, J.G.A., Ummenhofer, C.C., Corbeau, A. & Weimerskirch, H. (2021). [Albatrosses respond adaptively to climate variability by changing variance in a foraging trait](https://doi.org/10.1111/gcb.15735). *Glob. Change Biol.*, 27, 4564–4574.

Pettorelli, N., Hilborn, A., Duncan, C. & Durant, S.M. (2015). [Chapter Two - Individual variability: The missing component to our understanding of predatorprey interactions](https://doi.org/10.1016/bs.aecr.2015.01.001). In: *Advances in Ecological Research*, Trait-Based Ecology - From Structure to Function (eds. Pawar, S., Woodward, G. & Dell, A.I.). Academic Press, pp. 19–44.

Phillips, R.A., Lewis, S., González-Solís, J. & Daunt, F. (2017). [Causes and consequences of individual variability and specialization in foraging and migration strategies of seabirds](https://doi.org/10.3354/meps12217). *Mar. Ecol. Prog. Ser.*, 578, 117–150.

Reid, A., Seebacher, F. & Ward, A. (2010). [Learning to hunt: The role of experience in predator success](https://doi.org/10.1163/000579509X12512871386137). *Behaviour*, 147, 223–233.

Schreiber, S.J., Bürger, R. & Bolnick, D.I. (2011). [The community effects of phenotypic and genetic variation within a predator population](https://doi.org/10.1890/10-2071.1). *Ecology*, 92, 1582–1593.

Snell-Rood, E.C. (2013). [An overview of the evolutionary causes and consequences of behavioural plasticity](https://doi.org/10.1016/j.anbehav.2012.12.031). *Anim. Behav.*, Including Special Section: Behavioural Plasticity and Evolution, 85, 1004–1011.

Tinker, M.T., Bentall, G. & Estes, J.A. (2008). [Food limitation leads to behavioral diversification and dietary specialization in sea otters](https://doi.org/10.1073/pnas.0709263105). *PNAS*, 105, 560–565.

Tinker, M.T., Mangel, M. & Estes, J.A. (2009). Learning to be different: Acquired skills, social learning, frequency dependence, and environmental variation can cause behaviourally mediated foraging specializations. *Evol. Ecol. Res.*, 11, 841–869.

Toscano, B.J., Gownaris, N.J., Heerhartz, S.M. & Monaco, C.J. (2016). [Personality, foraging behavior and specialization: Integrating behavioral and food web ecology at the individual level](https://doi.org/10.1007/s00442-016-3648-8). *Oecologia*, 182, 55–69.

Weimerskirch, H. (2007). [Are seabirds foraging for unpredictable resources?](https://doi.org/10.1016/j.dsr2.2006.11.013) *Deep Sea Research Part II: Topical Studies in Oceanography*, Bio-logging Science: Logging and Relaying Physical and Biological Data Using Animal-Attached Tags, 54, 211–223.

Wilson-Rankin, E.E. (2015). [Level of experience modulates individual foraging strategies of an invasive predatory wasp](https://doi.org/10.1007/s00265-014-1861-1). *Behav Ecol Sociobiol*, 69, 491–499.

Woo, K.J., Elliott, K.H., Davidson, M., Gaston, A.J. & Davoren, G.K. (2008). [Individual specialization in diet by a generalist marine predator reflects specialization in foraging behaviour](https://doi.org/10.1111/j.1365-2656.2008.01429.x). *J. Anim. Ecol.*, 77, 1082–1091.