Analysing individual specialisation and flexibility in predator hunting mode and its effect on hunting success using an online multiplayer videogame

Maxime Fraser Franco1, Francesca Santostefano1, Clint D. Kelly1, Pierre-Olivier Montiglio1

###### Groupe de Recherche en Écologie Comportementale et Animale (GRECA), Département des Sciences Biologiques, Université du Québec à Montréal, Montréal, QC, Canada

###### 1Correspondence: Pavillon des Sciences Biologiques (SB) SB-1805, 141 Avenue du Président-Kennedy, Montréal (Québec), Canada, H2X 1Y4

###### 1Corresponding author: maxime(dot)fraser(dot)franco(at)hotmail.com

# Abstract

This is my abstract paragraph

Keywords: individual variation, hunting success, foraging mode, hunting tactics, predator-prey behaviour, online videogames

# Introduction

Predator hunting mode plays a crucial role in structuring ecological communities and ecosystems (Huey & Pianka 1981; Preisser *et al.* 2007; Schmitz 2008; Romero & Koricheva 2011; Kersch‐Becker *et al.* 2018). Experimental studies in the field show that contrasting hunting modes, such as active vs sit-and-wait hunting, can cause opposing trophic cascades and act at different trophic levels (Schmitz 2008). For instance, predators may differ in the amount of individuals, species, or in the type of prey they capture relative to their hunting mode (Miller *et al.* 2014; Donihue 2016; Glaudas *et al.* 2019). Predator hunting modes are classified in three categories: 1) Active/patrolling hunters who usually search, follow, and chase prey on long distances, 2) sit-and-pursue hunters who remain motionless and pounce on prey that are within chasing distance, and 3) sit-and-wait (ambush) hunters who wait for prey to be within immediate capture distance (McLaughlin 1989). There has recently been a growing interest in investigating how ecological factors shape individual variation in hunting behaviour within populations, and its consequences for predator-prey interactions (Pettorelli *et al.* 2015; Toscano *et al.* 2016; Schmitz 2017). Experimental evidence show that individual predator behavioural type can mediate consumptive and nonconsumptive effects during trophic interactions (Preisser *et al.* 2007; Griffen *et al.* 2012; Toscano & Griffen 2014). However, empirical studies still tend to classify predator species either as active or sit-and-wait hunters based on their average behaviour (Bolnick *et al.* 2011; Pettorelli *et al.* 2015; Schmitz 2017). Thus, accounting for individual variation in hunting mode is a pressing need if we aim to understand the community consequences of predation.

Individual variation in hunting mode can be driven by specialisation when predators in a given population display consistent differences in their tactic use. Such differences are expected when individuals experience temporal and/or spatial fluctuations in the distribution, the availability, or the behaviour of their prey (Araújo *et al.* 2011; Carneiro *et al.* 2017; Phillips *et al.* 2017; Courbin *et al.* 2018). For example, prey activity/mobility level is an important mediator of encounter rates with predators (Gerritsen & Strickler 1977; Huey & Pianka 1981; Scharf *et al.* 2006). Hence, predators may specialise by using specific hunting modes to meet the energy/time required to successfully capture the type of prey they encounter. In this sense, the locomotor-crossover hypothesis (Huey & Pianka 1981) predicts that ambush predators should be more sucessful when they hunt fast-moving prey, while active predators should have greater success with sedentary prey (Scharf *et al.* 2006; Belgrad & Griffen 2016; Donihue 2016). If the individuals’ tactics allow them to reach similar capture rates, then predators with contrasting hunting modes may coexist within the same population (Kobler *et al.* 2009; Michel & Adams 2009; Chang *et al.* 2017). However, it may be difficult to test such an hypothesis at the individual level in wild populations of free ranging predators.

Habitat structure is a second important driver of individual differences in predator foraging mode, as it shapes opportunities of prey encounter and prey capture (Robinson & Holmes 1982; James & Heck Jr. 1994; Sargeant *et al.* 2007; Wasiolka *et al.* 2009; Donihue 2016). Hence, habitat caracteristics could be used to predict the tactic a predator should use. A growing body of evidence points that predators who hunt in open and homogeneous habitats tend to adopt an active mode, contrary to those hunting in heterogeneous and closed habitats who adopt an ambush strategy (James & Heck Jr. 1994; Wasiolka *et al.* 2009; Donihue 2016). Heterogeneous habitats are expected to favor sit-and-wait/sit-and-pursue hunters as they offer perches and hiding grounds 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, at the expense of being themselves more easily detected (Michel & Adams 2009).

Ceci implique donc un compromis entre les deux stratégies selon la situation, et la capacité d’ajustement des prédateurs devrait être critique pour leur succès face à des conditions environnementales changeantes.

paragraphe switching

# References

Araújo, M.S., Bolnick, D.I. & Layman, C.A. (2011). The ecological causes of individual specialisation. *Ecology Letters*, 14, 948–958.

Belgrad, B.A. & Griffen, B.D. (2016). Predator–prey interactions mediated by prey personality and predator hunting mode. *Proceedings of the Royal Society B: Biological Sciences*, 283, 20160408.

Bolnick, D.I., Amarasekare, P., Araújo, M.S., Bürger, R., Levine, J.M. & Novak, M. *et al.* (2011). Why intraspecific trait variation matters in community ecology. *Trends in Ecology & Evolution*, 26, 183–192.

Carneiro, A.P.B., Bonnet-Lebrun, A.-S., Manica, A., Staniland, I.J. & Phillips, R.A. (2017). Methods for detecting and quantifying individual specialisation in movement and foraging strategies of marine predators. *Marine Ecology Progress Series*, 578, 151–166.

Chang, C.-c., Teo, H.Y., Norma-Rashid, Y. & Li, D. (2017). Predator personality and prey behavioural predictability jointly determine foraging performance. *Scientific Reports*, 7, 40734.

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. *Ecology Letters*, 21, 1043–1054.

Donihue, C.M. (2016). Aegean wall lizards switch foraging modes, diet, and morphology in a human-built environment. *Ecology and Evolution*, 6, 7433–7442.

Gerritsen, J. & Strickler, J. (1977). Encounter probabilities and community structure in zooplankton: A mathematical model. *Journal of the Fisheries Board of Canada*, 34.

Glaudas, X., Glennon, K.L., Martins, M., Luiselli, L., Fearn, S. & Trembath, D.F. *et al.* (2019). Foraging mode, relative prey size and diet breadth: A phylogenetically explicit analysis of snake feeding ecology. *Journal of Animal Ecology*, 88, 757–767.

Griffen, B.D., Toscano, B.J. & Gatto, J. (2012). The role of individual behavior type in mediating indirect interactions. *Ecology*, 93, 1935–1943.

Huey, R.B. & Pianka, E.R. (1981). Ecological consequences of foraging mode. *Ecology*, 62, 991–999.

James, P.L. & Heck Jr., K.L. (1994). The effects of habitat complexity and light intensity on ambush predation within a simulated seagrass habitat. *Journal of Experimental Marine Biology and Ecology*, 176, 187–200.

Kersch‐Becker, M.F., Grisolia, B.B., Campos, M.J.O. & Romero, G.Q. (2018). Community-wide responses to predation risk: Effects of predator hunting mode on herbivores, pollinators, and parasitoids. *Ecological Entomology*, 43, 846–849.

Kobler, A., Klefoth, T., Mehner, T. & Arlinghaus, R. (2009). Coexistence of behavioural types in an aquatic top predator: A response to resource limitation? *Oecologia*, 161, 837–847.

Laurel, B.J. & Brown, J.A. (2006). Influence of cruising and ambush predators on 3-dimensional habitat use in age 0 juvenile Atlantic cod Gadus morhua. *Journal of Experimental Marine Biology and Ecology*, 329, 34–46.

McLaughlin, R.L. (1989). Search modes of birds and lizards: Evidence for alternative movement patterns. *The American Naturalist*, 133, 654–670.

Michel, M.J. & Adams, M.M. (2009). Differential effects of structural complexity on predator foraging behavior. *Behavioral Ecology*, 20, 313–317.

Miller, J.R.B., Ament, J.M. & Schmitz, O.J. (2014). Fear on the move: Predator hunting mode predicts variation in prey mortality and plasticity in prey spatial response. *Journal of Animal Ecology*, 83, 214–222.

Pettorelli, N., Hilborn, A., Duncan, C. & Durant, S.M. (2015). Chapter Two - Individual variability: The missing component to our understanding of predator–prey interactions. 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. *Marine Ecology Progress Series*, 578, 117–150.

Preisser, E.L., Orrock, J.L. & Schmitz, O.J. (2007). Predator hunting mode and habitat domain alter nonconsumptive effects in predator–prey interactions. *Ecology*, 88, 2744–2751.

Robinson, S.K. & Holmes, R.T. (1982). Foraging behavior of forest birds: The relationships among search tactics, diet, and habitat structure. *Ecology*, 63, 1918–1931.

Romero, G.Q. & Koricheva, J. (2011). Contrasting cascade effects of carnivores on plant fitness: A meta-analysis. *Journal of Animal Ecology*, 80, 696–704.

Sargeant, B.L., Wirsing, A.J., Heithaus, M.R. & Mann, J. (2007). Can environmental heterogeneity explain individual foraging variation in wild bottlenose dolphins (Tursiops sp.)? *Behav Ecol Sociobiol*, 61, 679–688.

Scharf, I., Nulman, E., Ovadia, O. & Bouskila, A. (2006). Efficiency evaluation of two competing foraging modes under different conditions. *The American Naturalist*, 168, 350–357.

Schmitz, O. (2017). Predator and prey functional traits: Understanding the adaptive machinery driving predator–prey interactions. *F1000Res*, 6, 1767.

Schmitz, O.J. (2008). Effects of predator hunting mode on grassland ecosystem function. *Science*, 319, 952–954.

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. *Oecologia*, 182, 55–69.

Toscano, B.J. & Griffen, B.D. (2014). Trait-mediated functional responses: Predator behavioural type mediates prey consumption. *Journal of Animal Ecology*, 83, 1469–1477.

Wasiolka, B., Blaum, N., Jeltsch, F. & Henschel, J. (2009). Behavioural responses of the lizard Pedioplanis l. Lineoocellata to overgrazing. *Acta Oecologica*, 35, 157–162.