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

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# Abstract

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# Introduction

Predator hunting mode plays a crucial role in structuring ecological communities and ecosystems (Huey & Pianka 1981; Preisser *et al.* 2007; Schmitz 2008; Kersch‐Becker *et al.* 2018). Contrasting hunting modes, such as active vs sit-and-wait hunting, can cause opposing trophic cascades and act at different trophic levels (Schmitz 2008; Romero & Koricheva 2011). 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 studies show that individual predator behavioural type can mediate consumptive and nonconsumptive effects during trophic interactions (Smith & Blumstein 2010; 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 (Lima 2002; 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 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 tactics to meet the energy/time required to successfully capture the type of prey they encounter (Bowen *et al.* 2002; Tinker *et al.* 2008; Arthur *et al.* 2016). 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 cursorial 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, such an hypothesis may be difficult to test at the individual level in wild populations of free ranging predators.

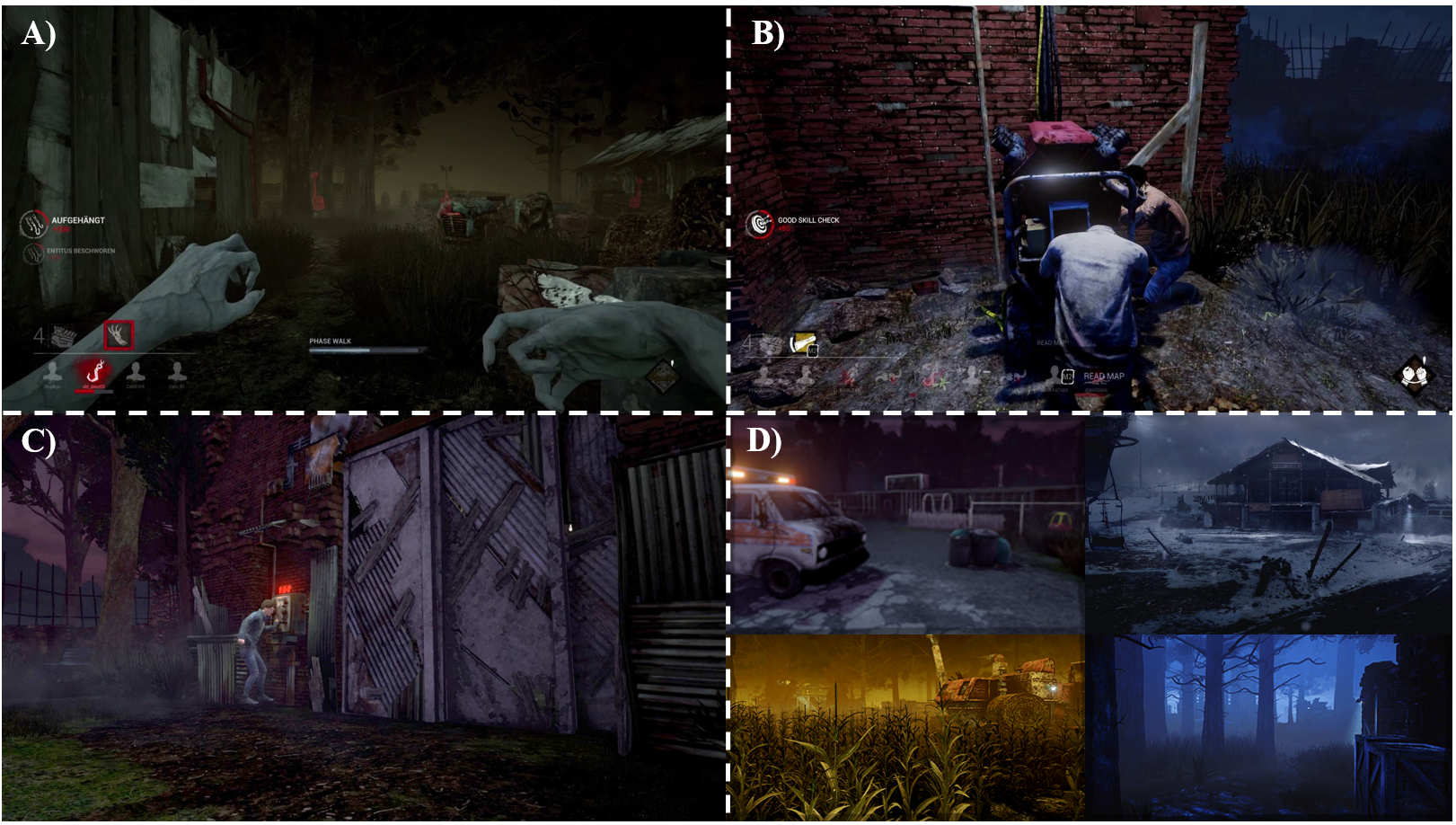
Habitat structure is a second important driver of individual differences in predator foraging mode, as it shapes opportunities of prey encounter and prey capture (Robinson & Holmes 1982; James & Heck Jr. 1994; Sargeant *et al.* 2007; Wasiolka *et al.* 2009; Donihue 2016). Hence, habitat caracteristics can 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 a cursorial strategy, contrary to those hunting in heterogeneous and closed habitats who use ambushes (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). This suggests that tradeoffs could mediate individual differences in hunting strategies as a function of habitat structure. Thus, predators could benefit from adjusting their strategy in accordance with habitat changes.

A wide range of predator taxa display flexible hunting behaviour (Helfman 1990; Heithaus *et al.* 2018). Foraging mode switching occurs when individual predators respond to prey or habitat changes within their lifetime to maintain optimal hunting success. Notably, foraging mode switching can be triggered as a function of prey density (Inoue & Marsura 1983), prey behavioural type (McGhee *et al.* 2013), prey condition (Wignall & Taylor 2008), seasonality (Phillips *et al.* 2017), or in response to changes in habitat structure (Wasiolka *et al.* 2009). In spite of the recent advancements in our understanding of the factors that promote foraging mode swithing, most research is conducted under controlled laboratory experiments, which may fail to capture the nuances and complexities of predator species’ ecology in the wild (Carter et al., 2013; Niemelä & Dingemanse, 2014). Understanding how and when predators balance specialisation vs switching in tactics would thus help us to better predict the type of prey predators should choose when they hunt.

Different challenges arise when researchers aim to investigate individual variability in hunting mode. To properly quantify multiple levels of variation in hunting tactics, it is necessary to repeatedly measure the behaviour of a large number of individuals under different environmental settings (Hertel et al., 2020). This may impose considerable financial, technical, and ethical challenges when studying larger or elusive wildlife, such as apex predators (Hertel et al., 2020). An additional challenge in empirical studies of predator-prey interactions is identifying traits in predators and prey that are easily observable, but also ecologicaly relevant.

We tackled the problems associated with investigating individual variability in predator hunting mode by using the multiplayer online videogame Dead by Daylight (DBD) as our study system. The use of online videogame data could provide multiple advantages for ecologists who aim to study the mechanisms driving individual variation in behaviour.

This game pits a single player (predator) against a group of four players (prey), where the predator’s objective is to capture prey (Cere et al., unpublished data). DBD reproduces realistic predator-prey interactions. Prey can use a wide range of behaviours such as cooperation or hiding in order to successfully escape. For example, they can cooperate to help conspecifics escape from capture (Cere et al., unpublished data), which predators may exploit to lure them in an ambush. These situations offer the possibility for predators to express different hunting tactics. For example, the speed and the rate of space covered by predators could represent active- pursuit tactics, while guarding captured prey could represent a sit-and-pursue tactic. Predators who successfully capture prey earn “points”, which provide an indicator of performance. We therefore applied the framework offered by traditional selection analysis to investigate the consequence of predator hunting tactic specialisation and flexibility for individual success in different game environments. Moreover, because matches occur within different environmental settings such as in urban areas or in forests, predators experience different prey encounter rates and thus are expected to benefit from changing their behaviour accordingly to maximize performance. Hence, DBD provides a study system that realistically mirrors the range of ecological situations in which predators and prey interact. It also offers the advantage of supplying large and unusually complete datasets on the hunting behaviour of individuals over long time windows.



**Figure 1. Images of the online videogame Dead by Daylight** **A)** The predator player’s first person vision. **B)** The prey (survivor) player’s third person vision. Prey can cooperate to repair generators. Once all generators are repaired, prey may activate one of the two **C)** doors in order to escape and win the match. **D)** Representative pictures of the different game environments where matches take place. The game environments settings vary between urban, farmland, and forest areas.

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