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), and usually consists of three main classes: 1) active/cursioral hunters who 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). Field studies show that predators with contrasting hunting modes (ex. cursorial vs ambush) 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). Following these observations, there has 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). Researchers who adressed these questions report 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, predator species still tend to be 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). Thus, accounting for individual variation in hunting mode during predator-prey interactions 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 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, predators specialise in specific tactics in order 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). Prey activity/mobility has shown to be an important trait influencing encounter rates with predators (Gerritsen & Strickler 1977; Huey & Pianka 1981; Scharf *et al.* 2006). Therefore, individual variation in encounter rates with prey activity-types may lead to nonrandom interactions between predator-prey behavioural types (Wolf & Weissing 2012). Such a mechanism in trophic interactions is described by the locomotor-crossover hypothesis (Huey & Pianka 1981), which 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 a same population (Kobler *et al.* 2009; Michel & Adams 2009; Chang *et al.* 2017). However, this hypothesis may be difficult to test at the individual level in wild populations of free ranging predators.

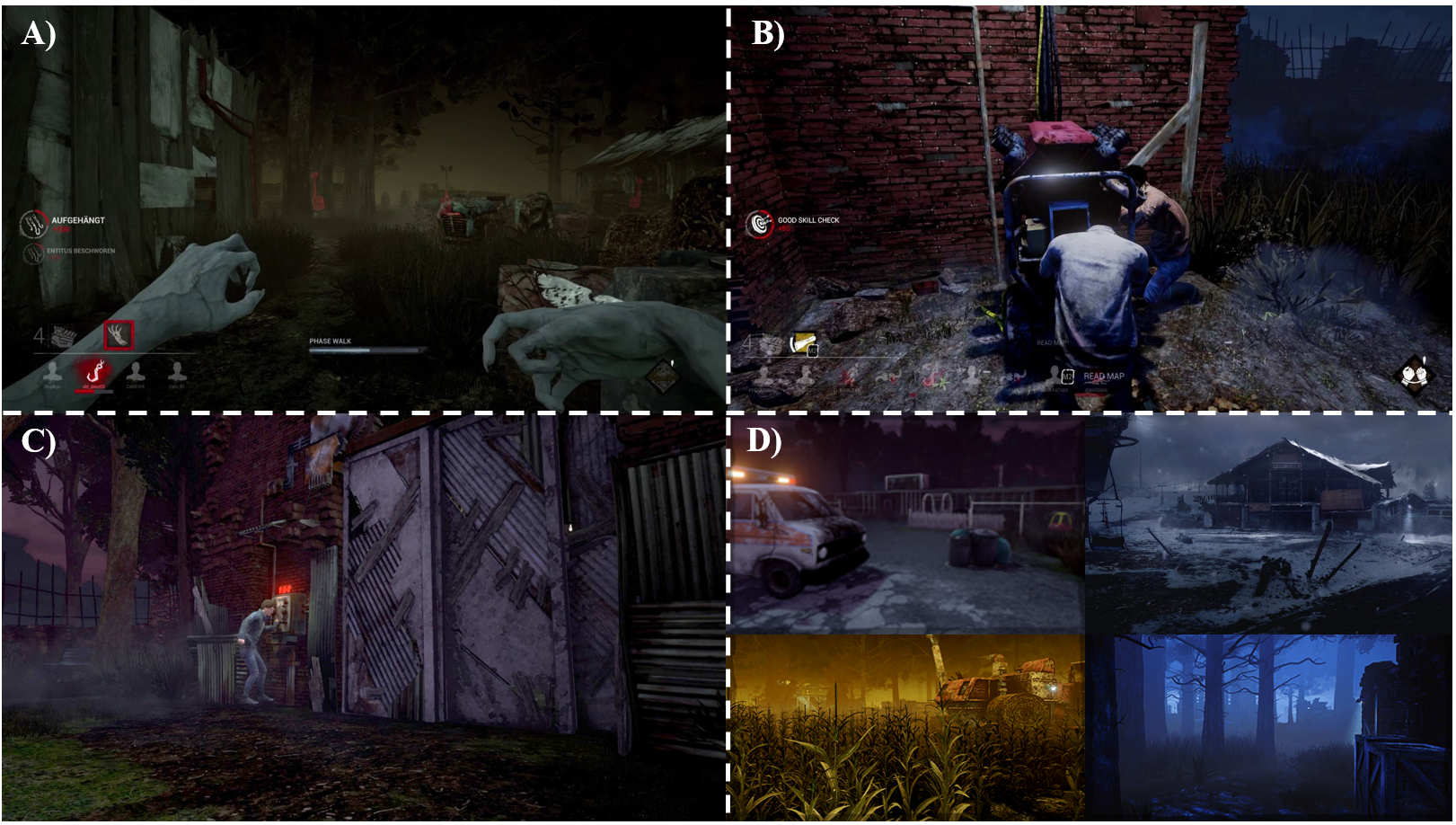
Habitat structure is a second important driver of individual differences in predator foraging mode, as it shapes opportunities of prey encounter and prey capture (Robinson & Holmes 1982; James & Heck Jr. 1994; Sargeant *et al.* 2007; Wasiolka *et al.* 2009; Donihue 2016). A growing body of evidence points 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). Hence, the habitat components of a predator’s hunting grounds can be used to predict the tactic he should use. Heterogeneous habitats are expected to favor sit-and-wait/sit-and-pursue hunters as they offer perches and hiding grounds 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, but 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. In this sense, predators could benefit from adjusting their strategy in accordance with short-term prey and 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 in order 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 (Miles *et al.* 2007; 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 switching, 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, and how these changes affect hunting success would help scientists to predict more precisely the community consequences of predation.

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 (sources?). 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 (sources?).

In light of the hurdles associated with the investigation of individual variability in predator hunting mode, we propose a novel approach based on the use of online multiplayer videogame data to make real-world predictions (Balicer 2007; Lofgren & Fefferman 2007; Oultram 2013; Ahmad *et al.* 2014; Ross *et al.* 2015). Multiplayer online videogame data could provide numerous opportunities for ecologists who aim to study general ecological phenonena, to mechanisms driving individual variation in behaviour (Barbe *et al.* 2020). First, online videogames provide vasts amount of repeated measurements from millions of individual players across temporal and environmental gradients, which takes in comparison a considerable amount of resources to gather for longitudinal ecological studies. This enables researchers to test ecological hypotheses that may be impossible to adress in the wild. Second, environmental settings are known and can be controlled for by the observer, which provide means to test experimentaly how specific components of the environment shape the phenomenon of interest. Third, videogames can reproduce realistic ecological settings where complex interactions among individuals take place. For instance, players may balance tradeoffs to successfully win matches, and may specialise in distinct tactics to reach their goals depending on how they interact with others (Barbe *et al.* 2020). In that end, we argue that videogames should not replace ecological studies in the field but be rather thought as a complementary study system, where specific hypotheses that are difficult to test with wild animals can be adressed. A classical example that set the stage for the scientific use of videogame data is the “Corrupted Blood” epidemic in the online videogame game *World of Warcraft*, where specific epidemiologic parameters such as transmission rate could be monitored to make predictions about the outbreak (Balicer 2007; Lofgren & Fefferman 2007). Following what Balicer et al. and Lofgren et al. proposed for epidemiological studies, we suggest that online videogames may be useful for ecologists by helping to bridge the gap between real-world ecological studies and large-scale computer simulations. Online videogames have generated interest in social, economical, and epidemiological sciences (Ross *et al.* 2015), but to our knowledge, we are the first study that uses one to test empirical hypotheses in ecology and evolution.

We used the online multiplayer videogame *Dead by Daylight* (*DBD*) as our study system. This game pits a single player (predator) against a group of four players (prey), where the predator’s objective is to capture prey (Fig. 1). The predator’s main objective is to search for and consume prey, while the preys’ objective is to escape the predator. Prey can use a wide range of behaviours such as cooperation or hiding in order to successfully escape (Fig. 1 B and C). 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. Moreover, each match in *DBD* occurs within a specific game environment. The different game environments vary from forests and farmlands, to urban areas. These environments differ in the heterogeneity and complexity of their structures (McCoy & Bell 1991), such as in the availability of perches and refugia, vegetation density, or surface area (Fig 1. D). Hence, predators may encounter prey that express different behaviours, and are expected to benefit from changing their behaviour accordingly to maximize hunting success.



**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.

In this study, we used an extensive and complete dataset on the hunting behaviour of predator players in *Dead by Daylight* to investigate individual and environmental variation in hunting mode, and how it affects hunting success. We used three hunting behaviours as proxies of hunting mode: travel speed, the rate of space covered in the environment, and the proportion of time spent in a guarding position. We applied the framework offered by behavioural syndrome analysis (Sih *et al.* 2004; Sih & Bell 2008; Dingemanse & Wolf 2013) to investigate the consequence of behavioural specialisation and flexibility for individual success in different game environments. This enabled us to quantify the structure and variability of predator foraging mode within populations along a continuum of hunting traits (Perry *et al.* 1990; Perry 1999; Butler 2005; Miles *et al.* 2007). Within-population variation would include a) the variation in tactic use arising when some individuals employ one tactic more often than the others (i.e. individual specialisation) and b) the variation arising from individuals adjusting tactic use over time in response to changes in environmental conditions or prey behaviour (i.e. individual flexibility). We hypothesized that individual predators would differ in their hunting mode. Thus, we predicted that the three measured behaviours would be correlated among- and within-individuals, reflecting specialisation and flexibility in the use of ambush and cursorial tactics along a continuum. The position of individuals (their foraging mode) along this continuum should be consistent over time, but also vary among game environments. Therefore, we expected to observe ambush tactics in smaller and heterogeneous environments, whether cursorial tactics should occur in open/wider and homogeneous environments. Lastly, following the locomotor-crossover hypothesis, we predicted that both ambush and cursorial predator-types may coexist in the population because individuals achieve similar hunting success by performing better against prey with the opposite locomotor tendency.

# Materials and methods

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