Multiplayer videogames to analyze behavior during ecological interactions

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Abstract

Behavior shapes population and community dynamics through feedbacks with habitat configuration and interaction networks. Work on this interplay includes longitudinal surveys, experiments, and models. Multiplayer online videogames foster real-time interactions among lots of players in virtual spaces. Data from these games could complement theoretical and empirical work but research on them is only emerging now. We highlight how these games allow us to track individual movement, decisions, interactions, and performance in a tractable environment. We use our work on the game *Dead by Daylight* as an example to show that social and predator-prey interactions can generate complex eco-evolutionary dynamics favoring an array of behavioral traits we often study in nature. These games can foster progress in eco-evolutionary and behavioral research.

A new approach to study ecological interactions

Animals (including our species) interact constantly, either as social partners, predators and prey, or hosts and parasites. Individual behavior during these interactions (e.g., prosocial behavior or foraging tactics) is central to our ability to explain and predict the dynamics of natural populations and communities. understanding the consequences of individual behavior is challenging because behavioral traits exhibit substantial phenotypic plasticity, indirect (genetic) effects, and social or multilevel selection (1). These processes create feedbacks among habitat configuration (i.e., the spatial arrangement and attributes of resources, refuges, or movement barriers), the behavior of individuals, and the network of interactions (i.e., who interacts with whom 2). For example, individual behavior varies with the configuration of the habitat and the network of interactions (3). In return, selection exerted on behavior varies based on the phenotypic composition of groups (2; 4) and habitat configuration (5).

Gaining a mechanistic understanding of this interplay requires monitoring individuals through multiple interactions in social and ecological environments with measurable features (6). Common complementary approaches to analyze this interplay include longitudinal individual-level surveys of wild animals, targeted laboratory experiments and mesocosms manipulating interaction or habitat configurations, and theoretical models investigating the selective consequences of specific ecological interaction scenarios and their impact on behavioral variation (2). These approaches have contributed tremendously to our understanding of individual behavior during ecological interactions, but they are still struggling with several limitations. Data from longitudinal surveys never fully capture the complexity of natural environments and interaction networks, and this constrains our ability to parse out the consequences of behavior at the level of populations and communities (7). Results from theoretical models rest on simplifying assumptions, and this limits our ability to apply these to explain the behavior of real animals in the real world (8).

Multiplayer videogames (see Glossary), offer a study system at the interface between theoretical and empirical work that could complement our efforts to analyze the interplay among the structure of the environment, the structure of interactions, and individual behavior. In these games, multiple players (ranging from 2 to several million) interact with each other in the same game or environment in real-time through digital characters (i.e., **avatars**; 9), to compete, hunt, or cooperate across a striking diversity of virtual habitats (Box 1; 10). Interactions among players are possible either on the same computer or console, on machines linked by a local network, or via the internet. Such games usually feature complex, persistent simulated environments, for example including several continents or solar systems, with rich spatial and temporal structures. Researchers already use videogame-like interfaces to study behavior (e.g., 11-12), but very few ecological and evolutionary studies have harnessed the possibilities of commercial multiplayer online videogames (but see 13).

Here, we highlight the strengths and particularities of multiplayer videogames, present where they lie relative to other research approaches, discuss some research opportunities that they offer, and review our work on predator and prey behavior in the game *Dead by Daylight* as worked examples. We hope this synthesis will help foster their use in ecological and evolutionary research on animal behavior.

What do multiplayer videogames have to offer?

Ecological interaction scenarios in virtual environments

Multiplayer online videogames are often set in open virtual ecosystems (14). Examples include the world in which *World of Warcraft* takes place (composed of several continents, harboring cities and habitats with lower densities of avatars) and the set of solar systems in which *EVE Online* is developed, which includes systems with varying abundances of resources and risk (i.e., habitats with differing configurations, Box 1). These environments are often large enough to require several hours or days of navigation to acquire resources or meet other players (15). In most of these games, players use an avatar that can accumulate artifacts, tools, skills, or abilities over several hours, sometimes years (Box 1; 16). Players must overcome challenges, manage their state, or negotiate trade-offs in the allocation of their time or resources to survive in the game. For example, in games like *Rust*, players manage their health, hydration, and energetic condition while competing among themselves for limited resources to survive. Players must also express a diversity of tactics to navigate complex social and ecological interaction scenarios such as competing for resources, avoiding predation, or coordinating efforts to secure resources. Players can choose to forage alone or collectively, or to rescue or heal other players while avoiding predation by another player in *Dead by Daylight* (17-18). Thus, these games involve the management of a limited set of state variables for players, constrained by simple ecological challenges, under several of the ecological interaction scenarios that we study in nature.

A central aspect of these games is that player behavior in response to these ecological challenges and interactions has consequences for performance (e.g., foraging success or survival; 19). Hence, multiplayer videogames allow us to analyze the behavioral decisions or tactics of individuals during interactions and to analyze the ecological agents generating selection on behavior in clearly defined ecological contexts. Game environments and mechanics are likely to exert predominantly **soft selection** pressures on player behavior (which is probably the most pervasive selection in nature; Box 2; 20-21), because games are designed to retain players irrespective of their performances. Thus, while videogames do not allow us to analyze the evolutionary response of player behavior, they allow us to study the process of selection and seek functional explanations of how behaviour could impact fitness. Games further implement competition, predation, or cooperation using a variety of detailed and complex game mechanics. Thus, analyzes on videogames could provide highly valuable insights into the importance and consequences of ecological interactions for natural populations (22). Of course, these analyzes would need to first validate that the mechanics of the game match the ecological interactions one is interested in studying in nature. For example, in the videogame *Dead by Daylight* the benefits that players acquire during social interactions can alter dramatically individual behavior and selection on cooperation (Box 2; 17). In sum, these games could complement our understanding of the consequences of behaviour on fitness (i.e., functional explanations).

Structured, realistic, and representative behavioral variation

Players within multiplayer videogames exhibit behavioral flexibility (11; 17), consistent individual differences (23), and behavioral specialization (24). Thus, the behavioral variation within multiplayer videogames is structured, with part of this variation observed among individuals, and part observed within individuals among games, much like natural behavioral variation in free-ranging animals. Further, this behavioral variation in videogames is generated by real decision rules and cognitive mechanisms paralleling those used by animals in nature. Hence, behavioral variation from multiplayer videogames should be biologically and ecologically realistic because it integrates the cognitive biases that animals often exhibit (e.g., pessimism or irrationality; 25). While players can sometimes behave to maximize ranking (19) or socialize (26), these facets of play behavior often align by design with the ecological challenges that games invoke (18). In fact, player behavior might exhibit a greater level of optimism (25) and a greater diversity than animal behavior in nature. Thus, analyzes of player behavior should allow us to analyze the full range of outcomes associated with ecological interactions. Mesocosms or laboratory captive experiments can achieve this but typically allow for much smaller datasets.

Player behavior is also representative of animal behavior in nature. First, animal and human behavior are studied within the same frameworks, highlighting their evolutionary similarities. Behavioral ecology, initially developed to explain non-human animal behavior, has been very fruitful when applied to humans (27), and econometric models, initially developed to make sense of human decisions, have led to major advances in our understanding of animal behavior (i.e., game theory; 8). Second, the behavioral variation in humans and in non-human animals is shaped by common mechanisms. Players transfer their skills about the assembly of technological artifacts (such as spaceships in *Space Engineers*, items in *Minecraft*, or combat tactics in *EveOnline*) from one avatar to the next, or from one game to another through personal learning, community forums, wikis, or blogs. These mirror learning, teaching, and cultural transmission mechanisms that we observe in several non-human animals (e.g., 28). Third, several common characteristics of humans and non-human species evolved through the same ecological routes. For example, cooperative breeding probably evolved from larger families in both clades (29-31). Finally, player behavior in virtual worlds is representative of human behavior in real life, and human behavior in real life is representative of animal behavior in nature. Indeed, videogames elicit neural and physiological responses that mirror those of interactions in real life (32-35). Furthermore, human behavior in competitive, trophic, or cooperative contexts is representative of animal behavior in natural populations (36) in part because they share common cognitive and endocrine mechanisms (e.g., oxytocin and prolactin systems; 37).

Where do multiplayer videogames fall relative to other research approaches?

Multiplayer online games are already used as systems for research in epidemiology, sociology, and psychology (38-41), and several researchers have pointed out their value in other fields (42-43). In ecological and evolutionary research, multiplayer videogames could complement other approaches (Figure 1a). Longitudinal surveys in nature consider real individuals in a complex environment but are hampered by a lack of manipulability and the difficulties of collecting sufficient and complete datasets. In contrast, theoretical models and simulations consider simplified individuals in a simplified environment, but their value is limited by their lack of realism. Videogames consider real individuals and realistic behavioral variation in a simplified environment. They would thus occupy a niche left out by observational work in nature and theoretical models and simulations.

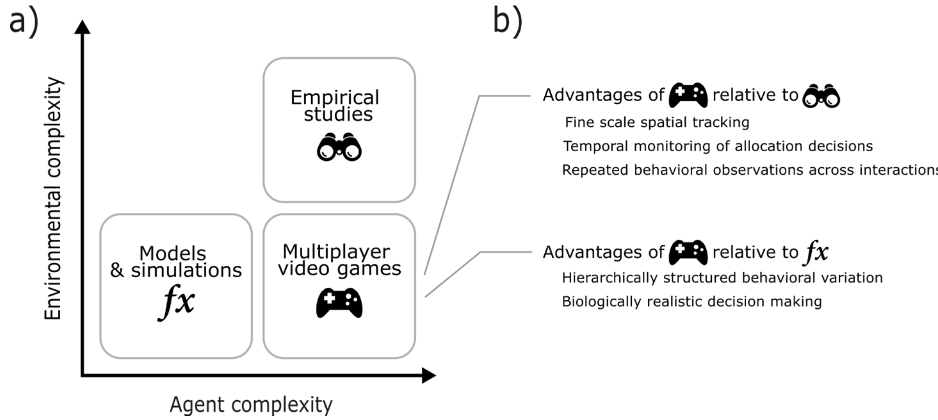

Figure 1: a) Complementary research systems to study the interplay among the structure of the environment, the structure of interactions, and individual behavior. Theoretical models (including numerical simulations) and empirical studies (including experimental work) are well-established approaches. Relative to these, videogames and robotics could provide interesting research opportunities, by allowing to consider agents with complex decision rules and realistic cognition within tractable and manipulable environments. b) Relative to these established systems, multiplayer videogames could help consider structured behavioral variation and its impact on the outcome of ecological interactions, integrate cognitive biases within theory, and allow deeper and more complete datasets tracking the movement, behavior, and allocation decisions of individuals across vast volumes of interactions.

Relative to empirical work conducted in nature, videogames offer several advantages (Figure 1b). First, we can track the position and movement of many individuals repeatedly in the environment over time (14-15), free from the logistical, ethical, and financial constraints associated with the use of telemetry in nature. Datasets typically available from these games often comprise the location and the time at which player actions or interactions happen, such as the collection of a resource or an attack by a player on another (15). Second, we can use points accumulated by players, and game metrics collected by game developers, to infer their behavior and interactions with a rare level of precision and replication. Point acquisition and game metrics are often directly associated with ecologically relevant behaviors and decisions. For example, players in the game *Dead by Daylight* accrue points for investing time to help others or acquire a resource (17-18). Such data can be acquired for several game sessions, eventually encompassing the whole time spent by players in the game over months or years. It is thus possible to curate longitudinal datasets tracking the behavior or performance of individuals and their dynamics over time with a resolution that we can rarely achieve in other study systems (e.g., 23). Third, individuals often accumulate currencies over time that they use to acquire items or skills for their avatars. For example, avatars in *EveOnline* can acquire abilities needed to attack others, defend themselves, or forage more efficiently over time. Tracking these decisions enables us to analyze how individuals allocate limited resources to various functions related to competition, safety, or foraging, and the consequences of these allocation decisions of success. Alternatively, one can use **non-player characters**, programmed to behave in a precise and standardized way, to study player behavior in response to standardized social environmental gradients such as intensity of agonistic interactions or predation intensity (see also 44-45, for a similar approach based on robotics).

Multiplayer videogames also offer several advantages relative to theoretical models and simulations (Figure 1b). First, these games harbor structured, realistic, and representative behavioral variation (see previous section). Thus, work on videogames should provide more conclusive or more generalizable results than models or simulations (8), because the latter often lack any structured variation (see also 38) or cognitive biases (25). In sum, multiplayer videogames, with their simple ecological interaction scenarios, their diversity of realistic behavior and tactics, and their huge volume of interactions could offer an interesting way to test and refine theory by questioning the **behavioral gambit** (27; 46). For example, one could assemble a dataset including all the occurrences where a player needs help by others for thousands of games. Alternatively, this dataset could include all the games played by a sample of several thousands of players to parse out the costs and benefits of helping others (17) and test theoretical predictions about the evolution of altruism (Box 2). This dataset could also include spatial data such as the distance between players as well as information on the structure of the environment such as the abundance of resources, their distribution, or the risk of predation. Finally, such datasets could also include the decision of players for each specific interaction and its impact on performance (i.e., survival or success) for the game session.

Data from these games can be acquired through partnerships with companies, the use of public **application programming interfaces** (i.e., APIs), and/or direct observation (e.g., scan sampling or focal observations; 4; 47). For example, we acquired the data on *Dead by Daylight* for our research (Box 2 & 3) directly from the publisher's database through a research collaboration (22; chapter 12 in 48). Examples of games providing a public API are *Age of Empire*, *Call of Duty*, and *Dota 2*. One can use these interfaces to gather data on a large number of games, or on specific games or players playing in a local network or server (13; chapter 2 in 48). Some multiplayer videogames even allow users to build custom scenarios and environments, which enables us to generate datasets tailored to specific research questions. Once acquired, datasets on multiplayer videogames should be treated like any other ecological or evolutionary dataset. These need be curated these into useable formats and checked for consistency, quality, and completeness. Most of these datasets are analyzable using common statistical and computational approaches, although some larger datasets might require approaches adapted for big data (48).

Which research questions can we ask using multiplayer videogames?

How does the habitat structure interactions?

Habitat configuration determines the distribution of organisms in space, the network of interactions, and thus the social/mating system at the population level or predator-prey dynamics at the community level. Analyzing individual-level responses to changes in habitat configuration is therefore critical to better predict population and community dynamics. Current efforts face the challenge of manipulating the configuration of replicated habitats to pinpoint its effect on individual behavior and interactions (49-50). This objective has generated theoretical models considering individual movement and behavior in landscapes (51) as well as longitudinal surveys tracking individual space use over time (52). These studies have rarely used an experimental approach on free-ranging animals, because, indeed, it is hard to manipulate habitat configuration at scales that are relevant for most of the animals we can track. Virtual environments supporting multiplayer online videogames are often generated procedurally based on pre-specified parameters defining the distribution and abundance of resources, the size and shape of habitats, or the barriers to movement in the habitat. Several games even enable players to design their own environment (e.g., *Minecraft*, or *Starcraft*). Thus, these games can offer replicated habitats with precise configurations. Datasets including the time and spatial location of interactions or events during gameplay (14; 48; 53) combined with information on the distribution of resources, predation, or competition could allow us to recreate the various layers of the biotic landscape (e.g., the landscape of fear) and analyze the impact of habitat configuration on these landscapes (e.g., 13; 54).

How do ecological interactions structure selection on behavior?

Explaining the ecological function of animal behavior requires quantifying the relationship between behavior and fitness or performance (i.e., selection gradient), and analyzing how ecological conditions shape this relationship. In a social context, selection regimes are extremely dynamic (55) and have the potential to explain puzzling behavioral adaptations such as altruism, spite, courtship displays, or patterns of behavioral plasticity (2). Classical modeling frameworks, such as game theory, have formalized several mechanisms through which interactions generate selection on behavior (56), but additional efforts are necessary to integrate more realistic behavioral variation within these models (8). In parallel, studies tracking individual behavior across social interactions have quantified dynamic selection regimes but struggled to pinpoint the exact agents of this selection (i.e., how the behavior of social partners shapes the performance of a given individual; 57). Multiplayer online videogames can provide complete and wide longitudinal datasets detailing individual selfishness, cooperation, altruism, and performance across vast volumes of interactions (17-18). Survival games (Box 1) could help us understand the viability selection exerted on behavior by predation risk and competition. Games where players compete in groups (e.g., 58, Box 1), could help us analyze changes in the selection exerted on resource acquisition or interference competitive behaviors as a function of the tactics used by competitors or teammates. Many of these games offer interaction scenarios analogous to those considered by game theoretical models (e.g., hawk-dove, common good, or prisoner dilemma). These games could be modified to assess the consequences of employing a given tactic more accurately, by instructing players to maximize a particular currency such as resources acquired or the area in space secured in the game, or by imposing additional rules or game mechanics on top of the ones already included in the game itself (see 17, for an example).

How do ecological interactions shape behavioral specialization?

Behavioral variation has consequences for community dynamics (e.g., 59), selection pressures (56), and evolutionary dynamics themselves (6). Much of this variation is observed among individuals and referred to as trophic or individual specialization (60-61) or personality, behavioral syndromes, and coping styles (62). The key challenge is explaining why some populations are composed of specialists while others are composed of generalists (6; 63), by investigating the development of individual behavioral profiles and the links between behavior and performance across interactions (e.g., 6; 57; 64). Models predict that within the life cycle of an organism, specialization can arise from learning (7; 65), feedbacks between behavior and state (66), and developmental plasticity in response to social or interspecific interactions (67). Individual behavioral variation also exists in multiplayer online games as a result of these mechanisms (14; 68-70; Box 3). Games offering competitive interactions or risky environments (i.e., survival games such as *Rust*; Box 1) would be especially well-suited to study how social interactions shape individual differences in behavior, the width of individual behavioral niches, or phenotypic plasticity. In some online role-playing games (Box 1), players maintain and develop a single avatar over extensive time windows. Datasets tracking individual aggressiveness or cooperation, social partners, and past performance over time would enable us to describe how past social experience shapes individual behavior. Because they often integrate characters programmed to behave in a precise and consistent way in their environments (non-player characters or NPCs), many games can also be used to study the social behavior of individuals, or their anti-predatory behavior, in a standardized way, much like the robots that are increasingly used with non-human animals (44). In games where play is divided into matches or trials, one could parse out the effects of past victory or defeat from those of associative learning (e.g., whether a player's hunting tactic led to prey capture or not) to clarify how learning and other forms of plastic changes determine players' tactics and strategies over time (Box 3).

Concluding Remarks

Multiplayer videogames allow us to track the movement, behavioral decisions, interactions, and performance of a large number of real organisms facing ecological challenges in a tractable environment. Data from these games could complement long-term population surveys (71) and theoretical models and simulations (8). Replicating and manipulating virtual environments will help us assess how habitat configuration determines the movement and distribution of individuals, or the consequences of this configuration for ecological interactions and social systems (Box Outstanding questions). Tracking the performance of players across interactions would help us to identify the role of competition or predation as agents of selection, determine the consequences of behavioral variation and cognitive biases for the outcome of ecological interactions, and to explain individual specialization. Recognizing the similarities between interaction scenarios faced by animals in nature and by players in virtual environments will allow us to seize the opportunities brought by these games. Indeed, when used with care and validation, multiplayer videogames can push forward our understanding of the interplay between habitat configuration, interaction networks, and behavioral variation in animals and humans (36; 72-73). This bridge could profit work on animals by providing theory or tools developed to analyze traits that are often seen as hallmarks of our species (e.g., contests, cooperation, cultural transmission, post-reproductive lifespan 74-77). In parallel, such analyzes might also help us improve our understanding of in-game behavior and its ecology or help to design virtual environments supporting more inclusive and enjoyable online interactions, which is a central societal problem (78-80).

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Declaration of interests

We declare no conflict of interest.

Box 1: Multiplayer videogames suitable for ecological and evolutionary research

Role-playing

Role-playing games (or massively multiplayer online role-playing games) are set in complex virtual ecosystems with their own economies (e.g., *EVE Online*) and political systems (10). Players usually use an avatar that they will develop over time (sometimes years) to acquire abilities and skills. Avatar development can determine players' **playstyle**, **tactics**, and space use in the game. Role-playing games generally offer several ecological challenges. For instance, in *World of Warcraft* (Figure Ia), players can interact in real time, either to cooperate during quests, accumulate artifacts, express a wide array of social roles, and/or optimize their skills and abilities.

Survival

In **survival games**, the main objective of the player is to survive for as long as possible in the virtual environment. Players often manage health, thirst, and hunger, while negotiating dynamic environmental conditions and predation by other players and non-player characters (e.g., *The Forest* and *Rust*). Survival games often encourage players to explore and interact with the environment extensively to collect resources while being at risk of attack. These games often comprise important components of resource management such as weapon and tool crafting, as well as shelter construction and maintenance. In some instances, players will converge in resource hotspots where they may have to fight to access rare items, leading to highly dynamic interactions with outcomes being determined by the level of cooperation or competition among players (e.g., cooperate and share the resource vs kill the other player's avatar to keep the resource).

Real-time strategy

Real-time strategy games such as *Age of Empires* or *StarCraft* require players to allocate their limited resources to build units and defeat an opponent. Players must constantly make decisions on how to invest their time and various types of resources, facing trade-offs between different strategies in the development of their population. Players often specialize on units with different characteristics depending on the resources they decide to collect. Such decisions, and the success of a strategy itself, are highly dependent on those adopted by the other players.

Sandbox

Sandbox games, such as *Minecraft* (Figure Ib) or *Space Engineers* are based on minimal concrete goals or narratives, and instead promote creativity and free play. They are often set in open-ended worlds that players can explore and modify. This gives rise to emergent gameplay from simple building blocks or game mechanics. In the online multiplayer game modes, players compete against each other, cooperate towards a common goal, or simply explore and socialize.

Figure I: Examples of multiplayer videogames. a) The role-playing game *World of Warcraft* offers players the possibility to develop an avatar acquiring skills, abilities, and artefacts. Through this avatar, players can interact in real-time with others in teams within a large virtual environment (credits: 81). b) The sandbox game *Minecraft* can be modified by players to create various objectives. In the original version of the game, players move in a spatially-explicit environment to secure resources, build refuges, and avoid attacks while managing their health and hunger levels (credits: Microsoft Corporation).

Box 2: Worked example: Quantifying and explaining selection on prey behavior in Dead by Daylight

In the game *Dead by Daylight* (Behaviour Interactive Inc.), five players interact in real-time (four prey, one predator, 22). The predator has to capture, handle, and consume the prey. Prey forage and accumulate resources distributed on several patches in the environment to unlock an escape while avoiding consumption by the predator. They can also help each other by healing or freeing injured or captured partners. The game ends when all prey have either escaped or been consumed by the predator. Virtual environments vary in the type and size of habitats and resource and refuge distributions.

In this game, prey antipredatory, foraging, and helping behavior are under a complex selection regime including social and natural linear and non-linear selection gradients (see Figure II, black arrows 18). Interestingly, the combined natural and social selection regime define three of the most common behavioral adaptations we observe in animal societies: Foraging effort is a cooperative behavior, beneficial for the individual and for its social partners; Predator avoidance is a selfish behavior, beneficial for the individual but detrimental to its social partners (18); Helping and defense are altruistic behaviors, detrimental to the individual but beneficial to its social partners (22). These behaviors are also under correlational (i.e., prey survival is affected by combinations of behaviors) and contextual selection (i.e., the consequences of prey behavior for survival varies with the behavior of social partners), which should structure behavioral variation (82). Hence, simple social interactions within a predator-prey context are sufficient to generate selection regimes consistent with the evolution of social behaviors we study in nature and with models. Predator hunting behavior further modulates the selection regime exerted on prey behavior (Figure II, purple arrows), suggesting that the selective mechanisms (i.e., the costs and benefits of behavior) generated by social and trophic interactions can cross ecological contexts. Work on the evolution of social behavior rarely considers this carry-over between social and predator-prey contexts (83-84).

Dissecting selection to quantify the relative contribution of several agents of selection is rarely achievable but very important to our understanding of evolution (83; 85). An experiment where players act either as purely selfish or altruistic prey show that helping others is costly because it results in a higher probability of injuries from the predator, and a lower investment into foraging (17). The benefits are also associated with the increased group size enabled by helping behavior. Such a group augmentation hypothesis has the potential to change our view of the evolution of altruism but is very challenging to test in natural systems (86). Altruistic individuals, by saving their social partners, foster larger prey groups, which increases group foraging efficiency and dilutes predation risk. Reciprocity among players within matches brings weak additional benefits. Taken together, these mechanisms account for most of the selection on helping behavior (17). Helping could be favored whenever it increases group size, even in the absence of any form of reciprocity nor repeated interactions among individuals.

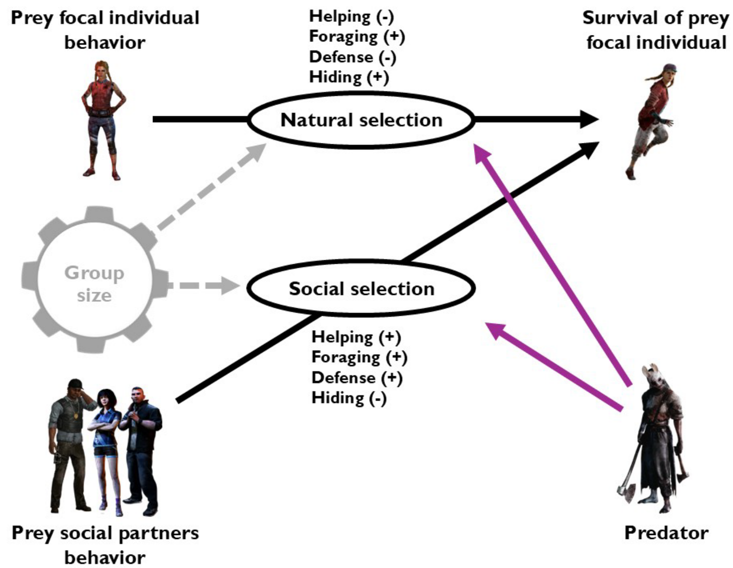

Figure II: Selection generated by social interactions among players in the game *Dead by Daylight*. The survival of prey focal individuals is determined by their antipredatory, foraging, and helping behavior (i.e., prey behavior is under natural selection, black arrow). + and - denote prey behavioral traits with a positive and a negative effect on prey focal individual survival. The survival of prey focal individuals is further determined by the antipredatory, foraging, defense, and helping behavior of their social partners (i.e., prey behavior is under social selection, black arrow). Considering natural and social selection on each of these traits identifies foraging effort as a cooperative trait, predator avoidance as a selfish trait, and defense and helping as altruistic traits. Most of the benefits of helping behavior by social partners are associated with an increase in group size. The survival costs of this behavior are associated with increased susceptibility to predation and a lower foraging effort. Predator hunting behavior modulates the selection regime exerted on prey behavior (purple arrows), most probably by modifying the costs and benefits of each behavior in terms of survival (gray arrow).

Box 3: Worked example: Analyzing the emergence of trophic specialization in Dead by Daylight

In this game, predators exhibit hunting tactics that are very similar to those observed in animals in nature (87-88). Predator players vary consistently in the proportion of ambush and cursorial tactics that they use to hunt other players (23). In nature, such alternative foraging modes or hunting tactics often emerge in response to variation in habitat configuration or prey mobility (see Figure III). However, few studies quantified how ecological conditions modulate the relationship between these tactics and foraging success. Analyzing the hunting success of predator players across a range of habitats, we showed that the relationship between predator behavior and hunting success varied as a function of prey space-use and movement but not habitat configuration. Hence, variation among prey should favor the emergence of alternative hunting tactics in predators, composed of a suite of correlated behaviors including space-use and speed of movement (23).

Ambush and cursorial tactics are both more successful against slower prey. This result challenges the predictions from one of the central hypotheses formulated to explain the emergence of a continuum of hunting tactics (i.e., the locomotor cross-over hypothesis 89) and emphasizes that predator and prey movement behavior interact in complex ways to determine hunting success. Indeed, the influence of prey behavior on the outcome of hunting tactics is also dynamic, suggesting that behavioral variation among individual prey favors predators with the ability to adjust their hunting tactic in response to prey. Hence, multiplayer videogames such as *Dead by Daylight* offer a great opportunity to dissect how prey and predator space-use interact with habitat configuration to shape behavioral evolution.

Individual predator players differ not only in their average hunting tactics but also in their level of hunting specialization. Over time, some predators specialize on cursorial hunting tactics, while some other predators become more flexible and use a wider range of hunting tactics (90). Expressing a wider range of tactics is associated with encountering prey with a wider range of phenotypes (90). Hence, seemingly random differences in the average and diversity of prey speeds encountered by predator players across their successive matches could lead some predators to specialize on a narrow range of hunting tactics, and some other predators to expand the range of hunting modes that they express in response to prey behavior (90). Predators need extensive experience in the game to develop expertise and reach their maximum hunting success (24), but we observed that flexible and specialized predators achieve a similar success (90). Thus, variation in prey behavior, coupled with the complex relationships linking hunting tactics and success, could allow for the coexistence of specialists and generalists within predator populations.

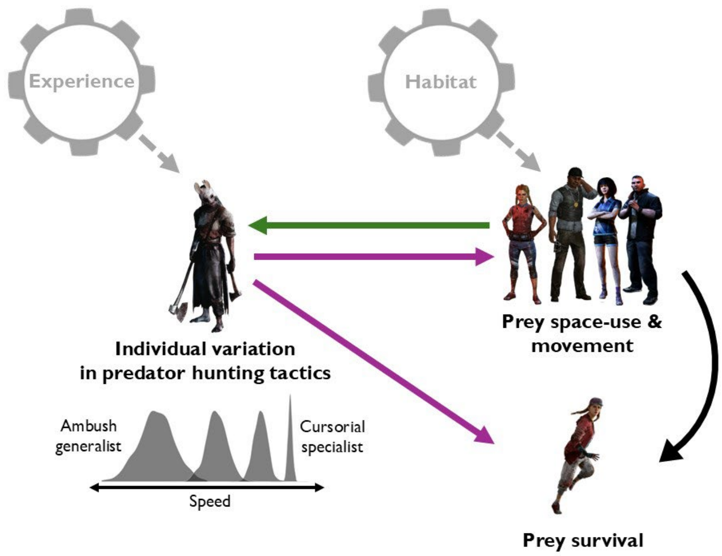

Figure III: The mechanisms generating trophic specialization in predators in *Dead by Daylight*. Over time and as they gain experience, individual predators develop as generalist ambush hunters, or specialized cursorial hunters (gray arrow). The degree of specialization in these tactics is also shaped by the behavior of the prey that predators encounter (green arrow), while predators also shape the behavior of their prey through their hunting tactic (purple arrow). Prey respond to habitat configuration (gray arrow), which indirectly influences the strategy of predators. Ultimately, the success of predators is determined by the interplay between their own strategy and the strategy of the prey that they encounter.

Glossary

Application programming interface: A set of protocols allowing the use of code to query data or send instructions from a software (e.g., a videogame) to another (e.g., a programming environment allowing data manipulation and analysis).

Avatar: A digital representation of a player in a virtual environment. Avatars can often be customized, differ in their abilities and be modified in response to past player decisions.

Behavioral gambit: A research approach assuming that the expression of adaptive behavior is not constrained by the psychological and cognitive mechanisms.

Non-player character: A character programmed by game designers to perform standardized actions when prompted or triggered by players during gameplay.

Multiplayer videogames: Games with a video interface where two or more players can interact in real time, often using avatars in a spatially structured virtual environment.

Playstyle: The tactics or behaviors that players use preferentially.

Real-time strategy games: Games where players allocate limited resources to build units and defeat an opponent.

Role-playing games: Players use an avatar that they develop over time to acquire abilities and skills across quests or missions.

Sandbox games: Games set in open-ended worlds that players can explore and interact without set objectives.

Soft selection: A form of selection where the fitness of an individual is determined by its phenotype relative to the phenotypic composition of its neighbors or social partners.

Survival games: Games where the main objective of the player is to survive in the virtual environment while managing health, thirst, and hunger.

Tactic: Player tactics refer to suites of short-term decisions made to overcome challenges and achieve objectives during gameplay.

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