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Predator–prey interactions paradigm: a new tool for artificial intelligence

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Abstract
Predator–prey interactions are probably one of the key mechanisms for explaining the evolution of organisms in their ecosystems. Scientific fields relevant to understanding the mechanisms of these interactions are as diverse as evolutionary biology, behavioral ecology, ecomorphology, molecular biology, phylogeny, neurosciences, physiology, biomechanics, and robotics. The difficulty in understanding these mechanisms lies therefore (1) in the multi- and interdisciplinary nature of this issue, and (2) in keeping up with very rapid developments in various scientific fields. This Special Issue provides an interdisciplinary approach to predator–prey interactions to identify how phenotypic traits of both types of organisms interact and how each can act as a selective pressure on the evolution of a population of organisms at the different levels of the trophic chain. Moreover, we show that confronting bodies of knowledge that a priori appear as remote as those of robotics and experimental biology or ecology may seem difficult but can provide reciprocal understanding.

Keywords
Evolution, adaptation, phenotypic trait, environment, artificial intelligence

1 Introduction

Together with sexual reproduction, one of the greatest innovations of life has been the emergence of heterotrophy by individuals collecting other organisms as food between 3.8 and 1.8 billion years ago. This innovation has complicated food webs by adding additional levels, that is, secondary consumers composed of predators and primary autotroph consumers, as widely demonstrated since the early works of Elton (1927). These tropho-dynamic networks consist of a set of interconnected food chains in an ecosystem or in linking ecosystems. Energy flow through the trophic levels occurs in a dynamic equilibrium of ecological communities into ecosystems involving phenomena such as “top-down” relationships that ensure regulation of resources by consumers and “bottom-up” relationships that limit resources available for these same consumers. Empirically, it is obvious that these interactions play one of the key roles in the dynamics of spatially structured populations (Clobert, Le Galliard, Cote, Meylan, & Massot, 2009). Three levels constitute the structural basis of the food chains: producers, consumers, and decomposers. Predation pressure in these chains is one of the major factors for shaping diversity and function of organisms (Agrawal, 2001). Symbiotic and parasitic interactions are also key factors of the functioning of food chains, as demonstrated since the 1950s (Crofton, 1971a, 1971b).

Complex relationships between trophic chains (Figure 1) within and between various ecosystems, often represented by simplified ecological pyramids, participate in the dynamics of all ecosystems. Simple models that consider food webs as a succession of more or less homogeneous trophic levels, from primary producers to successive consumers, cannot always predict the functioning of the networks of interactions between organisms belonging to various trophic levels. Indeed, these interactions are fundamentally nonlinear (Kooi, Kuijper, Boer, & Kooijman, 2002) because functional groups of organisms collected in the various levels of an ecological pyramid differ from each other in their diet, physiology, and vulnerability to predation (Davic, 2003). Predation is defined as a biological interaction between organisms where a predator approaches, hunts, captures, and swallows living resources called prey. Seed predation and egg eating are also often considered as predation because they

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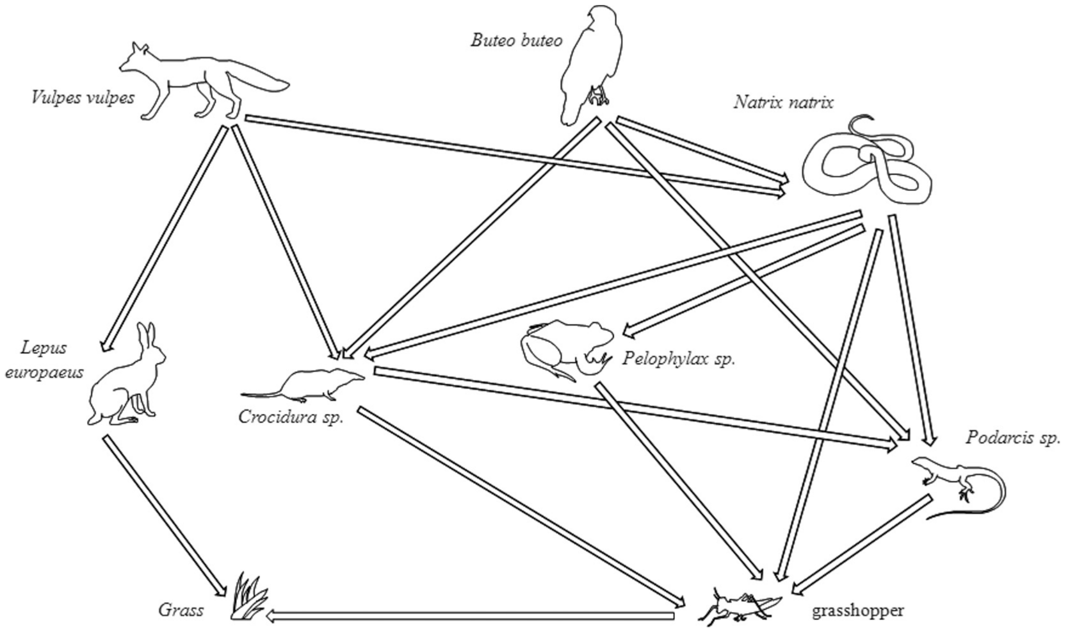

Figure 1. Simplified representation of an example of food webs in a French agricultural ecosystem. Each organism involved in successive levels, from consumers (i.e., *Lepus lepus*, grasshopper) to top predators (i.e., *Vulpes vulpes* and *Buteo buteo*), can be characterized by more or less complex feeding (or predatory) behaviors.

represent eating of potential organisms. Predation, from mode of prey capture (Bels, Chardon, Vandewalle, & Aerts, 1994; Schwenk, 2000; Figure 2) to density control of populations at each trophic level, is determined by the interplay between predator behavior and prey antipredator behavior. Consequently, the effects of such interplay fundamentally control ecosystem function including all exchanges characteristic within ecosystems (Schmitz et al., 2008), for example, energy flow and the biogeochemical cycle.

Predator hunting strategy, and consequently prey escape strategy, can be viewed as key functional traits that partly control the top-down interactions in ecosystems. These behaviors and their related energetic costs (e.g., acquisition and processing of information from the environment, locomotion, and development and maintenance of the musculo-skeletal systems) are probably important for the origin, functioning, and development of all food webs. How phenotypic traits, from structures to behaviors, of predators and prey involved in these interactions regulate the functioning of ecosystems remains a widely open field of interdisciplinary research. Therefore, one major current issue in evolutionary biology concerns the ecosystemic role of predator and prey behaviors in various environments (e.g., aquatic, terrestrial, and arboreal). The work done since the first standard models of predator–prey interactions (Volterra, 1928) has established increasingly complex mathematical models based on logistics equations. Many papers and textbooks within the last decades mention the evolution of traits of predators and prey and these provide valuable data to test theories about the evolution of predator–prey interactions (Abrams, 2000; Mitchell, 2009). However, we still need to integrate empirical and experimental data into sophisticated mathematical simulation of the behavioral responses of predator and prey to obtain more reliable models of predation. Studies of the responses of the predators and prey are needed to understand and model the effect of their phenotypic traits (i.e., morphological, physiological, energetic, and metabolomic) and their underlying genomic basis. For these reasons, the studies of the dynamics of predator–prey interactions need to become more and more integrative and to incorporate data from a wide array of fields ranging from molecular biology to behavioral ecology.

Predatory success at all trophic levels depends on a series of external factors (e.g., complexity of the environment, density of prey, temperature, and behavior of the prey) and phenotypic features (e.g., musculo-skeletal system, integration of sensory and motor systems, cognitive ability). During the whole process of predation, from approach to capture, these environmental factors require behavioral adjustments as a result of environmental variations at all the levels of the ecosystem's functioning. These variations can be global and long-term (i.e., climatic change due to global warming), or local, involving any unexpected condition of the nearby environment at the instant of predation. For all these reasons (e.g., phenotypic traits, environmental factors), models relying on artificial intelligence currently under development (Floreano &

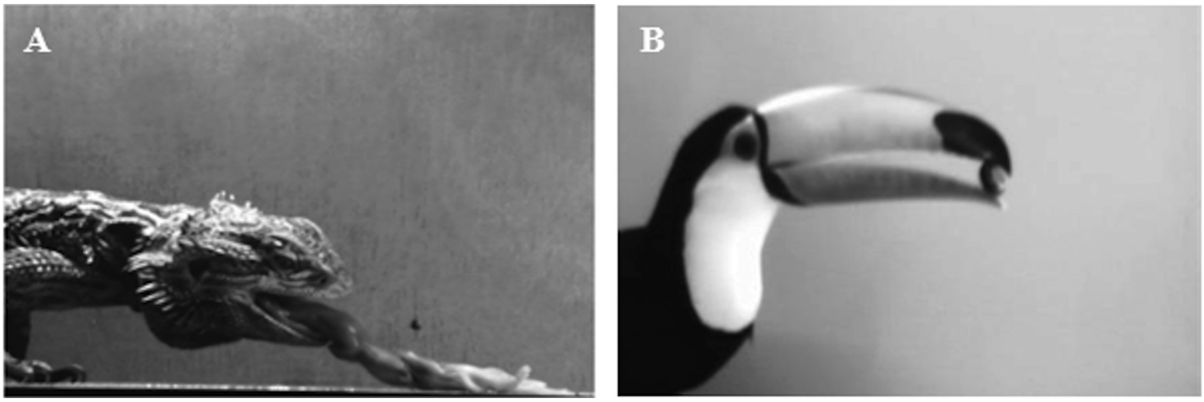

Figure 2. Examples of prey capture modes in vertebrate tetrapods in terrestrial environments. (a) Lingual prehension in *Pogona vitticeps*. (b) Beak prehension by *Rhamphastos toco*.

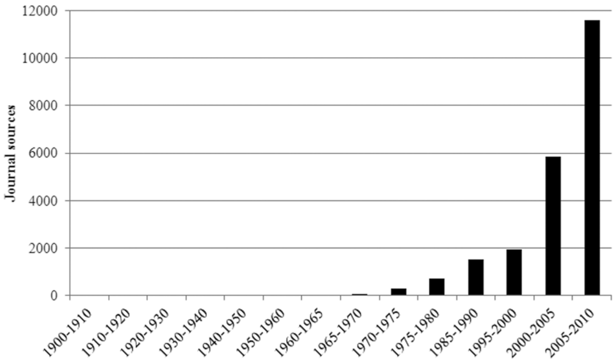

Figure 3. Time history of scientific references about predator–prey interactions from 1900 to 2010 (source Scirus, http://www.scirus.com/srsapp/).

Keller, 2010; Ijspeert, Crespi, Ryczko, & Cabelguen, 2007; Nolfi, 2012) must integrate a large amount of data, not only at the level of the population response, but also at the level of the individual involved in the predator–prey encounter. Therefore, these models are based on a large amount of empirical knowledge and must confront the experimental data obtained in the virtual world with those gathered in the field. An exhaustive review of the literature on experimental data on predator–prey interactions over the last century highlights the importance of this context in the study of evolutionary and adaptive mechanisms in animal biology (Figure 3).

Theories about the evolution of predator–prey interactions—including the dynamics and stability of populations in both trophic levels and responses of predators in relationship with their phenotypic and life traits—are of primary importance to better understand the processes that drive evolution of the behaviors of predator and prey and explain their interactions. Experimental study and confirmation by empirical observations in the field will improve our understanding of how predators exert evolutionary pressure on their prey, but also how prey develop evolutionary counter-measures.

The role of all phenotypic traits of organisms (predator and prey) involved in food webs is a blossoming research field. The term *phenotypic trait* here gathers all the observable and measurable characteristics of a living being. These traits are multiple (e.g., molecular, morphological, functional, and behavioral). The variation in these traits that characterize an organism is, undoubtedly, one of the essential elements on which natural and sexual selection can act. Without phenotypic variation, all individuals in a population would have the same fitness (selective value). Scientific fields relevant to understanding mechanisms in adaptation and evolution and their role in the phenotypic traits of organisms are as diverse as evolutionary biology, behavioral ecology, ecomorphology, molecular biology, phylogeny, neurosciences, physiology, biomechanics, and robotics. The difficulty in understanding these mechanisms lies therefore (1) in the multi- and interdisciplinary nature of this issue, and (2) in keeping up with very rapid developments in various scientific fields.

Adaptive and evolutionary mechanisms such as coevolution (Janzen, 1980), exaptation (Gould & Vrba, 1982; Okada, Sasaki, Shimogori, & Nishihara, 2010), functional trade-off (Ghalambor, Reznick, & Walker, 2004), and phenotypic plasticity and changes (Agrawal, 2001) are strongly related to predation. For example, behavioral responses in squamates result from evolutionary trade-offs (McElroy, McBrayer, Williams, Anderson, & Reilly, 2012). Also, weapon shape diversity for defense against predators in mammals (Stankowich, 2012) can be viewed as classical phenotypic change related to predation.

On 24th of August, 2010, in Paris, we organized a workshop entitled *Predatory and Antipredatory Behaviors: From Structures to Simulation* in the context of the *11th International Conference of Adaptive Behavior*. This was a unique opportunity for researchers working on predator–prey interactions with various methodological and conceptual approaches to better understand the predator–prey interactions and their effect on the function of ecosystems. The meeting also provided the basis for better understanding the function of the organisms and the effect of phenotypic traits on their fitness. Biological data on these topics can be compared with data collected from autonomous artificial systems. Confronting bodies of knowledge which a priori appear as remote as those of robotics and experimental biology or ecology may seem difficult, but we have shown that this provides reciprocal illumination.

2 From animals to animats

Between 1930 and 1950, the psychologist Clark Leonard Hull (Hull, 1937, 1950; see also Amsel & Rashotte 1984) explained that identical laws may govern the behavior of animals and machines. At the same time, the mathematician Norbert Wiener (1948) founded the new discipline of cybernetics, based on the analogy between information processing performed by natural and artificial systems. This analogy, made by these pioneers, led them to consider artificial entities as metaphors for living organisms and to study them from a positivist perspective that may excessively simplify their complexity. The exponential increase of our knowledge about the brain, thanks to advances in experimental neuroscience, quickly led to the reconsideration of this paradigm. A reversal of this paradigm took place during a meeting in Dayton (Ohio, USA), held from September 13th to 15th, 1980, as the result of the popularization of the concept of bionics. This launched comprehensive multidisciplinary research programs on how to design efficient artificial systems. The idea to reproduce the behavior of animals or to design bio-inspired robots is not new, as it is reported that in 1470 the German mathematician and astronomer Regiomontanus constructed a wooden eagle that flew from the city of Königsberg to meet the emperor Maximilian when he came into the free city of Nüremberg, saluted him, and returned. While this beautiful story is more likely myth than reality, it marks the emergence of the concept of "animats," that is, not intelligent robots, but something adaptive and able to cope with the real world. In this context, intelligence is not the result of a complex programming process of reasoning, but can emerge from the activation of simple behavioral modules that closely interact with the environment.

From a neurophysiological point of view, the behavioral response to the environment is often a simple reflex, although it is sometimes more sophisticated and then requires greater cognitive processes. One example developed in this Special Issue is the movement of a school of teleosts to avoid the attack of a predator (Marras, Batty, & Domenici, 2012). Experimental results show that group behavior is a trade-off between the behavior of the predator and of some individuals of the school. The cybernetic approach to such problems, which seem at first glance very complex, shows that the behavioral response of all individuals can partly be explained by a combination of binary reflex responses of individuals. Thus, simulation of the movement of clouds of animals or "boids," that is, virtual birds or fishes, on the basis of the combination of simple steering behaviors (Reynolds, 1987, 1999) allows the prediction of the actual behavior of the school, even if the behavior of some individuals remains unpredictable because of their phenotypic traits and the history of life (Buskey, Lenz, & Hartline, 2012; McElroy et al., 2012). This example shows that the a priori stochastic behavior of complex systems can emerge from the combination of simple behavioral responses to information taken from the environment (physical or social). So the question is often to identify emergent behaviors of the studied system (individual or group). Thus, according to Isaac Newton (2003), "we are to admit no more causes of natural things than such as are both true and sufficient to explain their appearances." Therefore, the research program of a series of biological disciplines, from ethology to physiology, is to extract the minimal behavioral laws that allow the emergence of complex behaviors such as predator escape strategies (Legreneur, Laurin, Monteil, & Bels, 2012) or weapon use for defense against predators (Stankowich, 2012). This knowledge is fundamental to the community of researchers in artificial intelligence because minimal behavioral laws present at least two qualities. The first is that these laws are simple to implement, which facilitates real-time simulation of the evolution of virtual agents. The second is that they are likely to apply to many systems. During evolution, despite changes in shape, structure, and motor controls of species, physical laws applying to individual locomotion are immutable (Goslow, Wilson, & Poore, 2000; Jamon, 2011; Lauder, 1991). Thus, for robotics, the evolutionary history of taxa is like a gigantic experiment that lasted hundreds of millions of years, but we do not know all the experimental conditions. The robust solutions that emerged during this long evolution have a very high probability of being nearly optimal in terms of energy use. In this context, characterization and study of resources required by individuals to maximize their success in predator–prey interactions are very important issues within the paradigm of bio-inspired robotics. That is why we have chosen, as part of this Special Issue, to present some widely different examples of predator–prey interaction strategies between terrestrial and aquatic species.

3 From animats to animals

As described above, researchers in artificial intelligence have long been interested in the strategies adopted by the living, either in terms of structure or behavior (Cordeschi, 2002). In contrast, the opposite approach of mathematically modeling these strategies to explore the causal relationships between structure and function is much more recent. The outstanding work of McNeill Alexander (2003) on animal locomotion was a forerunner in the biomechanical analysis of behavior. However, despite a detailed knowledge of the basic structures of living systems, it remains difficult to predict their behavior, other than by experience (Pouydebat, Laurin, Gorce, & Bels, 2008). This limitation reflects the difficulty in modeling the system using predictive equations because the number of parameters is great, and each can have a major influence on the behavior of the system (Bernstein, 1967). To predict predatory behavior, it is thus necessary to take several parameters into account, which amounts to performing a simulation of the studied system. In this context, it appears that research in behavioral biology in general should use the animat approach. Indeed, the increase in computing power of microprocessors, advances in embedded computing, and the use of new materials allowing a heuristic modeling of musculoskeletal systems of animals have led to the emergence of virtual animals (Ijspeert et al., 2007) that can interact in predator–prey relationships. Moreover, the optimization methods (genetic algorithms, neural networks) can help to understand the mechanisms that regulate the probability that traits appear during evolution. This leads to a better understanding of locomotor strategies and can identify optimal solutions for the selected shape (Nolfi, 2012).

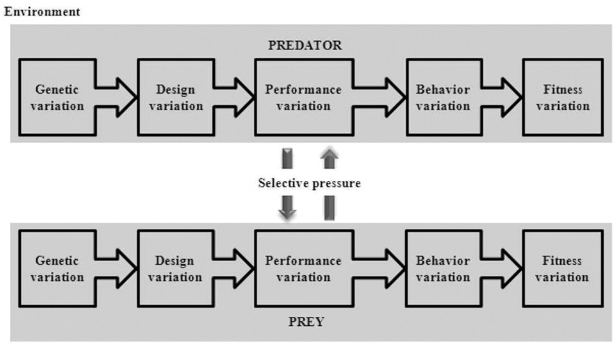

Figure 4. Schematic representation of the selective pressures of the predator on the prey and the prey on the predator. These pressures act on the structure versus performance versus fitness relationships of the individuals. The model path of predator and prey mainly interact at the level of the performances of the organisms. These performances are strongly related to structures, from molecular to gross morphological levels, of the organisms. The combinations of these performances constitute the predatory (predator) and escape (prey) behaviors.

4 Conclusion

In view of the interaction between structure, performance, and fitness (defined as adaptive value in biology), any structure can achieve a performance that has some fitness in light of the evolution of species (Arnold, 1983). In this context, the predator–prey interactions are probably one of the key mechanisms for explaining the evolution of organisms and their ecosystems. The predator acts as a selective pressure on the prey and the prey acts also as a selective pressure on the predator. A simple path model—morphology versus performance versus fitness—between predator and prey permits the modeling of the role of each of the organismal levels on the evolution of the trophic chain within ecosystems, and their functioning (Figure 4). The reciprocal influence of diet and predators focuses directly on one sort of expressed phenotypic trait (performance) of each organism included in the various trophic levels. Consequently, determining the plasticity of all traits (e.g., morphological, physiological, biochemical) is of primary importance for understanding the predator–prey interactions. For example, the predatory performances during hunting, from approach to capture, probably have a direct effect on the success of predation. For example, some squamates are able to use either jaw prehension or lingual prehension to capture prey. Such plasticity is not only related to the prey type (Montuelle, Herrel, Libourel, Reveret, & Bels, 2010), but can be selected by the predator for a same prey item (Smith, Kardong, & Bels, 1999).

Combined empirical experimental and field research, as described in this Special Issue, and associated simulations that permit the extraction of general laws, are needed to understand the primary role of predator–prey interactions in the evolution of ecosystems and the potential effects of any disturbance due to human activities. Therefore, the study of trophic relationships, by comparing the experimental results from the biological sciences with those predicted by artificial intelligence, is an extremely exciting area of research (Meyer, Doncieux, Filliat, & Guillot, 2003; Meyer & Guillot, 1994), as demonstrated within this Special Issue that we hope to be useful for future research in this field.

The multidisciplinary study of predator–prey interactions is also an important socio-economic issue today. Given that the sixth mass extinction event is currently in progress (Wake & Vredenburg, 2008), because of habitat destruction and global warming in particular, understanding the mechanisms that regulate trophic interactions is essential for effective conservation strategies (Domenici, Claireaux, & McKenzie, 2007). In fact, most evolutionary biologists now believe that predator–prey interactions have played a key role in the development of the history of life on Earth (Abrams, 2000; Bailey et al., 2011). Another exciting developing field is paleobiological inference of behavior in long-extinct species (Kelley, Kowalewski, & Hansen, 2003). More commercial uses of such data in artificial intelligence include development of video games, serious games, or robots able to work in constraint environments.

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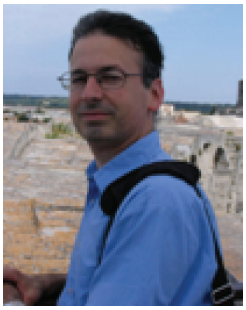

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