

Review

Predators as Agents of Selection and Diversification

Jerald B. Johnson * and Mark C. Belk 

Evolutionary Ecology Laboratories, Department of Biology, Brigham Young University, Provo, UT 84602, USA; mark_belk@byu.edu

* Correspondence: jerry.johnson@byu.edu; Tel.: +1-801-422-4502

Received: 6 October 2020; Accepted: 29 October 2020; Published: 31 October 2020



Abstract: Predation is ubiquitous in nature and can be an important component of both ecological and evolutionary interactions. One of the most striking features of predators is how often they cause evolutionary diversification in natural systems. Here, we review several ways that this can occur, exploring empirical evidence and suggesting promising areas for future work. We also introduce several papers recently accepted in *Diversity* that demonstrate just how important and varied predation can be as an agent of natural selection. We conclude that there is still much to be done in this field, especially in areas where multiple predator species prey upon common prey, in certain taxonomic groups where we still know very little, and in an overall effort to actually quantify mortality rates and the strength of natural selection in the wild.

Keywords: adaptation; mortality rates; natural selection; predation; prey

1. Introduction

In the history of life, a key evolutionary innovation was the ability of some organisms to acquire energy and nutrients by killing and consuming other organisms [1–3]. This phenomenon of predation has evolved independently, multiple times across all known major lineages of life, both extinct and extant [1,2,4]. Quite simply, predators are ubiquitous agents of natural selection. Not surprisingly, prey species have evolved a variety of traits to avoid predation, including traits to avoid detection [4–6], to escape from predators [4,7], to withstand harm from attack [4], to deter predators [4,8], and to confuse or deceive predators [4,8]. Predators, in turn, have co-evolved to become more adept at finding, killing, and consuming their prey [9,10]. Although we know a great deal about the effects of predation on the evolution of prey traits [11–13], much less is known about how predators more generally drive evolutionary diversification at different biological scales, including diversification within populations, diversification among populations that can lead to the formation of new species, and even adaptive radiations that can give rise to multiple species. In this Special Issue of *Diversity*, we present a variety of papers that shed light on this question.

To frame this collection of papers, we provide a brief overview here of the many ways that predators can act as diversifying agents of natural selection. Our list is almost certainly not exhaustive, but it does offer a glimpse into the importance of predation as a fundamental biological phenomenon that has led to local, regional, and even global patterns of biodiversity on Earth. Further, we recognize that predation can have both direct and indirect effects on evolutionary change, and that both are likely important in the generation of evolutionary novelty [14–16]. Some areas of research on predator-mediated evolution are well established, where others have received much less attention. Yet, what should be clear in all of this is that predation can play a key role in shaping biological diversity.

2. What is a Predator?

For our purposes, we limit the definition of predator to an organism that kills and consumes all or a part of another organism. Thus, grazing and parasitism are not included in our definition. We acknowledge that the consumptive actions of grazers and parasites can sometimes result in death and alter vital rates of organisms, and that grazers and parasites, thus, can be important selective agents [17,18]. However, we do not consider such interactions within the scope of this Special Issue.

To understand how predators affect evolutionary diversification, it is critical to first understand how these organisms function as agents of selection. Of course, no two predator species are identical, and variation among predator species inevitably leads to differences in how prey species respond [19–21]. This said, we have come to understand predators in general ways that provide an important context for understanding how they inflict mortality on their prey, and how they affect other aspects of biological systems that can influence reproduction or survival. Several excellent reviews have been published describing predation as a general ecological phenomenon [22–26]. Rather than try to summarize these here, we instead offer just a few key insights about predators as evolutionary drivers.

First, predators face a fundamental problem. Unlike organisms who secure energy and nutrients from inanimate sources, or consume resources without killing them, predators must capture, subdue, and kill their prey. Prey organisms can be highly vagile or difficult to contact, cryptic or difficult to detect, and inherently dangerous or large relative to predators. Hence, predators have evolved several traits that make them efficient in this process. Predators typically have the following traits:

Large Body Size—The easiest way to overpower and kill prey is to be larger and physically capable of killing by brute strength or consumption. The best examples of this are the whales and large fishes that consume large numbers of smaller prey at one time [27].

Enhanced Sensory Perception—To detect cryptic or widely scattered prey, predators often have enhanced vision, hearing, touch, or other sensory capabilities. Many unique sensory adaptations have evolved to detect prey, such as electrosensitive capabilities in some fishes [28], echolocation in bats and some cetaceans [29,30], infrared sensory capabilities in some snakes [31], and ultraviolet vision in some birds [32].

Cryptic Appearance or Behavior, and Luring—Capturing and subduing prey requires the predator to get close enough to launch an attack. Many predators rely on cryptic appearance or behaviors to aid in reducing the distance to prey. Some of the best examples are in so-called sit-and-wait predators such as large snakes, benthic fishes, mantids, and spiders. Other predators combine cryptic coloration with lures that attract potential prey [33–37].

Enhanced Weaponry or Predatory Behaviors—Killing prey sometimes requires enhanced weaponry, especially when prey are large relative to predators. Contact with prey can be dangerous to predators [38]. Thus, quick killing provides a selective advantage to predators. Enhanced weaponry typically entails enlarged jaws, beaks, or teeth (found in sharks, many advanced fishes, crocodilians), raptorial limbs (found in birds of prey and mantid insects), and evolution of toxins accompanied by highly evolved delivery systems (found in snakes, arachnids, scorpions).

Enhanced Social Behavior—An alternative to individual large body size is social behavior that allows multiple individuals to work together to find, capture, subdue, and kill prey [39]. Such social behaviors can range from coordinated feeding (e.g., predatory schooling fishes) to higher levels of sociality (e.g., mammalian Carnivora, cetaceans, Hymenoptera).

Second, predators usually adopt one of two ways of foraging. Some actively search for prey, moving across the landscape hunting for organisms to capture and consume [22]. These so-called “active foragers” rely on encountering their prey or detecting them through their senses, and then pursuing them with the potential of eventually capturing and consuming them. Other predators rely on hiding from their prey and waiting for the prey to come to them where they are essentially ambushed prior to capture. Although no review to our knowledge has been completed evaluating the frequency of these different tactics, it appears that both are effective as evidenced by their presence in a variety of taxonomic groups [22,40].

Finally, it is important to recognize that in stable ecological systems, predators are always less abundant than their prey. This is due to the conversion efficiency of prey biomass to predator biomass—the “10% rule” of trophic conversion frequently taught in ecology classes offers a rough context to understand why predators are generally uncommon [41]. This relative rarity of predators often creates conditions where natural selection can act on variation among individual prey without completely decimating prey populations, and, of course, prey species in turn are evolving traits that allow them to avoid mortality by predators.

The take home in all of this is that predators are effective agents of natural selection because they possess key traits that allow them to capture and consume their prey; they adopt different strategies to do so, and they are common, but not too common, such that they can drive prey evolution without driving prey species to extinction.

3. How Predators Affect Prey Evolution

Predation can have both direct and indirect effects on prey evolution [14–16]. Direct effects are those where predators interact directly with their prey, altering either prey survival or reproduction. Such interactions can drive a variety of prey traits, multiplying the potential combinations of traits that can vary among species within the constraints of history and tradeoffs. Here, we consider some of these traits, highlighting what we have learned about the role of predators as agents of selection in shaping these traits. We then suggest ways that predators might be equally influential through indirect effects on trait evolution. These indirect effects include cases where one predator species affects the efficacy of other predators, or where predators interact with other agents of natural selection that in turn shape prey evolution.

3.1. Direct Effects

3.1.1. Effects of Predation on Prey Morphological Traits

Some of our first evidence that predation can drive evolutionary diversification was in the form of morphological differentiation. There is abundant evidence that organisms have evolved an array of morphological traits in response to predators [4,5,22,42]. Spines, barbs, and other types of armament can protect prey species (e.g., catfishes and other spiny-rayed fishes, porcupines). Some prey species have evolved hardened body forms that certain predators cannot penetrate (e.g., turtles, gastropods). Still other prey species have evolved body shapes that predators either cannot handle, or that they cannot consume because it exceeds predator gape (e.g., crustaceans). Other morphological adaptations include adaptive coloration, such as camouflage (e.g., walking sticks, order Phasmatodea, leafhoppers, order Hemiptera) or warning colors that deter predators from attacking in the first place (e.g., many species of Hymenoptera). Interestingly, some of these defensive traits are induced by the presence of predators, whereas others are expressed constitutively.

3.1.2. Effects of Predation on Prey Behavior

Successful predators must detect, capture, and consume their prey. Hence, prey behavior often includes adaptations to avoid detection and capture, or to escape once detection has occurred [7,14,23,26]. Prey can avoid encounters by reducing or modifying their activity levels, or by restricting activity in space and time. Prey might also utilize habitats that predators are likely to avoid, including habitats that can be stressful to both predator and prey. Prey have also evolved traits to facilitate escape after encounters [43,44]. Some of these include deploying chemicals that make prey unpalatable to predators, or the use of evasive movements to confuse or confound predator attacks. Some prey species that live in groups also engage in shoaling or group movement that reduce individual mortality risk and make it more difficult for predators to successfully capture prey. Bird flocking, fish shoaling, and mammal herding are all thought to be driven by evolution on individual behavior resulting in emergent group properties that benefit members of the group.

3.1.3. Effects of Predation on Life History Traits

The theoretical and empirical history of life history research is intimately linked to predation as an agent of selection. Most models of life history divergence have focused on the nature of extrinsic mortality as a driver of life history evolution [45,46]. Moreover, there is abundant evidence demonstrating that where predator-mediated mortality differs among populations, divergent life history strategies have evolved [47]. Predators that inflict high adult mortality relative to juvenile mortality, for example, are known to favor individuals that mature early, invest more heavily in reproduction, and often have more and smaller offspring. These patterns have evolved independently, in multiple prey species. Interestingly, some evidence suggests that predator-mediated life history evolution may in fact contribute to speciation, suggesting that predation might not only be driving micro-evolutionary diversification within species, but could also contribute to macro-evolutionary change resulting in the formation of new taxa [48].

3.2. Indirect Effects

One of the most promising areas for research on predation and evolution is to consider the ways that predators might indirectly drive evolutionary change. We note that indirect effects can shape the same traits considered important for direct effects, including morphology, behavior, and life history traits. Although classic studies of predation focus almost exclusively on simple two-species predator–prey interactions [49], there is ample evidence that some prey species encounter more than one predator species. Similarly, many predators prey upon more than one prey species. This can create interesting dynamics where prey evolve traits that are in some ways a compromise to deal with a spectrum of selective agents. We know much less about how evolutionary diversification occurs under these scenarios. The indirect effects of one predator on the efficacy of another as a selective agent have also received very little attention beyond studies of intra-guild predation where competing predators sometimes feed upon the juvenile stages of their competitor [19,50].

Finally, predation is but one of the many ecological factors that prey species encounter. Predators likely have important effects on other ecological selective agents. For example, predators can alter the way prey species forage, which may affect the timing of feeding and the types of food items that prey species consume. Predators can also alter habitat use which can change prey density [51,52], alter mate choice dynamics [53,54], and modify the effective niche space that prey occupy [55,56]. We know almost nothing about how predators indirectly affect prey in terms of disease transmission, various social behaviors, and group dynamics. Hence, this area of “indirect effects” of predation on evolutionary diversification seems to hold much promise for future research.

4. Why a Special Issue on This Topic?

Clearly, research on predation itself has become more nuanced in recent years. Classic ecological studies that viewed predators as static entities that interact with prey in fixed ways resulting in predictable population dynamics are likely too simplistic. Today we recognize that both predator and prey populations evolve—and that this evolution can happen very rapidly, even on ecological time scales, often with more than two species involved. In this Special Issue, we invited authors to share research findings that explore the various ways that predation can lead to evolutionary diversification. Our invitation was answered with several interesting papers that capture some of the ways that predation contributes to the evolution and maintenance of biological diversity.

Some of this work underscores the strength of predation as a direct diversifying agent. Wisenden [57] shows that divergence among populations of convict cichlid fish in swimming performance and behavior is associated with differences in predation intensity between lake and river environments. This classic pattern of divergent selective pressures leading to evolutionary diversification reinforces the importance of selection as a driver of evolutionary change. Our paper [58] builds on this idea by showing that evolutionary diversification driven by the presence or absence of

predators within the livebearing fish species *Brachyrhaphis rhabdophora* is mirrored in the continued evolutionary diversification in two other *Brachyrhaphis* fish species that have already undergone speciation. In essence, this work suggests that predation itself has likely contributed to the formation of two new species. The paper by Lichti et al. [59] suggests that seed predators directly shape the evolution of plant dispersal strategies, revealing just how pervasive predation is as a selective agent.

Other papers in the Special Issue reinforce the importance of looking for both direct and indirect effects to explain patterns of phenotypic diversity observed in nature. Moreno-Rueda et al. [60] examined how predator-mediated crypsis in a lizard species changes across an elevational cline as predatory density and substrate composition co-vary with elevation. This is a clear example of the complex interplay between predator ecological constraints and prey adaptation in response to varying selective pressures. Kruschel and Schultz [61] censused Adriatic fish communities and found that aggressive predators appear to drive prey species to habitats where less aggressive predators are found, changing both the types of predators that they encounter and the ecological context in which they encounter these predators. This work shows how some predators indirectly affect the evolution of prey traits through other selective agents. Diel et al. [62] remind us that predators can induce phenotypic defenses in prey species in remarkable ways. They provide a detailed review of inducible defenses in zooplankton, including morphological, behavioral, and life history shifts completely mediated by the presence or absence of predators. This work makes it clear that much of the phenotypic diversity that we observe in zooplankton species is mediated by predation risk. Finally, Toscano et al. [63] used cleverly designed mesocosm experiments to examine how variation in prey behavior among individuals within an insect species and among individuals of different insect species can affect prey mortality risk. Their work clearly shows that how prey respond to their predators depends on the context of what other individuals do. This work reinforces the notion that adding real ecological complexity to predator-mediated evolution is essential to understand patterns of biological diversity in natural systems.

Of course, the papers published here are only some examples of the power of predators to drive evolutionary divergence in the wild. However, they do an excellent job of framing the importance of considering predation as a direct agent of selection, as well as an important ecological factor that can indirectly shape other potential drivers of evolution.

5. Current Challenges and Future Direction

Now is a promising time to study predation and its effects on biological diversification. Clearly, we have made important progress in this area. However, there are important challenges and questions that still need to be addressed. Studying predation as a selective agent requires quantifying the nature and strength of selection, which generally requires being able to estimate mortality rates in the wild. Such data are not commonly collected, at least in part because they are notoriously difficult to obtain, often requiring labor-intensive mark–recapture approaches. However, having a better understanding of the strength of predation as a selective agent would help us understand how quickly predation might drive evolutionary change. Similarly, we often know very little about the standing additive genetic variation in prey populations to know how rapidly and how completely prey populations will respond to selection when it does occur.

Another challenge is that most work carried out to date has focused on one predator species interacting with one prey species (but see [19,64]). Yet we know that species interactions are seldom this simple. Predators frequently rely on multiple prey species as a food source, and most prey are at risk from more than one predator. Understanding more complex, and more realistic, interactions between predators and prey should lead to better predictions about evolutionary change in both predators and prey species.

Finally, a quick survey of the literature reveals an unsurprising taxonomic bias in predation research. Extant mammals and extinct dinosaurs have long-captivated researchers as model predators [65–67]. We know much less about single cell species that prey upon other taxa and non-vertebrate species.

The ubiquity of predation in nature demonstrates the adaptive advantage of securing energy this way. However, without broad sampling of predation effects on evolutionary diversification across a variety of taxa, it remains unclear if the results in well-studied taxa are general.

Author Contributions: The authors made the following contributions: conceptualization, J.B.J. and M.C.B.; resources, J.B.J. and M.C.B.; writing—original draft preparation, J.B.J.; writing—review and editing, J.B.J. and M.C.B. Both authors read and agreed to the published version of the manuscript.

Funding: This research received no external funding.

Conflicts of Interest: The authors declare no conflict of interest.

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