Oikos 123: 1234–1243, 2014
doi: 10.1111/oik.01468

Subject Editor: James D. Roth. Accepted 27 May 2014

Towards a cohesive, holistic view of top predation: a definition, synthesis and perspective

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Research on the ecology of top predators – upper trophic level consumers that are relatively free from predation once they reach adult size – has provided regular contributions to general ecology and is a rapidly expanding and increasingly experimental, multidisciplinary and technological endeavour. Yet, an exponentially expanding literature coupled with rapid disintegration into specialized, disconnected subfields for study (e.g. vertebrate predators versus invertebrate predators, community ecology versus biological control etc.) increasingly means that we are losing a coherent, integrated understating of the role and importance of these species in ecosystems. This process of canalization is likely to hinder sharing of scientific discovery and continued progress, especially as there is a growing need to understand the generality of the top–down forcing, as demonstrated for some members of this group. Here, we propose ways to facilitate synthesis by promoting changes in mentality and awareness among specialists through increased debate and collaboration, conceptual reviews and a series of exemplary case studies. The strategy will rely on the collective contribution by all scientists in the field and will strive to consolidate and formalise top-order predation as a holistic, cohesive, cross-taxonomical field of research studying the ecology, evolution and behaviour of apex predators and their capability to exert top–down forcing on lower trophic levels.

Synthesis

The ongoing global loss of top predators and their recolonization of various regions are causing a rapid upsurge of studies on these species and a consequent fragmentation of this field into disconnected, specialized subcompartments: this will weaken efforts to produce synthetic generalisations of broader ecological interest. Here, we show that top predation provides regular contributions to general ecology, is well grounded in theoretical ecology and is a rapidly expanding and increasingly experimental, multidisciplinary and technological field of research. The novelty of this forum lies in providing a concise synthesis of this area of ecology, in attempting to formalise "top predation" as a specific, inter-connected area of investigation, and in proposing a marked change of mentality by stressing the need for cross-taxonomic approaches enabling broader views of the role of predators in ecosystems.

Modern ecology is developing through a rapid, progressive fission into specialized sub-disciplines, coupled with an exponential increase in the literature (Thompson et al. 2001, Graham and Dayton 2002, Nobis and Wohlgemuth 2004). While increasing specialization is important to gain detailed, mechanistic insights into ecological systems, it may nonetheless hinder progress in various ways. First, excessive research canalization causes scientists to be excessively 'myopic', losing sight of the broader picture (Kuhn 1962, Schmitz 2010). Second, an ever-increasing expansion of the literature challenges ones' ability to keep abreast of advances in one's own field of research, let alone other related ones. Third, the rapid rise in volume of literature leads progressively to past ecological studies and debates being overlooked or ignored (erasure of history or cultural amnesia, Holt 2007), leading to recycling of ideas (or worse recasting old ideas in new ways and claiming novelty); all of which is a waste because the basic principles and knowledge on which ecology must build become lost or ignored (Graham and Dayton 2002). Increasing specialization may also lead to overemphasis on analytical, methodological and technological advances, and under-emphasis on ensuring continued progress in conceptual thinking and theory development (Belovsky et al. 2004).

These trends in ecology have motivated increasing efforts aimed at providing better interdisciplinary integration of historical and modern advances in ecological concepts, themes and sub-disciplines (Nathan et al. 2008, Jones et al. 2010, Schmitz 2010, McCann 2012). These landmark efforts – books, review papers or special issues of journals – can become powerful tools to 1) synthesise a whole field of research, 2) frame it in a new paradigm, 3) consolidate it by overcoming taxonomic or methodological boundaries, 4) integrate it into broader understanding in ecology, 5) re-direct it to fill gaps of knowledge, 6) render it quickly available to non-specialists, and 7) provide better coordination of theoretical and empirical developments.

Here, we offer a synthesis to stress the need for more holistic and integrative approaches to the study of top predators and their role in respective ecosystems. This field of research is peculiar because of its traditional capability to attract the attention of scientific and popular audiences and to stimulate the development of general concepts in ecology ever since the early days of the discipline (Leopold 1943, Peckarsky et al. 2008). However, the field also faces fragmentation into a myriad of disconnected sub-compartments, specialist groups and research agendas that pull it progressively farther apart. To counter such drift, we propose that researchers in this field expand their awareness of research on a wider variety of top predatory groups, and increase emphasis on the broader implications of their studies through more collaborative, multidisciplinary and cross-taxonomic approaches, as recently accomplished in other fields (Nathan et al. 2008, Jones et al. 2010). This process will strengthen current research on predation as a platform of general ecological interest and as a more formal, cohesive and cross-boundary field of enquiry that transcends the ecology, evolution and behaviour of particular top predators and specific ecosystems, in an effort to understand the growing need to determine the capability of apex consumers to exert top–down forcing on lower trophic levels and how species that previously operated as mesopredators will emerge to function as top predators as food webs become flattened (Prugh et al. 2009, Estes et al. 2011, Ripple et al. 2014).

To place such issues and their importance into a broader context, in the next four sections we will: 1) define top predation; 2) provide a concise review of the history of research on top predation in order to highlight its traditional relevance to general ecology; 3) highlight the recurrent contribution of this field to the development of ecological theory; 4) demonstrate how top predation is receiving rapidly growing attention; and 5) suggest how to overcome the marked fragmentation suffered by this field of research, a fragmentation which may seriously hinder progress.

Defining top predation

A ‘predator’ is a species which captures, kills and consumes individuals of another species. We define top predators as those species that feed at or near the top of the food web of their supporting ecosystem (upper trophic level consumers) and that are relatively free from predation themselves once they reach their adult size. This definition mainly includes vertebrate predators such as large diurnal raptors and owls, seabirds, herons, mammalian carnivores, cetaceans and pinnipeds, sharks and other large predatory fishes, as well as many large snakes, crocodiles and varanids. However, it also encompasses invertebrates in contexts in which they can exert substantial top–down forcing on lower trophic levels or that represent the highest trophic level in small-scale, simplified or anthropogenically degraded ecosystems (Schmitz et al. 2000, Griswold and Lounibos 2006, O’Donnel et al. 2007, Zeidberg and Robison 2007). These include species such as large cephalopods, spiders, predatory Coleoptera and Hymenoptera, and larval dytiscids and odonates. We further use the term ‘top predation’ to refer to: 1) the behavioural act of predation by top predators and its ecological consequences; and 2) a field of research that studies all aspects of the ecology, evolution and behaviour of top predators. It is critical to note, however, that 1) not all ‘top predators’ included in the definition above are completely free of predation risk themselves, and that 2) these species may not be ‘top predators’ throughout their life history or across all habitats they are found in. The designation of ‘top predator’ is not a trait of a species, but rather a statement about the role of a species in a concrete environmental and community context. These distinctions are critical to studies of top predators, in as much as a failure to account for predation risk, even on large-bodied species considered top predators, could lead to invalid assumptions about factors driving distributions, behaviour, and ecological interactions (Heithaus et al. 2012).

A brief history of research on top predation and its contribution to general ecology

Throughout the first half of the 20th century, research on top predators was scant and mainly based on paleontological or qualitative life history accounts. The major emphasis was on the role of these species as ‘vermin’ or ‘pests’, because they were viewed as competitors of human beings that should be removed in order to enhance game populations or avoid destruction of livestock. In 1943 Aldo Leopold published an influential paper on the capability of top carnivores to limit populations of their ungulate prey, thus preventing them from causing habitat degradation through excessive browsing of vegetation. This was one of the first reports of species at higher trophic levels regulating populations of species of lower trophic levels (i.e. top–down control), with effects rippling through the ecosystem down to the lowest autotroph level (i.e. a three trophic-level effect, today defined as a ‘trophic cascade’). The paper was considered a landmark at the time and reported in several textbooks but, somehow, it failed to inspire further tests of its concepts in the coming decades (Ripple and Beschta 2005). This failure may have been associated with 1) the extinction of many top predators, caused by direct control and indirect poisoning concentrating at higher trophic levels; and 2) by the complementary views expressed at the time by Errington (1946), who argued that predation is often concentrated on a ‘doomed surplus’ of inferior, wounded, senescent or socially sub-dominant individuals, thus producing compensatory mortality with no dramatic effect on prey recruitment or standing crop.

In the 1950s and 1960s, studies of predator–prey dynamics resulted in three major theoretical advances. Holling (1959) developed conceptual advances by Solomon (1949) to formalise the type I, II and III functional responses of predators to changing prey abundance, which laid important foundations for theoretical developments based on the famous Lotka–Volterra formulations, so as the graphical and analytical predator–prey models of Rosenzweig and MacArthur (1963). These expanded the work of earlier ecologists (Nicholson and Bailey 1935) to predict coupled oscillations of predator and prey as an outcome of a top–down predatory interaction. The same period saw the birth of optimal foraging theory, which relied heavily on theoretical models of predators foraging for prey in a way that maximized individual predator fitness (MacArthur and Pianka 1966). Meanwhile, Hairston et al. (1960) proposed their "Green World hypothesis" by which the world is green because predators limit herbivore populations, thus preventing them from over-consumption of the vegetation. This hypothesis was quickly opposed by the "Plant defence hypothesis" by which the world is green because of the outcome of an arms race between herbivores and plants, mediated by chemical warfare through toxic substances evolved by plants to avoid consumption. These hypotheses have prompted decades of discussion about the importance of bottom–up versus top–down structuring processes (Schmitz 2010). At the same time, Paine (1966) helped to initiate the experimental tradition in ecology in general, and predator–prey ecology in particular, by illustrating the concept of keystone predation as a community structuring agent. Some long-term population monitoring programs were initiated in this period and later became landmark studies capable of integrating top predators as ecosystem components and structuring agents (e.g. studies of carnivores on Isle Royale, in the Serengeti and Yellowstone; cf. Mech 1981, Sinclair and Arcese 1995, Clark et al. 1999).

In the 1970s, theoretical developments further highlighted the capability of top predators to structure lower trophic levels, to confer stability to model systems and to cause rapid ecosystem shifts between alternative stable states (Rosenzweig 1973, May 1973, 1977). Such phase shifts were empirically demonstrated by a landmark study (Estes and Palmisano 1974) showing that the presence/absence of sea otter *Enhydra lutris* predation on herbivorous urchins could cause radical shifts in marine ecosystems between kelp forests and barren seascapes caused by excessive browsing. Even if much research funding still came from predator-control programs, this period saw a conceptual change of attitude from considering top vertebrate predators as mere vermin to be exterminated, to the perspective of them as intrinsically valuable, endangered, species worthy of sustained conservation effort; and of an enhanced appreciation of invertebrate (e.g. arthropods and spiders) predators as essential biological control agents of insect pests. This was paralleled by empirical emphasis on the negative effects of chemical contaminants and on the role of top predators as sentinels of ecosystem health (i.e. studies of bioamplification, Newton and Bogan 1974).

In the 1980s, there was a sea change in thinking, shifting from the 'competition paradigm' of the 1960s to 1970s, to predation as an additional structuring agent, in large measure due to an influential review by Sih et al. (1985) and further theoretical formalizations and empirical generalizations (Oksanen et al. 1981, Erlinge et al. 1984, Carpenter and Kitchell 1988). Much work during this period focused on predator-prey relationships, population dynamics and social behaviour (Mech 1981, MacDonald 1983, Erlinge et al. 1984, Korpimäki and Norrdahl 1989). Meanwhile, two decades of investigation on foraging theory led to its first reviews and generalizations (Stephens and Krebs 1986). This also spawned further recognition that predation risk can shape the foraging ecology and life-history of prey (Lima and Dill 1990) and the idea that predation risk alone can cause trophic cascades (Abrams 1984).

The 1990s saw a surge in studies of the ecological effects of predation risk (e.g. anti-predator behaviour as an individual foraging cost, behaviour-mediated trophic cascades, BMTC) and, commensurately, growing recognition of the capacity of predators to influence their surroundings solely as agents of intimidation (Lima 1998). This has recently matured into the broader theme of trait-mediated indirect interactions in communities (Ohgushi et al. 2012). Interestingly, however, this idea failed to take hold in some major areas of research (e.g. many studies on large marine predators; Dill et al. 2003), further underscoring the need for a unified approach to studying top predation.

The new millennium has brought an astonishing flourish of studies on top predatory species and a rapid branching into so many research areas that enumerating them all would be impossible. Such ramification makes it already difficult to sketch a simple history of main conceptual advances for the last 20 years. Among the main trends, the 'metapopulation paradigm' of the 1990s has inspired many powerful demonstrations of its application to large predators (Wootton and Bell 1992, Lahaye et al. 1994). This has directed much research towards spatial issues such as minimum habitat requirements, population viability analysis and the role of corridors for population persistence. Meanwhile, several studies have accumulated growing evidence of the capability of top predators to structure lower trophic levels, communities and even whole ecosystems, although the ubiquity of such effects and the conditions that promote them are still under debate (reviewed by Schmitz et al. 2000, 2010, Terborgh and Estes 2010, Estes et al. 2011, Ritchie et al. 2012, Ripple et al. 2014). Chesson and Kuang (208) for instance have convincingly argued that predation and competition should be viewed symmetrically as interactions which can either limit or foster the maintenance of biodiversity. Furthermore, such increasing attention to interactions across trophic levels has encouraged a blooming of empirical studies on interactions also within the predatory trophic level, especially in the form of intraguild predation (reviewed by Palomares and Caro 1999, Sergio and Hiraldo 2008, Ritchie and Johnson 2009). The application of spatial concepts to wide-ranging predators and the growing appreciation of their structuring ecosystem-role have progressively consolidated them as archetypes of large-scale conservation and ecosystem studies (Soulé and Terborgh 1999, Clark et al. 1999, Sergio et al. 2008). Further major trends in the last 20 years have included an increasing use of: 1) field-experiments for both ecological and behavioural investigations (Krebs et al. 1995, Hakkarainen and Korpimäki 1996, Sergio et al. 2011; reviewed by Korpimäki et al. 2004 and Salo et al. 2010); 2) semi-natural experiments (e.g. introductions or accidental removal of top predators; Estes et al. 1998, Terborgh et al. 2001, Beschta and Ripple 2009, Wallach et al. 2010, Ripple and Beschta 2012); 3) long-term datasets usually analysed to examine responses to global change (McLaren and Peterson 1994, Munson et al. 2008, Lehikoinen et al. 2011); 4) ever more multidisciplinary approaches and sophisticated technological devices, such as last generation GPS-satellite tags, geolocators, time-depth recorders and physiological-loggers (Cooke et al. 2004); 5) increasing focus on indirect measures of predator behaviour, necessitating heavy reliance on the aforementioned technology (e.g. pelagic marine systems) (Cooke et al. 2004); and 6) recognition that there can be considerable individual specialization within top predator populations that leads to markedly different roles in ecosystems (Matich et al. 2011, Tinker et al. 2012, Rosenblatt et al. 2013).

A few generalities emerge from this brief historical excursion. 1) Since the early days of ecology, this area of investigation has been well integrated into major conceptual debates about the functioning of ecological systems, showing its recurrent importance to a broad scientific audience. 2) Like the rest of ecology, it has developed from a qualitative initial approach to an increasingly quantitative, data-intensive, theory-demanding mode of investigation. 3) In line with major trends in ecology, it has caused a shift from an early focus on bottom–up structuring processes (physical nutrient forcing) to increasing attention to biotic and behavioural interactions, exerted both between and within trophic levels (e.g. trophic cascades, mesopredator release, intraguild predation), and mobile predators provide a key dynamical link among spatially separated ecosystems (Holt 2002, McCann 2012). 4) It is growing rapidly, and becoming increasingly experimental, technological and multidisciplinary. Finally, 5) since its inception, it has traditionally received much input from, and contributed heavily to, ecological theory, an aspect that we will expand in the next section.

Research on top predation and theoretical ecology

Research on top predation has been strongly intertwined with the development of two broad areas of theoretical ecology: predator–prey theory and spatial ecology. Predator–prey theory is one of the most traditional branches of theoretical ecology and includes themes as diverse as predator–prey population dynamics, optimal foraging theory, food-web structure, top–down forcing, and trophic cascades. Studies and debates in this field have spanned several decades and produced a wide array of results. Among the most notable contributions, theory has shown the potential of top predation to: 1) generate coupled oscillations between predator and prey (Rosenzweig and MacArthur 1963, Jansen 2002); 2) improve the stability of trophic interactions, for example through cross-ecosystem subsidies mediated by the mobility and behavioural flexibility typical of large predators (May 1973, McCoy et al. 2009, McCann 2012); 3) impose shifts between alternative stable states (May 1977, Holt 2002); and 4) structure whole communities and ecosystems through top–down forcing and trophic cascades (Hairston et al. 1960, Holt 2000). There is still lively debate about even basic aspects of predator–prey theory (Arditi and Ginzburg 2012).

In turn, this large body of literature has prompted a large number of empirical tests of the predictions generated by theoreticians (Boutin 1995, Soulé et al. 2003). The complexity, ramifications, broadness of interest and disputes that distinguish many of these research themes are epitomized by the protracted debate about the capability of predators to impart cycles to their prey. Already conceptualized through a verbal model 130 years ago (Forbes 1880), cycles of small mammals and grouse have been considered as the ecological signature of boreal ecosystems and are exemplified by the oscillations of snowshoe hares *Lepus americanus* in North America and voles in northern Europe (Krebs et al. 2001, Korpimäki et al. 2004). In both cases, decades of study have demonstrated the complexity of assessing causation in predator–prey systems and the importance of a pluralistic approach integrating theoretical predictions, long-term observation and large-scale experimentation (Krebs et al. 2001, Korpimäki et al. 2002, 2004). Current views integrate the effect of both bottom–up and top–down determinants of oscillations and their amplitude (reviewed by Krebs et al. 2001, Korpimäki et al. 2004).

Research on top predators has also given and received much theoretical input in the area of spatial ecology. This includes several areas of investigation such as metapopulation theory, source–sink dynamics, ideal despotic models, and conservation applications in the form of habitat-connectivity, corridor-design and spatially-structured population viability analyses. An excellent example of integration between empirical and theoretical advances is offered by the implementation of theoretical metapopulation models to field demographic data on spotted owls *Strix occidentalis* (Lande 1988). Although focused on a single species, this paper was extremely influential by showing ecologists, theoreticians, managers and politicians that an ecological process (dispersal in increasingly fragmented landscapes) could drive a population to extinction. Strongly grounded in theory and good data, it inspired in turn many empirical, conceptual and theoretical developments (Doak and Mills 1994, Lahaye et al. 1994). This chain of events demonstrates how the strategic exploitation of the charismatic status of many top predators, coupled with solid science, can be powerful tools to attract broad attention in the scientific and popular media. Another example where theoretical spatial modelling has inspired or received inspiration from top predation research include work on Iberian lynx *Lynx pardinus*, which has shown the interconnectedness of within- and between-patch movement and demography in determining metapopulation persistence (Revilla and Wiegand 2008) and, in turn, inspired theoretical models of broader applicability (i.e. not just to predatory species: Delibes et al. 2001).

It is often difficult to discern how much theoretical advances have promoted or been inspired by empirical findings. Decades of conceptual developments and empirical demonstrations of top–down forcing and trophic cascades have inspired a flourishing of field-studies and conceptual models on their constituent mechanisms and side-effects. This includes work on intraguild predation (Holt and Polis 1997), on the effect of multiple predators on prey (Sih et al. 1998), on extinction-waves caused by predator-removal (Borrvall and Ebenman 2006), on predator control of ecosystem nutrient dynamics (Schmitz et al. 2010), on the interactive impact of predator behaviour on prey escape tactics (Lima 2002), and on indirect, trait-mediated effects, such as the predation-landscapes generated by the "ecology of fear" (Abrams 2000, Brown and Kotler 2004, Morosinotto et al. 2010).

One of the most influential lessons taught by spatial research on vertebrate top predators to general ecology and conservation is that the wide-ranging mobility of these species functionally connects their population persistence to large-scale, multiple landscape components (Lande 1988, Revilla and Wiegand 2008, Schmitz et al. 2010, McCann 2012). This imposes the necessity to 'think large' to ensure long-term biodiversity preservation (Soulé and Terborgh 1999). In like manner, empirical studies have highlighted how top predators can dramatically modulate the flows of materials among ecosystems (McCauley et al. 2012). In this sense, research on predation has been permeated by an intellectual tradition of incorporating a spatially broad and temporally long-term view, making the perspective an archetype for understanding and monitoring landscape change, and an ideal tool to 'operationalize' decades of advances in theoretical ecosystem-level ecology (Minta et al. 1999, Lima 2002, Donlan et al. 2006). Along the same line, many national parks are now managed at the 'wider or greater ecosystem level' following the concept of the 'Greater Yellowstone Ecosystem' framed in response to the challenge of preserving the wide-ranging grizzly bears of Yellowstone (Keiter and Boyce 1991). Such intellectual tradition is rooted in the many whole-ecosystem studies in which top predators figured prominently in their role in the ecosystems and as a focus of research. Notable examples are the research programs developed in the Serengeti, Yellowstone, Bialowieza, Isle Royale, and at sites of the Antarctic, arid coastal Chile, the boreal forests of Europe and America and Shark Bay, Australia (Jaksic et al. 1993, McLaren and Peterson 1994, Sinclair and Arcese 1995, Jedrzejewska and Jedrzejewski 1998, Clark et al. 1999; Krebs et al. 2001, Korpimäki et al. 2004, Ainley 2007, Heithaus et al. 2012, Ripple and Beschta 2012). In all theses cases, top predators and their supporting ecosystems have been framed as interactive, cohesive components of a larger picture, and this has influenced the conceptual approach of other studies.

Finally, a further way in which research on top predators has contributed to theory and conceptual ecology is through exceptional landmark studies that have opened the way to major advances in some fields, catalyzing further developments. For example, work on information-transfer in anti-predator alarm calls and on social behaviour in coyotes *Canis latrans* has inspired decades of research on animal societies, communication and cognition (Seyfarth et al. 1980, Bekoff et al. 2002).

Based on the synthesis we have just described, the interaction between top predator research and theoretical ecology can be described as mutual and lively. Although a substantial gap between theoretical concepts and practical applications still remains, the incorporation of theoretical predictions into empirical studies seems to be increasing, as exemplified by the growing number of books on top predators that incorporate theoretical chapters and sections (Clark et al. 1999, Ray et al. 2005, Schmitz 2010, Terborgh and Estes 2010). This may have been further promoted by the increasing complexity, multi-disciplinarity and technological sophistication of studies on top predators, typical of an expanding field of research.

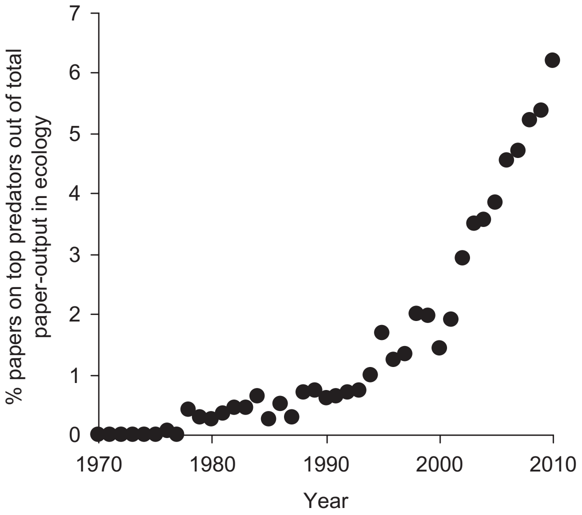

Figure 1. Percentage share of papers on top predators out of the total number of papers published over the last four decades in the area of 'Environmental Sciences and Ecology' (data from the Zoological Record – Web of Knowledge, accessed on December 2011).

Top predation as an expanding field of research

The recent growth and popularity of studies on top predators is probably promoted by their highly interactive nature, their capacity to trigger top–down effects on both herbivores and mesocarnivores, their ability to act as conservation umbrellas or as indicators of ecosystem health, and the value of their charisma to raise funds and attention. Furthermore, their role in ecosystems is receiving increasing attention given the growing emphasis in general ecology on the ecosystem-structuring capabilities of highly interactive species, such as many top predators (reviewed by Schmitz 2010, Terborgh and Estes 2010, Ritchie et al. 2012, Ripple et al. 2014). As a result, 'predator–prey interactions' have become one of the trendy-fields in general ecology (Nobis and Wohlgemuth 2004). Indeed, there has been a steady rise in the annual percentage of papers using the word 'top, apex or super predator' out of the annual total of papers produced in the area of ecology between 1970 and 2010 (Fig. 1). Such a growing share may bring a mix of good and bad news. On one hand, it implies a mounting interest by the scientific community for this functional group of species, increasingly seen as suitable models for ecological research of broad interest. On the other hand, with several hundreds of papers published in their field every year, scholars face a publication glut that growingly overwhelms their capability to absorb it, an 'information avalanche' already well known in ecology (Bartholomew 1986). As shown over and over (Graham and Dayton 2002, Fisher et al. 2012), such literature expansion leads to an impoverishment in creativity and innovation, and typically leads to growing fragmentation into specialized, disconnected groups. Such fragmentation is already apparent, we suggest, in top predator research.

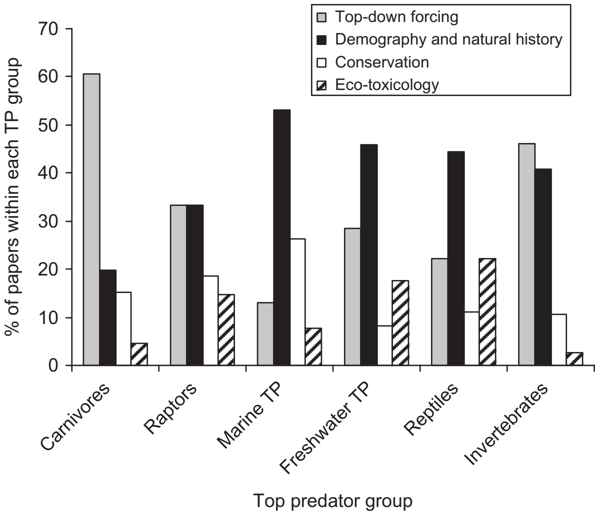

Figure 2. Percentage occurrence of papers on different groups of top predatory taxa according to four main research topics. Included are: 1) papers published between 2006–2010 inclusive; 2) with the word 'top predator', 'apex predator' or 'super-predator' in the title or abstract; and 3) that really focused on top predatory species upon detailed inspection (n = 565 papers from the Zoological Record – Web of Knowledge). The frequency of papers on different topics varied significantly among taxonomic groupings ($\chi^2_{20} = 114.0$, $p < 0.0001$). In the axes legends, TP = top predators.

Fragmentation of research on top predation

Current research on top predators is fragmented in disconnected subfields mainly by taxonomy. Taxonomic groups such as birds of prey, mammalian carnivores, predatory fishes, seabirds or invertebrate predators are characterized by a rich history of study, but each one with different dominant themes and strongholds. Thus, for example, spatial organization and predator–prey relations via intensive radio-tracking has been the traditional stronghold of mammalian carnivore research, while biological control has pervaded the literature on top predatory arthropods. This heterogeneity risks the development of subfields as though they have their own unique theoretical constructs and methodology.

Growing heterogeneity is confirmed by a review of the recent literature. Figure 2 shows all the papers published in the last five years (2006–2010) using the words 'top or apex or super-predator' in the title or abstract according to the Zoological Record. Publications were classified as belonging to four broad areas of research: top–down forcing; general natural history and demography; conservation and management; and eco-toxicology. A snapshot of recent research shows a disconcerting trend of different research agendas for different taxonomic groups. For example, research on carnivores and top predatory invertebrates is strongly dominated by studies on top–down forcing, such as trophic cascades and predator–prey relationships (Fig. 2). Investigation of marine top predators mostly focuses on general demography and conservation (Fig. 2), such as the globally generalised fishing-down of food-webs by industrial fisheries. Finally, eco-toxicological analyses occupy a relevant share of research on raptors, reptiles and freshwater top predators, but appear overlooked by mammalian carnivore and invertebrate biologists (Fig. 2). Furthermore, 14% of the 557 papers categorized in Fig. 2 report invertebrate taxa as top predators, whereas vertebrate ecologists often discount them as potential upper-level consumers that could have significant effects on ecosystems. Such segregation by taxonomic sub-sectors is problematic because it discourages cross-fostering of complementary perspectives and ideas. For example, it is often difficult to experimentally test theory over the vast landscapes that vertebrate apex predators exert their influence. Studies of invertebrate predators can thus provide important proofs of concept that can be extrapolated to larger-scale systems (Schmitz 2010). For example, mesocosm experiments revealing state-dependent risk-taking by tadpoles under threat from invertebrate predators served as the basis for theoretical simulations which predicted that a decline in near-surface fish-prey would induce vertebrate pinnipeds to increase their risk-taking by making deeper foraging dives, thereby incurring higher predation by deep-dwelling sharks (Frid et al. 2009). Overall, fragmentation into specialized sub-fields may lead to distorted or biased perspectives due to unavoidable biased representation of certain taxa in the scientific data.

Furthermore, when focusing on specific research areas, two trends are apparent. 1) Some themes have been researched intensively by specialists of one taxonomic group but not others, who are often unaware of them. The idea of trophic cascades has received enormous attention by mammalian, invertebrate and marine biologists but has only very recently been discovered by raptor ecologists (Schmidt 2006a, Ydenberg et al. 2007). The same applies to the 'greater ecosystem' concept, which is widely used in mammalian and marine carnivore research, but does not appear widely in the lexicon and work on other taxa. Similarly, use of predators to evaluate pollution effects in ecosystems (e.g. details of bioaccumulation of pesticides in the raptor and heron 'DDT-saga' of the 1960–1970s) are often not considered by carnivore or invertebrate researchers. 2) In other cases, the same research theme has been developed in parallel in different taxonomic groups but in a completely independent manner. For example, intraguild predation and alternative stable states are usually treated by mammalian carnivore research with little or no attention to other taxa (e.g. raptors or invertebrates) and vice versa (Polis and Holt 1992, Palomares and Caro 1999, Sergio and Hiraldo 2008). Clearly, lessons from one subfield often do not penetrate the others, hindering progress.

The results expected from this fragmentation are visible, for example, in claims by carnivore researchers of a lack of landscape-level studies (Minta et al. 1999), which are common in raptors, and in complaints by raptor researchers about the scarcity of intraguild predation studies (Sergio and Hiraldo 2008), which abound for carnivores and invertebrates. It is common to see research teams working at the same site on different taxonomic groups with minimum or no connection. The irony is that, while researchers do not interact, their study species surely and regularly do (Jaksic 1981). Thus, we hear of eagles limiting fox populations or changing diet in response to carnivore ecosystem-effects, of bears affecting the breeding performance of crocodilians, and of raptorial birds becoming cyclic in response to the oscillations of their grouse prey, in turn imposed by carnivore predation (Hunt and Ogden 1991, Newton 1998, Roemer et al. 2002, Anthony et al. 2008). However, studies that integrate multiple top predatory groups are still scarce, especially for the terrestrial realm (Prugh et al. 2007, Wirsing and Ripple 2009). Finally, fragmentation into subfields is accentuated by further specializations within each taxonomic group of expertise (e.g. experts in the movement ecology of carnivores, in the eco-toxicology of waterbirds, in invertebrate pest control, etc.). All the above issues take us back to the precipice of canalization, i.e. scientific myopia, erasure of history, lack of information circulation, recycling and reinventing of ideas (Graham and Dayton 2002).

Where do we go from here?

Research on predation provides regular contributions to general ecology and is a rapidly expanding, increasingly experimental, multidisciplinary and technological field of research. It is well grounded in theoretical ecology and in whole-ecosystem studies, it yields regular applications for conservation (e.g. by revealing that alien predators have a more detrimental effect on prey than native predators: Salo et al. 2007), but is subject to an 'information avalanche' coupled with rapid fragmentation into specialized, disconnected compartments. Meanwhile, while we learn that top predators are frequently the strong interactors much needed to forecast and restore ecosystem deterioration (Soulé et al. 2003, Donlan et al. 2006, Salo et al. 2008, Ritchie et al. 2012), these same species are rapidly declining with unknown ecological consequences (Myers and Worm 2003, Ainley 2007, Terborgh and Estes 2010, Ferretti et al. 2010, Estes et al. 2011, Ripple et al. 2014). Clearly, synthetic episodes capable of better integrating past and future theoretical and empirical developments and of instilling higher communication among scientists would return cohesiveness and generality to a rapidly disaggregating field. We propose four actions that are essential priorities to the goal of unifying and formalising research on top predation into a cohesive area of investigation of broader ecological interest.

Action 1. Cross-cutting reviews

Reviews can be powerful, trend-setting tools, and could promote strong shifts in attitude, awareness and approach by scholars in top predation. Reviews that succeed in integrating knowledge from different predatory groups in a cohesive and convincing way could set the right example and go a long way towards the consolidation of more holistic approaches. We believe that the time is perfect for such accomplishment. In a few years, we consider that the literature will have expanded so much that providing a thorough synthesis integrating past and current developments will be virtually impossible. Holyoak et al. (2008) give a good example of a field where publication overload already prevents a comprehensive synthesis and enforces reviews based on random sub-sampling of the literature.

Action 2. Conceptual, forum essays

A series of conceptual, forum papers, such as the one presented here, could draw the attention of the scientific community towards unifying themes that may communicate the need for more cohesive, collaborative and multidisciplinary approaches (Rotjan and Idjadi 2013 is a good example of an integrative attempt). Quantitative bibliographic analyses could be supporting tools to summarize the current state of the art for this field, propose ideas and highlight areas in need of expansion. Ideally, the ultimate goal of this action could be a formal proposition of a quantitative unifying paradigm, as accomplished in other research areas (Nathan et al. 2008, Jones et al. 2010). Given the diversity of top predation, it may be difficult to obtain consensus on a single framework, as witnessed in other fields (Jones et al. 2010). However, its proposition alone could lead to important debate and reinforce the need for cooperation, cross-taxonomic awareness and cohesiveness. Finally, there is a need to systematically strive to link ongoing detailed empirical studies to predator–prey theory, in a way that meta-analyses about top predator effects can be dynamically informed.

Action 3. Fostering dialog and collaboration: overcoming the vertebrate-invertebrate dichotomy

In our experience, many researchers of top predation live their studies in the conscious or unconscious conviction that their study species is THE top predator of the ecosystem, as if the (supposed) 'king-role' of their species translated into some higher status of the researcher. Such an approach sets a stage of unproductive competition and scepticism rather than interest and collaboration among scientists working on different taxonomic groups. In turn, this hinders the circulation of ideas and increases fragmentation. Breaking the wall of this 'collaboration inertia' will be paramount for the acquisition of ecological generalities about top predation that are truly general, i.e. valid across taxonomic groups. For example, trophic cascades have been demonstrated in a large number of studies on mammal, fish and invertebrate predators, but only in a handful of studies on reptiles or birds of prey (Schmitz et al. 2000, Terborgh and Estes 2010). We believe that this is not because raptors or reptiles are incapable of triggering cascades (Schmidt 2006a, Ydenberg et al. 2007, Sutherland et al. 2011). It is only because excessive specialization, fragmentation and low circulation of ideas have somehow prevented, until only very recently, raptor and reptile specialists from being part of the enormous advancements that were being operated by mammal, fish and invertebrate ecologists.

Cross-taxonomic absence of interaction probably reaches its utmost levels when considering specialists of vertebrate and invertebrate top predatory species. This is a major flaw in our research system for three reasons. First, the two groups may equally well act as top predators depending on the scale and characteristics of the ecosystem under study. For example, upon close inspection, few vertebrate ecologists would doubt that 50 kg squids can be currently top predators over vast areas of a trophically degraded ocean, that army ants *Eciton burchellii* can exert major top–down forcing in tropical forests, or that a larval dipteran or mosquito can be the top predator of a miniaturised tree-hole community (Griswold and Lounibos 2006, O'Donnel et al. 2007, Zeidberg and Robison 2007). Second, the two groups may function in profoundly different manners, offering stronger scope to reach emergent generalities on the ecology of top predation. For example, most invertebrates present complex life cycles with major ontogenetic shifts in trophic role, a concept that has been widely overlooked for their vertebrate counterparts (except fish). This could be exploited as a rich source of hypotheses in the search for ecological generalities rather than a cause of divide. For example, terrestrial vertebrate specialists could test whether their study subjects present similar ontogenetic variation in top predatory role, though mediated by different mechanisms (e.g. age-related changes in size or progressive improvements in hunting skills, as shown by several shark studies; reviewed by Grubbs 2010). Finally, invertebrate taxa are much more amenable to experimentation than large vertebrates. For example, as an extreme example, when will be the next time that 100 killer whales *Orcinus orca* are removed from a small area and the responses of prey are noted (Ainley et al. 2010)? Again, instead of discounting such manipulations for reasons of scale and extrapolation, experiments on invertebrates could be used as tools to 1) provide mechanistic, experimental tests of theoretical concepts that are impossible or unethical to perform on vertebrates (Schmitz et al. 1997), or 2) formulate working hypotheses that are then tested on vertebrates through natural experiments or more correlational analyses (Frid et al. 2009, Burkholder et al. 2013). Cross-taxonomic concordance of results across such sequential tests would imply a high degree of confidence in emergent conclusions, leading to more solid generalisations (Schmitz 2006b, Heithaus et al. 2008a, b, Wirsing and Ripple 2009). In sum, higher integration of cross-taxonomic scientists would bring major benefits in term of research realism, strength of conclusions, and broadness of implications.

In our view, the way ahead is to actively encourage scientists working on different groups to meet one another. This could be achieved by organizing generalised conferences on top predators, where researchers from all groups, realms and fields are actively invited to participate. Alternatively, key specialists of one taxonomic group could be invited to give review talks at specialized congresses of other groups.

Action 4. Exemplary case studies

Researchers setting up future programs could promote enormous advancement by setting up collaborative, cross-taxonomic studies that render examples of the importance of unifying approaches. A good example in this context is the articulate, long-term study on the trophic cascades triggered by sea otters. A series of sequential analyses on this system showed that killer whale predation could affect the capability of sea otters to trigger a trophic cascade capable of structuring the whole ecosystem configuration, with repercussions on the diet and foraging mode of top predatory species from other groups, such as eagles (Estes et al. 1998, 2011, Anthony et al. 2008). Future case studies could further focus on the competitive and predatory interactions occurring among predatory species from different taxonomic groups (e.g. carnivores and invertebrates). Ideally, such case studies could promote further progress by focusing on groups that have received less research attention, such as reptiles (Sutherland et al. 2011).

Conclusion

The above four actions would compose a flexible, cross-taxonomic and collaborative strategy. Its ambitious scope is unlikely to be attained by a single researcher or research team. Instead, it will depend on the collective effort by all scholars in this field, potentially propelled by good examples and increased awareness for the need of more holistic approaches. We hope that this note will help to promote such awareness.

Acknowledgements – We thank N. Owen-Smith and J. D. Roth for comments on a first draft of the paper. Writing of the first draft by FS was supported by Grant CGL2011–28103 of the Spanish Ministry of Science and Innovation and Excellence Project RNM 7307 of the Junta de Andalucía. RDH thanks the Univ. of Florida Foundation for support.

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