

# **SUPPLEMENTAL MATERIAL FOR THE DRAFT ENVIRONMENTAL IMPACT STATEMENT – PREDATOR DAMAGE MANAGEMENT IN IDAHO**

## **SUMMARY OF RELEVANT SCIENTIFIC LITERATURE: TROPHIC CASCADES**

The study of ecological trophic cascades is relatively new and very complex, with potentially many highly interrelated factors and inherent complications to developing and implementing robust studies and ecological computer models. Statistical analyses must be carefully chosen and applied to develop strong correlations and reasonable interpretation of study results. Different ecosystems may have inherently higher productivity than others, resulting in different comparative study outcomes. Each study looks at a very small question related to very broad and complicated interrelated systems, and a particular study addressing a specific question cannot be expected to provide an answer that can be applied broadly. Therefore, this review briefly summarizes the scientific literature relevant to the broader questions related to trophic cascades and related factors subsumed within that possible ecological relationship. It is not intended to be an impact analysis related to WS-Idaho PDM actions, but rather provides the context for the impact analysis in Section 3.8 of the *Draft Environmental Impact Statement: Predator Damage Management in Idaho*. This review focuses on peer-reviewed published scientific literature, but, also includes some unpublished or non-peer-reviewed documents because they are frequently raised by commenters.

### **1 WHAT FOUNDATIONAL ECOLOGICAL TOPICS INFORM THE DISCUSSION ON TROPHIC CASCADES?**

#### **1.1 How do Carnivores Contribute to Ecosystem Biodiversity?**

Large terrestrial mammalian carnivores, such as wolves, coyotes, and dingoes, have been historically seen as threats to human lives, property, and domestic livestock (Schwartz et al. 2003, Ray et al. 2005a, Prugh et al. 2009, Estes et al. 2011). Large mammalian carnivores have high metabolic demands due to being warm-blooded, and they have a large body size with large surface to volume ratio. Therefore, they typically require large prey and expansive, connected, unfragmented habitats. These characteristics often bring them into conflict with humans, their property, and livestock, and compete for wildlife that are also regulated game species.

Large carnivores are vulnerable to many human-created conditions, including habitat loss, degradation, and fragmentation, invasive and exotic species, climate change, and hunting, as well as to widespread lethal control conducted in response to human intolerance, often resulting in population depletion, extirpations, and extinctions (Ripple et al. 2014). Hunting by humans does not duplicate or replace natural predation because it differs in intensity and timing, resulting in dissimilar effects on prey behavior, age, and sex (Ray et al. 2005a, Ripple et al. 2014). However, where large carnivores were once seen as impediments to conservation goals, including for protection of endangered species, they are now increasingly considered as essential players in efforts to preserve ecosystem biodiversity through structuring ecosystem interactions and providing ecological services (Ray et al. 2005b, Wallach et al. 2009b).

#### **1.2 How are Ecosystems Structured?**

Ecosystems are structured through the dynamic interactions of abiotic factors such as weather, soil productivity, climate change, and surface and subsurface hydrology, natural perturbations such as wildfire, and the variety, composition, and abundance of fauna and vegetation present. Those dynamics change in abundance, variety, and distribution as components of the ecosystems change.

Studies suggest that large carnivores may directly and/or indirectly affect the populations of certain species in terms of presence, abundance, reproductive success, activities, and function within the ecosystem. These effects may partially result from their predatory activities on smaller animals, including other carnivorous predators (such as foxes, coyotes, and cats), animals that eat only vegetation (herbivores, such as rabbits and deer), and animals that eat both vegetation and meat (omnivores, such as bears, badgers, and raccoons). These effects can also change the biomass, variety, and productivity of the vegetation that is eaten by herbivores and omnivores. These relationships based on consumption is called a **food web**, which recognizes the web-like interaction of a set of interrelated food chains, including species that share the same foods and carnivores that consume other carnivorous species.

Within these webs, animals with similar food habits create **trophic levels**, where energy is transferred and transformed as animals from one level feed on animals or plants from a lower level. If interactions occur from one trophic level of the web to a higher or lower trophic level, this is considered a **vertical relationship**. If the interaction occurs within the same trophic level, such as when a larger predator kills or feeds on a smaller predator or omnivore, it is considered a **horizontal relationship**. Therefore, the large carnivores are considered apex predators (in the vertical relationship), because they are not naturally preyed on by other animals, except by humans (Duffy et al. 2007).

Therefore, an **apex or top predator** is defined as a species that feeds at or near the top of the food web of their supporting ecosystem and that are relatively free from predation themselves once they reach adult size (Sergio et al. 2014). As animals in each trophic level need to use some of the energy obtained through consumption for maintenance, growth, activities, and reproduction, a much smaller amount of energy is transferred from a lower trophic level to a higher one. This generally results in a fewer number of animals within each higher trophic level. The top trophic level of a food web generally has fewer species and smaller population sizes than lower levels (and typically larger body sizes), resulting in the need to feed on larger prey with less energy expended in order to meet their energy requirements for survival. Top carnivores also tend to be more vulnerable to sustained adverse perturbations in their environment and persistent high mortality rates, and therefore more susceptible to extirpation and extinction.

## 2 WHAT IS THE HISTORY OF THE STUDY OF ECOSYSTEM FUNCTIONS AND ROLES OF APEX PREDATORS?

The history of recognizing the ecological roles of apex predators as something other than vermin or pests is relatively new (Ray et al. 2005a). The concept was popularly introduced by Charles Darwin's *Origin of Species* (1859) in his concept of mutualism (domestic cats controlling mice, that that would otherwise eat bee honeycombs, affecting plants and pollinators; Ripple et al. 2016). In more contemporary times, the concept of top predators was publicized primarily by Aldo Leopold in 1943. In the 1950s and 1960s, relatively simple studies were conducted on the dynamic interrelationships of predators and their prey, using uncomplicated models and limited field experiments. In the 1970s, simple modeling and empirical field studies began to test the capabilities of top predators to ecologically structure lower trophic levels, evaluate the relationships between predator and prey, confer stability to populations, and cause ecosystem shifts between alternative stable states (e.g., Ballard et al. 1997, Stenseth et al. 1997).

In the 1980s, modeling and field studies expanded in complexity to include predator-prey relationships, population dynamics, and adaptive social behavior in response to the risk of being preyed, including how behavior changes affected foraging behavior and life history of prey and how these dynamics interrelate ecologically. Studies also began considering the potential for some predators to eat other predators, acknowledging a food web that interacts both vertically and horizontally, and the potential to cause trophic cascades. In the 1990s, these studies became increasingly complex, further investigating the roles of predation risk and anti-predator behavior adaptations, and how these affect the fitness of an

individual animals, populations, and communities, potentially contributing to behavior-mediated trophic cascades (Sergio et al. 2014).

Presently, studies are branching into increased use of field and interdisciplinary research to investigate more realistic community, food web, population, ecological community, and individual animal responses to manipulations, and intended perturbations of communities of predators and prey, including direct and indirect behavior adaptations, ecological roles, predators killing other predators, and individual and species specializations of apex predators. Empirical field studies are increasingly using more sophisticated technologies to study wide ranging and secretive top predators, such as GPS satellite tags and collars (Sergio et al. 2014).

Originally, field studies were conducted on mostly sessile or low mobility species and webs, such as invertebrates, spiders, plankton, and small fish in localized ecosystems in relatively high productivity streams, lakes, intertidal zones, grasslands, and agricultural areas (e.g., Schmitz et al. 2004, Ray et al. 2005a, Beschta and Ripple 2006). Expanding these studies to open ocean marine and terrestrial ecosystems with more wide-ranging predators and prey that are inherently more difficult to manipulate and create perturbations in, especially without causing moral, ethical, and political controversy, created extensive challenges in methodologies and complexity (e.g., Ray et al. 2005a, Brashares et al. 2010, Estes et al. 2011, Sergio et al. 2014). Researchers also questioned whether the correlative results of studies that are small-scale in time and/or space and conducted in ecologically relatively simple and localized ecosystems such as grasslands, agricultural fields, salt marshes, and marine intertidal zones could be extrapolated and applied to larger scale circumstances associated with trophic interactions in marine and terrestrial ecosystems across broad land and seascapes (e.g., Loreau et al. 2001, Srivastava and Vellend 2005).

It is extremely difficult to establish complex causal links between the indirect effects of top predators cascading over several trophic levels, and is still the subject of modern studies. Only recently have researchers conducted empirical studies of the roles of large carnivores in structuring communities, including the roles in ecosystem stability, biodiversity, and ecosystem functions (Ray et al. 2005a).

### 3 WHAT IS A TROPHIC CASCADE?

In theory, apex predators may shape major shifts in the structure and function of ecosystems, as their predation and behavior ripple down and across food webs. These apparent ripple effects can create alternative and possibly long-term ecologically stable states that differ from the original state before the perturbation to apex predators, which ultimately becomes the persistent state (**homeostasis**). These changes may progress smoothly over time as the changes themselves occur, or, more likely, may occur when some threshold or “tipping point” is reached, at which point the structure and/or function shifts to different stable condition. During this phase shift, the conditions may rapidly fluctuate and species populations may rapidly increase then crash, before settling into the subsequent new and persistent condition.

Theoretically, the loss of one or more apex predators may result in shorter links within the food web because the apex predator is no longer present. This can potentially result in the release (in terms of numbers, distribution, biomass, etc.) of smaller predator and/or omnivore species that the apex predator preyed upon or behaviorally controlled. **Behavioral control** means that the prey exhibited adaptive anti-predator behavior that lowered its ability to forage optimally or kept individual animals in chronic physiological stress, resulting in lower overall fitness at the individual and community levels. In other words, the species’ population was controlled by apex predators in such a way that the prey population could not reach the **carrying capacity**, or the maximum number of a species that the environment can support indefinitely (i.e., due to natural abundance of food and habitat resources). When the apex

predator is at too low an abundance or density to create ecological restrictions on the prey population, or is no longer present, the controlled predator species may be released from the top-down control formerly exerted by the apex predator, and typically becomes the apex predator of the now-shifted system.

Theoretically, populations controlled by the new top predator may now release control on their prey, which may be herbivores, small mammals, or even vegetation. For a simple example, coyotes may now exert a greater predatory pressure on red foxes, decreasing their numbers, which may then release control on small rodents, resulting in increasing rodent populations. If this release is sufficiently high, the small rodent population may then increase dramatically, which may subsequently suppress the species composition or biomass of the vegetation eaten by the mice. This vertical control from top predators that may ripple through the food web is called **top-down control**.

The web is further complicated by a horizontal interaction within a food web, when one predator preys upon or otherwise controls another predator. This sideways feeding is called **intraguild predation** or **IGP**. A **guild** is made up of species that tend to play similar roles within a food web, such as carnivore, omnivore, or herbivore. See Section F.8.1 for more information on IGP.

When the population of the smaller predator (intraguild prey) is released by the extirpation, extinction, or severe control of the intraguild predator, that dynamic is called **mesopredator release**. A mesopredator species tends to be an intermediate predator within a food web, one that is typically smaller than the lost apex predator species, more of a generalist in terms of diet, and may be small enough to exploit more potential food niches. Mesopredator species often have a relatively high intrinsic rate of increase because of high reproductive rates and/or because they respond with higher reproductive rates when their populations are below carrying capacity (called a **density dependent response**) and the populations are released from suppression. Examples of mesopredators that may be released when wolves (as top carnivore) are severely suppressed or extirpated from an area could be coyotes, badgers, foxes, raccoons, and feral and free-ranging cats, depending on the composition of the ecological community. Generally, under these circumstances, the coyote population then fills the trophic role of apex predator, alternatively exerting control and releasing species, depending on whether the impact is direct or indirect on the particular trophic level. See Section F.8.2 for more information on mesopredator release.

It is also possible that predator species may be indirectly controlled by lack of prey or low vegetative productivity. For example, a multi-year drought may reduce the plant forage of rabbits, reducing both the rabbit population and its intrinsic reproductive rate. This, in turn (with a lag time), may suppress the physiological fitness and intrinsic reproductive rate of its primary predator, for example, a coyote. This is called **bottom-up control**. Coyotes may then begin to feed more on foxes (an IGP situation occurring within the relatively same trophic level), which were not affected by the drought, because the plants that the small rodents fed on (different from the plants that the rabbits fed on) were more resistant to the effects of drought. If the IGP by coyotes on foxes is sufficiently high, the fox population may again be suppressed, releasing the mouse populations. Complicating this concept is that both top-down and bottom-up controls may occur simultaneously for the same and different components within the same ecosystem (Borer et al. 2005, Ritchie and Johnson 2009). Such top-down and bottom-up effects can be complicated by **interference competition** (where dominant predators interfere in the ability of subordinate predators to obtain resources), site productivity, behavioral adaptation to avoiding the risk of predation and obtaining high quality resources, and intrinsic “noise” in the ecosystem due to natural variation (Elmhagen et al. 2010). In the above example, coyotes could switch from rabbits to other smaller rodents and insects (prey switching) that foxes prey on and compete with the foxes for the same prey base.

These apparent up and down (or lateral) alternating trophic interrelationships (when one population increases, it may cause a decrease in another (a direct effect) and increase in a species in the next lower

trophic level (an indirect effect), which may indicate an interrelationship among trophic levels called a **statistical correlation** (Section F.6.1). However, such correlations do not indicate that one relationship is actually caused by the other. For example, large irruptions of mouse populations may be interpreted as being indirectly related to, for example, removal of a predator that feeds on mice, but may actually be caused by factors that were not considered, such as human food subsidies.

Polis et al. (2000) also recommend that researchers distinguish between potential cascading or rippling interactions at the species level (those occurring within a subset of the food web of a community, such that changes in predator numbers affect the success of one or more subsets of the plant species) and at the community level (those occurring where cascades considerably alter the distribution of plant biomass through the trophic levels of the entire system). This adds further complexity to empirical studies and interpreting results.

It is inherently extremely difficult, if not impossible in many circumstances, to develop and implement study protocols for field experiments resulting in statistically strong correlations. It is also inherently difficult to determine, even with replication of studies resulting in similar correlations, that inter- and intra-trophic relationships are caused by ecological perturbations, such as the removal of an apex predator, or that the removal results in a trophic cascade. Frequently, top-down effects do not appear as strong or to produce predicted cascading effects in terrestrial ecosystems due to the complexity of factors, such as the effects of dispersal and immigration, social regulation, and interference competition among predators, and abiotic factors, such as weather, soil, ecosystem productivity, and spatial and temporal habitat heterogeneity (Halaj and Wise 2001, Ray et al. 2005a, Berger et al. 2008, Estes et al. 2011).

Section F.13 details the inherent challenges of modeling and designing empirical field studies that determine statistically-correlated interrelationships between ecological factors. These studies may indicate needs for further investigation or potentially establish factors that can be shown to create a direct causation for the observed effect through study replications. Terrestrial ecosystems, food webs, and their processes are especially complex, with wide-ranging apex predators and intricate and adaptive predator and prey behaviors.

#### **4 WHAT IS THE HISTORY OF THE CONCEPT OF TROPHIC CASCADES AND ITS DEFINITIONS?**

Since the 1980s when Paine (1980) used the term “trophic cascade” to describe food webs in intertidal marine communities, trophic cascade has been a central or major theme of more than 2,000 scientific articles across many different ecosystems worldwide. Polis et al. (2000) and Ripple et al. (2016) expressed concern that, after decades of studies and modeling in many different ecosystems, the definitions and language used to describe trophic cascades have become inconsistent, obscuring and impeding both communication among researchers and the usefulness of the concepts for application in ecological management and conservation. To be useful and contribute to clarity, the definition must be both widely applicable yet sufficiently explicit to exclude extraneous interactions.

Ripple et al. (2016) provide a summary of the various definitions provided by researchers between 1994 and 2006. Trophic cascades were thought to only occur from upper trophic levels to lower trophic levels (top-down), until Terborgh et al. (2006) suggested that cascades can ripple either up or down a food web, with alternating negative and positive effects at successive levels. The first indirect effects of predators on plankton in lakes were suggested in the 1960s (Brooks and Dodson 1965, Hrbáček and Straškraba 1966). Subsequently, Estes and Palmisano (1974) described the role of sea otters in structuring nearshore communities of sea urchins and kelp, later modified to include orcas and sea lions, based on changes caused by humans (Estes et al. 1998), a frequently cited example in the literature to this day. The research on trophic cascades began to shift from being dominated by studies in freshwater systems and

old field grasslands and croplands to being dominated by terrestrial and marine systems in the early 2000s.

Based on a recent meta-analysis of scientific literature, Ripple et al. (2016) suggest trophic cascades be defined as indirect species interactions that originate with predators and spread downward through food webs. According to the authors, this definition does not require that trophic cascades begin with apex predators, nor that trophic cascades end with plants. The authors suggest that bottom-up effects are not downward trophic cascades, but what they call **knock-on effects**, in which effects spin-off from the main top-down interactions. Whether or not bottom-up effects are incorporated into the definition of trophic cascades (as suggested in Terborgh et al. 2001, Ripple et al. 2013, Ripple et al. 2015), research has indicated that effects may flow both directions at different times in dynamic ecological systems in which top and mesopredators are present and active. Such top-down and bottom-up effects can be complicated by **interference competition** (as mentioned in the coyote example above).

## 5 WHAT IS THE DIFFERENCE BETWEEN CORRELATION AND CAUSATION IN INTERPRETING STATISTICAL STUDY RESULTS?

Before evaluating the scientific literature, it is important to explicitly define the difference between correlation and causation in order to better understand the statistical results of these studies. These terms are often misunderstood and misused when interpreting scientific papers. This discussion on correlation and causation is adapted from the Australian Bureau of Statistics (2013).

### 5.1 Correlation

A **correlation** is a statistical measure (expressed as a number) that describes the size and direction of a relationship between two or more variables. A correlation is suggested by a positive or negative relationship – when one factor increases, another may also increase (**positive correlation**) or decrease (**negative**, or **inverse, correlation**). If an apparent correlation is observed statistically, it does not mean that one factor causes the other, only that the one factor either goes up or down in relation to the other factor.

The strength of the apparent correlation, or the indication that there truly is some level of interrelationship, is determined using statistical formulas that should meet assumptions pertinent to the context of the data and the system being studied. The formulae provide a figure, known as the square of the correlation coefficient, or  $R^2$ , which is always a number between 0 and 1. A value closer to 1 suggests that a stronger correlation exists, indicating that the relationship may warrant further investigation and study. However, it is possible to identify strong, but meaningless, correlations, and many other factors may introduce complexity into the relationships as well as confound the apparent results.

As an example of an apparent, but not necessarily actual, correlation, we can use the observance of the onset of cold weather in the winter and increasing numbers of colds. As the temperature decreases in December, it may appear that people get more colds, an apparent inverse correlation. That could be a correlation, and an  $R^2$  value may actually indicate a strong correlation. However, the cold temperatures also tend to occur during the holiday season. The suggested correlation between decreasing temperatures and increasing rates of illness may actually be more closely related to depressed immune systems from eating more sugar and increased exposure to viruses from greater contact with people. Despite an apparent correlation, it is also possible that decreasing December temperatures themselves do not directly cause increased rates of illness, and therefore wearing warmer clothes will not necessarily decrease the number of colds or the risk that an individual person will catch one.

The suggested statistical correlation can be confounded by many variables that may or may not have been incorporated into the statistical analysis, potentially resulting in misleading results. In another well-

known example, the  $R^2$  for the number of highway fatalities in the United States between 1996 and 2000 and the quantity of lemons imported from Mexico during the same period is  $R^2=0.97$  – a very strong correlation – but it is extremely unlikely that one causes the other. Generally, scientists and researchers will reject factors that show a weak correlation, but completely irrelevant factors can produce a statistically high  $R^2$  coefficient, potentially leading researchers in the wrong direction.

## 5.2 Causation

**Causation** indicates that one event is the result of the occurrence of the other event. Proving that a strong statistical correlation is directly responsible for an observed result requires more than a high  $R^2$  value. Once a strong correlation is indicated, researchers experimentally need to test their hypotheses for causation to determine if indeed the factor(s) considered in the statistical analysis caused the result (cause-and-effect relationship), rather than just suggesting a relationship. They need to determine that the result is not just varying up or down statistically in unrelated or potentially indirect ways, or that the results may be confounded by untested or unmeasured factors. For strengthening a potentially causal relationship, the tests must be replicated by other researchers using the same methods, scale, and contexts to determine if the results are truly causative.

A powerful research protocol is one that holds all factors constant but one, and then tests for statistically significant changes that indicate a causative relationship. The variable factor can also be changed and the results tested to further clarify a causative relationship. A statistically significant finding is one that would occur more often than it would if it were to occur randomly.

## 5.3 Conclusion

When relying on studies, it is critical to understand that statistical correlations, which are offered by researchers as suggestive or indicative results often without replication, are different from conclusions of statistically significant causation. Ray et al. (2005) state that researchers are often influenced by numerous factors, including their education, cultural background, and inherent conditions of the ecological systems on which they work. Ecologists who specialize in some systems often favor certain hypotheses, interpretations, and factors measured, and discount others developed, to inform work on other systems.

Misinterpreting weak, or even strong, correlations or the results of theoretical models as indicative of causation is inappropriate and does not credibly represent the state of the science or the robustness of data and research protocols. More importantly, it can lead to uninformed decision-making and poor choices regarding conservation and management actions that may have unintended and damaging consequences. APHIS-WS reviews the pertinent literature and places priorities on studies that accurately account for correlations, have relevant assumptions, and disclose study and statistical limitations and strengths.

## 6 WHAT DO RELEVANT STUDIES SUGGEST ABOUT TROPHIC CASCADES?

The following studies are representative of empirical field research conducted on large predators in terrestrial ecosystems that are useful for understanding the complexities of trophic cascades and contributing processes:

**Hebblewhite et al. (2005)**, in a study in Banff National Park (NP), suggested that human activity, including recreation, in one valley restricted the use of the area by wolves, while limited human activity in an adjacent valley allowed higher wolf use. Survival recruitment of female elk and recruitment of calves was higher in the valley with human activity and lower wolf numbers. Elk competed with beaver for willow in riparian areas could have important impacts on biodiversity and ecosystem function and

structure. The authors suspected wolves were the primary correlating factor in the observed cascading effect, but recognized that other predators may be implicated to an unknown degree.

**Ripple and Beschta (2006a)** hypothesize that an increase in human recreation in Zion NP resulted in a catastrophic regime shift to lower mountain lion densities and higher mule deer densities, higher herbivory on cottonwood trees, lower recruitment of young trees, increased bank erosion, and reductions in both terrestrial and aquatic species abundance. A top-down trophic cascade model would predict an increase in producer biomass following predator removal, while a bottom-up model would predict little or no change in consumer or producer biomass. Additionally, other likely interaction pathways include increased species interactions, improved nutrient cycling, limited mesopredator populations, and food web support for scavengers. The canyon with low human activity showed high recruitment of cottonwoods, hydrophytic plants, wildlife, amphibians, lizards, and butterflies along the creek, as well as presence of small endemic fish, with fewer eroded banks and altered channel widths. The diminishment of cottonwood forests in the riparian area reflects a potentially strong trophic cascade with ultimate effects on the structure and ecology of stream floodways, with decreased biodiversity. Without an appreciation of the potential for abrupt regime shifts and resulting new and persistent ecological stasis, the authors hypothesize that studies involving the removal of top predators are likely to provide conflicting results regarding function and structure of perturbed systems.

**Ripple and Beschta (2007)** reported evidence of reduced browsing and increased heights of young aspen, particularly at areas with high predation risk (riparian areas with downed logs) after wolves were reintroduced into Yellowstone NP. Young aspen in upland settings showed continued suppression, consistent with the combined effects of trophic cascades, mediated by adaptive behavior related to predator risk avoidance by elk and lower densities of elk, indicating a recovering ecosystem. Much of the aspen growth observed in riparian areas after the reintroduction of wolves appears due to reduced browsing by elk at sites with poor escape terrain and reduced visibility, rather than climate change or site productivity. The patchy recovery of as evidenced by increases in aspen height in the uplands as compared to riparian areas is consistent with recently reported patchy release of willow in Yellowstone (Ripple and Beschta 2006a). The authors suggest that elk may be avoiding browsing certain riparian areas as an anti-predator strategy. The authors recognized that the broad-scale application of the results of this study are limited by the lack of an experimental control (area with no wolves) since the entire area was recolonized by wolves and that the data most likely represent the beginning of aspen recovery and not aspen population responses across Yellowstone's northern range. Concurrent increases in bison populations in Yellowstone's northern range may also be affecting the status of aspen communities.

**Berger et al. (2008)**, in an often-cited article, suggested that wolf predation on coyotes in the Greater Yellowstone Ecosystem released the heavy coyote predation on pronghorn antelope fawns, resulting in increased pronghorn survival. The pronghorn population studied had not recovered from heavy market hunting, and the study found that fawn survival was four times higher in areas used by wolves where wolves preyed on coyotes than in areas not used by wolves. Observed differences in fawn survival in areas with wolves may be sufficient to reverse the currently declining pronghorn population.

**Kauffman et al. (2010)** suggest that contrary to Ripple and Beschta (2006, 2007), survivorship of young browsable aspen are not currently recovering in Yellowstone NP, even in the presence of a large wolf population. A marked reduction in elk followed wolf reintroduction at the same time that drought reduced forage availability and hunting by humans increased outside the park during and after winter elk migration, indicating that the difference in aspen recover may be based on factors other than response to predation. Contrary to findings of previous researchers, the authors suggest that much of the variation in aspen reproduction was not due to elk browsing levels in response to predation risk, but to site productivity. Patterns of aspen recruitment are consistent with the effects of a slow and steady increase in elk abundance following the end of market hunting in the late 1800s and wolf extirpation in the 1920s.



The authors' interpretation suggests that landscape level differences in habitat more strongly determined where wolves killed elk. Also contrary to Ripple and Beschta (2007), these authors suggest that aspen growth differences were due to the confounding patterns associated with abiotic factors such as soil moisture, mineral content or patterns of snow accumulations, which vary widely across the landscape. Aspen sucker survivorship was lower near wolf territory core areas, likely due to wolves maintaining territories in areas of high elk densities, limiting the cascading impacts of behavioral changes due to predation risk, which apparently occur only in response to the near imminent threat of wolf predation. The authors suggest that aspen recovery across the northern range of Yellowstone NP will occur only if wolves in combination with climate and other predators further reduce elk populations.

**Brown and Conover (2011)** conducted a large-scale removal of coyotes on twelve large areas in Utah and Wyoming to study effects on pronghorn antelope and mule deer populations. Their data suggest that coyote removal conducted during the winter and spring provided greater benefit than removals conducted during the prior fall or summer for increasing pronghorn survival and abundance. Unlike that for pronghorn, the data suggest that coyote removal during any season does not affect mule deer populations.

**Ripple et al. (2011)** suggest that it is possible that disrupted trophic and competitive interactions among wolves, coyotes, lynx and snowshoe hares after wolf extirpation may be sufficient to chronically depress hare and lynx populations; human-caused habitat fragmentation and livestock presence may have added to the depressed populations in Banff NP. With wolf extirpation, coyotes preyed on hares, competing with lynx. The authors hypothesize that warming climates may increase coyote predation on hares in areas with lower snowpack even at higher elevations typically used by lynx, because coyotes can better traverse areas with less deep snow.

**Beschta and Ripple (2012)** report that, following extirpation of large predators (wolves, mountain lion, and grizzly bears) in Yellowstone, Olympic, and Zion National Parks in the early 1900s, large ungulate populations irrupted, with increased herbivory on riparian cottonwood, willow, and aspen communities. Beavers abandoned willow communities, resulting in loss of pond habitat and deepening of streams with bank erosion within twenty years. Nearly two-thirds of Neotropical migrant birds depend on riparian vegetation during the breeding season, even though riparian systems make up 1% to 2% of total land areas in the western US. As streambanks eroded, the level of coarse streambed sediments decrease with an influx of finer sediments during the erosion of floodplains which effectively fill in gravel interstices, changing benthic habitats in streams, increasing water temperature degrading fish habitats with losses of stable overhanging banks and ripple flows with low sediment loads. If apex predators are reintroduced, the effects may or may not be reversible, depending on whether the level of reduced herbivory can be sufficiently maintained.

**Levi and Wilmers (2012)** analyzed 30 years of data involving intraguild predation involving wolves, coyotes, and foxes to determine any effect on trophic cascades found correlational interrelationships, based on a plausible mechanism of increased interference competition between closely-sized canids. Theory suggests that guild interactions with an even number of species will result in the smallest competitor being suppressed, while guild interactions with an odd number of species may result in the smaller predator being released (Levi and Wilmers 2012).

**Ripple and Beschta (2012)** repeat earlier aspen and cottonwood surveys and measure browsing heights to determine recovery of aspen in the northern range of Yellowstone NP. The authors suggest that browsing on the tallest aspen stems decreased from 100% in 1998 to averages of less than 25% in the uplands and less than 20% in the riparian areas by 2010, increasing aspen recruitment and growth. Synthesis of trophic cascade studies conducted in Yellowstone NP within 15 years after wolf reintroduction generally indicate that the reintroduction of wolves restored trophic cascade with woody browse species growing taller and canopy cover increasing in some areas. After wolf reintroduction, elk

populations decreased and beaver and bison populations increased. Despite indications that wolf reintroduction created substantial initial effects on both plants and animals, northern Yellowstone NP appears to be in the early stages of ecosystem recovery and results may differ over time.

**Squires et al. (2012)** question the interpretations of the data published by Ripple et al. (2011), finding the correlations between recovering wolf populations and benefits to lynx populations through reduced coyote populations and through reduced competition among ungulates and snowshoe hare have weak or contradictory empirical support in the available literature. The authors believe that these findings cast doubt on the usefulness of Ripple et al. (2011) hypotheses and demonstrate the importance of experimental and comparative documentation when proposing trophic cascades in complex food webs. The authors caution against “publishing unsupported opinions as hypotheses that concern complex trophic interactions is a potential disservice to lynx conservation through misallocated research, conservation funding, and misplaced public perception.”

**Callan et al. (2013)** suggest that deer in Wisconsin were more abundant at the peripheries of wolf territories, based on evidence of higher deer herbivory (deer feeding on plants) on the territory margins than in core wolf territories. Understory vegetation in white cedar stands may be more influenced by bottom-up hydrology and ecological edge effects than by trophic effects. Areas with high plant diversity may increase deer densities that then attract and maintain higher wolf densities. Addressing wolf impacts at the scale of wolf territory rather than at a regional scale (rather than studying results within particular wolf territory, studies are conducted on whether wolves are present in a larger area) could have implications for study results. Research is essential to determine the level of scale at which a pattern becomes detectable above the ambient noise of ecological variation for understanding relationships between patterns and process.

**Marshall et al. (2013)** refute conclusions of previous researchers regarding willow recovery after wolf reintroduction. In Yellowstone NP, the authors found that moderating browsing by elk alone is not sufficient to restore willows in riparian areas along small streams – such recovery depends on eliminating browsing and restoring hydrological conditions that occurred before wolves were extirpated. Beavers were common in the park, and interacted symbiotically with ecologically healthy riparian systems by the ecosystem. The riparian system provided tall willows that the beavers used to provide food and build dams, which created the hydrological conditions for healthy and sustained willow communities. Loss of beavers in the 20<sup>th</sup> century amplified the direct effects of herbivory by elk, lowered water tables, and compressed bare moist soils needed for willow establishment. In the absence of beaver creating necessary hydrologic conditions, ten years of total protection from elk browsing was not sufficient to allow willows to grow greater than two meters tall (resilient to browsing). This study indicated clearly that bottom-up control of willow productivity due to beavers exceeded top-down control by herbivory.

**Painter et al. (2015)** further and refute the conclusions of both Kauffman et al. (2010) and Ripple and Beschta (2007). The authors suggest that increased wolf predation on elk after wolf reintroduction played a role in substantial decreases in elk populations, interacting with other influences such as increased predation by grizzly bears, competition for forage with expanding bison populations, and shifting patterns of human land use outside the park towards irrigated agriculture (which become more important during droughts), reduced livestock densities, and increased hunting on the elk winter ranges. Currently, a large proportion of elk now winter on irrigated fields outside the park, a strong shift in distribution. Even with the near elimination of winter elk hunting after 2005, lower wolf numbers after 2007, mild winters after 1999, a major wildfire in 1988, and the end of the regional drought in 2007, the trend of declining elk density inside the park continued through 2012. Increasing bison populations inside the park (growth of three times between 1998 and 2012), either expanded into vacated elk winter range or perhaps displaced elk. The authors argue that research conducted by Kauffman et al. (2010) and Ripple and Beschta (2007) used protocols that differed in both timing and design, potentially missing patchy aspen recovery or

recovery that was in the initial stages. Where herbivory has been reduced, bottom-up factors such as site productivity may become more important drivers of young aspen and willow height. The authors conclude that changing elk dynamics and beginning aspen recovery are consistent with top-down control of large herbivores by large carnivores.

**Ripple et al. (2015)** suggest that increases in wolf numbers after reintroduction into Yellowstone NP resulted in decreased elk populations and increases in berry-producing shrubs, including serviceberry. Increases in serviceberry may partially be due to the 1988 wildfires or other factors. With increases in berries, grizzly bears increased fruit consumption, possibly in association with decreased whitebark pine nuts rather than the effects of trophic cascades. Evidence of a trophic cascade associated with increases in wolf populations, decreases in elk populations, and associated increases in berries, may have resulted in grizzly bears increasing consumption of berries. This may show both a top-down cascade from wolf-elk-berries, and a bottom-up response with increased berry production and grizzly bears switching to now-available berries during periods of low production of whitebark pine nuts.

**Benson et al. (2017)** suggest that eastern coyotes have ascended to the role of apex predators since the extirpation of wolves in northeastern North America. Eastern coyote packs consumed less ungulate prey and more human-provided food than wolf packs, being more generalists. Eastern coyotes are effective deer predators and are larger than western coyotes (eastern wolves are smaller than western wolves), but their dietary flexibility as generalists and low kill rates on moose suggest that they have not replaced the ecological role of wolves as apex carnivores in eastern North America. What is the Relationship of Intraguild Predation (IGP) and Mesopredator Release (MPR) to the Potential Occurrence of Trophic Cascades?

## 7 WHAT IS THE RELATIONSHIP OF INTRAGUILD PREDATION (IGP) AND MESOPREDATOR RELEASE (MPR) TO THE POTENTIAL OCCURRENCE OF TROPHIC CASCADES?

### 7.1 Intraguild Predation

**Interference competition**, also known as competitive exclusion (Polis et al. 1989, Arjo et al. 2002, Finke and Denno 2005), is a system in which species in a community use similar diets and/or space and one species interferes with the ability of the other to optimize the use of food and habitat. Individuals of one or both species attempt to avoid this competition by using different parts of the same habitat, using the habitat at different times, and/or shifting to different foods (**resource partitioning**).

The **competitive exclusion theory** implies that coexistence of closely-related competitive species depends on resource partitioning and the degree to which shared resources are limited (Arjo et al. 2002). This is especially important when one or more predators interfere with other predator(s), called **IGP**. Relative body size and degree of trophic specialization are the two most important factors influencing the frequency and direction of IGP (Polis et al. 1989). Inherent life history characteristics such as litter size, growth rates, social structure, and density dependent interactions may influence the strength and direction of IGP correlations. IGP interactions may be directed preferentially towards predators with the closest rate of competition, often with the larger predator being dominant over the smaller (Polis et al. 1989). A review of the IGP literature found that the effects of IGP vary across different ecosystems, with the strongest patterns of IGP in terrestrial invertebrate systems. However, it is difficult to compare across systems and literature because of differences among study scales, sample sizes, and sampling methods (Vance-Chalcraft et al. 2007).

Polis et al. (1989) identified the complexities of potential types of interactions and responses associated with IGP at the population level: intraguild predators may benefit from reduced competition, especially

when local resources are limited; IGP may be sufficiently intense to control populations of intraguild prey populations; intraguild predators may paradoxically increase populations of intraguild prey if the prey has density dependent responses to decreased abundance and competition; and/or presence of the IG predator may increase competition for habitat refugia.

At the community level, interactions over ecological and evolutionary time strongly influence the abundance of species. These interactions may influence distribution, resource use, and body structure, as intraguild prey often use habitat differently than their intraguild predator in space and time to avoid the risk of predation. In these early papers, Polis et al. (1989) and Arim and Marquet (2004) suggest that IGP is ubiquitous through various ecosystems, is not due to chance (found by Arim and Marquet 2004 to be statistically significant), and is a powerful interaction central to the structure and functioning of many natural communities.

Many researchers agree that the effect of IGP on trophic systems is understudied (e.g., Palomares et al. 1995, Litvaitis and Villafuerte 1996, Palomares et al. 1996, Finke and Denno 2005). IGP is more likely to occur in predator guilds with many predator species, which increases the chances of IGP interactions (the intra-guild predator competing for shared prey and predating on other predators) and the potential for dampening trophic cascades (Finke and Denno 2005, Daugherty et al. 2007). Based on a review of the literature on IGP theory and modeling, Holt and Huxel (2007) concluded that most models are oversimplifications of natural systems, including by not considering richer webs of interacting species across heterogeneous landscapes.

Wolves may control coyote populations through IGP and competition (Berger and Gese 2007 found a statistically significant correlation) in the Greater Yellowstone Ecosystem and Grand Teton NP. Survival rates of resident coyotes were higher than that of transient coyotes. Humans were responsible for 88% of all resident coyote deaths; predation caused 67% of all transient coyote deaths, with wolves causing 83% and mountain lions 17% of that predation. Despite IGP on coyotes by wolves, it is possible that coyotes may arrange their territories to overlap wolf activity areas, possibly in response to increased scavenging opportunities within wolf territories.

## 7.2 Mesopredator Release

Early studies related to the conservation effectiveness of removing large predators indicated that such removals may result in unintended increases of populations of smaller predators. The increase of smaller predator populations may have further impacts on the prey populations of those smaller predators. This concept is now referred to as **mesopredator release**.

Cote and Sutherland (1997), in an analysis of the literature, concluded that predator control is often the one factor, other than human exploitation, that can be directly managed (the others being climate, productivity, diseases and parasites, availability of territories, and accidents). Predator control may increase target populations of breeding birds, but not reliably, based on immigration and the availability of the area's carrying capacity to support more birds.

On closed systems associated with oceanic islands (systems with highly restricted opportunities for emigration and immigration) on which exotic predators such as feral cats or rats are introduced, removing the apex predator may result in irruptions of mesopredators (removing the cats eliminated the suppressive effects on rats), which may lead to extinction of the shared prey. Rats, being omnivores, may maintain high abundance and high levels of predation, even when bird populations are low (Courchamp et al. 1999, Bergstrom et al. 2009, Roemer et al. 2009). Release of mesopredators by removal of apex predators on insular islands may have many unintended consequences, including reducing nutrient subsidies from predation by small mammalian predators on large colonies of birds, altering vegetation communities; driving native species to extinction or extremely low abundance; filling niches that can no longer be filled

by apex predators; and creating reservoirs of diseases carried by mesopredators (Roemer et al. 2009). Despite these problems, Russell et al. (2009) argue that removing apex predators from oceanic islands may outweigh the negative effects of MPR.

Large mammalian carnivores are particularly vulnerable to extirpation and extinction in fragmented habitat due to human development, which may result in MPR of smaller predators, which are more resilient to extirpation (Crooks and Soule 1999, Roemer et al. 2009). In an area highly fragmented due to residential development, the authors found positive statistical correlation between coyote abundance and mesopredator abundance, especially opossums and foxes, and negative correlation between bird diversity and grey foxes, domestic cats, opossums, and raccoons. Mesopredators avoided areas of high coyote presence both temporally and spatially. Because domestic cats are recreational hunters subsidized by their owners, approximately 35 cats (from a neighborhood of 100 homes) were present in bird habitat fragments containing a very small number of birds (Crooks and Soule 1999).

Prugh et al. (2009) asserted that collapses in top predators caused by human influences are often associated with dramatic increases in the abundance of smaller mesopredators across many types of communities and ecosystems. The authors defined a **mesopredator** as a mid-ranking predator in a food web regardless of size or taxonomy. A mesopredator in one food web may be an apex predator in another and may not directly fulfill the original apex predator's ecological role in the web. The occurrence of a MPR is often symptomatic of fundamental ecological imbalances due to human activities, such as habitat fragmentation, introduction of exotic species, and provision of human subsidies. Overabundant populations of mesopredators are difficult to control because the species are usually characterized by the potential for high densities, high reproductive rates and rates of recruitment, and high rates of dispersal. The authors also assert that it is difficult to root out alternative explanations for mesopredator overabundance, such as habitat changes, that often occur with or cause the loss of apex predators. Uncertainty regarding the causal mechanisms underlying mesopredator outbreaks muddies prescriptions for management. In a commonly cited meta-analysis by Ritchie and Johnson (2009), the authors reported that more than 95% of the papers reviewed suggested evidence of MPR and/or suppression of mesopredator populations by apex predators. The only exceptions involved species with specialized defenses, such as skunks or those that use specialized structural niches, such as arboreal behavior. Apex predators can affect mesopredator abundance through killing (and sometimes eating) them; through forcing behavioral shifts in foraging or use of habitats in time and space; and through direct aggressive interactions. These changes can have effects on population growth, predation rates, fitness, and survival. Bottom-up effects of vegetation productivity and community composition and distribution can affect abundance of species at all trophic levels, including IGP, attenuating or exacerbating the nature, strength, and direction of interactions among species (Thompson and Gese 2007, Ritchie and Johnson 2009). Apex predators may be more effective in controlling mesopredators in productive ecosystems (Ritchie and Johnson 2009).

In another commonly cited meta-analysis, Brashares et al. (2010) found evidence that MPR is a common result of the loss of apex predators in many systems throughout the world. Many current apex predators in some systems are exotic or invasive species. Loss of apex predators may or may not result in MPR, depending on the context. Additionally, increased abundance of mesopredators may or may not cause prey populations to decline, with mesopredators gaining dominance in areas of low productivity and high habitat fragmentation, and apex predators having more resilience in areas with high productivity and low habitat fragmentation. If a high diversity of apex and mesopredators consume a wide variety of prey, the potential for MPR and trophic cascades is weakened. Challenges in detecting MPR is difficult because of short duration studies, inherent natural variation, complex interactions among trophic levels, and researchers often invoke MPR when the apex predator has already been extirpated.

Another recent meta-analysis conducted by Ripple et al. (2013) suggested that any MPR effects due to wolves could be dependent on the context, and may be influenced by bottom-up factors, such as the productivity of a system without wolves. Factors such as human-provided food subsidies, scavenging opportunities on livestock and large ungulates, and existence of alternative prey may confound results. The authors suggest that a link exists between wolf population declines and expansion in the ecological influence of coyotes. The strength of any trophic cascade created by wolf recolonization may be dependent on whether wolf populations may reach ecologically-effective densities (also suggested by Letnic et al. (2007)), the amount of unfragmented habitat available, levels of wolf harvests and removals, and presence of refugia and food subsidies available to coyotes.

In Australia, researchers have suggested that widespread and intensive control of dingoes using aerial distribution of 1080-poisoned baits has resulted in releases of mesopredators, especially introduced foxes and cats (Wallach et al. 2009a, Letnic et al. 2011, Brook et al. 2012), although Allen et al. (2014) argues that other plausible explanations may exist. Letnic et al. (2011) suggested factors that may also limit the control of dingoes on foxes include the abundance of prey (particularly introduced rabbits), seasonal activity patterns, levels of site and vegetation productivity, predator control regimes used, human food subsidies, and reproductive rates. Importantly, the authors argue that it is possible that top predators can ecologically express control over mesopredator populations only when apex predator population densities reach a certain threshold (also suggested by Ripple et al. 2013), which is likely to be above that at which apex predators pose a threat to livestock or human safety. Lack of human tolerance to predators may not allow that ecological threshold of abundance to be reached.

Similarly, Newsome et al. (2017) found that top predators suppressed mesopredators in areas where top predator densities were highest (core area), supporting the notion that removal of top predators can cause MPR. At areas outside the top predators core area, mesopredators and top predators have been shown to coexist, indicating that MPR may not occur when top predators are removed in those areas since mesopredators already had a realized ecological role. However, there is uncertainty with their results, since mesopredators could coexist in the high-density core of a top predator's territory, but those individual animals are thought to be difficult to detect. The authors note that abiotic factors, such as human disturbance and agriculture, caused both top predators and mesopredators to be absent from the area, dampening the strength of top-down forces enough to create a bottom-up driven system.

Wallach et al. (2009a) suggest that dingoes originally coexisted with two endangered species (a ground-nesting bird and a rock-wallaby), and extensive dingo baiting may be the unintended cause of Australia's extinction crisis due to MPR of introduced foxes and cats. Intensively baited dingoes may have managed to preserve pack cohesiveness due to learned behavior in response to human persecution, including becoming difficult to sample and highly secretive in areas of human presence and where they were expected to be exterminated. After intensive baiting of dingoes, endangered species may either crash (which is improperly attributed to the baiting program) or exhibit an exponential increase followed by a crash after a lag period (mesopredator populations increase during the lag period before adversely affecting the population of the endangered species). Brook et al. (2012) found evidence that controlled dingo populations hunted less at dusk (dusk being their common hunting period concurrent with prey activity), and therefore feral cats hunted more at dusk with higher efficiency. Cats may also have the additional behavioral advantage of climbing trees both to access prey and avoid predation by dingoes. Dingo densities may actually increase for a time following intense baiting due to dispersal of young dingoes.

Allen et al. (2013) demonstrated that the removal of dingoes did not result in increased mesopredator abundance. Further, Allen et al. (2014) argues that three often-cited studies purporting to provide evidence of MPR in Australia are actually plagued by imprecise sampling of predator populations. Additionally, none of the studies provide reliable evidence of MPR because there was no verification of

reduced dingo populations due to baiting. The authors assert that, despite broad patterns of MPR demonstrations in some contexts, MPR cannot be reliably separated from other equally plausible explanations for the suggested interrelationships among dingoes, foxes, and cats. Additional research by Allen et al. (2018) has indicated that bottom-up effects (habitat and food availability) have a greater influence on hopping-mice (prey item of mesopredators) than the abundance of dingoes.

## **8 WHAT IS THE RELATIONSHIP OF ADAPTIVE BEHAVIOR, RESOURCE PARTITIONING, AND HUMAN SUBSIDIES TO THE POTENTIAL FOR TERRESTRIAL TROPHIC CASCADES?**

### **8.1 Adaptive Behavior**

Since the late 1990s, researchers have recognized that individuals and groups of herbivorous and/or carnivorous prey animals use behavior that may be evolutionary-based or learned as part of a social system to reduce the risk of predation. Other non-consumptive and abiotic factors such as snowpack, system productivity, rainfall, and climate change may also affect how predators and prey (including predators as prey, or IGP) interact (Peckarsky et al. 2008). Although top predators will kill smaller predators, other factors, including behavioral responses such as shifting territories, adapting anti-predator behavior, and resource partitioning, are the primary mechanisms by which dominant predators can limit smaller predator populations (Casanovas et al. 2012).

Berger-Tal et al. (2011) suggest that adaptive behavior by predators and prey should be integrated into models of conservation theory, and recognize the role that human behavior plays in impacting animal behavior, such as overharvesting, habitat fragmentation, disturbance, and the introduction of exotic species. The key animal behaviors affecting survival, reproduction, and recruitment are changes in movements and use of space, behaviors related to foraging and avoidance of predation, and social behaviors.

Gese (1999) reported that elk and bison act more aggressively toward the alpha pair of wolves than toward betas and juveniles. Female elk with young act more aggressively toward predators than males to determine the most effective level of anti-predator behavior with the least use of energy (Gese 1999), perhaps responding to behavioral clues emitted by the predators themselves (Peckarsky et al. 2008). The type of hunting style use by different terrestrial large predators, such as “coursing” versus “sit-and-wait” may cause different anti-predator responses by prey. For example, it may be easier to respond with less energy to coursing predators, such as wolves and coyotes, because it is easier to know if they are present or absent from an area than an animal that may be hiding and waiting for prey to mistakenly enter their attack range (Schmitz et al. 2004, Ritchie and Johnson 2009). However, Orrock et al. (2010), working primarily with fish and invertebrates, suggested that predators may change prey movements and behavior by “remote threat,” even when the predator is not present (the predator causing a threat has been called a “keystone intimidator” by Peckarsky et al. 2008).

It is difficult to interpret the rationale for certain wildlife behaviors. Creel and Winnie Jr. (2005) disagreed with Hebblewhite and Pletscher (2002) interpretation of elk grouping behavior near and far from cover. The latter interpreted elk foraging in meadows as a means to avoid predator attacks emerging from cover, the former reinterpreted the same behavior as release from anti-predator behavior when the short-term risk of predation was low, providing an opportunity for foraging in the best habitats. Creel and Winnie Jr. (2005) suggested that elk can assess temporal variations in predation risk on a sufficiently fine scale to determine the daily comings and goings of wolves through the senses, patterns of predator presence, and/or distribution of prey carcasses.

Prey may change their behavior to avoid chronic predation, including by humans, by changing the timing of activity (temporal behavioral change during the day or night) or the how they use the available habitat spatially in relation to the activity of the larger predator (Kitchen et al. 2000, Wilson et al. 2010). For example, Kitchen et al. (2000) reported coyote populations being significantly more active during the time period when predators are not (for coyotes, more active during the night while their eyesight is more adapted for optimal hunting during the day or dawn). Social animals may also be forced into behavioral and associated physiological changes under heavy human predation. Wallach et al. (2009b) asserted that heavy predator control against dingoes (wolf-like canid) in Australia through aerial 1080 baiting fractured the social structure of packs, leading to changes in age composition, group size, survival rates, hunting abilities, territory size and stability, and genetic identity and diversity. When heavily controlled, dingoes learned to survive in areas deep in reserves and, conversely, directly near humans, livestock and areas of heavy baiting, utilizing additional food sources and passing on the anti-predator/human behavior to offspring.

Free-ranging domestic dogs were found to control distribution and habitat use of a small wild deer in South America due to high potential for harassment and attacks and resulting high lethality of attacks. Recreational hunting by subsidized domestic predators can cause behavioral and habitat shifts, reduction in fitness, and populations declines (Silva-Rodriguez and Sieving 2012).

Other important behaviors affecting the role of species abundance and recovery within trophic systems is dispersal, immigration into and out of a system or population, and territoriality. In species with social structures, such as wolves, dingoes, and coyotes, dispersal by beta and juvenile individuals may be due to little interaction with other pack members, lack of breeding opportunities, restriction to food resources by higher ranking members, and increased social aggressions from more dominant pack members (Gese et al. 1996a;b). Territories are areas that are defended from emigration by individuals that are not pack members, usually by the dominant pair, to limit or exclude competition for mates, food, and space (Gese 1998). Berger and Gese (2007) suggested that differential effects of wolf competition with coyotes on transient coyote survival and dispersal are important mechanisms by which wolves reduce coyote densities.

A challenge to interpreting the role of adaptive behaviors and other non-consumptive traits such as habitat or temporal shifts that are acquired over evolutionary time is that, when evaluating statistical correlations, these factors may have the same sign as consumptive factors (factors related to trophic interrelationships), moving in the same direction, so they may be overlooked or masked. Conversely, adaptive behaviors may also potentially increase the magnitude of trophic cascades that would otherwise be mediated by consumption. Non-consumptive effects may also be easily interpreted as bottom-up effects, or be considered as an afterthought to explain observations inconsistent with consumption-based theory, further confounding interpretation of study results (Peckarsky et al. 2008).

## 8.2 Resource Partitioning

Partitioning of resources in time and space are key behavioral methods for coexisting and minimizing competition between predators and prey, including predators that kill and/or eat other predators (IGP). Polis et al. (1989) identified **interference competition** (also called competitive exclusion; Arjo et al. 2002, Finke and Denno 2005, Brook et al. 2012), in which taxa in a community use similar diets and/or space and one interferes with the ability of the other to optimize the use of such resources. For example, hungry consumers may have greater movement in search of food, encountering predators or prey more frequently. Behavioral adaptations to minimize the risk of prey encountering predators can involve switching the use of habitats by using them at a time when it is likely that the predator would not be present (Palomares et al. 1996, Finke and Denno 2005, Hunter and Caro 2008) or switching their diet to minimize competition (Schmitz et al. 2004, Thompson and Gese 2007, Elbroch et al. 2015).



Several authors have reported that coyotes may eat smaller prey compared to wolves (such as deer, rabbits, or rodents rather than elk), while at the same time obtaining food directly provided by wolves through scavenging on large carcasses that the wolf pack cannot completely consume, such as elk and moose (Paquet 1992, Wilmers et al. 2003). Prior to wolf reintroduction in Yellowstone NP, coyotes depended on small mammals and scavenging carcasses late in the winter season, when animals were naturally weakened and died (Gese et al. 1996b, Wilmers et al. 2003). However, after wolves are reintroduced or they recolonize an area after extirpation, carcasses are provided throughout the winter, making direct interaction with wolves at a carcass, despite increased aggression and the risk of being killed, more energetically efficient than hunting (Arjo et al. 2002, Wilmers et al. 2003, Atwood et al. 2007, Thompson and Gese 2007). Food subsidies provided by scavenging introduces complexity into food webs. In Rocky Mountain National Park, over 30 species of mammalian and avian scavengers use wolf kills (Wilmers et al. 2003).

After reintroduction of wolves into Yellowstone NP, competition between mountain lions and wolves suggested that mountain lions significantly increased the proportion of deer in their summer diet and decreased the proportion of elk. Both wolves and mountain lions preyed on elk calves in the summer, but elk had shifted their winter range to irrigated fields outside the park, as well as institutionalized winter-feeding subsidies. This resulted in elk populations no longer being limited by natural carrying capacity, so neither wolf nor elk were limited in the summer by elk calf availability (Elbroch et al. 2015).

Atwood et al. (2007) found that mountain lions and wolves ate the same prey (elk) but in different habitats. Female mountain lions select habitat based on opportunities for hunting more than male mountain lions do. Lendrum et al. (2014) suggest that competition with reintroduced wolves in Yellowstone NP caused mountain lions to select habitat removed from known wolf pack territories and with buffers to reduce the potential for interactions with wolves. Avoiding wolves may result in use of less optimal habitat, especially for female mountain lions, which may have implications for survival of dispersing juvenile mountain lions and overall mountain lion dynamics.

Swift and kit foxes, closely related foxes that are much smaller than coyotes, are often killed by coyotes in areas where their home ranges overlap (Kamler et al. 2003, Moehrensclager et al. 2007, Kozlowski et al. 2008); however, fox populations having higher survival rates tended to use portions of the overlapping home ranges that had more heterogeneity, especially areas providing burrow and den refugia that allow rapid escape from coyotes. Home range sizes decreased as the availability of burrows increased, as it did in areas with lower shrub densities in which predators can be readily viewed and escaped more quickly (Moehrensclager et al. 2007, Kozlowski et al. 2008).

More than body size and behavior, especially in non-canid mammalian predators, may cause resource partitioning. Even when raccoon and coyote home ranges overlapped, researchers found little evidence of coyotes killing raccoons, and little evidence that raccoons avoided coyotes. Since raccoons are opportunistic omnivores, there is little potential for direct competition. Raccoons also climb trees, which may provide a structural habitat partitioning (Gehrt and Prange 2007). Skunks avoid direct predation by larger carnivores through distinctive coloration and toxic emissions (Hunter and Caro 2008, Ritchie and Johnson 2009).

Human influence on habitat use, especially habitat fragmentation, human activity, and human food subsidies, is an important consideration for how individuals and populations interact and thrive (Litvaitis and Villafuerte 1996, Palomares et al. 1996, Fedriani et al. 2001, Fischer et al. 2012).

### **8.3 Human Food Subsidies**

A review of the literature by Newsome et al. (2015b) found that 36 terrestrial species in 34 countries used food provided by humans, such as discarded food, livestock carcasses, crops, and landscaping. With such

subsidies, predator abundance increased (no longer limited by resources), diets were altered to include human-provided food, survival increased, and social interactions shifted to either the benefit or disadvantage of the predator. Predators also changed their home ranges, activity, and movements. Subsidies can result in induced behavioral or population changes and may result in trophic cascades, causing predator populations to no longer cycle with prey cycles. Top predators used primarily livestock, mesopredators used livestock carcasses and waste food, cats continued to use live prey, and bears mostly used crops, waste foods, and carcasses. Prey also used human presence and activities as shields from predators in some cases.

Fedriani et al. (2001) found that areas in southern California with high and patchy human residential development provided sufficient human food subsidies through trash, landfills, livestock, and domestic fruit, as well as providing subsidized habitat for rabbits. The study also found that coyote densities were eight times higher than in more natural areas (also, Fischer et al. 2012). As predator size increases, human tolerance tends to decrease (Fischer et al. 2012).

In urban areas, coyotes tended to avoid urban and crop areas, using safer corridors between patches of forest areas used for cover during the day and hunting (Arim and Marquet 2004, Gehrt et al. 2009). Gehrt et al. (2009) found mostly “invisible” coyotes avoiding humans and human-provided food in core areas of downtown Chicago and at O’Hare International Airport (similar to Wallach et al. 2009a, Wallach et al. 2009b). Raccoons, however, heavily used dumpsters and trashcans at night in areas with high human activity during the day (Gehrt et al. 2009). Bino et al. (2010) found that foxes, when human food subsidies were rapidly removed, responded by increasing or shifting their home ranges or dispersing from the area, and that fox densities in the urban area decreased substantially within a year.

## **9 HOW DO PREDATOR POPULATION AND SOCIAL DYNAMICS AFFECT ECOSYSTEM STRUCTURE AND FUNCTION?**

The territory of an animal has been defined as the area that an animal will defend against individuals of the same species (Mech 1970). Since the Knowlton and Stoddart (1983a) study (and further clarified by Gese 1998), it is clear that the territorial alpha pair is the basic unit of wolf and coyote populations. According to Gese (1998), the alpha pair is responsible for monitoring and defending the territory and its resources from other conspecific predators from adjacent packs through patrolling and scent marking. Pack size varies geographically, with wolf packs more commonly composed of more individuals than coyote groups. Ecologically, the socially intact and operating wolf pack, not individual animals or even the alpha pair, is the unit that appears to control the structure and function of the ecological system (Wallach et al. 2009b).

Maintaining the structure of the pack is critical for ensuring that the pack has the needed resources through shared hunting strategies and scavenging, collaborative care of the alpha pair’s young, and learned behavior of the young for hunting efficiency and wariness of novel changes in the territory. In coyotes, only the alpha pair breeds and only 10% of the young from a given pair need to survive and reproduce to replace the pair. The remaining 90% of the beta (subdominant) and transient animals either stay in the pack without reproducing, die, or disperse, and often die before establishment in a new territory (Knowlton et al. 1999). Therefore, in the absence of human hunting, territories and associated population densities tend to remain relatively stable over time.

Population control of socially complex species like wolves may have profound ecological impacts that remain largely invisible if only abundance is considered. Heavy predator control (in this case intensive aerial baiting of dingoes with 1080) can seriously fracture pack social structure, leading to changes in age composition, group size, survival rates, hunting abilities, territory size and stability, social behavior, genetic identify, and diversity. Controlled populations tend to have a higher proportion of young

breeding pairs and litters due to loss of dominant adults in the pack structure controlling access to breeding. Packs may disperse after the loss of the breeding pair and territory boundaries may weaken or dissolve, creating transient individuals that are more vulnerable to predation. The pack may also shift to another area under heavy exploitation and breakup of territories. Learned and practiced coordinated hunting behaviors within packs may be lost due to loss of social structure and changes to social traditions. A symptom of pack disintegration may be a decreased ability to take down larger prey and predators may shift to smaller and or more vulnerable prey. Smaller packs may reduce success at scavenging in the winter due to competition from larger predators. Intensive human removals may teach remaining animals to be highly secretive (Wallach et al. 2009b).

Studies suggest that coyote territories do not remain vacant for very long after members are removed. Gese (1998) noted that adjacent coyote packs adjusted territorial boundaries following social disruption in a neighboring pack, thus allowing for complete occupancy of the area within a few weeks, despite removal of breeding coyotes. Blejwas et al. (2002b) noted that a replacement pair of coyotes occupied a territory in approximately 43 days following the removal of the alpha territorial pair. Williams et al. (2003) suggested that temporal genetic variation in coyote populations experiencing high predator removal indicated that localized removal did not negatively impact population size. Gese (2005) found that after heavy removal rates (populations reduced between 44% and 61% over two years) there was a younger age structure in packs and increased reproduction by yearlings, with pack size and density rebounding to pre-removal levels within eight months post-removal. The author attributed some of the response to immigration of animals from outside the territory and increased lagomorph prey availability that apparently increased mean litter size in both the removal and control areas. Young animals, which are low in the social structure and subjected to lower resource accessibility, and some betas with no potential for becoming breeding alpha members of the pack, generally disperse (Gese et al. 1996b), which may also keep genetic diversity high as dispersing animals fill vacated openings within another pack.

While it is true that wolf removal can have a short-term disruptive impact on pack structure, that disruption does not appear to result in adverse impact on the overall wolf population (Nadeau et al. 2008, Nadeau et al. 2009, Mack et al. 2010). Pack resilience to mortality is inherent in wolf behavioral adaptation and reproductive capabilities (Brainerd et al. 2008). Based on mean pack size of eight, mean litter size of five, and 38% pups in packs, Boertje and Stephenson (1992) suggested 42% of juveniles and 36% of adults must be removed annually to achieve population stability. Researchers have indicated declines may occur with human-caused mortality at 40% or less of autumn wolf populations (Peterson et al. 1984, Ballard et al. 1997).

The data on wolf mortality rates suggest some wolf populations tend to compensate for losses and return to pre-removal levels rapidly, potentially within a year. Wolf populations have sustained human-caused mortality rates of 30% to 50% without experiencing declines in abundance (Fuller et al. 2003). In addition, Brainerd et al. (2008) found that 62% of packs in recovering populations retained territories despite breeder loss. Furthermore, pup survival was primarily dependent on size of pack and age of pup because multiple pack members feed pups despite loss of an alpha breeder. Pup survival in 84% of packs with breeder loss was similar or higher than packs without breeder loss (Mech and Boitani 2003).

Wolves and coyotes with strong social structures can be resilient in the face of moderate levels of exploitation, and can recover abundance relatively rapidly. However, it is not known at what population densities these species can exert top-down control through the ecosystem. Many populations are simply too small to actually cause top-down trophic cascades (Ray et al. 2005a, Letnic et al. 2011, Ripple et al. 2013).

## 10 WHAT IS THE RELATIONSHIP OF TROPHIC CASCADES TO ECOLOGICAL BIODIVERSITY AND ECOSYSTEM FUNCTION?

Humans are the top predator in all systems, but the roles humans play as predator in trophic cascades, biodiversity, and ecosystem function are rarely considered (Ray et al. 2005a). Most predators cannot directly and intentionally change their habitats and condition to serve their own purposes; only humans can do that.

Humans are altering the composition, ecosystem structures, and impacted diversity of biological communities through a variety of activities, such as logging, agriculture, grazing, development, climate change, loss of native species and additions of exotic or invasive species, with new functions that increase the rates of species invasions and extinctions, at all scales. Many human-altered ecosystems are difficult and expensive to recover, or may be impossible to reverse (Hooper et al. 2005, Ritchie et al. 2012). Biodiversity is declining a thousand times faster now than at rates found in the fossil record, and is becoming increasingly confined to formally protected areas, which may fail to function as intended due to size and lack of connectivity to other protected areas (Balvanera et al. 2006, Estes et al. 2011). Concern is growing that the loss of ecosystem services provided by biodiversity are adversely impacting human well-being (Hooper et al. 2005, Balvanera et al. 2006, Cleland 2011).

Despite compelling experimental evidence, the relationship of biodiversity to ecosystem functioning and provision of ecological services has great uncertainty and is still contentious among researchers because the differences in experimental design, the results obtained, and interpretations of those results have not been consistent or universally accepted among the research community (Hooper et al. 2005, Balvanera et al. 2006).

Biodiversity can be described at many scales, from genetic to global (Hooper et al. 2005, Cleland 2011). Biodiversity can be measured in many ways as well, including **species richness** (the number of species in a system), richness of functional groups (the number of ecological functions performed by groups of species in a system), **evenness** (the distribution of species or functional groups across the system), species composition (the identity of species occurring in the system), and diversity indices (comparative measures, using whatever factors are measured). Typically, biodiversity is measured in terms of species richness, because it can be readily measured and compared, but that measurement ignores the complex interactions among species, population, communities, and abiotic factors (Ray et al. 2005a, Balvanera et al. 2006, Cleland 2011).

The five top reasons for losses of biodiversity are human-caused habitat loss, fragmentation, and conversion; climate change; introduction of invasive and exotic species; pollution and nutrient enrichment (such as additions of farm fertilizers to aquatic systems); and overharvesting (Srivastava and Vellend 2005). However, these effects can be mediated to a degree by immigration and dispersal (France and Duffy 2006). The effects of biodiversity change in ecosystem processes are weaker at the ecosystem level than at the community level, and have a negative correlation at the population level (Balvanera et al. 2006).

Four mechanisms that account for biodiversity can influence the combined densities of predators and prey and their resources: sampling effects; resource partitioning; indirect effects caused by IGP, including diverse ecosystems with multi-trophic levels and multiple indirect effects; and non-additive effects resulting from consumers with non-linear complex functional responses (Ives et al. 2005).

Biodiversity can enhance the reliability and stability of ecosystem services and functions through more diverse communities and spatial heterogeneity (France and Duffy 2006). **Ecosystem stability** is defined as a system that changes little, even when disturbed; **ecological resilience** is defined as a system that, when perturbed, can recover to its original stasis (Cleland 2011). Ecosystems with low biodiversity have

low resilience and are sensitive to disruptions, including perturbations caused by humans (Ritchie et al. 2012). Having a variety of species, including top predators, which responds differently to environmental perturbations can stabilize ecosystem processes (Hooper et al. 2005, Duffy et al. 2007).

**Ecosystem functioning** is a broad term that encompasses a variety of processes and reflects how the interrelated ecosystems involving biotic and abiotic factors work together. It depends on biodiversity and is the basis of the capability of the ecosystem to provide ecological services of value to humans (Hooper et al. 2005). Variation in ecosystem functions and processes can result from natural annual environmental fluctuations, directional correlational changes in conditions, and abiotic and biotic disturbances (Hooper et al. 2005).

**Functional redundancy** of species refers to the degree to which organisms do similar things within a system and that one species can potentially compensate for the loss of another (Hooper et al. 2005, Casula et al. 2006, Cleland 2011). A relevant example of lack of functional redundancy involves human hunting (with human as the top predator) and natural predation. Human hunting cannot replace the roles that top predators play because the timing and intensity of predation is different; different age and sex classes are targeted; hunting does not generally result in impacts to mesopredators; trapping can result in take of non-target animals; hunting requires infrastructure such as roads that have effects on animals and vegetation (such as mortality caused by collisions with vehicles). In many cases, human hunting and poaching are unsustainable in many parts of the world (Ray et al. 2005a).

It is suspected that greater variations in response to changes in biodiversity occur than is reported in the literature, based on inherent complexities associated with variations in prey use patterns, prey use rates by predators, predator abundance, and predator-prey distributions and interactions. This complexity results in many plausible theoretical explanations for results obtained by modeling biodiversity (Casula et al. 2006), none of which are certain. Studies incorporating multi-trophic levels that more realistically reflect nature and that consider interrelationships are still rare in this discipline (Hooper et al. 2005).

**Ecosystem services** are the conditions and processes through which natural ecosystems and the species that comprise them sustain and fulfill human life, including purification of air and water, support of soil fertility, decomposing waste, climate regulation, pollination, regulation of pests and human diseases, creating conditions of aesthetic beauty, and maintenance of biodiversity (Srivastava and Vellend 2005, Balvanera et al. 2006). As human populations increase and human domination of the biosphere expands, managing ecosystems for human services will become increasingly important to prevent shortages of water, energy, and food, while attempting to decrease disease and war (Kremen 2005).

Substantial theoretical and empirical evidence exists that biodiversity is able to effect ecosystem function for plant communities, but it is not clear if these patterns hold for conditions involving large predator extinctions, multi-trophic communities, or larger spatial scales (Loreau et al. 2001, Ray et al. 2005a, Srivastava and Vellend 2005). The major challenge is to determine how the dynamics of biodiversity, ecosystem function, and abiotic factors interact, especially with steadily increasing human-caused ecosystem degradations. Considering factors other than species abundance and richness (the number of species occurring in an ecosystem and the number of animals in each species), a more predictive science might be achieved if researchers developed an appropriate classification of ecosystem function integrating changes in biodiversity, ecosystem function, and abiotic factors into a single, unified theory that can be empirically tested (Loreau et al. 2001). This is extremely difficult to develop.

Understanding how biodiversity affects ecosystem function requires integrating diversity within trophic levels horizontally and across trophic levels vertically. Multi-trophic interactions may produce a richer variety of diversity and functioning relationships, depending on the degree of dietary generalization and specialization, trade-offs between competitive ability and resistance to predation, IGP, and

immigration/dispersal. Little is known about how reducing the number of trophic levels or species or removing predator species affects ecosystem processes. Integrating more mobile large carnivores into research is an especially difficult challenge empirically (Duffy et al. 2007).

Experiments are often conducted at small scales with insufficient duration to account for turnover of the components in order to provide evidence for true change (as opposed to inherent natural variation), and biodiversity often includes exotic and invasive species. The effects of biodiversity on ecosystem function depend on the system being studied and the functions that are sampled and measured. Few studies have been conducted considering interactive effects of extinctions between two trophic levels, and those studies have mixed results (Srivastava and Vellend 2005).

Srivastava and Vellend (2005) conclude that biodiversity is declining at global scales, but the scales at which empirical studies are being conducted are not scaled up to appropriate levels to reflect nature. The results of studies are inconsistent on whether biodiversity has positive effects on ecosystem function, especially because it is not known how these studies are being scaled up; ecosystem effects of extinctions in multi-trophic food webs are difficult to predict because of numerous and complex indirect effects and the likelihood of simultaneous or cascading extinctions through the trophic levels; and human-caused drivers of extinction effect ecosystem function to a large magnitude directly and indirectly.

Decreases in biodiversity often lead to reductions in ecosystem functions, then in the resultant ecosystem services. Declines in providing services are initially slow, but become more rapid as species from higher trophic levels are lost at faster rates. Different ecosystem services respond differently to losses of habitat and biodiversity, introductions of exotic or invasive species, and the variety of interactions among species within and between trophic levels. Because different ecosystem services tend to be performed by species at different trophic levels, and trophic webs tend to first thin before collapsing from top to bottom, the processes should be predictable and foreseeable. The best way to address biodiversity and ecosystem function is to ensure that the ecosystems remain viable for species with larger area requirements that tend to have less readily identifiable economic value, such as large carnivores (Dobson et al. 2006).

Sustainable and healthy populations of large predators have the potential to restore ecosystem stability and confer resiliency against global processes, including climate change and biological invasions (Duffy et al. 2007). Because the roles of predators are dependent on their context, the emphasis of research must be more focused on predator functions in ecosystems, including the importance of social structures and adaptive behaviors in influencing the dynamics of trophic interactions, and less on the identities and abundance of species. There is great variability and uncertainty surrounding the ecological functions of predators, including unpredictable and even counter-intuitive outcomes that may be caused by species interactions such as IGP and mesopredator release (Ritchie et al. 2012). However, it is inappropriate to assume that the mere presence of large carnivores ensures persistence of biodiversity (Ray et al. 2005a).

The first species that tends to be lost or rendered ecologically extinct in both terrestrial and marine systems is almost invariably the large carnivorous predator, primarily due to their intrinsic rarity at the top of the trophic web, small population sizes, restricted geographic ranges, generally slow population growth rates, and specialized ecological habits. Top predators are especially vulnerable to human-caused habitat destruction and fragmentation, as well as exploitation and persecution due to conflicts with humans (Duffy 2003). Humans, as the top predator, have eliminated the largest predators from over 90% of the Earth, globally extinguishing ecological functions (Pace et al. 1999, Ray et al. 2005a).

Evidence suggests that the loss of one or more large carnivorous predator species often has impacts comparable in magnitude to impacts associated with a large reduction in plant diversity. This results in large changes in community organization, ecosystem properties and system functions (Duffy 2003). Apex predators tend to be the determinants of biodiversity structure and function, and the most

challenging to conserve (Ray et al. 2005a). Studying the results of the impacts of the loss of large carnivores on the structure and function of ecosystems is extremely difficult because of a complexity in trophic interactions. Evidence from ecological studies indicate that the largest contribution of changes in biodiversity on ecosystem function occurs when humans introduce exotic or invasive plant and/or animal species, which may increase the number of species in a system (species richness), while reducing ecosystem functions. Biodiversity will continue to erode under human influence (Duffy 2003).

Despite increasing research on the tangled complexity of food webs and trophic interactions, we have no better understanding of how to apply the results to conserving biodiversity and ecosystem function. Marine ecosystem cascades are generally caused by overexploitation of species eaten by humans; in terrestrial ecosystems, changes in biodiversity are generally caused by human-caused habitat destruction, fragmentation, and conversion. Large carnivores are generally not specialized in function or diet, so pristine conditions are not needed for survival; large carnivores are mostly resilient in the face of human perturbations, provided they have their basic baseline conditions. The primary problem with restoring large carnivores is competition with humans for space, resources, and property such as livestock (Ray et al. 2005a), which can often lead to legal and illegal removals, concerns with human health and safety, and further pressures on endangered species (Ritchie et al. 2012).

Biodiversity, broadly defined, and the roles of large predators potentially contributing to biodiversity, clearly has strong effects on ecosystem functioning and provision of ecosystem services, which must be communicated to those charged with economic and policy decision-making to avoid ineffective and costly management actions (Hooper et al. 2005).

However, researchers have identified the need for consideration of ecological complexities in study designs for better determining true levels of biodiversity and their roles within ecosystems, including factors such as resource partitioning, indirect and additive effects (including IGP and MPR), multiple effects, social stability of packs of socially complex top predators, and multi-trophic systems. Studies must also be upscaled to more realistically represent larger systems, the results of which may then overturn the more general findings of the current studies of simplified systems (Ives et al. 2005, Srivastava and Vellend 2005, Wallach et al. 2009b). More studies are also needed on the sequence of system collapse and replacement of ecosystem services as systems are further degraded (Dobson et al. 2006). The ecological roles of predators in supporting ecosystem biodiversity and functions and providing ecosystem services to humans are substantially unknown.

## **11 WHAT SHOULD BE THE ROLE OF TOP PREDATORS IN CONSERVATION PLANS?**

Predator management is characterized by complex ecological, economic, and social tradeoffs that are often not readily apparent or mutually exclusive, as well as being very expensive. Large carnivore conservation is impeded because much of the habitat is already destroyed or has uses that conflict with predators, they can be perceived to be threatening to human safety, and they kill game species and livestock (Prugh et al. 2009, McShane et al. 2011, Ritchie et al. 2012). Replicating the full suite of influences provided by apex predators is exceptionally challenging if not impossible.

The ability to better predict mesopredator responses to reintroduction or gradual recolonization of apex predators would enhance effectiveness of management efforts. The daunting task of conservation of top predators requires substantial habitat restoration, greater public acceptance of large carnivores, and compromises among people most directly affected by these predators (Prugh et al. 2009). Also, little is known about the impact of trophic interactions, particularly predator-prey and predator-predator interactions on the relationship of biodiversity and ecosystem functioning in natural systems. Increasing predator diversity could promote trophic cascades if predator species act additively or hide trophic cascades if IGP is likely to occur in diverse predator assemblages (Finke and Denno 2005).

Because top predators need lots of room, have symbolic value, and can structure ecosystems under certain circumstances, they have the potential to gain public support for conservation programs to achieve higher scale conservation goals to restore degraded ecosystems. Large scale conservation should not be confused with the ecological roles and importance of apex predators to conservation. In areas where top predators were extirpated but the system was protected, such as in national parks, top predators may be effective in improving biodiversity and ecosystem function.

In areas with high levels of human-caused habitat change, development, and relatively unlimited prey (large populations of deer), gradual recolonization by top predators, such as by wolves in the northern Midwestern US, often increase the potential for conflicts with humans. The ability of top predators to reach a threshold density to play an ecological role for conservation may be limited by population reductions in response to human conflicts, including in areas surrounding reserves. The conservation goal must focus on reaching population levels and distribution of top predators that the threshold for creating ecological structure is reached and sustained (Ray et al. 2005a, Letnic et al. 2011, Ripple et al. 2013).

The best chances for using top predators for conservation purposes is where the extirpation of predators has been clearly shown to result in adverse ecosystem impacts and where the system has not been degraded by other factors. In terrestrial systems, where habitat conversion has created so many changes to biodiversity, the return of top predators may require long periods of time to reach conservation objectives, if recovery can be achieved at all (Ray et al. 2005a).

The precautionary principle when designing conservation plans is important, shifting the burden of proof to those who discount the ecological role of predation, because thresholds of change may result in large and sudden phase shifts that may be impossible to reverse (Ray et al. 2005a, Estes et al. 2011).

The most important questions regarding conservation of large predators, biodiversity, and ecosystem function remain unanswered:

1. In what locations and under what conditions do large carnivores play an ecologically significant role?
2. In what locations and under what conditions would restoration of large carnivores result in restoration of biodiversity?
3. What densities of large carnivores are necessary to produce the desired restoration of biodiversity?
4. What are the interactions between hunting by carnivores and hunting by humans? (Ray et al. 2005a).

## **12 WHAT ARE THE CHALLENGES ASSOCIATED WITH INTERPRETING AND APPLYING THE RESULTS FROM STUDIES CONDUCTED IN DIFFERENT ECOSYSTEMS?**

Regardless of the context, Litvaitis and Villafuerte (1996) warn researchers not to confuse declines in apex predators and changes in lower trophic level species abundance as a cause-and-effect relationship, as both are likely a response to human activity, including collisions with vehicles, legal and illegal take, habitat fragmentation, development, and/or human subsidies. Interpretations of results must look for factors beyond those naturally occurring in the study area.

A primary challenge to testing the presence and strength of a trophic cascade involves removing predators from systems in which they are abundant or adding them to systems where they are absent, creating an intended perturbation that can be tested statistically (Estes et al. 2011, Ripple et al. 2016). With large



free-ranging carnivores, intended removal of predators as part of a study is typically socially, ethically, and politically challenging or impossible (Ray et al. 2005a, Estes et al. 2011). Therefore, many studies rely on areas in which large apex predators were extirpated and either reintroduced or rapidly recolonized the area, while the original conditions remain substantially the same, such as in older national parks, including Yellowstone National Park, Zion NP, and Banff NP (e.g., Hebblewhite et al. 2005, Ripple and Beschta 2006a, Berger et al. 2008, Estes et al. 2011, Beschta and Ripple 2012, Ripple et al. 2015).

Another challenge involved with conducting studies that provide statistically-strong results involves the temporal scale of the study, which must be of sufficient duration to incorporate the generation times of the component species, especially plants. While predator impacts have been observed over weeks and months in lakes, streams, and nearshore marine systems, decades or even centuries may be required for terrestrial systems where the base autotrophs may be shrubs or trees (Duffy 2003, Schmitz et al. 2004, Briggs and Borer 2005, Ripple et al. 2016, Engeman et al. 2017).

### 12.1 Relevant Publications Outlining Challenges

**Ecosystems are more complex than first thought:** Pace et al. (1999) suggested that cascades are more likely to be non-linear and food webs to be probabilistic due to highly variable conditions that promote and inhibit the transmission of the effects of predators on food webs (called trophic dynamics), including complicating and confounding factors such as differences in inherent primary productivity (the nutrition provided by the plant communities), adaptive predator-avoidance behavior, the potential for ecological compensation, and the availability of anti-predator refugia for prey. In other words, researchers began to understand that ecological interrelationships among biotic and abiotic components of ecosystems had blurred what had appeared to be clear boundaries and interconnections.

**Top-down effects appear to dissipate faster on terrestrial ecosystems than in freshwater ecosystems:** Polis et al. (2000) suggest that this may be the result of aquatic systems better fitting the simplifying assumptions of trophic cascade models (such as incorporating discrete homogeneous environments and short regeneration periods for predators, and simple and trophically-stratified systems with strong and clearly identifiable interactions among species). They also suggest that most terrestrial systems are more complex and heterogeneous, with fuzzy boundaries between trophic levels, having variable prey and predator dynamics, and weak and diffuse interactions between species (except in human-designed agricultural systems). Species that have greater defenses against predation or herbivory tend to become dominant, weakening the link between predators and prey. The authors argue that, even at the species level, support for the presence of trophic cascades is limited in terrestrial systems (also, Halaj and Wise 2001). Conclusions about the strength of top-down effects may be an artifact of the plant-response being measured, not a response that actually exists in the environment. Schmitz et al. (2004), based on a meta-analysis, reports that a conclusion that a cascading effect may be weak or non-existent or existent and strong may be an artifact of the way the species in a system are categorized and aggregated by the researcher (for example, whether a species is a mesopredator or an apex predator, or which predator species feeds on which prey species), and the conclusion may be dependent on the system topology as conceptualized for the specific web.

**Certain ecological dynamics that occur in terrestrial ecosystems may not occur in aquatic ecosystems:** The additions of the concepts of IGP (Section N.7.1) and mesopredator release (MPR; Section N.7.2), in addition to non-consumptive factors such as adaptive anti-predator behavior and beneficial foraging behavior (Section N.7) in the face of differing predation risk based on the type of predator hunting behavior (“coursing” compared to “sit-and-wait”), further complicate the concept of trophic cascades in heterogeneric terrestrial ecosystems with socially complex and wide-ranging predators and prey (Ripple et al. 2016).

**Some effects, though appearing in both ecosystems, may be weaker in terrestrial ecosystems:** A meta-analysis of research papers conducted by Halaj and Wise (2001) related to terrestrial arthropod-dominated food webs found extensive support for the presence of trophic cascades in terrestrial communities, but that the effects on biomass of primary producers are weaker in terrestrial communities than in aquatic food webs. A meta-analysis of 102 scientific publications across different types of ecosystems (lakes/ponds, marine, stream, lentic and marine plankton, and terrestrial agricultural and old fields) conducted by Shurin et al. (2005) reported high variability among ecological systems, and that predator effects were apparently strongest in benthic communities in lakes, ponds and marine ecosystems, and weakest in marine plankton and terrestrial food webs (also Borer et al. 2005). The complexity of terrestrial food webs within which large wide-ranging and adaptable carnivores are at the top of the web may further weaken the statistically observable presence of predator-driven effects (Halaj and Wise 2001).

**Tradeoff behavior may be specific to the type of ecosystem and may contribute to the variability in the nature and strength of cascading effects:** Schmitz et al. (2004) conducted a meta-analysis of 41 studies conducted in aquatic and terrestrial ecosystems that indicated that one mechanism addressing the uncertainty about the ultimate mechanisms driving trophic cascades may be the trade-off behavior associated with prey avoiding the risk of predation while also attempting to forage optimally. Knowing the habitat and resource use by prey with regard to the presence of one or more predators, and the hunting mode of the predator (“coursing/patrolling” compared to “sit-and-wait”) may help explain the considerable variability on the nature and strength of cascading effects among systems. Different hunting modes force prey to balance the energetic effects of reacting through vigilance, ceasing foraging and moving away, or exhibiting aggression. Prey responding to active, coursing predators may be the least risk averse, determining that foraging is more important than maintaining constant vigilance, especially later in the winter, when fitness is inherently reduced. Different predators apply different rules of engagement based on hunting mode and habitat use, which then drive adaptive behavioral responses and associated trophic effects (Schmitz et al. 2004, Peckarsky et al. 2008).

**Studies may study small subsets of communities for short periods of time, making interpreting results difficult.** Borer et al. (2005) conducted a meta-analysis of 114 studies in terrestrial agricultural and grassland/shrub ecosystems mainly involving arthropods, lake, marine, and stream benthic communities. Of all the studies reviewed, only the marine benthic and grassland studies involved warm-blooded predators, and only one included a warm-blooded herbivore. The authors found evidence that the strongest cascades involved warm-blooded vertebrates (otters and humans), but these communities were primarily in marine environments. However, the authors reported that most studies only evaluate interactions within a small subset of a community, potentially resulting in too little variability in the species manipulated to detect relationships between diversity and the strength of cascades. Most studies were also of insufficient duration and study area size to actually detect ecological impacts that could be suggested to be different from inherent natural variability.

## **12.2 Challenges to Conducting and Interpreting Research and Modeling on Complex and Dynamic Ecological Systems**

Many researchers and theoretical ecologists have identified the challenges associated with attempting to study and reach conclusions about very complex and interrelated systems. Ray et al. (2005a) finds that determining the ecological effects of large carnivores on the biodiversity, structure, function, and dynamics of ecological systems and any associated ecosystem services may be highly challenging or even impossible to discern. Reasons provided by various researchers include:

It is difficult to design suitable experiments with spatial and temporal dimensions that are appropriate for the species, populations, communities, and systems involved. This is especially difficult for large

carnivore species that are wide-ranging and socially and behaviorally complex, and that use large heterogeneous integrated habitats that may change seasonally (Ray et al. 2005a, Ripple and Beschta 2006a, Vance-Chalcraft et al. 2007, Engeman et al. 2017).

Determining change in systems requires that perturbations be created and the results tested, with replications, which may be socially, morally, ethically, and politically impossible with systems involving large carnivores (Ray et al. 2005a, Estes et al. 2011).

Baselines on which to compare changes to determine causal relationships are often already damaged or eliminated, with no remaining or known natural benchmarks against which to measure effects, restricting the ability to discern short-term and long-term equilibrium states with and without predators (Ray et al. 2005a, Kozlowski et al. 2008, Estes et al. 2011).

Finding matched comparison study areas that are sufficiently similar over large spatial areas and over a sufficiently large temporal duration may be difficult and costly at best, and realistically impossible (Ray et al. 2005a).

The existence of many confounding factors can make strong predictions about effects and causation impossible, including abiotic factors such as climate change; weather; differences in site and area productivity; naturally occurring environmental oscillations and “noise”; soil mineralization; and surface and subsurface hydrological dynamics (e.g., Ray et al. 2005a, Ripple and Beschta 2006a, Kauffman et al. 2010, Orrock et al. 2010, Miller et al. 2012, Ripple et al. 2013, Allen et al. 2014, Engeman et al. 2017).

Human impacts are often discounted or are considered tangentially, despite their often dominant and pervasive influence (Vitousek et al. 1997, Estes et al. 2011), and can confound the ability to experimentally discern functional roles of predators, such as: human actions that have historically caused extirpations or extinctions; habitat fragmentation, especially by development and agriculture; introduction of livestock and/or exotic and invasive species into systems; hunting, poaching, persecution, and roadkill; human intolerance, especially of larger predators; human competition for prey of predators; depletion of prey needed by predators; providing food and structural subsidies; creating predator guilds made up of free-ranging carnivorous pets (cats and dogs) that are subsidized, are recreational killers, and often live in developments bordering large fragmented habitats with already stressed prey populations; and large-scale resource exploitation (e.g., Litvaitis and Villafuerte 1996, Palomares et al. 1996, Fedriani et al. 2001, Ray et al. 2005a, Estes et al. 2011, Fischer et al. 2012, Allen et al. 2017, Haswell et al. 2017).

Some potentially strong and important correlations related to non-consumptive factors that are in the same statistical direction as commonly recognized correlations may be masked and not considered in interpretation of study results (Peckarsky et al. 2008).

Valid comparisons of studies evaluated in meta-analyses of multiple studies (where researchers review and reconsider the results of many studies to look for patterns and problems) have been difficult to make because of differences in spatial and/or temporal scale, differences in factors measured, differences in statistical methods and assumptions, and differences in study methodologies, among other reasons (Briggs and Borer 2005, Hooper et al. 2005, Vance-Chalcraft et al. 2007, Brashares et al. 2010).

Most models are oversimplifications of natural systems, and do not include complexities such as anti-predator behavior, more multi-trophic community models, and richer webs of interacting species across heterogeneous landscapes (e.g., Holt and Huxel 2007).

Much of the research related to trophic cascades is often conducted at a small scale and is of short duration in relation to the inherent biological characteristics of the species, communities, and populations

(such as reproduction, immigration, generational turnover, or developing ecologically meaningful changes in abundance), and on species that are small, sessile, or localized and easily manipulated (adding or removing individual predator species or guilds), such as invertebrates, arthropods, localized fish populations, and plankton, and are typically in high productivity systems such as streams, lakes, and marine intertidal ecosystems (e.g., Duffy 2003, Schmitz et al. 2004, Briggs and Borer 2005, Ray et al. 2005a, Beschta and Ripple 2006, Brashares et al. 2010, Estes et al. 2011, Ritchie et al. 2012).

Research conducted in small temporal and/or geographic scales is difficult or inappropriate to scale up or apply generally to large marine or terrestrial systems, especially for guilds involving wide-ranging, often socially complex predators (for example, bluefin tuna (*Thunnus thunnus*), sharks, wolves, dingoes, or coyotes) (e.g., Schmitz et al. 2004, Ripple and Beschta 2006a, Brashares et al. 2010, Engeman et al. 2017).

Research in various systems is being published so rapidly in the last 20 years that it is difficult for researchers to be aware, let alone familiar with, that level of new research results (“information avalanche”), especially if the research is conducted on systems outside of their own disciplinary area (Sergio et al. 2014).

Statistical analyses, assumptions, and interpretations of results are often appropriately re-evaluated and challenged by other researchers, yet the original papers are cited by other researchers without recognizing these challenges (e.g., Litvaitis and Villafuerte 1996, Palomares et al. 1996, Hooper et al. 2005, Balvanera et al. 2006, Ripple and Beschta 2006a;2007, Kauffman et al. 2010, Wielgus and Peebles 2014, Painter et al. 2015, Poudyal et al. 2016).

The role of outbreaks of parasites and pathogens in ecosystem function is often ignored, although they may be strong mediators of trophic competition and, in some systems, keystone species for driving ecological structure and/or function through acting as a small biomass predator on other larger predatory species within the food web (for example, canine parvovirus in wolves on Isle Royale) (e.g., Ray et al. 2005a).

Several studies identify that predator population must reach a certain threshold level at which they become ecologically effective at creating trophic and ecosystem changes, but no one is attempting to determine the threshold level and its effect on humans and livestock (Ray et al. 2005a, Estes et al. 2011, Letnic et al. 2011, Ripple et al. 2013).

Researchers even disagree on the appropriate definitions of and factors involved in ecological functions, trophic cascades, and intraguild predation causing miscommunication among researchers, sampling of inappropriate factors, and misinterpretation of and challenges to cited correlations (Ray et al. 2005a, Ripple et al. 2016).

Poor population sampling to reflect true presence/absence and abundance, resulting in misinterpretations of results, and differences in sampling protocols among studies, making comparisons difficult (e.g., Vance-Chalcraft et al. 2007, Wallach et al. 2009a, Allen et al. 2014).

Publication bias, where only positive results are published, may result in important information being withheld that could provide insight into the findings of other studies (Polis et al. 2000, Brashares et al. 2010).

Not considering adaptive behavior for predator avoidance (for example, changing circadian patterns of activity or habitats used or climbing trees) or increasing predator efficiencies (for example, scavenging),

and morphological and biological traits (such as toxic chemicals used by brightly patterned skunks) (e.g., Schmitz et al. 2004, Peckarsky et al. 2008, Berger-Tal et al. 2011).

Many papers repeatedly use the same few examples of trophic cascades, such as studies conducted in Yellowstone NP, Isle Royale, orca-otters-urchins-kelp (e.g., Ray et al. 2005a, Peckarsky et al. 2008, Estes et al. 2011, Allen et al. 2014, Allen et al. 2017).

Confusing the roles of, failing to consider, or making inappropriate interpretations of immigration and emigration to account for changes in consumer, competitor or prey abundance; the levels and rates of immigration is very difficult to measure (e.g., Duffy 2003, Briggs and Borer 2005, Ray et al. 2005a).

Few studies have attempted to evaluate or quantify the short term and long terms costs of loss of apex predators and mesopredator release (Brashares et al. 2010).

Confusing and misinterpreting the trophic level and functions that a particular predator plays in a specific food web that may poorly reflect on actual roles in nature (Polis et al. 1989, Ray et al. 2005a, Ripple et al. 2016).

The differences in studying large carnivore-driven system structure and function in relatively unchanging and protected areas in which they were previously extirpated and rapidly reintroduced for management purposes (for example, wolves in Yellowstone National Park), areas in which large carnivores gradually immigrated that are dynamic and largely impacted by humans (for example, wolves in Wisconsin and Minnesota immigrating into areas with high levels of habitat fragmentation and human and livestock densities), urban areas with high levels of human-provided subsidies and habitats, human persecution, intense levels of habitat fragmentation, and/or high levels of subsidized carnivorous pets exist, and neotropical islands (e.g., Ripple and Beschta 2007, Berger et al. 2008, Beschta and Ripple 2012, Fischer et al. 2012, Newsome et al. 2015b).

The repeated citation of a few studies as examples throughout the literature, some of which have been challenged regarding validity of interpretations of results or factors considered (Peckarsky et al. 2008, Prugh et al. 2009, Allen et al. 2017).

Consideration of whether ecological change to system structure and function occur in a smooth dynamic way or reach thresholds at which major, and possibly irreversible, shifts and perturbations occur (e.g., Ray et al. 2005a, Estes et al. 2011, Ripple et al. 2016).

### **13 WHAT RELEVANT COMMONLY CITED ARTICLES ARE NOT INCLUDED IN SUMMARY BECAUSE OF STUDY DISCREPANCIES?**

Several commonly cited papers in support of the occurrence of trophic cascades in terrestrial systems have serious discrepancies that create problems with the use of their results.

**Clark (1972):** This early study collected field data on coyote densities, food habits, fecundity, and population growth in relation to prey densities. Documented limitations of the study included inconsistent time spent looking for dens between year, and small sample sizes for the size of the breeding female cohort and litter sizes. Despite these methodology weaknesses, this paper is often cited for its conclusion that long term coyote densities in the Great Basin of Utah appeared to be partly a function of food base, in this case jackrabbits. The study suggests that coyotes did not control jackrabbit populations.

**Henke and Bryant (1999):** This study conducted in Texas involved heavy removal of coyotes with between 26 and 55 coyotes removed every third month between 1990 and 1992, reducing coyote density

from approximately 0.12 coyotes/km<sup>2</sup> to 0.001 coyotes/km<sup>2</sup> (coyote density on untreated control area was 0.14 coyotes/km<sup>2</sup>). In addition to such heavy and chronic removals, the authors suggest caution should be used in interpreting the results reported of a substantial decrease in rodent prey richness within nine months of coyote removals. A drought occurred in 1989 through 1990, which decreased forage and may have facilitated dominance of the highly competitive Ord's kangaroo rat over other species present before treatment began. Also, the authors state that logistical and financial constraints limited the number of replications performed, resulting in a low statistical power associated with the results. However, they state that the "weight of evidence" suggested that coyotes exerted top-down influence on the prey community with only weak empirical evidence. The authors also stated that, to consistently lower coyote densities, an annual removal rate of at least 75% is needed.

**Mezquida et al. (2006):** This paper discusses a potential negative effect of coyote control on sage grouse conservation through release of mesopredators (foxes, badgers, and ravens) that prey on sage grouse and eggs, depending heavily on Henke and Bryant (1999) and an internal unpublished report prepared by the wildlife biologist at a large private ranch in Utah (Danvir 2002). Rather than coyote predation being either directly or indirectly involved in adversely or positively affecting sage grouse, Danvir (2002) actually places the primary concern with heavy jackrabbit browsing in sagebrush habitat. Golden eagles, another predator of sage grouse, and coyote abundance seemingly increased in response to variability of jackrabbits and ground squirrels. His final conclusion is that he did not consider predator-prey interactions to be the cause of the increase in sage grouse, instead emphasizing the habitat manipulations that had been performed on the ranch to benefit sage grouse was the primary factor. Danvir (2002) suggests that weather drives sage grouse population dynamics relating to vulnerability to predators, especially in winters with deep snow and during spring nesting season, and that the way sagebrush steppe ecosystems are managed related to the quality of sage grouse habitat can magnify or minimize the effects of severe droughts, severe winters, and predation.

**Atwood and Gese (2008):** In Yellowstone NP after wolf reintroduction, socially dominant coyotes (alpha and beta) responded to wolf presence by increasing the proportion of time spent vigilant while scavenging, with alphas more diligent than betas. Alphas fed first on carcasses, then betas, then others. Increased vigilance, reduced foraging time, changes in group size and configuration, pre-emptive aggression, and retreat to refugia are crucial behaviors to mediating interspecific interactions. Coyotes would aggressively confront wolves, with numerical advantage by coyotes and the stage of carcass consumption influencing whether coyotes were able to displace wolves. In confrontation bouts that coyotes won, both alpha coyotes were present, there were more coyotes than wolves, and wolves were not very invested in winning. These observations are on one wolf pack and should not be generalized to coyote-wolf interactions at a broader scale without further study.

**Miller et al. (2012):** This paper suggested that coyotes avoided a wolf den, and that coyote predation on rodents away from the wolf den indicated a top-down effect by wolves on coyotes and subsequently on rodents, claiming that restoration of wolves could be a powerful tool for regulating predation at lower trophic levels. The authors argue that making comparisons over time as wolf numbers increase, especially when coupled with spatial comparisons in the study area, can provide evidence that the changes are due to the treatment, and not another confounding factor. These conclusions are based on studying coyote interactions with one wolf den in Grand Teton NP, which is not a sufficient sample size for making conclusions with any correlational strength.

**Allen et al. (2014):** In Australia, three particular published case studies are commonly cited in support of the mesopredator release theory. Problems exist in each study, including use of circumstantial evidence for MPR of introduced red fox or feral cat coinciding with dingo control. The authors conclude that an absence of reliable evidence that top predator control induced MPR. In the last 10 years, 22 literature reviews and extended opinion pieces were published. Only three of the 22 discussed caveats or

methodological limitations of these three case studies, while other call them anecdotal or circumstantial. Pettigrew (1993) concluded that shooting dingoes increased abundance of feral cats. Abundance sampling was imprecise (800 cats removed from trees, but only 229 observed in sampling surveys), and large bursts of cat abundance occurred in years following rainfall-induced increases in prey availability. Cats shot were prime adults, indicating a large-scale immigration of nonresident cats rather than increased rapid reproduction. Lundy-Jenkins et al. (1993) stated that dingo control resulted in fox detection and extinction of a protected species after dingo control. The study was small scale and the experimental design insufficient for inferring changes in predator population abundance. To suggest that lethal dingo control caused a MPR of foxes from a single opportunistic observation of fox tracks is to extend inferences far beyond the limitations of the data. To infer from the data that dingo control caused the local extinction of the protected species does not recognize the persistence of a nearby colony that did not go extinct in response to baiting but was destroyed by wildfire. Christensen and Burrows (1995) stated that dingo and fox poisoning resulting in an increase in feral cat abundance. The experimental design (imprecise sampling of predator populations) precludes reliable inference because increases in cat abundance coincided with the beginning of 1080 baiting (which does not target cats) after cessation of cyanide baiting (which targets cats, dingoes, and foxes), substantial rainfall events increasing prey densities, and a change in the physical location of the unbaited treatment area, all confounding the results.

The three case studies provide no reliable evidence of MPR because of little reliable evidence that dingo populations were affected by the control to any substantial degree, limitations to the experimental designs and predator sampling methods meant that the studies were incapable of reliably evaluating predator responses to dingo control, and MPR remains only one of several plausible explanations for the observations. Although broad patterns among top predator, mesopredators, and their prey have been demonstrated in some contexts and there are good reasons to suspect that these processes also occur for dingoes, MPR cannot be reliably separated from other equally plausible alternative explanations for the suggested interrelationships among dingoes, foxes, and cats. The authors advocate for evidence-based wildlife management approaches that do not unduly risk valuable environmental and economic resources, such as threatened species and livestock.

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