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Science & Society

Co-Adaptation Is Key to Coexisting with Large Carnivores

Neil H. Carter^{1,*} and John D.C. Linnell²

There is a pressing need to integrate large carnivore species into multi-use landscapes outside protected areas. However, an unclear understanding of coexistence hinders the realization of this goal. Here, we provide a comprehensive conceptualization of coexistence in which mutual adaptations by both large carnivores and humans have a central role.

Coexistence and Global Carnivore Recovery

Protected areas are crucial to large carnivore conservation. However, the vast ranges required by these animals mean that co-occurrence with humans is, and has been, common in shared landscapes outside protected areas (Figure 1). Given that shared landscapes often represent a vital part of their remaining geographic distribution [15], eradication of large carnivore species from these areas threatens their conservation. Despite this, the need for conservation of large carnivores in proximity to human populations often generates intense debate, with a key point of contention being whether, and to what degree, the negative impacts humans and large carnivores have on each other can be sufficiently minimized. Thus, operationalizing human–carnivore coexistence in shared landscapes is essential to global carnivore recovery efforts and maintaining (or improving) human wellbeing [1–3]. Yet, a clear understanding of what coexistence means is lacking despite its wide use in both popular and scientific literature. In

part, this is because coexistence can be interpreted very differently when viewed from either a social or natural science perspective. An unclear, inconsistent, or naïve conceptualization of coexistence hinders the ability of opposing stakeholder groups to engage in dialog and precludes the much-needed development of strong and comparable efficacy criteria for different coexistence strategies.

A Comprehensive Concept of Coexistence

Based on our combined experience of working on large carnivore conservation issues, we conceptualize coexistence as a ‘dynamic but sustainable state in which humans and large carnivores co-adapt to living in shared landscapes where human interactions with carnivores are governed by effective institutions that ensure long-term carnivore population persistence, social legitimacy, and tolerable levels of risk’. Our concept of coexistence includes both human–carnivore and human–human interactions, helping to unify disparate interpretations of coexistence from different disciplines. Indeed, coexistence emerges from the interactions within coupled socioecological systems, in which the human and natural systems are fundamentally integrated [3]. Specifically, mutual adaptations between humans and large carnivores are key mechanisms facilitating coexistence in space and time. Flexible institutions (i.e., the formal and informal rules that govern human behavior) have an essential role in fostering human adaptation to carnivores. Although our concept of coexistence might be difficult to achieve in reality, it can serve as a benchmark to strive towards. Here, we highlight key topics informing our concept of coexistence.

Coexistence and Risks from Carnivores

Coexistence does not preclude risks from carnivores; rather, it necessitates human tolerance of these risks and bringing risks to tolerable levels. The most common

risks from carnivores are those associated with damage caused by depredation on livestock, competition with hunters, and attacks on humans. These risks are thought to directly lead to intolerant behaviors by humans, such as illegal killing of carnivores, which can jeopardize carnivore recovery efforts [4]. Managers have access to several technical solutions to mitigate carnivore-related risks; however, recent studies have demonstrated that human tolerance of carnivores is sometimes strongly related to social, cultural, cognitive, and emotional factors, and not only to the economic and material interactions with carnivores *per se* [4]. Despite livestock depredations by snow leopards (*Panthera uncia*), for example, Tibetan Buddhist monasteries protect snow leopards and their habitats in certain areas because of their significant cultural and religious values [5]. Furthermore, the recent comeback of large carnivore species to regions of the USA and Europe after being nearly eradicated [1,2] indicates that changes in human tolerance to carnivores (e.g., operationalized in the form of public support for more protective policies) have implications on long-term carnivore persistence. Given that evidence indicates that the long-term viability of large carnivore populations in shared landscapes is related to human tolerance, learning more about human tolerance to carnivores is an important future research activity.

Conflicting Priorities, Governance, and Coexistence

Coexistence is influenced not only by human–carnivore interactions, but also human–human interactions that affect carnivores [6]. A variety of human attitudes toward carnivores and their conservation simultaneously exist among humans within and across regions and cultures. This plurality in attitudes can give rise to multiple and conflicting priorities and goals regarding the presence of carnivores in shared landscapes. For example, the international community might endorse policies promoting more carnivores in multi-use landscapes, whereas local



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Figure 1. Examples of Large Carnivore Species that Inhabit (either Persisting or Recovering) Multi-Use Landscapes outside Protected Areas. These examples are nonexhaustive but illustrate the fact that a range of carnivore species are currently sharing landscapes with humans around the world. Negative effects and conflicts associated with these carnivores vary greatly in each of these landscapes, but can sometimes be severe. The importance of shared landscapes for global carnivore recovery efforts necessitates a more holistic conceptualization of human–carnivore coexistence that can be operationalized on the ground. See the supplemental information online for references. Photos reproduced courtesy of Emmanuel Keller via Flickr/Creative Commons.

communities might not be willing to share their landscapes with carnivores because of the risks to human livelihood and safety. Failure to address the disparity in human norms, attitudes, and knowledge about carnivores among different human groups can undermine coexistence. For example, conflicts between stakeholder groups and reduced trust in the authorities in parts of Scandinavia are thought to be major causes of illegal killing of large carnivores [7]. One study in Sweden found that illegal killing of wolves (*Canis lupus*) accounted

for approximately half of the total mortality of the wolf population [8].

A variety of measures exist to reduce the impacts on humans of having large carnivores in shared landscapes, ranging from economic compensation and incentives, information campaigns, spatial zoning (e. g., habitat protection from human development), technical changes to livestock husbandry, the restoration of wild prey populations, and allowing limited hunting of large carnivores, among others. While

these measures can be useful, our concept of coexistence suggests that they should be supplemented with interventions that address the human and ethical facets more directly, such as efforts to engage diverse stakeholder groups, build trust and dialog between groups of humans with different viewpoints toward carnivores, or the adoption of novel decision-making structures that ensure participation and legitimacy. For example, participatory processes, characterized by bottom-up representation and

legitimization, have proven successful at negotiating outcomes that are viewed as acceptable, especially if some form of upward and downward accountability exists [9]. Such interventions have the potential to address issues of scale in governance. For example, overall goals of carnivore conservation in shared landscapes can be defined at a supranational or national scale, while local communities can adopt more specific, locally adapted policies and practices that are constrained by those broader-scale goals and limitations. In short, a wider array of interventions, such as, those mentioned above, can encourage coexistence by improving institutional fit; that is, the alignment of institutions and carnivore-occupied ecosystems, and between sets of stakeholders [10].

Coexistence through Co-Adaptation

Given the complex and dynamic nature of human–carnivore interactions, we contend that mutual adaptations between humans and carnivores in shared landscapes are crucial to achieving and maintaining coexistence. Instead of a purely evolution-based denotation, adaptation in this context means that humans and carnivores are able to change their behavior, learn from experience, and pursue their own interests with respect to each other. Humans and carnivores have adapted thus to each other for millennia; for example, carnivores feeding on domestic livestock or humans lethally removing carnivores to reduce risks. However, in terms of facilitating coexistence, we are concerned with mutual adaptations that result in minimal negative impacts of humans and carnivores on each other (carnivore impact on human livelihood and safety, and human impact on carnivore population persistence).

Recent studies have documented a surprising ability of large carnivores to adapt to humans. For example, cougars (*Puma concolor*) navigate through areas in

California with high human densities by using riparian woodlands [11]. Wild dogs (*Lycaon pictus*) living on community lands outside protected areas were found to maintain energy requirements by shifting their diet to smaller wild prey species instead of feeding on livestock [12]. Tigers spatially overlapped with large numbers of local humans collecting natural resources from forests inside and outside Chitwan National Park, Nepal [13]. Spatial overlap did not always lead to encounters between tigers and humans because the latter were most active during the day and tigers at night. This was also seen with the leopards (*Panthera pardus*) sharing space with humans in Maharashtra, India [14]. These examples are encouraging signs that large carnivores can adapt to humans on shared landscapes; however, more research is needed to assess how such adaptations affect large carnivore population viability as well as large carnivore regulation of prey, smaller carnivores, and ecosystems.

Although some large carnivore species can adapt to human-modified landscapes given sufficient prey and habitat, this capacity can increase the likelihood of negative encounters between humans and carnivores. Human response to negative encounters with large carnivores has often entailed the reduction of carnivore numbers through lethal methods, such as poisons. However, during humanity's long history of interacting with carnivores, we have also learned to adapt to carnivore presence, minimizing the need to reduce their population sizes. Examples of such human adaptation to carnivores include the use of livestock-guarding dogs, bomas, and nonlethal repellents (e.g., placing lights over livestock corrals). Other examples include avoiding potentially risky situations by understanding carnivore behavior (e.g., not jogging with a dog in cougar territory), reducing the amount of human-produced food accessible to carnivores (e.g., through bear-proof trash bins or by disposing of livestock

carcasses away from human settlements), or having adults herd livestock rather than children. An unwillingness (e.g., due to risk intolerance) or inability (e.g., due to lack of resources or knowledge) of individuals to behaviorally adapt to the presence of carnivores on shared landscapes are major challenges to coexistence, because not doing so is more likely to aggravate conflict. Therefore, overcoming these hurdles might rely on local community leaders to endorse behavioral adaptations or conservation organizations to implement various programs, such as social marketing campaigns. Moreover, institutions tasked with ensuring that the benefits (tangible and intangible) of large carnivores are available to current and future citizens can incentivize (e.g., performance payments) and regulate (e.g., enforcing societal mandates) human adaptations to large carnivores.

Concluding Remarks

Many questions remain about how to evaluate and operationalize coexistence. For example, what spatial scale is most relevant (e.g., supranational, national, or subnational) for different contexts and in which cases is coexistence more strongly related to the behaviors and habitat conditions of large carnivores or to governance institutions and human risk tolerances? The concept of coexistence presented here can be a starting point from which to advance both the interdisciplinary theory and practice of coexistence, which is increasingly urgent in an ever more human-dominated world. First steps should comprise studies from a range of cultural and/or institutional settings, and from a broad range of species other than carnivores, such as wild herbivores, to identify factors promoting, and inhibiting, sustainable interactions between humans and wildlife in general. Insights from such studies can help reconcile debates about wildlife conservation in shared landscapes and advance broader discourses in conservation, such as those related to rewilding, novel ecosystems, and land-sharing versus land-sparing.

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Science & Society Coexistence with Large Carnivores Informed by Community Ecology

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Conserving predators on an increasingly crowded planet brings very difficult challenges. Here, we argue that community ecology theory can help conserve these species in human-dominated landscapes. Letting humans and predators share the same landscapes is similar to maintaining a community of predatory species, one of which is humans.

Biodiversity is facing a major crisis and conservation efforts are failing to reverse the 6th mass extinction caused by the increasingly destructive impact of humans on the biosphere [1]. Species such as large-bodied predators at the tops of food chains bring additional conservation challenges, raising the question of whether these species will survive the 21st century [2]. Large carnivores have particular ecological characteristics, such as low densities, large home ranges, or limited reproductive potential, that require their conservation to be planned accordingly at a landscape level [3]. In addition, large carnivores frequently enter into conflict with humans by competing for game, predating livestock and pets, or threatening public safety. As a result, due mainly to direct persecution and habitat loss, most large carnivores are experiencing a dramatic decline globally in their populations and ranges [2]. Many large carnivore species are at risk of extinction [2] and arguably the most charismatic of all large carnivores, the lion (*Panthera leo*), is now

extinct in most parts of Africa and is threatened in its remaining strongholds [4]. Still, concurrent with this global decline, one continent is seeing an unexpected large-scale recovery of its previously lost large carnivore populations. Despite being densely populated (ca. 100 inhabitants/km²) and having few, if any, areas free from human activities, Europe today hosts growing populations of bears (*Ursus arctos*), lynx (*Lynx lynx*), and wolves (*Canis lupus*), accounting for more than 40 000 individuals altogether [5]. Interestingly, most European countries, despite being culturally, economically, and politically diverse, share a common approach to large carnivore conservation: they allow large carnivores and humans to share the same landscape, or at least do not actively prevent them from doing so on a large scale.

We term this conservation approach 'coexistence' and define it as the lasting persistence of self-sustaining large carnivore populations in human-dominated landscapes. In such landscapes, we propose that coexistence is similar to the maintenance of a community of predatory species comprising large carnivores and humans. Ecologists have shown that communities of competing species will converge to single-species communities when one species displays strong competitive abilities and has limited niche differentiation from the other species [6]. By contrast, species can coexist when they show moderate competitive abilities and large niche differentiation. We argue that conserving large carnivores in the Anthropocene is a question relevant for community ecology: can a hyperpredator (humans) [7] avoid displacing other competing predatory species (large carnivores) by becoming less competitive and adopting higher niche differentiation?

In the context of coexistence, the competitive ability of humans refers to the over-exploitation of large carnivores and destruction of their habitats. Human