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Editorial

Wolves across borders

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Introduction

The ongoing recovery of wolf populations in parts of Eurasia and North America represents one of the most controversial issues in wildlife ecology, management, and conservation. The grey wolf *Canis lupus* once ranged across most of the Northern Hemisphere, but due to human persecution wolf populations began to decline and their range contracted around the late 19th and early 20th centuries (Ripple et al. 2014). However, changes in human attitudes and the subsequent implementation of effective legislation have facilitated the recovery of wolf populations across some of their historic range (Ripple et al. 2014). This has been driven by both natural recolonization in parts of Europe and North America (Chapron et al. 2014) as well as active reintroductions in North America, such as in Yellowstone National Park (Smith and Bangs 2009) and Colorado (https://cpw.state.co.us/bringing-wolves-back-colorado). Expanding and increasing wolf populations attracted broad interest in wolf ecology, while growing public concerns and human–wildlife conflicts prompted the need for new and adaptive management approaches.

Wolves have always been at the centre of human–wildlife conflict, with their management often entangled in deep social and political divisions. Compounding this complexity, wolf populations span a wide range of countries, each with distinct ecosystems, cultures, government systems, and economic priorities. This is particularly true in Eurasia, where wolves cross between the borders of over 50 different countries. Differences in societal values, policy objectives, monitoring strategies, and knowledge of local wolf populations make transboundary management complex. The challenges posed by the large spatial extents over which wolves roam, and their implications for management, were the main themes of the 'Wolves Across Borders International Conference on Wolf Ecology and Management'

*Guest Editors for the 'Wolves Across Borders' special issue led by AT, all others listed in alphabetical order.

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(Wolves across Borders) held in Stockholm, Sweden, in May 2023. The goal of 'Wolves Across Borders' was to facilitate open conversation and knowledge exchange between nations that support wolf populations and the researchers, managers, non-profit organisations, and stakeholders that work with wolf ecology, management, and conflict resolution.

This special issue compiles papers related to the core topics represented at the 'Wolves Across Borders' conference, offering a diverse range of professional perspectives on wolves from various disciplinary and cultural viewpoints. The contributions to this special issue reflect current themes in wolf research, covering topics from wolf ecology and behaviour to the human dimensions of wolf management and governance. We hope the insights from 'Wolves Across Borders' will contribute to the development of more evidence-based, adaptive, and integrative wolf management and conservation policies worldwide.

Intrinsic versus extrinsic population regulation: a longstanding debate

Nothing fosters scientific understanding quite like alternative hypotheses, especially when presented by leading experts in the field. As the renowned physicist Richard Feynman stated, '*The first principle is that you must not fool yourself – and you are the easiest person to fool*'. With this in mind, we open this special issue with a longstanding scientific debate that was highlighted at the 'Wolves Across Borders' conference: are wolf populations regulated by intrinsic or extrinsic factors? Here, researchers David Mech and Douglas Smith came together to discuss whether intrinsic or extrinsic mechanisms play a greater role in shaping wolf populations worldwide. On stage, Mech presented the viewpoint most common in the current scientific literature. In short, Mech proposed that wolf populations are predominantly regulated by access to prey biomass, an extrinsic factor, but that density is limited via behavioural mechanisms such as dispersal and intraspecific strife. Smith countered that wolf populations are likely regulated by both extrinsic and intrinsic factors, noting that wolf life history traits meet all the characteristics required for intrinsic population control, as hypothesized by Wolff (1997). Specifically, intrinsically regulated species are expected to have non-mobile young and a protected rearing space, males often remain in the social group, and they display territoriality, infanticide, delayed juvenile emigration, and reproductive suppression to avoid inbreeding (Wolff 1997). Smith further suggested that under 'natural conditions', i.e., in the absence of human-driven landscape change and predator and prey population regulation, wolf populations would likely be more regulated by such intrinsic social factors.

In the special issue follow-up papers, Mech (2024) contended that while wolf density may be self-limiting, wolf populations are not. In other words, wolf populations are extrinsically limited by prey biomass, but that wolf density will be limited by behavioural factors such as dispersal and range expansion that keep wolf densities at a level that prey biomass can support. Smith and Cassidy (2024) examined the history of research surrounding this long-standing debate and presented the perspective that wolf population regulation likely results from a dynamic interplay between both intrinsic and extrinsic factors. Importantly, they suggest that the best way to study this interplay is longitudinally by monitoring one population through time.

Wolf avoidance of humans

Papers in the next section of the special issue examined wolf behaviour and movement in human-dominated landscapes in various parts of Europe. Sunde et al. (2024) reported that wolves in densely populated Denmark, where spatial opportunities to avoid humans are limited, invest heavily in temporal avoidance of humans and hence nocturnality. In a study from Turkey, however, Blount et al. (2024) reported that wolves do not necessarily increase their nocturnality or change their home range sizes in response to seasonal changes in human pressure, indicating that human avoidance is not the only driver of temporal and spatial behaviours in wolves. As wolves can be sensitive to human disturbance, researchers should seek to understand how their fieldwork and handling methods might affect their study populations. A study by Gable et al. (2024) found that brief visits to wolf dens, to handle pups for research purposes, did not have measurable effects on recruitment and pack size. Future research should further investigate the potential short- and long-term impacts of researchers' field activities on wolf behaviour and fitness.

Wolf populations in human landscapes

In major parts of Eurasia, wolves occur in landscapes heavily dominated by humans. Vorel et al. (2024) looked into the spatial ecology of re-colonising wolf populations across central Europe, pointing out that although wolves are spreading rapidly, their permanent recovery remains uncertain because of conflicts with the human population. Therefore, areas of high habitat quality will remain essential for wolf recovery in central Europe. As reported by Planillo et al. (2024) using demographic data from Germany, the reproductive output of wolves is determined by habitat suitability and the experience of females, suggesting that conservation efforts should focus on high-quality areas as sources for sustaining the population. This is further supported by Hulva et al. (2024) who found genetic admixture between formerly isolated central European and Alpine wolf populations, driven by secondary contact and interbreeding, with protected areas playing a key role in their recolonization and genetic diversity across Europe. Changes in the political landscape, however, may threaten the connectivity of wolf populations. Nowak et al. (2024a) highlighted how the recent construction of a border fence between Poland, Russia, and Lithuania may isolate wolves from the broader Baltic population, potentially threatening their long-term viability. Miltz et al. (2024) explored how future wind power developments in Scandinavia could impact territorial wolves. They found that proximity to proposed turbine sites varied by season and social status; during the denning period breeding wolves were less likely to overlap

with proposed turbines than non-breeders, probably because breeders restricted their movements to the den site, while the opposite was the case in winter, when breeders tended to use larger parts of their home range than did non-breeders. Unlike *Canis lupus*, other species of wolves may be less adaptable to human landscapes: Marino et al. (2024) reported that the Ethiopian wolf *C. simensis* is restricted to six isolated populations within fragmented Afroalpine habitats and faces significant extinction risks from habitat loss due to encroaching subsistence agriculture, disease, and human-related mortality. To promote their long-term survival, the authors recommended implementing translocations to facilitate dispersal between these isolated populations.

Wolf feeding habits

Overall, wolves rely mainly on large ungulates. This is also true in human-dominated landscapes, where the consumption of domestic over wild ungulates can sometimes be related to the availability of wild ungulates. For example, in a study based on scat analysis in Poland, Nowak et al. (2024b) found that in a large pine monoculture characterized by a diverse wild ungulate community, roe deer *Capreolus capreolus* made up almost half of the wolf diet, followed by red deer *Cervus elaphus* and wild boar *Sus scrofa*, while livestock was not recorded in the samples. Reyes Díaz et al. (2024), also analysing scat content, reported that reintroduced Mexican wolves primarily fed on the large prey available in the reintroduction area, including livestock, and that the presence of deer and diversionary feeding reduced the likelihood of cattle depredation. In a camera trap study, Wikenros et al. (2024a) found that wolves in Scandinavia made limited use of moose *Alces alces* viscera left over from annual hunts, preferring predation to scavenging, while smaller carnivores such as red foxes *Vulpes vulpes* and pine martens *Martes martes* were more frequent scavengers benefiting from human-subsidised food resources.

Effects of wolves and wolf predation

Wolves can depredate domestic livestock and affect economically and culturally important big game species which can exacerbate conflict with farming and hunting communities. Understanding the effects of wolf predation on both wild and domestic prey is therefore essential for informed management practices. Smit and Kuijper (2024) documented the first observed wolf–cattle interactions in the Netherlands, showing that free-ranging Galloway cattle exhibited anti-predator behaviours such as grouping, vigilance, and even chasing wolves without any cattle losses. These two documented interactions suggest that some free-ranging cattle can quickly develop protective behaviours against wolves, offering important insights for conservation and grazing management. Ausilio et al. (2023) investigated the major mortality factors of moose calves in Scandinavia which included large carnivore predation, hunter harvest, and climate-related factors. They found that the combination of wolf presence and deep snow cover, as well as areas of high human hunting risk and the migratory behaviour of female moose, were linked to higher moose calf mortality. These factors highlight the need for better understanding of the mechanisms driving moose populations in light of expanding large carnivore populations and climate change. In a related study, Wikenros et al. (2024b) examined factors influencing hunter harvest of moose in Sweden and Norway, finding that higher densities of wolves and brown bears *Ursus arctos* negatively impacted moose harvest, while a high density of roe deer as an alternative prey had positive effects on moose harvest rates. Differences in moose management between these two countries highlighted the need to enhance understanding and management of ungulate populations shared across bordering countries.

Studies on wolves have been instrumental in clarifying the role of apex predators in terrestrial ecosystems, increasing our understanding of trophic cascades and their implications for biodiversity and ecosystem functioning (Ripple and Beschta 2012). However, the cascading effects of large carnivores have been primarily studied in low-human-impact regions. Gerber et al. (2024) reviewed the evidence for non-consumptive effects of wolves on wild ungulates and subsequent cascading effects on vegetation in European landscapes. They emphasize the need to include human factors in such studies as well as in management approaches to better understand how non-consumptive predator effects could help restore ecosystem complexity. Root-Gutteridge et al. (2024) investigated the acoustic interactions among three sympatric canids – wolves, coyotes *Canis latrans*, and dogs *Canis familiaris* – revealing that rather than silencing each other, these species actively respond to one another's vocalizations. They suggest that interspecific communication and risk perception among canids are more nuanced than previously thought.

Human dimensions and wolf management

The success of wolf management depends largely on how people perceive and interact with wolves. Different groups – such as farmers, hunters, conservationists, and local residents – can have varied attitudes towards wolves. For example, farmers may be concerned about livestock losses, hunters about competition for game, and conservationists about maintaining wolves as a keystone species, while local residents may fear for their safety. Therefore, understanding the human side of wolf conflict is essential for effective management. As Aldo Leopold (1966) remarked: '*The problem of game management is not how we shall handle the deer – the real problem is one of human management. Wildlife management is comparatively easy; human management difficult*'.

Therefore, the papers in the last section of this special issue might be the most relevant for advancing adaptive wolf management. They report on various aspects of the human dimensions of wolf management in case studies from across Europe. In Switzerland, Cracco et al. (2024) compared multiple social research approaches to explore public perceptions and values surrounding wolves, revealing that the depictions and prominence of wolves varied significantly among methods. This suggests a need for diverse social science methodological approaches to better understand community sentiments in wolf management and conservation efforts. Ferrão da Costa et al. (2024) evaluated wolf

monitoring programmes in Portugal to assess their effectiveness in identifying the potential impacts of human infrastructure developments on the endangered wolf population within the framework of 'Environmental Impact Assessments'. They identified a disconnection between the stated objectives and the outcomes of monitoring programmes, along with a reliance on possibly misleading relative indices and summary statistics. To improve monitoring accuracy and effectiveness, they recommended implementing standardized protocols and utilizing statistical methods accounting for imperfect detection. The study by Grossman and Patko (2024) combined the 'Conflict Intervention Triangle Model' and the 'Logical Framework Approach' to evaluate outcomes of the LIFE EuroLargeCarnivores project, which focuses on human–wildlife conflict mitigation across 14 European countries. The results reveal positive developments in stakeholder perceptions, with significant differences in levels of confidence among nature conservationists, hunters, and livestock raisers, highlighting the importance of rigorous long-term evaluations to maximize conflict resolution outcomes and ensure efficient resource use in wildlife conservation efforts. Finally, Grente et al. (2024) evaluated the efficiency of wolf culling on livestock depredation, focusing on the Western Alps as a case study. Findings from an integrated individual-based model suggest that culling can maintain low wolf population sizes and low depredation risk, but may also reduce wolf dispersal by accelerating pack settlement, indicating that the timing and selectivity of culling significantly affected population resilience.

Discussion

The diverse perspectives and research presented in this special issue reflect the complexity of wolf ecology and management, particularly in human-dominated landscapes. The ongoing debate regarding the regulation of wolf populations – whether driven by intrinsic or extrinsic factors – highlights the need for a multi-faceted understanding of these dynamics. Mech (2024) contends that wolf populations are limited by extrinsic rather than intrinsic factors, and highlights the importance for management in settling this long-standing scientific debate. Smith and Cassidy (2024) emphasized the importance of considering both factors, suggesting that successful management strategies must account for the interplay between ecological conditions and behavioural responses.

The studies on wolf avoidance of humans underscore the adaptability of wolves in navigating human impacts, as seen in Blount et al. (2024) and Sunde et al. (2024), indicating that the effects of human presence are nuanced and context-dependent. This adaptability raises important questions about the management of wolf populations in human landscapes, particularly in areas like central Europe where habitat quality remains critical for recovery (Planillo et al. 2024, Vorel et al. 2024). Furthermore, the findings regarding wolf feeding habits and predation effects illustrate the broader ecological implications of wolves as apex predators. The studies on cascading effects of wolf presence on ungulate populations and vegetation dynamics emphasize the need to include human factors into such studies as well as integrate ecological knowledge into management practices, particularly in light of anthropogenic changes in land use (Gerber et al. 2024).

The human dimensions of wolf management are equally critical, as public perceptions and stakeholder attitudes significantly influence management outcomes. As highlighted by Cracco et al. (2024) and Ferrão da Costa et al. (2024), employing diverse methodologies to gauge community sentiments is essential for crafting effective management strategies. The emphasis on standardized monitoring protocols and rigorous evaluations, as advocated by several studies, is crucial for enhancing the effectiveness of wolf management initiatives.

In conclusion, this special issue underscores the importance of interdisciplinary approaches that integrate ecological science, social dynamics, and management practices. Effective wolf management requires not only a solid understanding of the ecological aspects but also a commitment to engaging with human communities coexisting with wolves and addressing their concerns. Future research should continue to explore the intricate relationships between wolves and their environments, while fostering collaboration among stakeholders to ensure the long-term viability of wolf populations across the Northern Hemisphere.

We hope that readers find this special issue of *Wildlife Biology* to be as stimulating and thought-provoking as we do.

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