Large Carnivore Ecology and Conservation in the High Mountains of Central Asia

Shannon Matthew Kachel

A dissertation
submitted in partial fulfillment of the
requirements for the degree of

Doctor of Philosophy

University of Washington
2021

Reading Committee:
Aaron Wirsing, Chair
Beth Gardner
Thomas McCarthy

Program Authorized to Offer Degree
School of Environmental and Forest Science

University of Washington

Abstract

Large Carnivore Ecology and Conservation in the High Mountains of Central Asia

Shannon Matthew Kachel

Chair of the Supervisory Committee
Aaron J. Wirsing
School of Environmental and Forest Sciences

Predators shape their ecosystems through myriad interactions with prey, other predators, and humans. However, the effects of these interactions may be contingent on multiple contextual factors, hindering prediction in any given community and impeding a general understanding of the ecological effects of predators. Despite their prominence as conservation flagship in the mountains of Central Asia, even basic aspects of snow leopard (*Panthera uncia*) ecology remain underexplored and poorly understood. The ecology of wolves (*Canis lupus*), sympatric with snow leopards throughout that species' range, has been even more neglected in the region, notwithstanding the significant impact of livestock depredation on pastoralist communities. This dissertation examines the interactions underlying the coexistence of wolves and snow leopards, including those with humans and their joint effects on prey, with the broader goal of improving our understanding of the context-dependence of the non-consumptive effects (NCEs) of predators. In Chapter 2, I explore the patterns of spatial, temporal, and dietary niche overlap between wolves and snow leopards in the Eastern Pamir Mountains of Tajikistan. I show that in light of dietary and temporal overlap, the two predators' coexistence may depend on strong spatial partitioning. In Chapter 3, I explore the consequences of this spatial partitioning by investigating how shared prey with distinct escape tactics, ibex (*Capra sibirica*) and argali (*Ovis ammon*), navigate the tradeoffs posed by the two predators in the Central Tien Shan Mountains of Kyrgyzstan. Each ungulate responded to each predator in a manner that was predictable based on the compatibility of their respective evasion and hunting-mode traits, suggesting that non-consumptive predator effects depend not on predator hunting mode or prey escape tactics, but rather on their interaction. Furthermore, short-term predation risk may upend each ungulates' long-term risk avoidance strategy, suggesting that emergent effects of multiple predators may have important consequences in this system. In Chapter 4, I develop a novel approach to investigate large-scale patterns of livestock depredation risk and occurrence for wolves and snow leopards, but also lynx (*Lynx lynx*) and bears (*Ursus arctos*), in the Western Pamirs of Tajikistan. Livestock depredation was commonplace, with most communities exposed to multiple predators, highlighting that conservation efforts meant to reduce conflict between people and carnivores should aim to reduce depredation as it is experienced by human communities – a threat from the entire carnivore guild. Overall, my results suggest that single-species approaches to conservation in the mountains of Central Asia may be inadequate for ecosystems *and* people. This dissertation advances the cause of conservation in Central Asia by providing an empirical perspective on how snow leopards and wolves coexist and shape their ecosystems, and by providing practical insight into the challenge of livestock depredation and conflict, a primary threat to wolves and snow leopards in the region. By showing that the non-consumptive effects of predators cannot be predicted based solely on prey escape tactics or predator hunting mode alone, it also contributes to a more comprehensive understanding of the role of predators in shaping ecosystems.

ACKNOWLEDGEMENTS

The research described in this dissertation relied on the collaborative efforts of many dozens of individuals and communities, to whom I am indebted. Foremost among these are the people of Uch-Koshkoon and Ak-Shyyrak in Kyrgyzstan, and of the Gorno-Badakshan Autonomous Oblast in Tajikistan, who graciously shared their stories, hospitality, and knowledge.

I am profoundly grateful to Drs. Thomas McCarthy and Aaron Wirsing who together took a bold chance on my risky – or perhaps more accurately, foolhardy – ambitions. Your support, confidence, and expertise, made this endeavor possible, and helped me see it to completion in the face of serial setbacks and challenges. My committee members, Drs. Beth Gardner, Brian Kertson, and Tim Essington provided invaluable insight, perspective, and mentorship that I'm lucky to have received. So too, Dr. Byron Weckworth, an honorary committee member to be sure, provided cherished mentorship and friendship in equal measure. Likewise, my fellow students in the Predator Ecology Lab and SEFS, and particularly C. Shores, L. Satterfield, J. Smith, C. Robins, L. van Eeden, A. Craig, V. Buschman, T. Ganz, and M. Parsons all contributed in key ways to my intellectual and personal development, in many cases simply by providing a solid belay, both literally and metaphorically.

Six individuals are deserving of special recognition here. Rana Bayrakcısmith, Khalil Karimov, Zairbek Kubanychbekov, Rahim Kulenbekov, Tanya Rosen, and Qobiljon Shokirov each made singularly invaluable contributions to this work and provided welcome companionship in the rarefied mountain air. I count myself fortunate to call you friends and colleagues. You give me optimism for the future of conservation in Central Asia and beyond.

The following individuals all contributed to field data collection efforts: S. Abdodova, M. Alidodov, K. Anderson, S. Aqdodova, J. Bahriev, O. Barker, R. Bayrakcismith, Dr. R. Berlinski, Dr. K. Castle, Dr. D. Cooper, S. Cross, D. Dahlgren,K. Davlatmamadov, D. Fraleigh, Q. Gadoliev, Dr. T. Georoff, Dr. M. Gilbert, J. Gulmamadov, T. Humphries, K. Karimov, S. Kennerknecht, P. Kortsalo, M. Khudoberdieva, Z. Kubanychbekov, R. Kulenbekov, C. Meyer, A. Nazrishoeva, Dr. J. Ochsenreiter, N. Oshurmamadov, Dr. S. Ostrowski, T. Rosen, Dr. Q. Shokirov, Dr. A. Tanweer, K. Toshbekova, Dr. B. Weckworth, and the rangers and staff of Zorkul Zapovednik in Tajikistan and Sarychat-Ertash Zapovednik in Kyrgyzstan. It's no exaggeration to say that the rangers of Sarychat – Omurbek, Tesha, Askat, Urmat, Mishka, Kamchibek, Kolya, Temurlan, Joki, and Ulan – kept both me and this project alive. Thank you all. Спасибо вам всем болшое. Ташаккури зиёд ба ҳама. Баарыңарга чоң рахмат.

I am deeply grateful for the material and financial support of Panthera, the National Science Foundation (DEG-125608), and Drs. Benjamin and Margaret Hall via the Hall Conservation Genetics Research Fund. I am intimidated the vast array of practical, bureaucratic, and logistical considerations underlying this work, and grateful to those individuals and organizations who helped navigate those hurdles, namely R. Bayrakcismith, Z. Kubanychbekov, K. Karimov, and T. Rosen, as well as M. Musaev at Sarychat-Ertash Zapovednik in Kyrgyzstan, R. Sidle and D. Butabekov at the MSRI/UCA Tajikistan, K. Sharma and K. Jumabay-uulu at SLT/SLFK, and A. Davletbakov at the National Academy of Sciences of the Kyrgyz Republic.

Lastly, I would never have completed this project with the love, support, perspective, and inspiration of my family, and in particular, of my partner Anissa, and our daughter Juniper, for whom I am most grateful of all.

CONTENTS

CHAPTER 1

INTRODUCTION

Predators shape their ecosystems not only through their consumptive effects on prey, but also through non-consumptive effects (NCEs) on prey traits – including behavior (Charnov et al. 1976, Lima and Dill 1990, Lima 1998). In both cases, the consequences can propagate throughout food webs to indirectly affect other species in the community. Beyond the now familiar example of trophic cascades, in which predators induce changes in prey density, foraging intensity and/or habitat use that are reflected in subsequent changes in plant communities (Ripple and Beschta 2004, Hebblewhite et al. 2005), predators can subsidize scavenger communities via carrion provisioning (Wilmers et al. 2003), alter the distribution and cycling of nutrients (Schmitz et al. 2010), reduce disease prevalence in prey populations (Packer et al. 2003), and suppress mesopredator populations (Prugh et al. 2009). Where multiple predators occur together, as is typical of many natural ecosystems, non-linear multiple predator effects (MPEs) may emerge as prey responding to one predator inadvertently modify their exposure to others (Sih et al. 1998). These same prey responses may serve to mediate indirect interactions between predators themselves: predator facilitation if prey incur additional risk exposure, or trait-mediated exploitation competition if prey responses reduce their exposure. Yet, despite the conservation and management implications of MPEs and indirect predator interactions in any ecosystem, NCEs from multiple predators have received limited attention in large terrestrial vertebrate systems (*sensu* Montgomery et al. 2019).

Despite considerable conservation investment and attention, snow leopards (*Panthera uncia*) remain poorly understood (McCarthy et al. 2017). A top predator inhabiting the high mountains of Asia – the highest mountains on Earth – the species' naturally low densities, cryptic habits, and affinity for rugged, logistically challenging habitats present considerable obstacles to scientific inquiry. In the face of evident anthropogenic threats, but persistent uncertainty and disagreement regarding the snow leopard's overall conservation status (e.g., Ale and Mishra 2018, Suryawanshi et al. 2019), most ecological research on the species has been devoted to counting and surveillance monitoring (Robinson and Weckworth 2016, Sharma and Singh 2020). Thus, while it is now clear that there are likely more snow leopards in the world than was previously thought (Mallon and Jackson 2017), neither the ecological mechanisms that sustain those animals, nor their impacts on ecosystems, have been well described. Yet, as with other large terrestrial carnivores, those impacts may be substantial.

Snow leopards, however, are not the only large carnivores in high mountains of Asia – throughout their range, snow leopards are sympatric with wolves (*Canis lupus*). With the help of conservation efforts motivated in part by the supposed ecological benefits the species may provide, wolves in Europe and North America are recovering from historic extirpations (Ripple et al. 2014). By contrast, wolves were never eradicated from Central Asia, and have been largely overlooked by scientific and conservation efforts in the region (Werhahn et al. 2019). Indeed, it has only recently become clear that wolves on the Tibetan Plateau and in the Himalayas represent a unique and ancient genetic lineage, and likely a unique species (Werhahn et al. 2020). High elevation wolves outside of these ranges, in the Pamirs and Tien Shan Mountains of Central Asia for example, are probably correctly classified as grey wolves, but introgression from Himalayan wolves has left these populations with genetic adaptations to their low-oxygen environments not shared by their lowland counterparts.

Like many large carnivores, wolves and snow leopards in the high mountain ecosystems of Asia are threatened by retaliatory killing and the loss of wild ungulate prey (McCarthy et al. 2017, Werhahn et al. 2019). Wolves, posing a perceived danger to pastoral livelihoods and human lives, are further subject to organized culling efforts (Sputnik News, 2020) and bounty programs (Goldthorpe 2016). Accordingly, investigation of wolf and snow leopard ecology in the region has predominantly focused on just two phenomena – food habits (e.g., Lyngdoh et al. 2014, Johansson et al. 2015, Tiralla et al. 2021) and human-wildlife conflict (e.g., Suryawanshi et al. 2017, Kusi et al. 2020). Beyond its relevance to conservation, inquiry into predation in a strict sense – killing and consuming prey – is clearly warranted: predation is the fundamental interaction by which predators shape their ecosystems. And yet, conservation of these two apex predators may ultimately require a more comprehensive understanding of their ecology.

The competitive exclusion principle predicts that two coexisting species competing for the same resources or niche (Hutchinson 1957) must partition the niche space available to them over the long term (Gause 1934). Without this partitioning, the competitively dominant species will drive the subordinate species to extinction. Like most terrestrial large carnivores, snow leopards and wolves prey primarily on large ungulate prey, resulting in substantial dietary overlap in low-diversity, low-productivity mountain ecosystems (Jumabay-Uulu et al. 2013, Bocci et al. 2017, Chetri et al. 2017, Werhahn et al. 2019). If prey resource limitation arises (Wiens 1993), exploitation competition between snow leopards and other predators may thus become a critical concern for their conservation. Indeed, in the Himalayas, high dietary overlap between snow leopards and common leopards (*Panthera pardus*) has been interpreted as evidence that snow leopards will be negatively impacted by exploitation and interference competition in the coming decades, as presumably dominant common leopards are expected to keep pace with rising tree lines encroaching upon snow leopard habitat (Lovari et al. 2013). Similarly, dietary overlap between wolves and snow leopards has been cited as evidence that climate change and declining prey populations will intensify competition between the two, to the detriment of snow leopards (Bocci et al. 2017). These interpretations may be oversimplified, however.

Diet is only one of the dimensions that shape a species' niche (Schoener 1974). If prey availability is limiting, high dietary overlap may indicate strong numerical and/or behavioral exploitation competition, and potentially interference competition as well, but if not, it may simply reflect an abundance of prey (Wiens 1993). On the other hand, high dietary overlap among predators that partition space – but not time (Kohl et al. 2019) – is predicted under predator facilitation (Charnov et al. 1976, Kotler et al. 1992), which can simultaneously drive emergent risk-enhancing MPEs on prey themselves, whereby the numerical impacts of multiple predators hunting the same prey exceed the sum of their individual effects (Sih et al. 1998). Patterns of niche overlap across multiple dimensions may thus be predictive of MPEs in ecosystems and of indirect interactions between predators (Schmitz et al. 2017). The conservation implications, for predators and for prey, of these various scenarios are altogether divergent. To more fully anticipate the potential impacts of sympatric large carnivores on one another, and to inform conservation accordingly, there is a need to consider and describe niche differentiation not only in dietary dimensions, but in time and space as well.

Contrasting habitat use between snow leopards and other sympatric carnivores is expected as an outcome of niche partitioning to reduce competition, but also as a result of predators selecting spaces that maximize their hunting success (Jumabay-uulu et al. 2013), which is only partially determined by prey abundance (Hopcraft et al. 2005, Balme et al. 2007, Davidson et al. 2012). The broken, rugged terrain used by snow leopards almost certainly facilitates its stalking mode of hunting by providing cover that is otherwise scarce in arid mountain landscapes (Jackson and Hunter 1996). Likewise, the gentle, rolling terrain more typically used by wolves (Viripaev and Vorobiev 1983) may be critical to the efficacy of its cursorial, chasing hunting mode (Jumabay-uulu et al. 2013). By implication, the two predators pose spatially contrasting risks to their prey; a contrast theory predicts should give rise to emergent effects on predators and prey alike (Sih et al. 1998). Terrestrial and aquatic mesocosm experiments across diverse taxa support the theory of multiple predator effects and indirect predator interactions mediated by prey behavior (Losey and Denno 1998, Eklöv and VanKooten 2001, Kotler et al. 2004), as do some empirical investigations of large terrestrial vertebrate systems (Leblond et al. 2016, Mumma et al. 2017, Gehr et al. 2018). Yet, others highlight how prey may use contrasting periods of inactivity among temporally contrasting predators to break the apparent tradeoff of spatially contrasting risk (Lone et al. 2017, Kohl et al. 2019). Broadly, empirical investigations of how prey respond to predation risk from multiple predators remain limited, impeding a comprehensive understanding of the factors that influence potential indirect NCEs (Montgomery et al. 2019, Wirsing et al. 2021).

Prey spatial responses to predation risk are a key mechanism by which NCEs propagate through ecosystems (Lima and Dill 1990, Schmitz et al. 1997, Preisser et al. 2005, Wirsing et al. 2010). Predation risk can be decomposed into two basic components, both of which may be perceptible to prey: the probability of an encounter between predator and prey, and the conditional probability of death given an encounter (Lima and Dill 1990, Hebblewhite et al. 2005). An immediate implication of this decomposition is that prey may maximize their fitness by using spaces where encounters with predators are frequent but their intrinsic lethality is low, if encounter risk can be decoupled from kill risk (Lima 1992). For example, prey species for tiger sharks (*Galeocerdo cuvier*; a cursorial predator) proactively and divergently shift their habitat use patterns when sharks are present: prey with agility- and speed-based escape tactics select habitats that favor the efficacy of those tactics despite higher encounter rates, whereas prey with evasion tactics that do not effectively decouple encounter and kill risk instead select habitats that minimize encounter rates altogether (Heithaus et al. 2009). By implication, prey responses to predation risk are contingent on their unique escape tactics (Wirsing et al. 2010).

Predator traits, i.e., hunting mode, present another potential source of contingency: stalking and ambush predators may exert stronger antipredator responses than cursorial predators (Preisser et al. 2007). For example, in a diverse African predator-prey community, small ungulates avoided all predators, while larger conspecific ungulates avoided areas used by stalking leopards and lions (*Panthera leo*), but not by cursorial cheetahs (*Acinonyx jubatus*) and wild dogs (*Lycaon pictus*) (Thaker et al. 2011). Unaddressed in this example, however, is the potential role of prey escape tactics. By contrast, Dröge et al. (2017) found that the strength of prey vigilance was best explained by the interaction of predator and prey identities, suggesting that neither predator hunting mode nor prey escape tactics alone are sufficient to understand prey responses and NCEs, but rather, it is their relative compatibility that matters. Although there is increasing recognition in the literature that the NCEs of predators on prey and ecosystems are contingent on properties of all three, empirical inquiry into how these various drivers of contingency interact is lacking, but it is nonetheless necessary to more fully understand the impact of predators in their ecosystems (Wirsing et al. 2021).

For the pastoralist human communities that share their mountain landscapes, livestock depredation is arguably the most important ecological impact of snow leopards and wolves. The cycle of human-carnivore conflict (HCC), in which carnivores kill livestock and humans retaliate by killing carnivores, threatens carnivore populations around the world, but also the health and livelihoods of human communities (Woodroffe et al. 2005). Indeed, pastoralist communities living alongside carnivores are often unable to absorb the stochastic shock of livestock depredation (Dickman et al. 2011).

Ultimately, the ecology of depredation is the ecology of predation in a human context. Just as wild prey species contend with potential tradeoffs in risk from multiple predators, pastoralists seeking to protect their herds and livelihoods from predators must also navigate potentially contrasting risks posed by different predators while simultaneously ensuring that their herds have access to adequate forage. But whereas wild prey may mediate indirect resource interactions between predators, humans can fundamentally restructure the mechanisms facilitating carnivore coexistence (Sévêque et al. 2020). For example, alternative domestic prey can expand available dietary niche space and reduce intraguild competition (Manlick and Pauli 2020) and human activity and habitat conversion can constrain the spatiotemporal habitat available to carnivores and presumably increase competition (e.g., Shores et al. 2019, Parsons et al. 2019). Human persecution can even mediate apparent competition between predators; for example, indiscriminate traps and poisons set for wolves have been repeatedly implicated in snow leopard poaching cases (Li and Lu 2014, Nowell et al. 2016).

As human populations and their effects on ecosystems grow, the viability of large carnivore populations may increasingly depend on human capacity for coexistence (Inskip and Zimmerman 2009). Building that capacity may depend, in part, on understanding the ecological and anthropogenic underpinnings of depredation – the primary trigger for conflict (Treves et al. 2011). The combination of interview-based wildlife detection data with occupancy modelling

(MacKenzie et al. 2002) may be an ideal approach to do just that (Karanth et al. 2009, Zeller et al. 2011). Extensions of the occupancy approach can potentially be leveraged to disentangle the probability of species occurrence from not only the imperfect probability of detecting species, but also the probability of falsely detecting species inherent to interview data (Royle et al. 2006, Petracca et al. 2017). Further extensions can enable joint estimation of multiple species' distributions (Zipkin et al. 2009), or of occurrence probability and livestock depredation risk (Nichols et al. 2007, Srivathsa et al. 2019). Given that livestock depredation is ultimately nothing more than predation with complicating human factors (Gervasi et al. 2020), decomposing depredation risk in this way into its constituent parts – the probability of site use and conditional probability of depredation (i.e., encounter and kill risk; Lima and Dill 1990) – may offer novel insights into the ecology of livestock depredation while providing a probabilistic approach to prioritizing conservation actions for snow leopards and other carnivores.

To help shed light on the ecology and conservation of wolves and snow leopards in the mountains of Central Asia, I first explored patterns of niche partitioning and overlap between the two predators, in time, space, and diet on the high plateau of the Eastern Pamir Mountains in Tajikistan (Chapter 2). I subsequently investigated how their shared ungulate prey in the Central Tien Shan Mountains of Kyrgyzstan – ibex (*Capra sibirica*) and argali (*Ovis ammon*) – respond at fine spatial scales to the contrasting risk posed by each predator in order to understand if and how prey might mediate indirect interactions between them, but also to explore how the interaction of predator hunting mode and prey escape tactics might contribute to a more comprehensive understanding of non-consumptive predator effects (Chapter 3). Lastly, I used interview-data in a novel extension of the occupancy framework to jointly large-scale patterns of habitat use and livestock depredation by wolves, snow leopards, lynx (*Lynx lynx*), and bears

(*Ursus arctos*) across the Western Pamirs, with an eye toward understanding the implications and challenges for pastoralists living with multiple predators (Chapter 4). The chapters that follow amount to the first in-depth description of the ecology, and ecological implications of, coexisting wolves and snow leopards. Taken together this work highlights multiple mechanisms of interaction between the two species and underscores the need for conservation approaches that recognize the significance of these interactions for wolves, snow leopards, humans, and their shared ecosystems.

Literature Cited

Ale, S.B. and Mishra, C. (2018). The snow leopard's questionable comeback. *Science*, 359, 1110–1110.

Balme, G., Hunter, L. and Slotow, R. (2007). Feeding habitat selection by hunting leopards Panthera pardus in a woodland savanna: prey catchability versus abundance. *Anim. Behav.*, 74, 589–598.

Bocci, A., Lovari, S., Khan, M.Z. and Mori, E. (2017). Sympatric snow leopards and Tibetan wolves: coexistence of large carnivores with human-driven potential competition. *Eur. J. Wildl. Res.*, 63, 92.

Charnov, E.L., Orians, G.H. and Hyatt, K. (1976). Ecological Implications of Resource Depression. *Am. Nat.*, 110, 247–259.

Chetri, M., Odden, M. and Wegge, P. (2017). Snow leopard and Himalayan wolf: food habits and prey selection in the Central Himalayas, Nepal. *PloS One*, 12, e0170549.

Davidson, Z., Valeix, M., Loveridge, A.J., Hunt, J.E., Johnson, P.J., Madzikanda, H., *et al.* (2012). Environmental determinants of habitat and kill site selection in a large carnivore: scale matters. *J. Mammal.*, 93, 677–685.

Dickman, A.J., Macdonald, E.A. and Macdonald, D.W. (2011). A review of financial instruments to pay for predator conservation and encourage human–carnivore coexistence. *Proc. Natl. Acad. Sci. U. S. A.*, 108, 13937–13944.

Dröge, E., Creel, S., Becker, M.S. and M'soka, J. (2017). Risky times and risky places interact to affect prey behaviour. *Nat. Ecol. Evol.*, 1, 1123–1128.

Eklöv, P. and VanKooten, T. (2001). Facilitation among piscivorous predators: effects of prey habitat use. *Ecology*, 82, 2486–2494.

Gause, G.F. (1934). Experimental Analysis of Vito Volterra's Mathematical Theory of the Struggle for Existence. *Science*, 79, 16–17.

Gehr, B., Hofer, E.J., Pewsner, M., Ryser, A., Vimercati, E., Vogt, K., *et al.* (2018). Hunting-mediated predator facilitation and superadditive mortality in a European ungulate. *Ecol. Evol.*, 8, 109–119.

Gervasi, V., Linnell, J.D.C., Berce, T., Boitani, L., Cerne, R., Cretois, B., *et al.* (2020). Ecological and anthropogenic drivers of large carnivore depredation on sheep in Europe. *bioRxiv*, 2020.04.14.041160.

Goldthorpe, G. (2016). *The wolf in Eurasia: a regional approach to the conservation and management of a top predator in Central Asia and the South Caucusus* (Technical Report). Flora and Fauna International.

Hebblewhite, M., White, C.A., Nietvelt, C.G., McKenzie, J.A., Hurd, T.E., Fryxell, J.M., *et al.* (2005). Human Activity Mediates a Trophic Cascade Caused by Wolves. *Ecology*, 86, 2135–2144.

Heithaus, M.R., Wirsing, A.J., Burkholder, D., Thomson, J. and Dill, L.M. (2009). Towards a predictive framework for predator risk effects: the interaction of landscape features and prey escape tactics. *J. Anim. Ecol.*, 78, 556–562.

Hopcraft, J.G.C., Sinclair, A.R.E. and Packer, C. (2005). Planning for success: Serengeti lions seek prey accessibility rather than abundance: Prey accessibility in Serengeti lions. *J. Anim. Ecol.*, 74, 559–566.

Hutchinson, G.E. (1957). Concluding remarks - Population studies: Animal ecology and demography. *Cold Spring Harb. Symp. Quant. Biol.*, 22, 415–427.

Inskip, C. and Zimmermann, A. (2009). Human-felid conflict: a review of patterns and priorities worldwide. *Oryx*, 43, 18–34.

Jackson, R. and Hunter, D.O. (1996). *Snow leopard survey and conservation handbook*. Second Edition. International Snow Leopard Trust and United States Geological Survey, Seattle, WA, USA and Fort Collins, CO, USA.

Johansson, Ö., McCarthy, T., Samelius, G., Andrén, H., Tumursukh, L. and Mishra, C. (2015). Snow leopard predation in a livestock dominated landscape in Mongolia. *Biol. Conserv.*, 184, 251–258.

Jumabay-Uulu, K., Wegge, P., Mishra, C. and Sharma, K. (2013). Large carnivores and low diversity of optimal prey: a comparison of the diets of snow leopards Panthera uncia and wolves Canis lupus in Sarychat-Ertash Reserve in Kyrgyzstan. *Oryx*, 48, 529–535.

Karanth, K.K., Nichols, J.D., Hines, J.E., Karanth, K.U. and Christensen, N.L. (2009). Patterns and determinants of mammal species occurrence in India. *J. Appl. Ecol.*, 46, 1189–1200.

Kohl, M.T., Ruth, T.K., Metz, M.C., Stahler, D.R., Smith, D.W., White, P.J., *et al.* (2019). Do prey select for vacant hunting domains to minimize a multi-predator threat? *Ecol. Lett.*, 22, 1724–1733.

Kotler, B.P., Blaustein, L. and Brown, J.S. (1992). Predator facilitation: the combined effect of snakes and owls on the foraging behavior of gerbils. *Ann. Zool. Fenn.*, 29, 199–206.

Kotler, B.P., Brown, J.S. and Bouskila, A. (2004). Apprehension and Time Allocation in Gerbils: The Effects of Predatory Risk and Energetic State. *Ecology*, 85, 917–922.

Kusi, N., Sillero-Zubiri, C., Macdonald, D.W., Johnson, P.J. and Werhahn, G. (2020). Perspectives of traditional Himalayan communities on fostering coexistence with Himalayan wolf and snow leopard. *Conserv. Sci. Pract.*, 2, e165.

Leblond, M., Dussault, C., Ouellet, J.-P. and St-Laurent, M.-H. (2016). Caribou avoiding wolves face increased predation by bears - Caught between Scylla and Charybdis. *J. Appl. Ecol.*, 53, 1078–1087.

Li, J. and Lu, Z. (2014). Snow leopard poaching and trade in China 2000–2013. *Biol. Conserv.*, 176, 207–211.

Lima, S.L. (1992). Life in a multi-predator environment: some considerations for anti-predatory vigilance. *Ann. Zool. Fenn.*, 29, 217–226.

Lima, S.L. (1998). Nonlethal Effects in the Ecology of Predator-Prey Interactions. *BioScience*, 48, 25–34.

Lima, S.L. and Dill, L.M. (1990). Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.*, 68, 619–640.

Lone, K., Mysterud, A., Gobakken, T., Odden, J., Linnell, J. and Loe, L.E. (2017). Temporal variation in habitat selection breaks the catch-22 of spatially contrasting predation risk from multiple predators. *Oikos*, 126, 624–632.

Losey, J.E. and Denno, R.F. (1998). Positive predator–predator interactions: enhanced predation rates and synergistic suppression of aphid populations. *Ecology*, 79, 2143–2152.

Lovari, S., Minder, I., Ferretti, F., Mucci, N., Randi, E. and Pellizzi, B. (2013). Common and snow leopards share prey, but not habitats: competition avoidance by large predators?: Interactions between two leopard species. *J. Zool.*, 291, 127–135.

Lyngdoh, S., Shrotriya, S., Goyal, S.P., Clements, H., Hayward, M.W. and Habib, B. (2014). Prey Preferences of the Snow Leopard (Panthera uncia): Regional Diet Specificity Holds Global Significance for Conservation. *PLoS ONE*, 9, e88349.

MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Royle, J.A. and Langtimm, C.A. (2002). Estimating Site Occupancy Rates When Detection Probabilities Are Less Than One. *Ecology*, 83, 2248.

Mallon, D.P. and Jackson, R.M. (2017). A downlist is not a demotion: Red List status and reality. *Oryx*, 1–5.

Manlick, P.J. and Pauli, J.N. (2020). Human disturbance increases trophic niche overlap in terrestrial carnivore communities. *Proc. Natl. Acad. Sci.*, 117, 26842–26848.

McCarthy, T.M., Mallon, D.P., Jackson, R.M., Zahler, P. and McCarthy, K.P. (2017). *Panthera uncia.* The IUCN Red List of Threatened Species 2017: e.T22732A50664030.

Montgomery, R.A., Moll, R.J., Say-Sallaz, E., Valeix, M. and Prugh, L.R. (2019). A tendency to simplify complex systems. *Biol. Conserv.*, 233, 1–11.

Mumma, M.A., Gillingham, M.P., Johnson, C.J. and Parker, K.L. (2017). Understanding predation risk and individual variation in risk avoidance for threatened boreal caribou. *Ecol. Evol.*, 7, 10266–10277.

Nichols, J.D., Hines, J.E., Mackenzie, D.I., Seamans, M.E. and Gutiérrez, R.J. (2007). Occupancy Estimation and Modeling with Multiple States and State Uncertainty. *Ecology*, 88, 1395–1400.

Nowell, K. (2016). *An ounce of prevention: snow leopard crime revisited.*

Packer, C., Holt, R.D., Hudson, P.J., Lafferty, K.D. and Dobson, A.P. (2003). Keeping the herds healthy and alert: implications of predator control for infectious disease. *Ecol. Lett.*, 6, 797–802.

Parsons, A.W., Rota, C.T., Forrester, T., Baker-Whatton, M.C., McShea, W.J., Schuttler, S.G., *et al.* (2019). Urbanization focuses carnivore activity in remaining natural habitats, increasing species interactions. *J. Appl. Ecol.*, 56, 1894–1904.

Petracca, L.S., Frair, J.L., Cohen, J.B., Calderón, A.P., Carazo-Salazar, J., Castañeda, F., *et al.* (2017). Robust inference on large-scale species habitat use with interview data: The status of jaguars outside protected areas in Central America. *J. Appl. Ecol.*

Preisser, E.L., Bolnick, D.I. and Benard, M.F. (2005). Scared to death? The effects of intimidation and consumption in predator–prey interactions. *Ecology*, 86, 501–509.

Preisser, E.L., Orrock, J.L. and Schmitz, O.J. (2007). Predator Hunting Mode and Habitat Domain Alter Nonconsumptive Effects in Predator–Prey Interactions. *Ecology*, 88, 2744–2751.

Prugh, L.R., Stoner, C.J., Epps, C.W., Bean, W.T., Ripple, W.J., Laliberte, A.S., *et al.* (2009). The Rise of the Mesopredator. *BioScience*, 59, 779–791.

Ripple, W.J. and Beschta, R.L. (2004). Wolves and the Ecology of Fear: Can Predation Risk Structure Ecosystems? *BioScience*, 54, 755.

Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., *et al.* (2014). Status and Ecological Effects of the World's Largest Carnivores. *Science*, 343, 1241484–1241484.

Robinson, H.S. and Weckworth, B.V. (2016). Landscape ecology: Linking landscape metrics to ecological processes. In: *Snow leopards*, Biodiversity of the world: conservation from genes to landscapes (eds. McCarthy, T. and Mallon, D.). Academic Press is an imprint of Elsevier, London ; San Diego, CA, pp. 395–405.

Royle, J.A. and Link, W.A. (2006). Generalized Site Occupancy Models Allowing for False Positive and False Negative Errors. *Ecology*, 87, 835–841.

Schmitz, O.J., Beckerman, A.P. and O'Brien, K.M. (1997). Behaviorally Mediated Trophic Cascades: Effects of Predation Risk on Food Web Interactions. *Ecology*, 78, 1388.

Schmitz, O.J., Hawlena, D. and Trussell, G.C. (2010). Predator control of ecosystem nutrient dynamics. *Ecol. Lett.*, 13, 1199–1209.

Schoener, T.W. (1974). Resource Partitioning in Ecological Communities. *Science*, 185, 27–39.

Sévêque, A., Gentle, L.K., López-Bao, J.V., Yarnell, R.W. and Uzal, A. (2020). Human disturbance has contrasting effects on niche partitioning within carnivore communities. *Biol. Rev.*, 95, 1689–1705.

Sharma, R. and Singh, R. (2020). *Over 100 years of snow leopard research: a spatially explicit review of the state of knowledge in the snow leopard range.* WWF, Gland, Switzerland.

Shores, C.R., Dellinger, J.A., Newkirk, E.S., Kachel, S.M. and Wirsing, A.J. (2019). Mesopredators change temporal activity in response to a recolonizing apex predator. *Behav. Ecol.*

Sih, A., Englund, G. and Wooster, D. (1998). Emergent impacts of multiple predators on prey. *Trends Ecol. Evol.*, 13, 350–355.

Sputnik News. (2020). *Нападение волков на жителей в ГБАО. Sput. News*. Available at: https://tj.sputniknews.ru/country/20200110/1030523065/gbao-ohotniki-zastrelili-volki-foto.html. Last accessed 28 October 2020.

Srivathsa, A., Puri, M., Karanth, K.K., Patel, I. and Kumar, N.S. (2019). Examining human–carnivore interactions using a socio-ecological framework: sympatric wild canids in India as a case study. *R. Soc. Open Sci.*, 6, 182008.

Suryawanshi, K.R., Khanyari, M., Sharma, K., Lkhagvajav, P. and Mishra, C. (2019). Sampling bias in snow leopard population estimation studies. *Popul. Ecol.*

Suryawanshi, K.R., Redpath, S.M., Bhatnagar, Y.V., Ramakrishnan, U., Chaturvedi, V., Smout, S.C., *et al.* (2017). Impact of wild prey availability on livestock predation by snow leopards. *R. Soc. Open Sci.*, 4, 170026.

Thaker, M., Vanak, A.T., Owen, C.R., Ogden, M.B., Niemann, S.M. and Slotow, R. (2011). Minimizing predation risk in a landscape of multiple predators: effects on the spatial distribution of African ungulates. *Ecology*, 92, 398–407.

Thirgood, S., Woodroffe, R. and Rabinowitz, A. (2005). The impact of human–wildlife conflict on human lives and livelihoods. In: *People and Wildlife* (eds. Woodroffe, R., Thirgood, S. and Rabinowitz, A.). Cambridge University Press, Cambridge, pp. 13–26.

Treves, A., Martin, K.A., Wydeven, A.P. and Wiedenhoeft, J.E. (2011). Forecasting Environmental Hazards and the Application of Risk Maps to Predator Attacks on Livestock. *BioScience*, 61, 451–458.

Viripaev, V. and Vorobiev, G. (1983). *Волк в Киргизии: эколого-географический очерк*. Ilim, Frunze, Kirghiz SSR.

Werhahn, G., Kusi, N., Li, X., Chen, C., Zhi, L., Lázaro Martín, R., *et al.* (2019). Himalayan wolf foraging ecology and the importance of wild prey. *Glob. Ecol. Conserv.*, 20, e00780.

Werhahn, G., Liu, Y., Meng, Y., Cheng, C., Lu, Z., Atzeni, L., *et al.* (2020). Himalayan wolf distribution and admixture based on multiple genetic markers. *J. Biogeogr.*, 47, 1272–1285.

Wiens, J.A. (1993). Fat times, lean times and competition among predators. *Trends Ecol. Evol.*, 8, 348–349.

Wilmers, C.C., Crabtree, R.L., Smith, D.W., Murphy, K.M. and Getz, W.M. (2003). Trophic facilitation by introduced top predators: grey wolf subsidies to scavengers in Yellowstone National Park. *J. Anim. Ecol.*, 72, 909–916.

Wirsing, A.J., Cameron, K.E. and Heithaus, M.R. (2010). Spatial responses to predators vary with prey escape mode. *Anim. Behav.*, 79, 531–537.

Wirsing, A.J., Heithaus, M.R., Brown, J.S., Kotler, B.P. and Schmitz, O.J. (2021). The context dependence of non-consumptive predator effects. *Ecol. Lett.*, 24, 113–129.

Zeller, K.A., Nijhawan, S., Salom-Pérez, R., Potosme, S.H. and Hines, J.E. (2011). Integrating occupancy modeling and interview data for corridor identification: A case study for jaguars in Nicaragua. *Biol. Conserv.*, 144, 892–901.

Zipkin, E.F., DeWan, A. and Royle, J.A. (2009). Impacts of forest fragmentation on species richness: a hierarchical approach to community modelling. *J. Appl. Ecol.*, 46, 815–822.

CHAPTER 2

PREDATOR NICHE OVERLAP AND PARTITIONING AND POTENTIAL INTERACTIONS IN THE MOUNTAINS OF CENTRAL ASIA[1]

Abstract

Direct and indirect interactions among predators affect predator fitness, distribution, and overall community structure. Yet, outside of experimental settings, such interactions are difficult to observe and thus poorly understood. Patterns of niche overlap among predators reflect and shape community interactions and may therefore help elucidate the nature and intensity of intraguild interactions. To better understand the coexistence of two apex predators, snow leopards (*Panthera uncia*) and wolves (*Canis lupus*), we investigated their spatial, temporal, and dietary niche overlap in summer in the Pamir Mountains of Tajikistan. We estimated population-level space use via spatial capture-recapture models based on non-invasive genetics and camera traps, diel activity patterns based on camera trap detections, and diet composition from prey remains in carnivore scats, from which we estimated coefficients between 0 and 1 for overlap in space, time, and diet, respectively. Snow leopards and wolves displayed moderate spatial partitioning (0.26, 95% CI: 0.17-37), but overlapping temporal (0.77, 95% CI: 0.64-0.90) and dietary (0.97, 95% CI: 0.80-0.99) niches. Both predators relied on seasonally abundant marmots (*Marmota caudata*) rather than wild ungulates, their typical primary prey, suggesting that despite patterns of overlap that were superficially conducive to exploitation competition and predator facilitation, prey were likely not a limiting factor. Therefore, prey-mediated interactions, if present, were unlikely to be a major structuring force in the ecosystem. By implication, carnivore conservation planning and

---

[1] Kachel, SM, Karimov K, Wirsing AJ. *In press*. Predator niche overlap and partitioning and potential interactions in the mountains of Central Asia. Journal of Mammalogy.

monitoring in the mountains of Central Asia should more fully account for the seasonal importance of marmots in the ecosystem.

Introduction

Intraguild interactions among predators can affect individual fitness (Holt and Polis 1997), population abundance and distribution (Linnell and Strand 2000; Vanak et al. 2013), and community structure (Cody and Diamond 1975). Direct interactions, like interference competition, can lead to spatial and temporal avoidance with potentially significant demographic impacts (Palomares and Caro 1999). Yet, the overall fitness effects of indirect prey-mediated interactions, namely exploitation competition, may outweigh those of direct interactions (Levine 1976). Despite their relevance to conservation and ecology, intraguild interactions among carnivores are difficult to observe and quantify. Accordingly, investigators typically rely on more observable patterns of niche overlap and partitioning to characterize and anticipate potential interactions within predator guilds (Schmitz et al. 2017), even if the realized nature and strength of those interactions is expected to shift with varying conditions and resource levels (Wiens 1993). In light of ongoing global losses of intact large carnivore guilds and prey communities (Wolf and Ripple 2016, 2017), and the role of anthropogenic disturbance as a mediator of intraguild interactions (Mannick and Pauli 2020; Seveque et al. 2020), assessing patterns of niche partitioning is critical to large-carnivore conservation planning (Lahkar et al. 2020).

Under the competitive exclusion principle (Gause 1934), sympatric predators should partition dietary, spatial, and/or temporal niche dimensions (Chesson 2000) to achieve some threshold of resource independence that enables stable coexistence (Case and Gilpin 1974; Schoener 1974). Dietary overlap, most likely to occur in ecosystems with low prey diversity, is indicative of a scenario in which exploitation competition should be anticipated should prey resources become limiting (Wiens 1993). Spatial (Vanak et al. 2013) and temporal (Hayward and Slotow 2009) partitioning likely arise as adaptations to reduce both exploitation and interference competition (Carothers and Jaksic 1984). Although numerical competition for prey may be the ultimate driver of interference (Donadio et al. 2006), partitioning in space and time has important repercussions for the interpretation of niche segregation patterns. For example, dietary overlap is consistent with both positive and negative prey-mediated interactions, depending on the extent to which prey limit predators (Wiens 1993), and on spatial and temporal partitioning. Namely, if prey availability is limiting, high dietary overlap may indicate strong exploitation competition (and, by extension, interference competition), but if not, dietary overlap may be detached from competition (Wiens 1993). Alternatively, high dietary overlap among predators with low spatial (Sih et al. 1998) but high temporal (Kohl et al. 2019) overlap could reflect predator facilitation (Kotler and Brown 1992), but (again) only if prey are a limiting factor, and only if prey move freely between predator domains (Schmitz et al. 2017). Given the divergent conservation implications of predator facilitation and competition, there is a clear need to consider multiple niche dimensions in parallel, particularly where humans have restructured ecological communities.

Ample evidence reveals that humans alternatively impede, destabilize, and reinforce patterns of predator niche partitioning in spatial, temporal, and dietary dimensions depending on the nature of the disturbance (Seveque et al. 2020). For example, livestock grazing can expand dietary niche breadth by providing alternative domestic prey (Manlick and Pauli 2020), hunting and recreational activity can shift temporal activity patterns (e.g., Shores et al. 2019), and habitat conversion can constrain available habitat, increasing spatial overlap (Parsons et al. 2019). Thus, assessing niche partitioning and overlap is immediately relevant to carnivore conservation in landscapes they share with humans.

Here, we investigate patterns of dietary, spatial, and temporal overlap and partitioning between sympatric snow leopards (*Panthera uncia*) and wolves (*Canis lupus*) in a shared landscape managed for both seasonal pastoralist livestock grazing and wildlife conservation in the high mountains of Central Asia. At large scales, snow leopards are sympatric with wolves throughout the range of the former, often with substantial overlap in their reliance on large ungulate prey, leading investigators to infer the potential for exploitation competition (Jumabay-Uulu et al. 2013; Bocci et al. 2017; Chetri et al. 2017). However, partitioning in alternative niche dimensions, namely space and time, remains unexplored. Snow leopards and the wild ungulates on which they rely are the focus of considerable conservation attention and investment, with declining prey availability regarded as a primary threat to snow leopards in many areas (McCarthy et al. 2017). The conservation status of wolves in the region, by contrast, is not well understood, though recent molecular evidence suggests Himalayan wolves and gray wolves are taxonomically distinct (Werhahn et al. 2018). Given their dietary overlap with snow leopards, wolves may also be vulnerable to prey declines, and both carnivores and their wild prey are potentially at risk from livestock grazing and the associated potential for depredation-driven conflict with humans (Mishra 1997). The mechanisms by which the two carnivores coexist is, however, are not well understood. The low diversity of ungulate prey in the mountains of Central Asia suggests that strong prey-mediated interactions between snow leopards and wolves are likely.

To better understand the coexistence of snow leopards and wolves, we explored how the two carnivores partition space, time, and diet during the summer. We estimated overlap in the spatially-explicit distribution, prey composition, and diel activity patterns of the two predators using camera traps, non-invasive genetics, and fecal microscopy in the Pamir Mountains of Tajikistan, a landscape in which we previously documented evidence of anthropogenic impacts on ungulate habitat use (Karimov et al. 2018). We hypothesized, based on low prey diversity and differing hunting modes, that wolves (cursorial pursuit hunters) and snow leopards (stalking hunters) are likely to occupy similar dietary niches, but unique spatial and temporal habitats suited to maximizing hunting success. Accordingly, we predicted that we would observe distinct spatial distributions and temporal activity patterns, but similar prey composition.

Methods

Study area.—Zorkul Reserve (Fig. 1) is a mixed-use protected area in the Pamir Mountains, encompassing about 887 km² in the Big Pamir Valley in Tajikistan. Altitudes range from 4000 meters to over 5500 meters. Wetland and meadow habitats, often degraded due to livestock grazing, typify the valley floor, while rocky slopes, ridges, glaciers, and cirques characterize the two surrounding mountain ranges. Local communities have used the reserve as seasonal pasture for generations and continue to do so despite the protected area designation. The flora is typified by graminoids, forbs, and low-lying shrubs. In addition to snow leopards, wolves, and their ungulate prey – argali (*Ovis ammon*) and Asiatic ibex (*Capra sibirica*) – the mammal community includes brown bears (*Ursus arctos*), red foxes (*Vulpes vulpes*), long-tailed marmots (*Marmota caudata*), tolai hares (*Lepus tolai*), and large-eared pika (*Ochotona macrotis*).

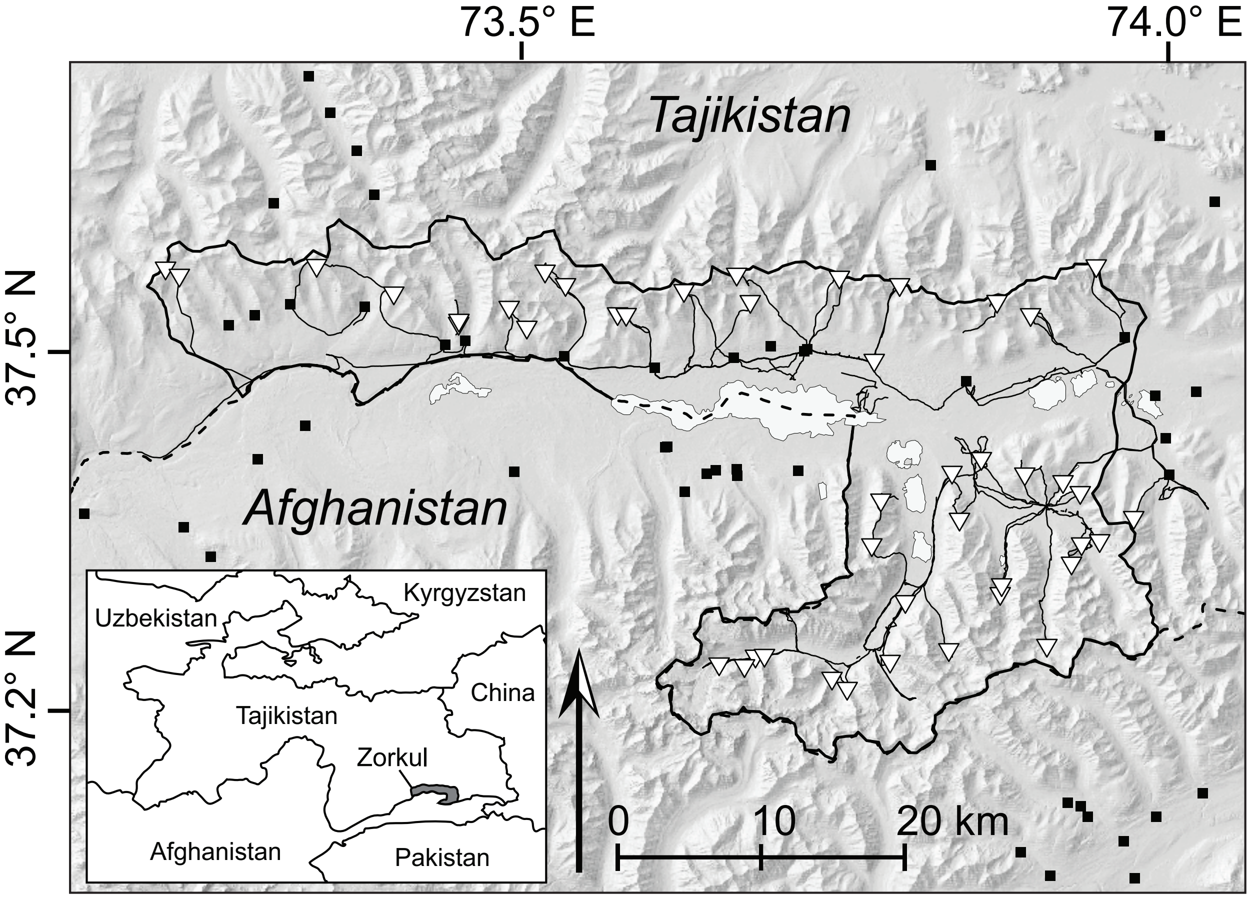

Fig. 1. Snow leopard (*Panthera uncia*) and wolf (*Canis lupus*) niche overlap sampling, Aug-2015 to Nov-2015, in Zorkul Reserve, Tajikistan (solid black line). Thin black lines indicate GPS tracks of opportunistic fecal search paths, white triangles indicate camera trap sites, and black points indicate permanent settlements and seasonal livestock stations.

Camera trapping.—To sample snow leopard density, and temporal activity patterns of both carnivores, we deployed 45 camera traps throughout the reserve over a 100-day period from 1 August to 8 November 2015 (for details, see Karimov et al. 2018). Cameras were functionally deployed for a total of 2839 trap nights, with variable operational performance (mean = 63.9 trap nights ±31.1 SD). We constructed spatial encounter histories for individual snow leopards over 10 consecutive 10-day sampling occasions, measured from 12:00 noon local time. We used 10-

day occasions to speed model run times. To maximize detections, we deployed cameras at sites with evidence of snow leopard or wolf use (e.g., scrapes and scent posts) or where we expected carnivore use based on evidence of ungulate presence or features characteristic of carnivore marking sites (e.g., trail junctions, ridgelines, outcroppings, and prominent boulders).

Scat sampling.—We used an opportunistic search-encounter design to locate putative carnivore scats from 1 August to 15 August 2015 in order to sample snow leopard and wolf diet and to evaluate wolf density. We divided the study area into a grid of 1 km^2 cells; in each cell, crews recorded search paths with handheld GPS units during all periods of active searching. We avoided collecting scats that we suspected were deposited prior to spring snowmelt, but we could not objectively determine the deposition age of scats found. Instead, we assumed that fecal material was too old to sample unless corroborating evidence was found indicating that samples were fresh, such as color, consistency, moisture content, and the presence of tracks. We followed this rule to adhere as best as possible to temporal population closure considerations (Royle et al. 2014). As detailed in Karimov et al. (2018), we collected 3-7 ml of each putative scat for genetic analysis in 10 ml vials with 3-5 ml of silica desiccant. For dietary analysis, up to 15 ml of additional fecal material was collected for prey identification via fecal microscopy. Carnivore species identification from scats was conducted at the Conservation Biology Lab (Seattle, Washington, USA) and at the Center for Conservation Genetics (New York, New York, USA); in both cases, genetic material was extracted using Qiagen's DNeasy Tissue kit (Qiagen, Valencia, California, USA), and PCR amplification of the carnivore-specific ATP6 region of the mitochondrial genome was used to determine species (Chaves et al. 2012). Domestic dogs (*C. lupus familiaris*) were differentiated from wolves using 4 single nucleotide polymorphisms in the cytochrome B region (Witt et al. 2015). Individual identification of wolves was based on further

PCR amplification with 6 microsatellite markers in 2 different multiplex sets using Qiagen's Multiplex kit.

Spatial overlap.—To quantify spatial partitioning, we estimated a coefficient of niche overlap using population-level space use estimated via spatial capture-recapture (SCR) models built using the 'oSCR' package (Sutherland et al. 2019) in R (R Core Development Team 2016). Motivated originally by problems of population estimation, SCR models are hierarchical models that consist of a spatial model for individual encounter probability and a spatially-explicit model for the distribution of those individuals (Efford 2004; Royle et al. 2014). We incorporated covariate effects on the spatially-explicit distributions of snow leopard and wolf activity centers, from which we calculated an index of spatial overlap between the two species.

We modeled each species separately, using an identical discrete state-space of 1 km^2 cells extending 18 km beyond all camera trapping and scat sampling activity (with cells corresponding to water bodies >1 km^2 removed) covering a total of 5,592 km^2. In initial trials, parameter estimates were insensitive to increasing the state-space buffer size beyond 18 km. We hypothesized that wolf and snow leopard distributions would be positively associated with ungulate distributions (Sharma et al. 2015), as indexed by plant primary productivity (Pettorelli et al. 2011), and with terrain characteristics like elevation, slope, and ruggedness (Chetri et al. 2019), but negatively linked to metrics of human impacts (Alexander et al. 2015). We considered the following remotely-sensed covariates: elevation (NASA JPL 2009), terrain ruggedness, slope, and Normalized Difference Vegetation Index (NDVI; NASA LP DAAC 2016). For wolf models, we calculated the per-pixel average NDVI over the presumed sampling period 1 May to 15 August 2015, and for snow leopard models, over the known sampling period 1 August to 8 November 2015. We relied on a validation of the relationship between NDVI and plant biomass in Western China (Liu et al. 2017). Raw covariates, which were measured at a resolution finer than the state-space, were recalculated as the weighted mean of the covariate grid cells intersecting with each state-space pixel. We considered possible anthropogenic influences on carnivore distributions by including the distance to permanent settlements and seasonal camps as an additional covariate. We screened for correlation using Pearson's coefficient for all pairwise comparisons; only those covariates derived from elevation were strongly correlated ($|r| > 0.7$). We standardized all covariates to mean 0 and unit variance.

We modeled encounter rate as a Poisson process, such that the number of detections of individual i at trap j on occasion k was y_{ijk}~Poisson(λ_{jik}), for snow leopards (or y_{ij} ~ Poisson(λ_{ij}) for single-occasion sampling of wolves) under a half-normal detection function where the expected number of detections was $\lambda_{ijk} = \lambda_0 \times \exp(-d^2_{ij}/2\sigma^2)$ and d_{ij} was the distance between a trap and an individual's activity center as scaled by σ (Royle et al. 2014). Under this formulation, n trap-level covariate (x_n) effects on encounter rates are incorporated via a log-linear model, $\log(\lambda_{0,ijk}) = \alpha_0 + \Sigma(\alpha_n x_n)$. For wolves, we included a measure of effort in each encounter model (Royle et al. 2014) – the length of search transect walked per 1 km^2 cell – and additionally considered a quadratic effect to allow for potential thresholds in the presumed positive relationship between search effort and detection. For snow leopards, we accounted for camera operation and considered binary covariates indicating the camera site-specific detection or non-detection of ibex and argali.

For each carnivore, we specified an inhomogeneous point process for the distribution of individual activity centers (Borchers and Efford 2008). N, the number of activity centers in a given pixel, was a Poisson random variable dependent on density, D, of activity centers in pixel s, such that $N(\boldsymbol{s})\sim Poisson(D(\boldsymbol{s}))$. Density was allowed to respond to n landscape covariates under a log-linear model, $\log(D(\boldsymbol{s})) = \beta_0 + \Sigma(\beta_n x_n(\boldsymbol{s}))$. We considered the covariate effects of elevation, slope, ruggedness, settlement proximity, and NDVI.

We used a two-stage model selection approach to first select among encounter (sub)models under a null density model, and subsequently to select among density models built with the top encounter model. At each stage we dismissed models with uninformative covariate parameters (i.e., the 85% confidence interval for β included 0) from further consideration, even if ΔAIC<2 (Arnold 2010). In any single wolf encounter model, we considered effort in paired combination with each camera site covariate, whereas for snow leopards we considered only single effects from the available site covariates (trap operation was already accounted for in the null snow leopard model). For density models, we considered single or paired covariates, accounting variously for vegetative productivity, potential anthropogenic impacts, and physical terrain characteristics (elevation, slope, or ruggedness), but we avoided combinations with multiple terrain-derived variables in any given model, as these variables were strongly collinear with each other. In total we built 7 encounter rate candidate models and 13 density candidate models for each species.

Using the top-ranked SCR model for each species, we calculated Schoener's (Schoener 1970) coefficient of spatial overlap, $D_{Overlap}$, where values close to 0 indicate strong partitioning, and values close to 1 indicate strong overlap. Across all $\boldsymbol{s}$ pixels of the state-space, we calculated $D_{Overlap} = 1 - 0.5 * \Sigma|u_{sl} - u_w|$ where u_{sl} and $u_{w,}$ for snow leopards and wolves, respectively, were the pixel-specific proportions of all N individual activity centers, distributed across a Gaussian smoothing kernel with a species-specific standard deviation of σ – the population-level realized space use implied by the SCR model. To approximate uncertainty in this index, we estimated a 95% confidence interval from 1000 bootstrap samples, obtained by resampling N individuals from the individual-level realized densities of all observed and unobserved individuals, and sampling values of σ from a random normal distribution with mean and standard deviation corresponding to model estimates for that parameter. Because the scat deposition (wolf model) and camera trapping (snow leopard model) periods only partially overlapped, we investigated the sensitivity of our spatial overlap estimates to the duration of the sampling session by following the same model selection process for a 40-day (four 10-day occasions) period starting 1-Aug, and calculated corresponding $D_{Overlap}$. We ultimately opted to use the full 100-day period in order improve precision and to explicitly include as many known snow leopard individuals (and by implication, their explicit space use) as possible in our estimates of realized space use for the species. Because the goal was realized – rather than predicted – space use, we made a tradeoff between including explicit information about the locations of real individual animals in the population that were only detected later in the camera trapping period, and relying more heavily on the assumption that animal activity centers did not substantially shift between the scat and camera periods.

Temporal activity pattern overlap.—We used camera trap photo captures to investigate 24-hour activity pattern overlap between wolves and snow leopards, estimating non-parametric kernel density for each species in order to derive a coefficient of overlap, Δ_1 (preferred for small sample sizes; Ridout and Linkie 2009), between 0 and 1 in the R package 'overlap' (Meredith and Ridout 2014), where values close to 1 indicate strongly overlapping activity patterns. We calculated Δ_1 as the area of overlap beneath both kernel density functions, and estimated uncertainty from 1000 bootstrap samples. We adjusted clock times to more biologically-relevant "sun times," relative to sunrise and sunset, prior to the overlap analysis (Nouvellet et al. 2012).

To better contextualize predator activity patterns, we also visualized temporal kernel density functions for ibex, argali, and marmot photo detections.

*Dietary overlap.—*We estimated dietary overlap using only genetically-confirmed wolf and snow leopard scats. First, we estimated the percent dietary biomass contribution of each prey species, based on the dietary scat analysis data of Karimov et al. (2018), who reported uncorrected prey frequencies of occurrence from our wolf and snow leopard scat samples; scat analysis uses microhistological characteristics of prey remains in scats to determine prey identity by comparison with reference specimens (Weiskopf et al. 2016). We adjusted for predator- and prey-specific variability in scat production by applying correction factors derived from prey weights compiled by (Weiskopf et al. 2016) and feeding trials of wolves (Weaver 1993) and pumas (Ackerman et al. 1984) as an analogue for snow leopards (Jumabay-Uulu et al. 2013). Because, in calculating correction factors, we assumed that ungulates detected in carnivore scats were adults, we evaluated the sensitivity of our diet composition to prey weights assuming ungulates were neonates. We calculated Pianka's index of dietary overlap (Pianka 1973), and estimated confidence intervals based on 1000 bootstrap samples.

Results

*Camera trapping and scat sampling.—*We built spatial capture histories of 13 individual adult snow leopards, detected an average of 2.38 times (SD = 1.12) at an average of 1.85 sites (SD = 0.64) and identifiable in 31 of 37 independent photo capture events at 14 total sites. Of the remaining events, 1 event included a single cub detected alone, and the other 5 were not clear enough to identify individuals. Wolves were independently detected 32 times at 7 camera sites, typically with multiple individuals per event. We collected 135 putative wolf and snow leopard scats from 736 km walked in August 2015 during the camera-trap deployment phase, from which we confirmed species identity for 18 snow leopard scats, and 75 wolf scats. We constructed spatial genetic capture histories of 35 individual wolves, detected on average 2.03 times (SD = 1.6) at 1.66 sites (SD = 0.8), based on 71 scats for which we were able to identify individuals.

Spatial niche partitioning.—The top wolf encounter model incorporated linear and quadratic effort terms, whereas the top model for snow leopard encounter rate included a positive effect of camera site-level ibex presence (Table 1). According to the top-ranked models (Tables 2, 3), snow leopard density was positively associated with NDVI and elevation, whereas wolf density was positively associated with distance to human settlements and seasonal camps and negatively associated with terrain ruggedness (Table 3; Fig. 2). Top-ranked models estimated an average density of 1.72 wolves/100 km^2 (SE = 0.84) and 0.41 snow leopards/100 km^2 (SE = 0.37). The estimated scale of movement for wolves was $\sigma_{wolf} = 5.03$ km (SE = 0.49), and for snow leopards was $\sigma_{snow\ leopard} = 8.82$ km (SE = 1.31). Spatially-explicit overlap between the two species was estimated at $D_{Overlap} = 0.26$ (Bootstrap 95% CI: 0.17-0.37). The best model for the 40-day truncated subset of the snow leopard data (Appendix Tables S1-S3) contained the same density covariates (Elevation, NDVI) as the overall top model (albeit with less precision in coefficient estimates and different detection covariates), and produced a similar estimate of interspecific overlap: $D_{40} = 0.29$ (Bootstrap 95% CI: 0.19-0.40).

Temporal niche partitioning.—Wolves and snow leopards both displayed crepuscular temporal activity patterns, as estimated from camera trap detection times (Fig. 3). Daily activity pattern overlap between the two species was $\Delta_1 = 0.77$ (Bootstrap 95% CI: 0.64-0.90). Ibex, argali, and marmot activity patterns were strongly diurnal (Fig. 4).

Table 1. Model selection summary for spatial capture-recapture models of snow leopard and wolf photographic and genetic encounter rates in Zorkul Reserve, Tajikistan, Aug-2015 to Oct-2015.

Species	Encounter rate model	Log likelihood	*n* parameters	ΔAIC
Snow leopard	*~Ibex*	134.12	4	0.00
	~Elevation	136.27	4	4.31
	~(Null)	137.65	3	5.07
	~Slope	136.71	4	5.18
	~NDVI	137.24	4	6.25
	~Argali	137.48	4	6.73
	~Rugged	137.61	4	7.00
Wolf	*~Effort + Effort*^{2}	313.14	5	0.00
	~Effort + Elev	313.52	5	0.76
	~Effort + Rugged	315.74	5	5.21
	~Effort + Slope	316.56	5	6.84
	~Effort (Null)	319.21	4	10.14
	~Effort + NDVI	318.44	5	10.60
	~Effort + Corral	319.21	5	12.14

Ibex and argali = binary variables indicating detection of each species (*Capra sibirica* and *Ovis ammon*); Effort = length of opportunistic scat search paths walked within a given 1 km^2 sampling cell; Null model for snow leopard detection accounted only for trap operation.

Table 2. Model selection summary for spatial capture-recapture density submodels of snow leopard and wolf encounter data in Zorkul Reserve, Tajikistan, Aug-2015 to Oct-2015.

Species	Density model	Log likelihood	*n* parameters	ΔAIC
Snow leopard	*~NDVI + Elevation*	130.08	6	0.00
	~Camp Distance + Elevation	131.76	6	3.35
	~(Null)	134.12	4	4.07
	~Elevation	133.72	5	5.29
	~NDVI + Rugged	132.87	6	5.57
	~NDVI	133.90	5	5.63
	~Camp Distance	133.96	5	5.77
	~Rugged	134.08	5	5.99
	~Slope	134.08	5	6.00
	~NDVI + Slope	133.16	6	6.15
	~Camp Distance + Rugged	133.49	6	6.82
	~Camp Distance + Slope	133.61	6	7.05
	~Camp Distance + NDVI	133.89	6	7.62
Wolf	*~Camp Distance + Rugged*	306.85	7	0.00
	~Camp Distance + Slope	306.88	7	0.05
	~Camp Distance + Elevation	309.18	7	4.64
	~Camp Distance + NDVI	310.81	7	7.90
	~(Null)	313.14	5	8.57
	~NDVI + Slope	311.44	7	9.18
	~Slope	312.63	6	9.55
	~Camp Distance	312.67	6	9.62
	~Elevation	312.80	6	9.88
	~Rugged	312.84	6	9.96
	~NDVI	313.14	6	10.56
	~NDVI + Rugged	312.35	7	10.99
	~NDVI + Elevation	312.67	7	11.63

CampDistance = distance to the nearest human settlement or seasonal camp; NDVI = average Normalized Difference Vegetation Index; Null models contained no density covariates.

Table 3. Maximum likelihood estimates and standard errors (in parentheses) of parameters included in the top AIC-ranked spatial capture-recapture models for snow leopards and wolves Zorkul Reserve, Tajikistan, Aug-2015 to Oct-2015.

Parameter	Snow leopard	Wolf
Movement scale:		
log (σ)	9.015 (0.159)	8.523 (0.097)
Encounter rate: log (λ_{ijk})		
α_0	-3.050 (0.401)	-3.311 (0.244)
α_{Effort}	--	0.961 (0.229)
$\alpha_{Effort^\wedge 2}$	--	-0.401 (0.136)
$\alpha_{Ibex\ Presence}$	1.000 (0.373)	--
Density: log($E(D)$)		
β_0	-9.709 (2.604)	-8.888 (2.752)
β_{NDVI}	2.034 (0.818)	--
$\beta_{Elevation}$	4.648 (1.888)	--
$B_{Ruggedness}$	--	-4.427 (1.762)
$\beta_{Camp\ Distance}$	--	1.878 (0.388)

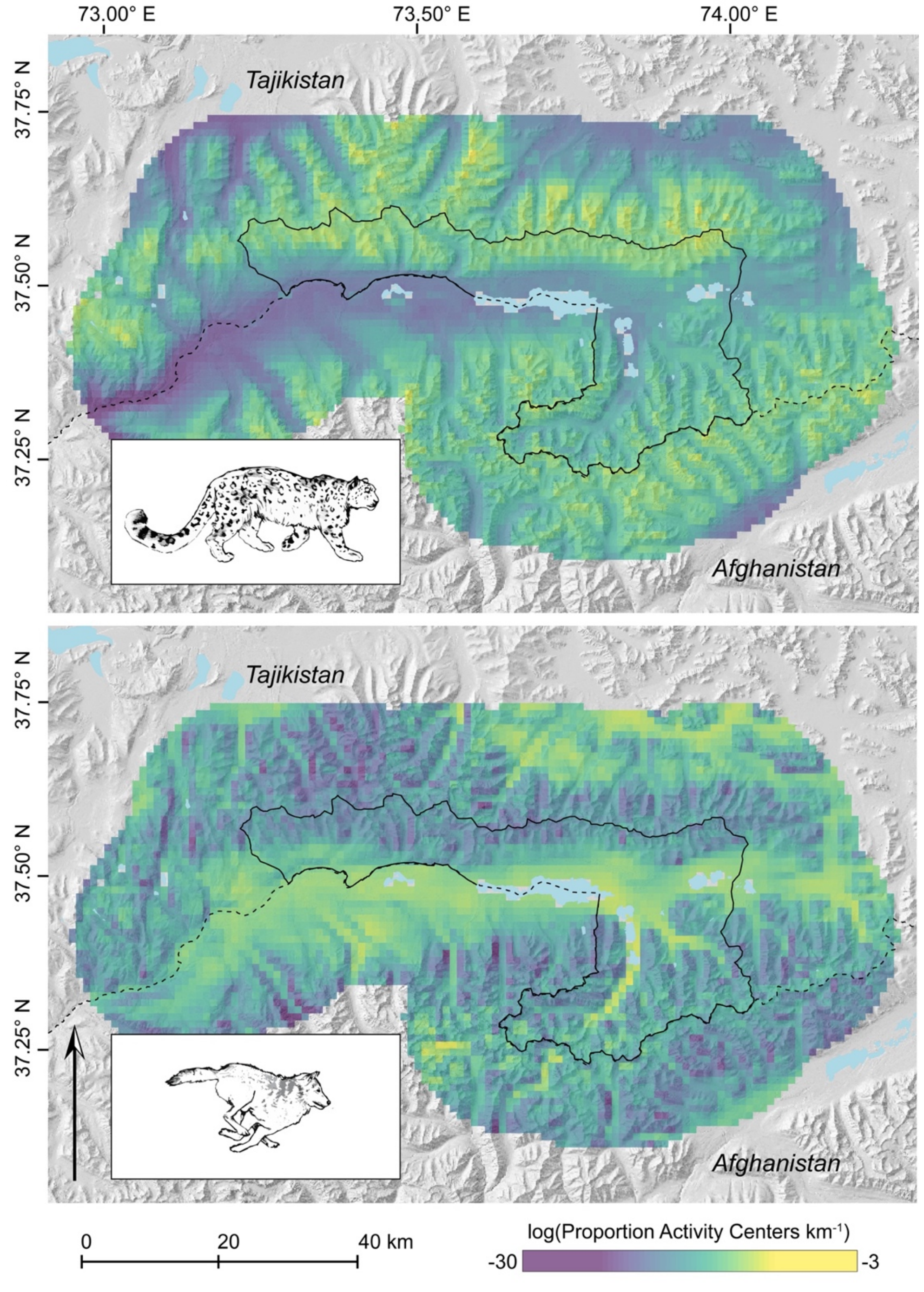

Fig. 2. Relative realized densities of snow leopard (top) and wolf (bottom) activity centers in Zorkul Reserve, Tajikistan, based on top-ranked spatial capture-recapture models built, respectively, from photographic (Aug-2015 to Oct-2015) and opportunistic fecal genetic (Aug-2015) data.

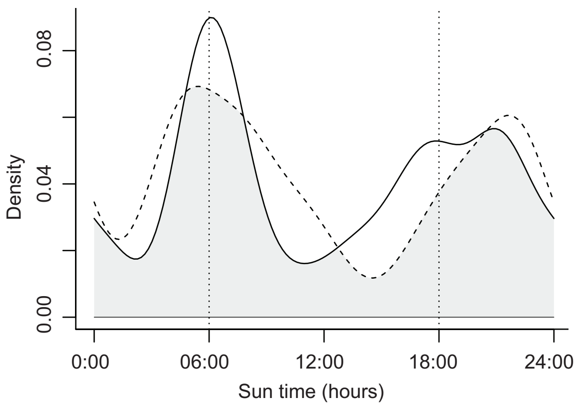

Fig. 3. Temporal activity kernel density of snow leopards (dashed line) and wolves (solid line) detections at camera traps in Zorkul Reserve, Tajikistan from Aug-2015 to Oct-2015. Photo capture times are adjusted to time relative to sunrise (06:00) and sunset (18:00). The shaded area corresponds to the coefficient of overlap, $\Delta_1 = 0.83$ (Bootstrap 95% CI: 0.70-0.96).

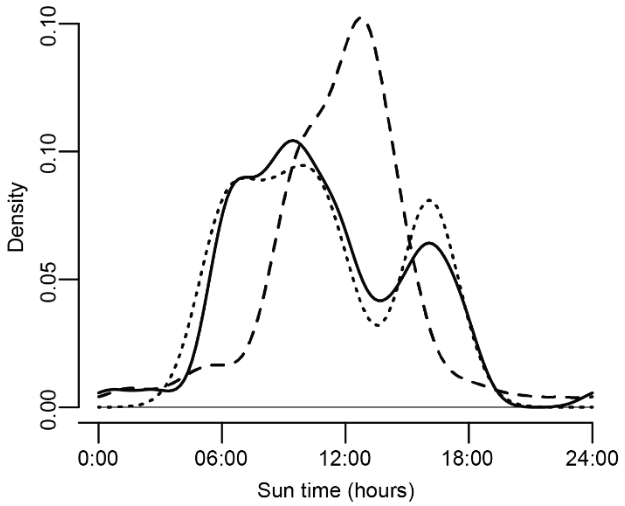

Fig. 4. Temporal activity kernel density of argali (*Ovis ammon*, solid line), ibex (*Capra sibirica*, dotted line), and marmot (*Marmota caudata*, dashed line) detections at camera traps in Zorkul Reserve, Tajikistan from Aug-2015 to Oct-2015. Kernel densities for both ungulates were adjusted to time relative to sunrise (06:00) and sunset (18:00).

Dietary niche overlap.—Pianka's index of dietary overlap was 0.97 (Bootstrap 95% CI: 0.80-0.99), with marmots, and to a lesser extent, argali providing the bulk of summer dietary biomass for each predator, despite the presence of alternative prey (Fig. 5).

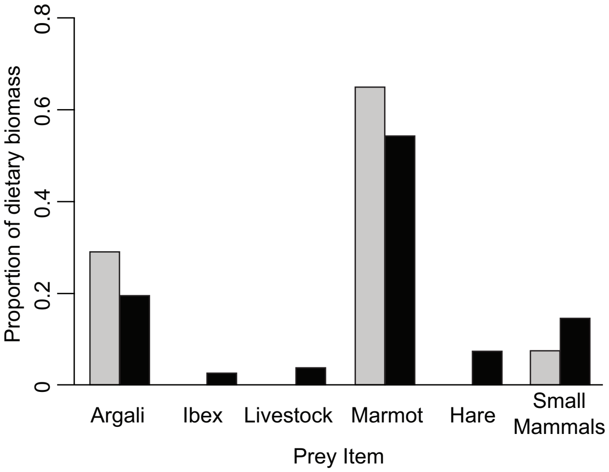

Fig. 5. Estimated proportion of summer dietary biomass contribution of different prey items for snow leopards (gray) and wolves (black) in Zorkul Reserve, Tajikistan, from scats collected Aug-2015.

Discussion

We observed spatial – but not temporal or dietary – summer niche partitioning between snow leopards and wolves in the Zorkul Reserve landscape, in keeping with our predictions. Counter to our expectations, however, marmots – not ungulates – were the most important prey by estimated dietary biomass for both predators, suggesting that despite patterns of niche segregation consistent with prey-mediated interactions between the two predators, the limiting conditions required for exploitation competition and the interchange of prey between predator habitats required for predator facilitation were weak or absent during summer. Instead, the spatial distribution and crepuscular activity patterns we observed can both be explained by predators seeking to maximize access to prey by focusing on spatial locations and daylight conditions most conducive to capturing prey, irrespective of potential competition. However, evidence of landscape-scale wolf avoidance of areas close to humans suggests that humans have the potential to influence niche partitioning between these carnivores even in protected landscapes.

Marmots accounted for more than 50% of each predator's estimated summer dietary biomass, and more than double the biomass contribution of wild ungulates – preferred prey, regionally, for snow leopards and wolves alike (Lyngdoh et al. 2014; Werhahn et al. 2019). Even if all detected ungulate prey were neonates (~5 kg; leading to increased estimates of overall dietary biomass contribution in light of scat production correction factors) we would still estimate marmots to contribute equal biomass compared to ungulates (~45% each) to each carnivore's diet. Dietary overlap may be lower than estimated, however, if there were major differences in the demographic composition of ungulate prey for the two predators. Relative to wolves and snow leopards, long-tailed marmots have small home ranges (0.03 km^2; Blumstein and Arnold 1998). In light of spatial partitioning, it is therefore unlikely that marmots mediate any short-term interactions between the predators. Our findings are potentially reflective of low ibex (generally preferred by snow leopards given shared habitat preferences; Lyngdoh et al 2014) abundance relative to other prey, but also of a landscape saturated with an easily available alternative. We did not directly estimate relative abundance or availability of different prey species, but in our camera data we detected ibex at only 16% of camera sites, whereas marmots and argali were detected at 78% and 56% of sites, respectively, reinforcing support for the marmot saturation explanation. If prey availability is limiting for predators during winter (when marmots are hibernating), we anticipate that the four-fold greater density of wolves could amplify the magnitude of exploitation competition for snow leopards.

Temporal displacement is regularly observed in carnivore species pairs with clear dominance hierarchies (Caro and Palomares 1999; Hayward and Slotow 2009). The lack of such displacement here suggests that interference was not an important factor driving either predators' activity patterns. Instead, activity patterns more likely reflected temporal constraints imposed by prey availability, which was strongly diurnal for wild ungulates and marmots alike. Thus, the observed crepuscular activity peaks probably help both carnivores optimize hunting success during periods when prey are at least somewhat active, and light is sufficient to see, yet low enough to provide some camouflaging cover (Hayward and Slotow 2009).

The pattern of contrasting space use we estimated is compatible with two explanations, namely that the two predators either use space in a manner that maximizes the efficacy of their contrasting hunting modes and access to prey, or alternatively that snow leopards use marginal habitats in order to avoid interference interactions with dominant competitors (Lovari et al. 2013). The positive spatial effect of NDVI – a good predictor of marmot distributions in similar landscapes (Lu et al. 2016) – on snow leopard distribution supports the first explanation, as does the negative effect of terrain ruggedness on wolves. A preponderance of empirical evidence indicates that snow leopards have a consistent and close association with rugged alpine terrain (tightly correlated with elevation in our landscape) at multiple spatial scales throughout their range (Fox and Chundawat 2016), suggesting that to the extent that interference from sympatric carnivores does inform the snow leopard space use, its influence is secondary to the interaction of terrain and hunting mode. By contrast, the cursorial hunting mode of wolves is best suited to less rugged terrain; however, our evidence of human impacts on wolf space use suggest that wolves may constrain their spatial niche to limit interference interactions with humans.

Human disturbance may impede, destabilize, or facilitate niche-parititoning among carnivores (Seveque et al. 2020). We found evidence of human influence on wolf space use, but the consequences of this association for wolf-snow leopard interactions, and conservation of both carnivores more broadly, remain unclear. Generally, this finding, and similar relationships inferred by Karimov et al. (2018) between humans and argali, suggest that pastoralism and associated anthropogenic impacts constrain the spatial niche used by wildlife in Zorkul. Conversely, evidence from elsewhere in Central Asia suggests that pastoralists may inadvertently facilitate wolves by subsidizing as much as 90% of their diet with livestock (Ekernas et al. 2017); we cannot dismiss the possibility of such anthropogenic facilitation in winter here, as livestock are present year-round on the Afghan side of the Big Pamir. Indeed, as with the role of wild prey, we expect that any anthropogenic impacts on snow leopards and wolves are likely greater during the winter, when wild prey availability is reduced by marmot hibernation.

Although marmots are only available to mountain carnivores for a short period each year, the view that they are “sub-optimal” secondary prey (compared to ungulates; Lyngdoh et al. 2014) for snow leopards may be oversimplified – this summer pulse of abundant, albeit smaller, prey is likely a major structuring force in predator communities in many high mountain landscapes across Asia. Given their importance in this ecosystem, we see a need for greater scrutiny of marmots to better monitor and safeguard populations, particularly in light of their susceptibility to high-mortality epizootic die-offs, eradication programs, competition with livestock, and conflict with pastoralists (Davidson et al. 2012). In Mongolia, for example, overexploitation led to a 70% decline in marmot populations nationwide in a single decade

(Wingard and Zahler 2006). Similar changes in marmot numbers in the Pamirs could dramatically reorganize predator and prey communities.

Three caveats weigh on the interpretation of our findings. First, our SCR models described heterogeneity in the distribution of animal activity centers, but the space use submodel simplified individual habitat use to a simple gaussian kernel around the activity center; more realistic models of fine scale habitat use (Royle et al. 2017) could alter predictions of overlap. Second, the temporal mismatch between wolf and snow leopard density models (May-August; August-October) was potentially problematic if there were differences in the spatial distribution of either predator between sampled periods. These first two concerns are alleviated somewhat by the fact that only 1 of 45 camera sites yielded detections of both carnivores (naïve trapsite overlap = 0.07); from these data Karimov et al. (2018) estimated fine-scale (0.0625 km^2) site use for both species, finding snow leopard use increased with slope, whereas wolf use declined with terrain ruggedness. Additionally, estimates of temporal overlap for both species and spatial overlap based only on the first 40 days of camera trap data for snow leopards were indistinguishable from those based on the full data (although SCR model estimates were less precise; Appendix Tables S1-S3). Third, lacking an objective tool to determine scat age during camera deployment, crews relied on subjective assessments of fresh vs. old scats. In a similar landscape, Chetri et al. (2019) found that >99% of putative snow leopard scats revisited 6-7 months after initial discovery had completely decomposed, reducing some of our concern around uncertain sample period here. Additionally, the prevalence of marmots in both carnivore's scats suggests that the majority of samples we collected did in fact correspond to the target period. However, the growing popularity of non-invasive genetics for monitoring snow leopard populations highlights a need for reproducible methods to ascertain or estimate the age of carnivore scats.

The prospect of interference and exploitation competition between wolves and snow leopard could have important consequences for their conservation, particular in light of the threat of declining prey availability (McCarthy et al. 2017; Werhahn et al. 2019). The patterns of niche partitioning and overlap we documented were consistent with conditions predicted to give rise to prey-mediated interactions when prey resources are limited, but this did not appear to be the case here. A full understanding of indirect interactions between snow leopards and wolves will benefit from investigations of patterns of niche segregation during periods of likely prey limitation (i.e., winter), and of prey responses to those patterns. Given that the data collected for this analysis were not suitable for a winter analysis, however, full consideration of the diets of and interactions between these two predators will require further investigation. Nonetheless, the dietary significance of marmots that we documented for both predators adds to a growing recognition of the potential conservation value of small-bodied prey for large carnivores (e.g. Newsome et al. 2016). Although ungulates are likely the primary prey for snow leopards and wolves in the high mountains of Asia on an annual basis, carnivore conservation efforts should not overlook the potential importance of marmots and other alternative prey.

Literature Cited

Ackerman B.B., Lindzey F.G., Hemker T.P. 1984. Cougar food habits in Southern Utah. Journal of Wildlife Management 48:147-155.

Alexander J.S., Gopalaswamy A.M., Shi K., Riordan P. 2015. Face value: Towards robust estimates of snow leopard densities. PLoS One 10:e0134815.

Arnold T.W. 2010. Uninformative parameters and model selection using Akaike's Information Criterion. Journal of Wildlife Management 74:1175–1178.

Bocci A., Lovari S., Khan M.Z., Mori E. 2017. Sympatric snow leopards and Tibetan wolves: coexistence of large carnivores with human-driven potential competition. European Journal of Wildlife Research 63:92.

Borchers D.L., Efford M.G. 2008. Spatially explicit maximum likelihood methods for capture-recapture studies. Biometrics 64:377–385.

Burnham K.P., Anderson D.R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer.

Case T.J., Gilpin M.E.. 1974. Interference competition and niche theory. Proceedings of the National Academy of Sciences of the United States of America 71:3073–3077.

Chaves P.B., Graeff V.G., Lion M.B., Oliveira L.R., Eizirik E. 2012. DNA barcoding meets molecular scatology: short mtDNA sequences for standardized species assignment of carnivore noninvasive samples. Molecular Ecology Resources 12:18–35.

Chetri M., Odden M., Sharma K., Flagstad Ø., Wegge P. 2019. Estimating snow leopard density using fecal DNA in a large landscape in north-central Nepal. Global Ecology and Conservation:e00548.

Chetri M., Odden M., Wegge P. 2017. Snow leopard and Himalayan wolf: food habits and prey selection in the Central Himalayas, Nepal. PloS One 12:e0170549.

Cody M.L., Diamond J.M., editors. 1975. Ecology and evolution of communities. Harvard University Press.

Davidson A.D., Detling J.K., Brown J.H.. 2012. Ecological roles and conservation challenges of social, burrowing, herbivorous mammals in the world's grasslands. Frontiers in Ecology and the Environment 10:477–486.

Efford M. 2004. Density estimation in live-trapping studies. Oikos 106:598–610.

Ekernas L.S., Sarmento W.M., Davie H.S., Reading R.P., Murdoch J., Wingard G.J., Amgalanbaatar S., Berger J. 2017. Desert pastoralists' negative and positive effects on rare wildlife in the Gobi: Pastoralists' effects on wildlife. Conservation Biology 31:269–277.

Fox J., Chundawat R. 2016. What is a snow leopard? Behavior and ecology. In: McCarthy T., Mallon D., editors. Snow leopards, biodiversity of the world: Conservation from genes to landscapes. Elsevier; p. 13–21.

Hayward M.W., Slotow R. 2009. Temporal partitioning of activity in large african carnivores: tests of multiple hypotheses. South African Journal of Wildlife Research 39:109–125.

Holt R.D., Polis G.A.. 1997. A theoretical framework for intraguild predation. The American Naturalist 149:745–764.

Jumabay-Uulu K., Wegge P., Mishra C., Sharma K. 2013. Large carnivores and low diversity of optimal prey: a comparison of the diets of snow leopards *Panthera uncia* and wolves *Canis lupus* in Sarychat-Ertash Reserve in Kyrgyzstan. Oryx 48:529–535.

Karimov K., Kachel S.M., Hackländer K. 2018. Responses of snow leopards, wolves and wild ungulates to livestock grazing in the Zorkul Strictly Protected Area, Tajikistan. PLoS One 13:e0208329.

Kohl M.T., Ruth T.K., Metz M.C., Stahler D.R., Smith D.W., White P.J., MacNulty D.R. 2019. Do prey select for vacant hunting domains to minimize a multi-predator threat? Ecology Letters 22:1724–1733.

Kotler B.P., Blaustein L., Brown J.S.. 1992. Predator facilitation: the combined effect of snakes and owls on the foraging behavior of gerbils. Annales Zoologici Fennici 29:199–206.

Levine S.H. 1976. Competitive interactions in ecosystems. American Naturalist 110:903–910.

Linnell J.D.C., Strand O. 2000. Interference interactions, co-existence and conservation of mammalian carnivores. Diversity and Distributions 6:169–176.

Liu S., Cheng F., Dong S., Zhao H., Hou X., Wu X. 2017. Spatiotemporal dynamics of grassland aboveground biomass on the Qinghai-Tibet Plateau based on validated MODIS NDVI. Scientific Reports 7.

Lovari S., Minder I., Ferreti F., Mucci N., Randi E., Pellizzi B. 2013. Common and snow leopards share prey, but not habitats: competition avoidance by large predators? Interactions between two leopard species. Journal of Zoology 291:127–135.

Lyngdoh S., Shrotriya S., Goyal S.P., Clements H., Hayward M.W., Habib B.. 2014. Prey preferences of the snow leopard (*Panthera uncia*): Regional diet specificity holds global significance for conservation. PLoS One 9:e88349.

McCarthy T.M., Mallon D.P., Jackson R.M., Zahler P., McCarthy K.P. 2017. *Panthera uncia*. In: IUCN 2020. The IUCN Red List of Threatened Species 2020. www.iucnredlist.org. Accessed 13 December 2020.

Meredith M., Ridout M.S. 2014. Overlap: estimates of coefficient of overlapping for animal activity patterns. R package version 0.3.2.

Mishra C. 1997. Livestock depredation by large carnivores in the Indian Trans-Himalaya: conflict perceptions and conservation prospects. Environmental Conservation 24:338–343.

NASA JPL. 2009. ASTER Global Digital Elevation Model. NASA JPL. lpdaac.usgs.gov/node/1079. Accessed 23 April 2018.

NASA LP DAAC. 2016. MODIS/Terra Vegetation Indices 16-Day L3 Global 250m SIN Grid. http://modis.gsfc.nasa.gov. Accessed 23 April 2018.

Nouvellet P., Rasmussen G.S.A., Macdonald D.W., Courchamp F. 2012. Noisy clocks and silent sunrises: measurement methods of daily activity pattern: Measurement of activity pattern. Journal of Zoology 286:179–184.

Palomares F., Caro T.M. 1999. Interspecific killing among mammalian carnivores. The American Naturalist 153:492–508.

Pettorelli N., Ryan S., Mueller T., Bunnefeld N., Jedrzejewska B., Lima M., Kausrud K. 2011. The Normalized Difference Vegetation Index (NDVI): unforeseen successes in animal ecology. Climate Research 46:15–27.

Pianka E.R. 1973. The structure of lizard communities. Annual Review of Ecology and Systematics 4:53–74.

R Development Core Team. 2016. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. www.R-project.org/.

Ridout M.S., Linkie M. 2009. Estimating overlap of daily activity patterns from camera trap data. Journal of Agricultural, Biological, and Environmental Statistics 14:322–337.

Royle J.A., Chandler R.B., Sollmann R., Gardner B. 2014. Spatial capture-recapture. Elsevier.

Royle J.A., Fuller A.K., Sutherland C.. 2017. Unifying population and landscape ecology with spatial capture–recapture. Ecography 41:444–456.

Schmitz O.J., Miller J.R.B., Trainor A.M., Abrahms B.. 2017. Toward a community ecology of landscapes: predicting multiple predator-prey interactions across geographic space. Ecology 98:2281–2292.

Schoener T.W. 1970. Nonsynchronous spatial overlap of lizards in patchy habitats. Ecology 51:408–418.

Schoener T.W. 1974. Resource partitioning in ecological communities. Science 185:27–39.

Sharma R.K., Bhatnagar Y.V., Mishra C. 2015. Does livestock benefit or harm snow leopards? Biological Conservation 190:8–13.

Sih A., Englund G., Wooster D. 1998. Emergent impacts of multiple predators on prey. Trends in Ecology and Evolution 13:350–355.

Sutherland C., Royle J.A., Linden D.W. 2019. oSCR: A spatial capture-recapture R package for inference about spatial ecological processes. Ecography 42:1459–1469.

Vanak A.T., Fortin D., Thaker M., Ogden M., Owen C., Greatwood S., Slotow R. 2013. Moving to stay in place: behavioral mechanisms for coexistence of African large carnivores. Ecology 94:2619–2631.

Weaver J.L. 1993. Refining the equation for interpreting prey occurrence in gray wolf scats. Journal of Wildlife Management 57:534–538.

Weiskopf S.R., Kachel S.M., McCarthy K.P. 2016. What are snow leopards really eating? Identifying bias in food-habit studies: Bias in snow leopard diet. Wildlife Society Bulletin 40:233–240.

Werhahn G., Senn H., Ghazali M., Karmacharya D., Sherchan A.M., Joshi J., Kusi N., López-Bao J.V., Rosen T., Kachel S., et al. 2018. The unique genetic adaptation of the Himalayan wolf to high-altitudes and consequences for conservation. Global Ecology and Conservation 16:e00455.

Werhahn G., Kusi N., Li X., Chen C., Zhi L., Lázaro Martín R., Sillero-Zubiri C., Macdonald D.W.2019. Himalayan wolf foraging ecology and the importance of wild prey. Global Ecology and Conservation 20:e00780.

Wiens J.A. 1993. Fat times, lean times and competition among predators. Trends in Ecology and Evolution 8:348–349.

Wingard J, Zahler P. 2006. Silent Steppe: the illegal wildlife trade crisis in Mongolia. Mongolia discussion papers, East Asia and Pacific Environment and Social Development Department. World Bank, Washington, DC.

Witt K.E., Judd K., Kitchen A., Grier C., Kohler T.A., Ortman S.G., Kemp B.M., Malhi R.S. 2015. DNA analysis of ancient dogs of the Americas: Identifying possible founding haplotypes and reconstructing population histories. Journal of Human Evolution 79:105–118.

Appendix

Table S1. Model selection summary for encounter rate submodels of spatial capture-recapture models of snow leopards based on the first 40 days of camera trap data (1 Aug – 9 Sept 2015).

Species	Encounter rate model	Log likelihood	*n* parameters	ΔAIC
Snow leopard	*~Slope*	66.40	4	0.00
	~Elevation	66.65	4	0.49
	~Rugged	67.42	4	2.03
	~NDVI	67.87	4	2.94
	~(Null)	69.24	3	3.67
	~Ibex	68.24	4	3.69
	~Argali	68.80	4	4.80

Ibex and Argali = binary variables indicating detection of each species; Effort = length of opportunistic scat search paths walked within a given 1 km^2 sampling cell; Null model for snow leopard detection accounted only for trap operation.

Table S2.– Model selection summary for density submodels of spatial capture-recapture models of snow leopards based on the first 40 days of camera trap data only (1 Aug – 9 Sept 2015).

Species	Density model	Log likelihood	*n* parameters	ΔAIC
Snow leopard	*~NDVI + Elevation*	64.09	6	0.00
	~(Null)	66.40	4	0.62
	~ Elevation	65.87	5	1.57
	~ Rugged	66.31	5	2.45
	~Slope	66.32	5	2.46
	~Camp Distance	66.38	5	2.58
	~NDVI	66.39	5	2.61
	~Camp Distance + Elevation	65.51	6	2.85
	~NDVI + Rugged	65.66	6	3.14
	~NDVI + Slope	65.76	6	3.35
	~Camp Distance + NDVI	66.29	6	4.41
	~Camp Distance + Rugged	66.31	6	4.44
	~Camp Distance + Slope	66.32	6	4.45

Camp Distance = distance to the nearest human settlement or seasonal camp; NDVI = average Normalized Difference Vegetation Index; Null models contained no density covariates.

Table S3.– Top spatial capture-recapture model for snow leopards based on the first 40 days of camera trap data only (1 Aug – 9 Sept 2015).

Parameter	Estimate	Standard error
Movement scale:		
log (σ)	8.878	0.207
Encounter rate: log (λ_{ijk})		
α_0	-2.464	0.519
α_{Slope}	0.712	0.362
Density: log($E(D)$)		
β_0	-9.187	3.097
β_{NDVI}	1.583	0.941
$\beta_{Elevation}$	4.060	2.330

CHAPTER 3

UNGULATE SPATIOTEMPORAL RESPONSES TO CONTRASTING PREDATION RISK FROM WOLVES AND SNOW LEOPARDS

Abstract

Spatial responses to risk from multiple predators can precipitate positive and negative emergent consequences for prey (i.e., multiple-predator effects, MPEs) and mediate indirect predator facilitation and competition between predators. How prey respond to risk from multiple predators may therefore have important ramifications for understanding the propagation of non-consumptive effects through ecosystems. The interaction of contextual factors such as predator hunting mode and prey escape tactics has emerged as a potentially key driver of anti-predator behavior but remains underexplored in large vertebrate systems, particularly where sympatric prey share multiple predators. We explored how two mountain ungulates with different escape tactics, vertically-agile, scrambling ibex (*Capra sibirica*) and sprinting argali (*Ovis ammon*), responded to predation risk from two shared carnivores with contrasting hunting modes, cursorial wolves (*Canis lupus*) and stalking snow leopards (*Panthera uncia*), the latter being globally threatened by declining prey availability and retaliatory killing to protect livestock. Contrasting risk posed by the two predators presented prey with clear tradeoffs. Ibex selected for greater exposure to long-term risk from snow leopards, and argali for wolves, in a nearly symmetrical manner that was predictable based on the compatibility of their respective traits. Yet, short-term risk from the same predator upended these long-term strategies, increasing each ungulates' exposure to risk from the alternate predator in a manner consistent with the conflicting anti-predator behaviors theorized to precipitate risk-enhancing MPEs and to mediate

predator facilitation. By contrast, reactive responses to wolves led ibex to reduce their exposure to risk from both predators – a risk-reducing MPE. Evidence of a similar reactive effect for argali vis-à-vis snow leopards was lacking, suggesting that MPEs and prey-mediated interactions between predators are contingent on the interplay of hunting mode and prey escape tactics. Further investigation of interactions among various drivers of contingency in NCEs will contribute to a more comprehensive understanding of the ecological effects of predators.

Introduction

Prey behavioral responses to predation risk are potentially significant drivers of the effects of predators in ecosystems over instantaneous, ecological, and evolutionary time scales (Lima and Dill 1990). Often taking the form of habitat shifts, these responses may help prey balance safety and resources within risky habitats, but they can also decrease access to food, increase stress levels, and negatively affect survival and reproductive success (Brown and Kotler 2004). In addition to these non-consumptive effects (NCEs) of predation on prey themselves, prey responses to tradeoffs between prey safety and resource acquisition can transmit indirect effects among species in communities (Schmitz et al. 1997, Ripple and Beschta 2004, Hebblewhite et al. 2005, Heithaus et al. 2008). For example, conflicting antipredator responses to contrasting patterns of predation risk from multiple predators may lead to positive indirect interactions between otherwise competing predators (i.e., predator facilitation; Charnov et al. 1976, Kotler et al. 1992, Eklöv and VanKooten 2001). Yet, empirical investigations of antipredator behavior and its potential consequences disproportionately focus on single predator-prey pairs (Montgomery et al. 2019), hindering investigation of this kind of predator facilitation (c.f. Atwood et al. 2009, Tornberg et al. 2011, Meadows et al. 2017, Gehr et al. 2018) and, more broadly, a comprehensive understanding of NCEs (Wirsing et al. 2021).

Predation risk, prey's per capita instantaneous probability of being killed by a predator at a given point in space and time, emerges from processes operating in multiple spatiotemporal dimensions (Moll et al. 2017). At long-term temporal scales, overall predation risk can be decomposed as the product of two basic probabilities, both of which may be perceptible to prey: the probability of encounter with a predator and the conditional probability of death (i.e., kill risk) given an encounter (*sensu* Lima and Dill 1990, Hebblewhite et al. 2005). At short-term scales, on the other hand, predation risk may depend on predator proximity, presence, or activity levels (Creel et al. 2008, Kohl et al. 2019), indicators of potential "encounter situations" when one or both species could detect the other's presence and react (Wirsing et al. 2021). Although spatiotemporal responses to predation risk are commonly hypothesized to reflect outright avoidance of high-risk situations (Lima 1998), they may instead reflect management of predator encounter risk separately from kill risk (Lima 1992), as well as dynamic interactions between short- and long-term risk (Lima and Bednekoff 1999), in a manner contingent on the interactions between predator hunting mode and prey escape tactics (Wirsing et al. 2021). Given the tradeoffs imposed by unevenly distributed risk and resources, prey utilizing proactive and/or reactive spatiotemporal habitat selection as a form of antipredator behavior may be expected alternatively to: dynamically avoid situations that place them in close proximity to predators irrespective of long-term spatial risk (the "risky times" hypothesis; Creel et al. 2008); chronically avoid areas with high long-term risk (the "risky places" hypothesis; Creel et a. 2008); or dynamically respond to the interaction of short- and long-term risk, thereby enabling prey to exploit predator absence in order to access resources in areas of high long-term risk (the "risk allocation" hypothesis; Lima and Bednekoff 1999). Empirical evidence across diverse taxa showing prey use and avoidance of risky places dependent on short-term risk (Lima and Dill 1990, Brown and Kotler 2004, Kohl et al. 2019) lends support to the role of risk allocation in prey space use.

Free-living prey typically contend with multiple predators, however, adding further complexity to the tradeoffs they face. Antipredator behaviors that incur only non-consumptive costs (e.g., lost foraging opportunity) in a single-predator setting may instead contribute to non-linear risk enhancement or reduction in a multi-predator setting (i.e., emergent multi-predator effects, MPEs; Sih et al. 1998). Furthermore, empirical evidence suggests that predator hunting mode is an important source of contingencies in antipredator behavior (Wirsing et al. 2021), in particular because stalk-and-ambush (or sit-and-pursue) predators, such as many large felids, have relatively discrete hunting domains that make risk more predictable compared to the relatively unpredictable risk from cursorial predators such as many canids (Preisser et al. 2007). Confronted with multiple predators, prey have been hypothesized to use: spatiotemporal gaps between predator domains, where the instantaneous per capita lethality of all predators is minimized (the "gap" hypothesis; Cresswell and Quinn 2013, Kohl et al. 2019); the domain of the least lethal predator (the "lethality" hypothesis; Relyea 2003); or the domain of cursorial predators (the "predator identity" hypothesis; Priesser et al. 2007). Experimental and observational findings are largely consistent with the prediction that stalking predators exert stronger proactive avoidance than coursing predators (e.g., Thaker et al. 2011, Kuijper et al. 2015, Luttbeg et al. 2020). Yet, despite the theoretical importance of such contingencies for predicting NCE's and the potential conservation and management significance of MPE's and their associated indirect effects among predators, empirical investigations of wild prey responses to multiple predators remain limited (Montgomery et al. 2019).

Further contingencies arise from the diversity of prey escape tactics (Lima 1992, Heithaus et al. 2009, Wirsing et al. 2010, Wirsing et al. 2021): certain tactics may effectively reduce predator lethality to such an extent that prey reap the greatest fitness benefit by selecting space with high encounter probability. That is, sympatric prey species with different escape tactics should make different habitat choices in response to risk from the same predator (Heithaus et al. 2009, Wirsing et al. 2010). However, the efficacy of any given repertoire of escape tactics is unlikely to be equally well-suited to multiple predator hunting modes (Wirsing et al. 2021). In this light, a refined formulation of the lethality hypothesis emerges, which we term the "risky contingencies" hypothesis. Namely, prey navigating multi-predator landscapes should generally eschew predator domains where, because of the predator's hunting mode or landscape features, their escape tactics are less effective post-encounter; instead, they should favor the domain of the predator for which their evasion tactics are better-matched or compatible. Paradoxically, despite lower intrinsic lethality, this "compatible" predator would most likely pose a greater per capita realized risk as measured by total mortality. Investigations in natural systems tend to focus not on the interaction between hunting mode and escape tactics (and thus, their compatibility; but see Dröge et al. 2017) but rather on one or the other (e.g., Thaker et al. 2011, Christianson et al. 2018, Dellinger et al. 2018). To better generalize our understanding of how predators influence their ecosystems, there is a clear need to consider multiple sources of contingencies in risk effects (Wirsing et al. 2021), for example by considering how multiple prey with different escape tactics respond to risk from multiple predators with different hunting modes.

We explored how short-term risk interacts with long-term risk from two predators with differing hunting modes - stalking snow leopards (*Panthera uncia*) and coursing gray wolves - to affect habitat use by two ungulate species with differing escape tactics – vertically-agile, scrambling Siberian ibex (*Capra sibirica*) and sprinting argali (*Ovis ammon*). Throughout their range across the high mountains of Central Asia, snow leopards, classified as "Vulnerable" under IUCN Red List guidelines, are sympatric with wolves (McCarthy et al. 2017). Retaliatory killing and declining wild prey abundance and availability are among the major threats to snow leopards; in recent years the species has been the focus of considerable conservation attention (McCarthy et al. 2017). Wolves are widely persecuted throughout Central Asia, justified primarily to protect livestock but also wild ungulate populations, under the presumption that they regulate the latter (Goldthorpe 2016). Despite potentially high dietary overlap arising from a shared reliance on large ungulate prey, and thus the potential for exploitation competition (Jumabay-uulu et al. 2013), wolves use less rugged spaces in shared landscapes compared to snow leopards, implying that spatial partitioning enables the two species to coexist (Kachel et al. *in press*). Likewise, argali are associated with gentler, flatter habitats compared to ibex (Fedosenko and Blank 2001, 2005). Within this context, we sought to elucidate how spatial responses of the two prey in winter might mediate multiple predator effects for the prey themselves and indirect interactions between the two predators, specifically if one or both ungulates displayed conflicting reactive spatial responses to short-term risk necessary to mediate indirect predator facilitation.

We modelled ibex and argali daytime habitat selection in response to short- and long-term predation risk from snow leopards and wolves as estimated from predator telemetry data, kill site investigations, and direct observations of ungulates. For each predator-prey pair, we considered two alternative characterizations of long-term predation risk representing the relative probability of encountering the predator and the relative probability of a lethal encounter between predator and prey (i.e., the realized risk of predation). Although previous investigations of ungulate responses to predation risk have used a variety of indices and model outputs as proxies for predation risk (Moll et al. 2017), the uncertainty associated with these estimated metrics is typically ignored (e.g., Leblond et al. 2016, Lone et al. 2017, Mumma et al. 2017). Accordingly, we used a novel Bayesian approach to propagate this estimation uncertainty throughout our analysis. We compared multiple competing hypotheses regarding prey responses to short- and long-term predation risk to explore how unique predator-prey match-ups of interacting hunting modes and escape tactics may have influenced those responses. Based on traits of predators and prey, we predicted that argali and ibex would generally select space that exposed them to greater long-term risk from wolves and snow leopards, respectively, and minimize their exposure to the other predator. We further predicted that reactive adjustments in response to short-term risk could undermine those long-term strategies, exposing argali to greater snow leopard risk, and ibex to greater wolf risk.

Methods

Study Area

We collected data from October 2015 to September 2018 in and around the 1491 km^2 Sarychat-Ertash Zapovednik (hereafter Sarychat), Kyrgyz Republic (Fig. 1). The topography is characterized by a U-shaped central river valley and its tributaries, draining steep, glaciated mountains. Elevations range from 2500 to 5500 m. Xerophytic grasses, forbs, and dwarf shrubs dominate the vegetated parts of the landscape. In addition to the focal species, the mammal community of Sarychat includes brown bears (*Ursus arctos*), Eurasian lynx (*Lynx lynx*), red fox (*Vulpes vulpes*), wild boar (*Sus scrofa*), manul (*Otocolobus manul*), marten (*Martes foina*), and marmots (*Marmota baibacina*) (McCarthy et al. 2010). Surrounding areas are managed variously for livestock grazing, large-scale mining, ecotourism, and ungulate trophy hunting.

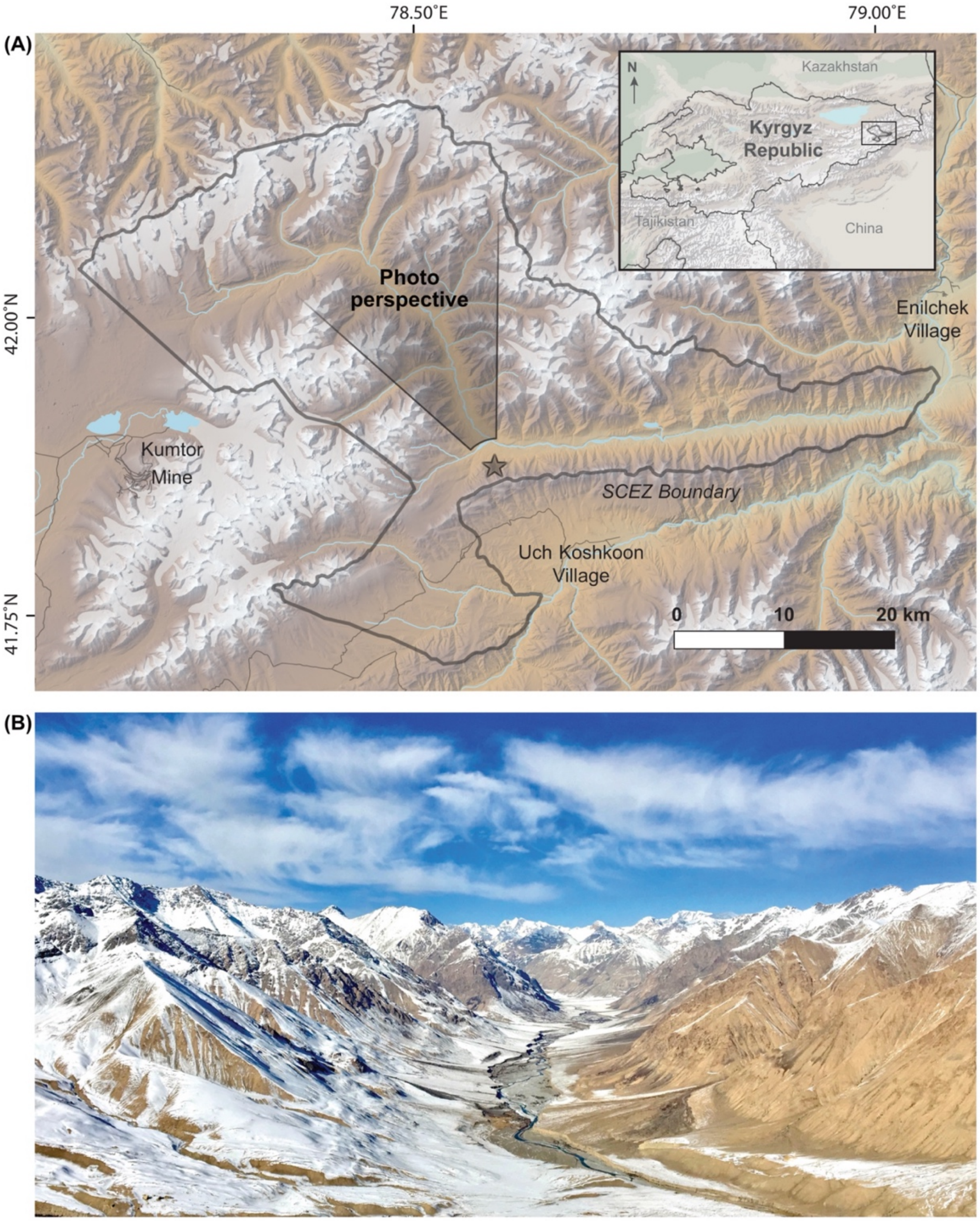

Figure 1. A. Sarychat-Ertash Zapovednik (SCEZ) in the central Tien Shan Mountains, Kyrgyz Republic. B. Characteristic landscape juxtaposing steep, rugged slopes and gentle valley bottom terrain.

Overview

We used a two-stage approach to explore ibex and argali spatial responses to snow leopard and wolf predation risk. First, we built predictive generalized linear models (GLMs) of the two different characterizations of long-term spatial risk: predator encounter risk, an estimate of the relative probability of a wolf or snow leopard using a given point on the landscape, comparing spatial attributes at GPS-collar locations and a random sample of background points; and realized predation risk, a predator-prey pairwise estimate of the relative probability of an ibex or argali being killed by a wolf or snow leopard at a given point on the landscape, comparing spatial attributes at confirmed kill sites against the background landscape. In the second stage, we compared models representing specific hypotheses explaining ungulate spatial resource selection to indices of primary productivity, snow cover, and predation risk: probabilistic predator occurrence, a proxy for encounter risk (Decesare 2012); probabilistic kill occurrence, a proxy for realized risk as estimated by comparing kill locations with a grid of background locations (Moll et al. 2016); and the proximity of the nearest predator as an index of short-term risk (Dröge et al. 2017, Moll et al. 2017). We limited our investigation to the seasonal period from September through April when marmots, an important alternate prey for both predators (Jumabay-uulu et al. 2013, Kachel et al. *in press*), were inactive.

Predator capture, handling, and kill site searches

We collected GPS-collar relocation data from seven adult snow leopards (4 female, 3 male) and two adult wolves (both female) captured using modified Aldridge foot snares (snow leopards) and padded leghold traps (wolves), in compliance with University of Washington Institutional Animal Care and Use Committee Protocol No. 4226-07. Animals were immobilized using a combination of 3 mg/kg of ketamine and 0.08 mg/kg of medetomidine (snow leopards) or 2 mg/kg of tiletamine/zolazepam and 0.4 mg/kg medetomidine (wolves), and fitted with GPS collars (GPS Plus, Vectronic Aerospace GmbH, Berlin, Germany) programmed to attempt a fix for 180 seconds every 4 or 5 hours for wolves and snow leopards, respectively. Upon completion of the handling process, the medetomidine was antagonized with 0.4 mg/kg (snow leopards) or 0.15 mg/kg (wolves) of atipamezole-hydrochloride. We screened collar data to omit locations with likely location errors (2-D locations; DOP>5; Lewis et al. 2007).

To locate ungulate kill sites, we modified Knopff et al.'s (2009) algorithm to identify predator GPS collar relocation clusters as ≥2 locations less than 100 m (snow leopards) or 200 m (wolves) apart within a 24-hour period. We subsequently visited a random subset of clusters to determine, via standard search methods (Anderson and Lindzey 2003, Johansson et al. 2015), if the cluster was associated with a kill, and if so, to determine prey species. We additionally searched for evidence that prey remains had been moved by predators (drag marks, disarticulated remains spread over large areas), and if found, we recorded the kill location at the beginning of the drag marks, at the location of the rumen, or the location of the spinal column. We considered all carcasses as killed by the collared predator if the decomposition state matched the dates of the location cluster, with some exceptions. Ambiguous evidence (e.g., hair and blood) was considered insufficient to classify a site as a kill. Alternatively, wolf rendezvous sites often contained the disarticulated remains (typically long bones and feet) of many different prey imposing an additional standard by which we made the determination to classify a site as a kill - disarticulated legs and feet in wolf beds were not counted as kill locations. If multiple collared animals visited the cluster, we assumed that the kill was attributable to the first animal recorded there.

Ungulate observations

To sample ibex and argali habitat use, field crews walked transects and visited prominent viewpoints at random times spanning the interval from 30 minutes before sunrise and after sunset (Appendix Fig. S1). For point counts, observations were made from predetermined locations that afforded broad views. At such points, two observers scanned the landscape with binoculars and spotting scopes for 20 minutes, not counting time spent monitoring ungulates once detected. For transects, observers stopped and scanned the landscape every 500 m in side valleys, or every 1000 m in broad central valleys. If ungulates were detected between set scan points, observers stopped and scanned the landscape for 20 minutes. Observers recorded observation time, observer location, weather conditions, ungulate group location at first detection (determined using a compass and rangefinder in conjunction with topographic maps), species, group size, and dispersion. Observations of animals moving in response to observers at the time of detection were excluded, as were the 5% of observations made at distances >3 km.

Long-term predation risk

As a proxy for predator encounter risk, we estimated wolf and snow leopard resource selection functions (RSFs, Manly et al. 2002, Hebblewhite et al. 2005) comparing collar locations with random background points, drawn from within a 99% isopleth of an autocorrelated kernel density estimate (aKDE) of the seasonal home range (Calabrese et al. 2016), conditioned on an anisotropic Ornstein-Uhlenbeck foraging process movement model (Fleming et al. 2015). Under appropriate conditions (with sufficient background points) the logistic RSF approximates the intensity function of an Inhomogeneous Poisson Process (IPP), the typical focus for inference in resource selection studies (Hooten et al. 2017). To determine the number of background points needed to reach stable coefficient estimates, we ran the models using 10 unique sets each of 5, 10, 25, 50, and 100 randomly sampled available points per used location and, maximally, 1 available point per 100 m throughout each animal's aKDE. The sign and uncertainty around coefficient parameter estimates converged for both species at a ratio of 25:1, but stability of the estimates continued to improve up to a ratio of 100:1, which we used in final models. We converted location timestamps to "sun times" relative to sunrise and sunset (Nouvellet et al. 2012), and excluded all locations collected between 18:30 and 05:30 on this adjusted scale in order to avoid mischaracterizing the encounter risk relevant to our daylight-only observations of ungulate spatial responses.

We built predator RSFs using Bayesian binomial GLMs where encounter risk, p, was the relative probability of selection, such that for snow leopards the use (1) or availability (0) of the ith location was $y_{ij} \sim \text{Bernoulli}(p_j)$, and $\text{logit}(p_j) = \beta_j \boldsymbol{X}$ where $\boldsymbol{X}$ was the design matrix, β_j was the vector of coefficients for jth individual, drawn from a population-level distribution, i.e., $\beta_j \sim \text{Normal}(\mu_\beta, \sigma_\beta)$ (Hooten et al. 2017), with weakly informative priors $\mu_\beta \sim \text{Logistic}(0,1)$ (Northrup and Gerber 2018) and $\sigma_\beta \sim \text{half-Cauchy}(1^2)$ (Gelman et al. 2014). Given that only two wolves were collared, a full random effects structure was inappropriate (Ogle and Barber 2020). Instead, for wolves, $\text{logit}(p_j) = \beta_{0j} + \beta \boldsymbol{X}$, with Logistic(0,1) priors on covariate β's and β_{0j}, the fixed intercept for the jth individual (Muff et al. 2020).

We modeled realized predation risk separately for each predator-prey pair using RSFs (Moll et al. 2016) comparing kill locations (1) identified from carnivore GPS-collar cluster searches (Appendix Table S1) with background points (0). We drew background points from a 100 m resolution grid covering the combined 99% aKDEs for each predator species (preliminary estimates using random backgound points were sensitive to the random set even at high use-available ratios). For each predator-prey pair, this relative probability of a kill occurring at a given location was a logit-linear function of spatial covariates; i.e., $\text{logit}(p_i)=\beta\boldsymbol{X}$, with $\beta\sim\text{Logistic}(0,1)$. Unlike encounter models, we included all kill locations in realized risk models, regardless of diel timing, as we lacked the temporal resolution necessary to confidently delineate between daytime and nighttime kills (Appendix Fig. S2).

Because our purpose for modelling predation risk was predictive, we built both sets of models with a shared, global set of covariates. These covariates were linked solely to physical terrain structure (derived from elevation; JAXA EORC 2020) because a) preliminary model checking suggested a lack of fit (and/or unacceptably strong multicollinearity) for models incorporating other available remotely sensed covariates (e.g., land cover covariates), and b) other potential covariates of interest relating to snow cover and vegetation were reserved for modelling potential bottom-up responses in ungulate RSFs (see below). Following a preliminary modelling step in which individual covariates were set aside owing to a lack-of-fit (see below), or to strong collinearity with other variables (Pearson's $|r| \geq 0.6$), the final global covariate set for included linear effects for 50-m topographic position index (TPI; Dickson et al. 2005) and vector ruggedness (Sappington et al. 2007), and linear and quadratic effects for 2000-m TPI and slope.

Short-term predation risk

We calculated the distance between each ungulate RSF location (see below) and imputed locations of collared predators over the preceding 12-hour time interval as a measure of short-term risk (Valeix et al. 2009). Imputation, akin to a weighted interpolation, was necessary to approximate the position of collared snow leopards and wolves between collar fixes. To do so, we used the multiple imputation procedure of McClintock (2017), implemented in the R package 'momentuHMM' (McClintock and Michelot 2018), to generate imputed locations between collar locations, at 1-hour intervals, from a single state continuous time movement model. We did not impute locations for gaps in collar fixes >10 hours. For some observation sessions, field crews observed the location of carnivores through direct observations. Because the effect of predator distance should itself weaken with distance, we used the negative log of distance (hereafter proximity) to represent short-term predation risk in ungulate response models (with the negative multiplier aiding in coefficient interpretation). Given that only a fraction of the carnivores in the study area were collared at any given time, predators were almost certainly closer to the observed ungulates than we were able to discern in some cases. In these cases, we would expect prey responses to predator proximity to be masked rather than falsely detected, increasing the probability of Type II errors, but not Type I errors (Creel et al. 2013). Although prey can exploit diel variation in predation risk associated with predator resting times (e.g. Kohl et al. 2019), we did not consider that variation here, as there was substantial overlap in the temporal distribution of kills by both predators (Appendix Fig. S2).

Ungulate resource selection functions

We built spatiotemporally-paired, Bayesian logistic RSFs comparing observed ungulate locations (Appendix Fig. S3) with unused background points. The ith used (1) or background (0) location associated with the jth observation was a random variable, y_{ij}~Bernoulli(p_j), where logit(p_j) = $\beta_{0j} + \beta\boldsymbol{X}$, with weakly informative prior, β~Logistic(0,1), on covariate effects and observation-level fixed intercepts, β_{0j}~Logistic(0,1), where covariates, $\boldsymbol{X}$, were various estimates of short- and long-term predation risk (and their interactions), in addition to Normalized

Difference Vegetation Index (NDVI; NASA LPDAAC 2016), and the percentage of days with snow cover in the preceding 8-day period (hereafter snow cover; Hall and Riggs, 2016). We standardized all covariates to zero mean and unit variance. Because direct observations are only possible in locations with a clear line of sight to the observer, we drew background points only from the intersection of the area visible to observers (up to 3 km) at the time of observation, and a 2 km buffer around the location of the observed animals, at which distance ungulate responses to nearby predators may attenuate (Valeix et al. 2009, Basille et al. 2015). Coefficient estimates in preliminary sensitivity analyses similar to those described for predator RSFs suggested sensitivity to randomly sampling background points, even at use-available ratios of 1:500; we instead drew background points for ungulate RSFs at regular 100 m intervals to ensure full representation of the spatial context available for each observation (Aarts et al. 2013).

Because we used derived estimates of long-term predation risk as covariates in ungulate response models, we propagated the estimation uncertainty arising from encounter and realized risk models into the ungulate spatial response models by treating these covariates as random distributions defined by the posterior distributions of parameters in the predation risk models (see *Implementation*). To understand the impact of propagating this uncertainty, we compared our models against "naïve" models that treated point estimates from risk models as fixed measures. To check for potential multicollinearity among these distributions (as well as other covariates), we approximated the distribution of pairwise Pearson's correlations by calculating r_P for 500 random draws from the posterior distributions of kill and encounter risk models (Appendix Figs. S4 and S5). For all models considered, median $|r_P|$ was <0.6 for all covariate pairs, which we considered evidence of sufficient independence.

In total, we considered six models representing alternative hypotheses to explain ungulate responses to predation risk from multiple predators with contrasting hunting modes. All models contained NDVI and snow cover covariates as potential bottom-up drivers of ungulate space use; the null model, representing the “bottom-up” hypothesis that space use is independent of predation risk, contained only these covariates. The “risky times” model additionally contained short-term risk covariates. We considered both the “risky places” and “risk allocation” hypotheses under the two alternative characterizations of long-term risk from each predator (encounter risk and realized risk), under the expectation that realized risk would better explain ungulate resource selection compared to encounter risk, which might overestimate perceived predation risk (Moll et al. 2017). For those models containing long-term risk covariates, the sign of estimated coefficients provided evidence for or against various hypotheses explaining prey responses to multiple predators : under the “gap” hypothesis, where risk responses are independent of predator identity, we expected similar responses to risk from both predators; under the “hunting mode” hypothesis, where responses are independent of prey escape tactics, responses of ibex and argali should be identical; under the “risky contingencies” hypothesis responses are dependent on traits of predator and prey alike, and we expected to observe unique NCEs from each predator for each ungulate (Table 1 and Appendix Table S2).

Spatial responses to predation risk potentially provide a mechanism necessary to mediate predator facilitation between snow leopards and wolves and thus risk-enhancing MPEs for ibex and argali. If the hypothesized predator facilitation and risk-enhancement were present, we expected model selection to favor risk allocation models generally with positive and negative coefficients, respectively, for intra- and inter-specific short- and long-term risk interactions. Model selection favoring risk allocation models built with realized risk covariates specifically would represent the strongest possible evidence in our data for conditions consistent with predator facilitation. By contrast, a positive coefficient for interspecific interactions would indicate a potentially competitive interaction between the predators (and a risk-reducing MPE), as prey responses to one predator help reduce risk from the other as well.

Table 1. Predicted effects (+/–) of short- and long-term predation risk on ungulate space use under models representing competing hypotheses of risk responses under the "risky contingencies" hypothesis of multiple-predator responses (refer to Appendix Table S2 for predictions under the "gap" and "hunting mode" hypotheses). Parentheses indicate responses predicted to be weak or unimportant, as wholesale avoidance of long-term risk obviates the need for reactive responses. As an illustrative example, under the risk allocation hypothesis with risk-enhancing multiple predator effects and predator facilitation, argali are predicted to proactively avoid areas of high long-term risk from snow leopards and to instead select areas with greater wolf predation risk except when short-term risk (proximity) is high, in which case they should avoid long-term wolf risk and favor long-term snow leopard risk.

		Bottom-up Factors		Long-Term Risk		Predator proximity		Predator proximity – long-term risk Interactions			
Species	Hypothesis	NDVI	Snow-cover	Snow leopard	Wolf	Snow leopard	Wolf	Snow leopard - Snow leopard	Snow leopard - Wolf	Wolf - Snow leopard	Wolf - Wolf
Argali	*Bottom up*	+	–								
	Risky Times	+	–			–	–				
	Risky Places	+	–	–	+						
	Risk Allocation	+	–	–	+	(–)	–	(–)	(+)	+	–
Ibex	*Bottom up*	+	–								
	Risky Times	+	–			–	–				
	Risky Places	+	–	+	–						
	Risk Allocation	+	–	+	–	–	(–)	–	+	(+)	(–)

Implementation

We built and ran all models using 'Nimble' v.0.10 (de Valpine et al. 2017), accessed via R (R Core Team 2018). For RSF and realized risk models, we ran 2 chains with 40,000 iterations, 15,000 burn-in. For ungulate response models, we ran 2 chains of 50,000 iterations, 20,000 burn-in. We propagated the estimation error arising from modelling (rather than measuring) predation risk covariates in ungulate response models using customized MCMC samplers to draw, with 100% acceptance, from normal distributions defined by the means and standard deviations of the population-level posterior distributions of the coefficients of those first-tier models. Thus, within each iteration, we sampled long-term risk covariates from the posterior distributions of encounter risk and realized risk models without exposing them to updating informed by ungulate responses. To maintain consistent coefficient scales and achieve convergence, we standardized these uncertain covariates within each MCMC iteration.

Model checking, predictive performance, and selection

To evaluate model convergence, we visually inspected posterior trace and density plots and calculated potential scale reduction factors, where $\hat{R}$>1.1 indicated acceptable convergence (Gelman et al. 2014). To evaluate goodness-of-fit, we calculated Bayesian P-values (P_B) based on chi-square test statistics comparing observed data (y) and data simulated from model parameters (y_{new}) against model expectations (p), where

$$\chi^2_{new} = \sum_i \frac{(y_i - p_i)^2}{p_i}$$

and values of the expression $Pr(\chi^2_{new} \geq \chi^2_{data})$ outside of the interval 0.1-0.9 indicate a potential lack of fit (Hooten and Hobbs 2015). If lack of fit was indicated, we used binned residual plots of known used locations (or kills) to identify problematic covariates, which were then removed from the models.

In lieu of formal model selection for predator RSFs and realized risk models, we formulated “global” covariate sets (shared across species), as our goal for these models was primarily predictive, not inferential. After winnowing the covariates based on our model checking procedure, we used *M*-fold cross validation to assess predictive performance (Boyce et al. 2002), where *M*=6, or 7 for the snow leopard RSF). We evaluated predictive accuracy using the mean Spearman rank correlation (r_s) of (equal-area) quantile-binned RSF values across the background landscape and the frequencies of used locations in each bin calculated for *M* subsets withheld data. We used 20 quantile bins for RSF models, but only 5 for kill models, given the sparsity of kills for some species pairs. We interpreted $r_s \geq 0.7$, indicating strong correlation between observed used locations, as representing acceptable predictive performance for predator encounter models; for realized risk models we used a less-stringent standard of acceptable performance, $r_s \geq 0.6$. We used WAIC (Watanabe 2010) to select among competing models of ungulate responses to predation risk, where lower scores indicated superior models (Hooten and Hobbs 2015).

Results

Predation risk models

Contrasting patterns of wolf and snow leopard habitat use (Fig. 2) were associated with divergent responses to slope (wolves selected flatter spaces, snow leopards selected steeper spaces) and snow leopard selection for more rugged features (Table 2). Clear drivers of kill site locations in realized risk models (as defined by 95% CRIs of coefficient estimates that did not overlap zero) were apparent in each predator-prey pair (Table 2). For both ungulates, kills by both predators were associated with negative values of 2000-m TPI, corresponding to large scale topographic minima such as river valley bottoms; argali kill occurrence was further associated with 2000-m TPI via a negative quadratic relationship. Negative quadratic relationships were also apparent with respect to slope for all pairs (although only moderately so for wolves and ibex). Wolf kills were negatively associated with slope. Snow leopard kills were associated with negative values of 50-m TPI, corresponding to fine-scale escarpment and drainage features, and with steeper slopes (although there was only moderate evidence of this relationship for argali).

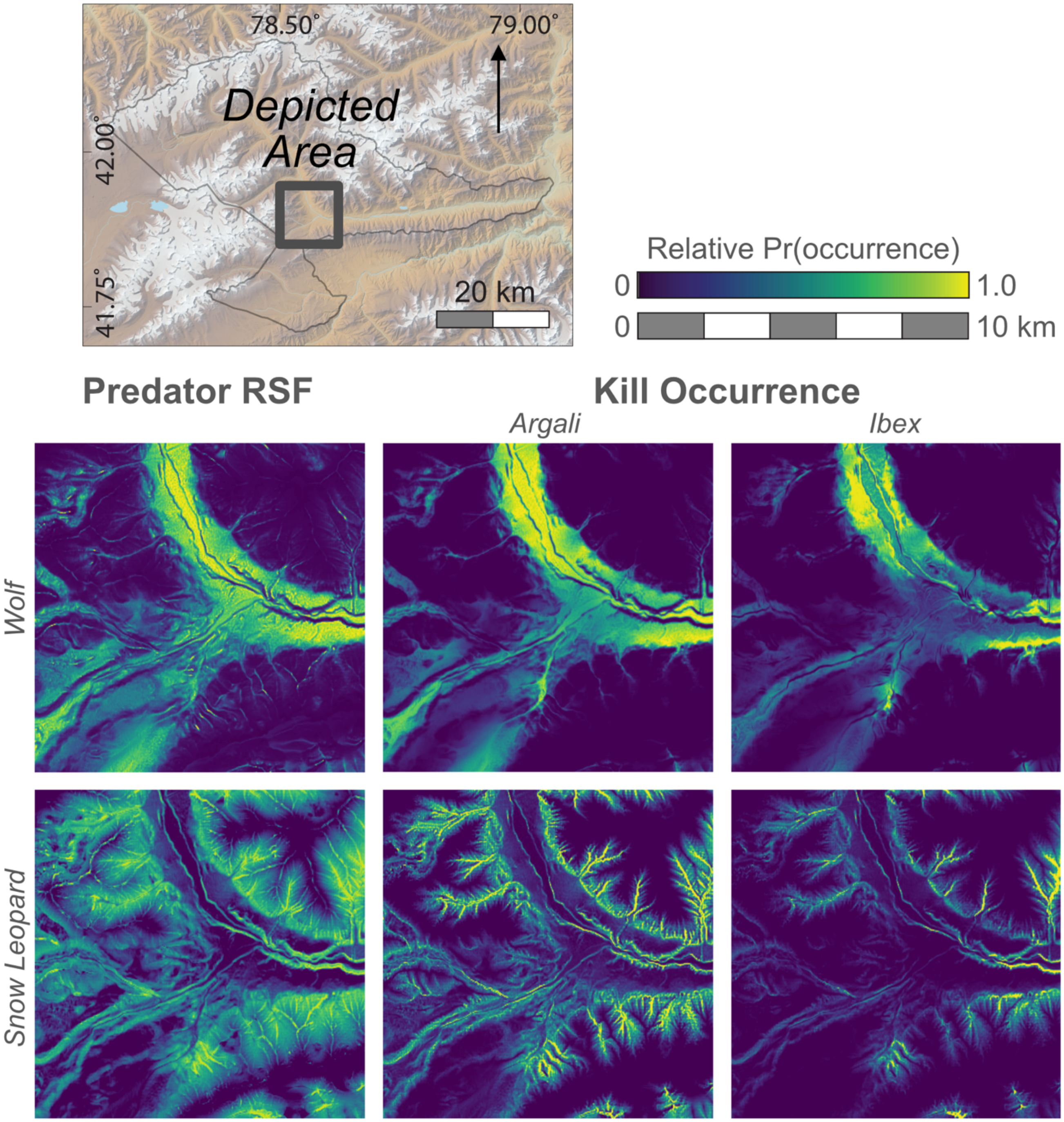

Figure 2. Predicted relative probability (scaled 0-1) maps of wolf and snow leopard occurrence (encounter risk) estimated from predator RSFs, and kill occurrence (realized risk) estimated from RSFs comparing kill sites and background lcoations.

Table 2. Posterior predictive checks, cross-validation scores, and covariate coefficients (with 95% credible intervals in parentheses) for snow leopard and wolf RSF (encounter risk) models and predator-prey pairwise kill site (realized risk) models for ibex and argali. Bayesian P-values (P_B) <0.1 or >0.9 suggest a lack of fit, whereas cross-validation scores ≥ 0.6 indicate strong Spearman rank correlation between predicted and observed locations of collared animals (encounter models) or kill sites (realized risk models), and thus acceptable predictive performance for withheld data. TPI-50, and -2000 indicate topographic position index across 50-, and 2000-m scales. Bold text highlights coefficients with 95% CRIs that did not overlap 0.

			Covariate effect coefficients (β's)					
Risk component	P_B	Cross-validation score	TPI-2000	TPI-2000^2	Vector Ruggedness	Slope	Slope^2	TPI-50
Snow leopard encounter	0.83	0.78 (0.63–0.89)	**-0.83** **(-1.27 – -0.36)**	-0.28 (-0.61 – 0.05)	**0.31** **(0.22 – 0.40)**	**0.52** **(0.26 – 0.75)**	**-0.29** **(-0.50 – -0.09)**	**0.21** **(0.10 – 0.31)**
Wolf encounter	0.23	0.92 (0.89–0.95)	**-0.63** **(-0.76 – -0.52)**	**-0.17** **(-0.24 – -0.11)**	0.05 (-0.03 – 0.12)	**-1.14** **(-1.28 – -1.00)**	**-0.29** **(-0.41 – -0.18)**	**0.25** **(0.17 – 0.34)**
Argali – snow leopard kill	0.35	0.73 (0.43–0.96)	**-1.60** **(-2.59 – -0.76)**	**-0.89** **(-1.61 – -0.30)**	-0.04 (-0.42 – 0.28)	0.26 (-0.24 – 0.72)	**-0.46** **(-0.97 – 0.05)**	**-0.45** **(-0.85 – -0.08)**
Argali - wolf kill	0.22	0.87 (0.68–0.98)	**-1.61** **(-2.33 – -0.92)**	**-0.42** **(-0.75 – -0.12)**	-0.24 (-0.74 – 0.15)	**-1.66** **(-2.59 – -0.96)**	**-0.61** **(-1.20 – -0.12)**	-0.12 (-0.55 – 0.27)
Ibex – snow leopard kill	0.80	0.89 (0.82–0.96)	**-1.42** **(-1.88 – -1.02)**	-0.12 (-0.36 – 0.09)	0.09 (-0.10 – 0.26)	**0.69** **(0.43 – 0.94)**	**-0.25** **(-0.54 – -0.14)**	**-0.33** **(-0.54 – -0.14)**
Ibex - wolf kill	0.56	0.62 (0.40-78)	**-1.85** **(-3.63 – -0.49)**	-0.19 (-0.85 – 0.34)	-1.18 (-3.17 – 0.06)	-0.52 (-1.59 – 0.38)	-0.62 (-1.60 – 0.19)	0.11 (-0.84 – 1.01)

Ungulate responses to predation risk

For both ungulates, the best supported models included interactions between short- and long-term predation risk (i.e., the "risk allocation" hypothesis), with long-term risk characterized by the relative probability of kill occurrence (i.e., realized risk) (Table 3). For argali, the risk allocation model with risk characterized by predator occurrence (i.e., encounter risk) yielded a nominally lower WAIC score, but the posterior check suggested a lack of fit (B_P=0.96). Consistent with our expectations under the "risky contingencies" hypothesis, both ungulates displayed unique spatial responses to risk from each predator (Table 4). Ibex selected areas with greater long-term snow leopard predation risk, whereas argali selected areas of greater long-term wolf risk. For both ungulates, avoidance of long-term risk posed by the alternate predator was primarily evident in the interaction between short- and long-term risk for that predator. We found strong evidence, in the form of a positive coefficient between short-term snow leopard risk and long-term wolf risk, that ibex selected areas of greater long-term wolf risk when snow leopards were nearby, consistent with predator facilitation. Similar evidence for argali, with respect to wolf proximity and snow leopard risk, was somewhat equivocal but nonetheless apparent (Fig. 3). By contrast, a negative selection coefficient for ibex for the interactive effect of wolf proximity and long-term snow leopard risk, indicated the potential for a risk-reducing multiple predator effect. Bottom-up factors were only obviously important in ibex models, where selection was positively associated with NDVI, despite a 95% credible interval nominally overlapping zero.

Propagating estimation uncertainty from predation risk models into ungulate RSF models did not produce qualitatively different results from estimation uncertainty models and naïve models (Fig. 3, Appendix Table 3). However, under the estimation uncertainty model for ibex we were >99.9% certain that ibex respond positively to the interaction of long-term wolf risk and snow leopard proximity, compared to only 85.9% certain under the naïve model. By contrast, under the naïve approach we would have been 90.5% confident that argali responded positively to the interaction between wolf proximity and snow leopard kill risk, whereas we were only 85.6% confident of the same relationship when accounting for estimation uncertainty (Fig. 3., Appendix Table S3).

Table 3. Model selection results for argali and ibex spatial response models. All models included covariates for NDVI and Snow Cover. Risky times models included predator proximity covariates. Risky places and risk allocation models included covariates representing long-term predation risk, estimated using either predator location data (RSF) or kill site locations (Kills). Risk allocation models additionally included predator proximity and interactions between predator proximity and long-term predation risk. Bayesian P-values (P_B) <0.1 or >0.9 indicate potential lack-of-fit. Lower values of WAIC correspond to better-supported models. Results for naïve models, which ignored estimation uncertainty in long-term predation risk covariates, are presented for comparison only.

		Estimation Uncertainty Model		Naïve Model	
Species	Model	P_B	WAIC	P_B	WAIC
Argali	Bottom-up	0.64	4313.17		
	Risky Times	0.55	4314.53		
	Risky Places - RSF	0.84	4157.26	0.92	4158.33
	Risky Places - Kills	0.80	4160.36	0.96	4158.19
	Risk Allocation - RSF	0.96	4153.90	0.94	4154.50
	Risk Allocation - Kills	0.87	4154.03	0.89	4148.98
Ibex	Bottom-up	0.65	3198.22		
	Risky Times	0.63	3193.48		
	Risky Places - RSF	0.75	3171.85	0.68	3178.44
	Risky Places - Kills	0.41	3179.91	0.51	3185.15
	Risk Allocation - RSF	0.72	3157.52	0.75	3161.82
	Risk Allocation - Kills	0.57	3136.67	0.69	3172.80

Table 4. Ibex and argali RSF selection coefficient estimates and credible intervals under the risk allocation and risky contingencies model.

Covariate	β posterior mean (95% Credible Interval)			
	Argali		Ibex	
Vegetation & climate				
NDVI	-0.04	(-0.17 - 0.11)	0.17	(-0.01 - 0.31)
Snow cover	0.04	(-0.10 - 0.18)	-0.03	(-0.18 - 0.11)
Long-term predation risk				
Snow leopard	-0.02	(-0.25 - 0.17)	0.12	(0.01 - 0.23)
Wolf	0.49	(0.37 - 0.61)	-0.10	(-0.26 - 0.06)
Short-term predation risk				
Snow leopard proximity	0.16	(-0.07 - 0.37)	0.38	(0.13 - 0.61)
Wolf proximity	-0.09	(-0.44 - 0.24)	-0.31	(-1.05 - 0.42)
Interactions - Snow leopard proximity...				
...× Snow leopard	-0.08	(-0.22 - 0.06)	-0.07	(-0.17 – 0.02)
...×Wolf	-0.01	(-0.12 - 0.12)	0.35	(0.19 - 0.56)
Interactions - Wolf proximity...				
...×Snow leopard	0.12	(-0.10 - 0.39)	-0.20	(-0.43 - 0.00)
...×Wolf	-0.14	(-0.32 - 0.04)	-0.38	(-0.72 - -0.08)

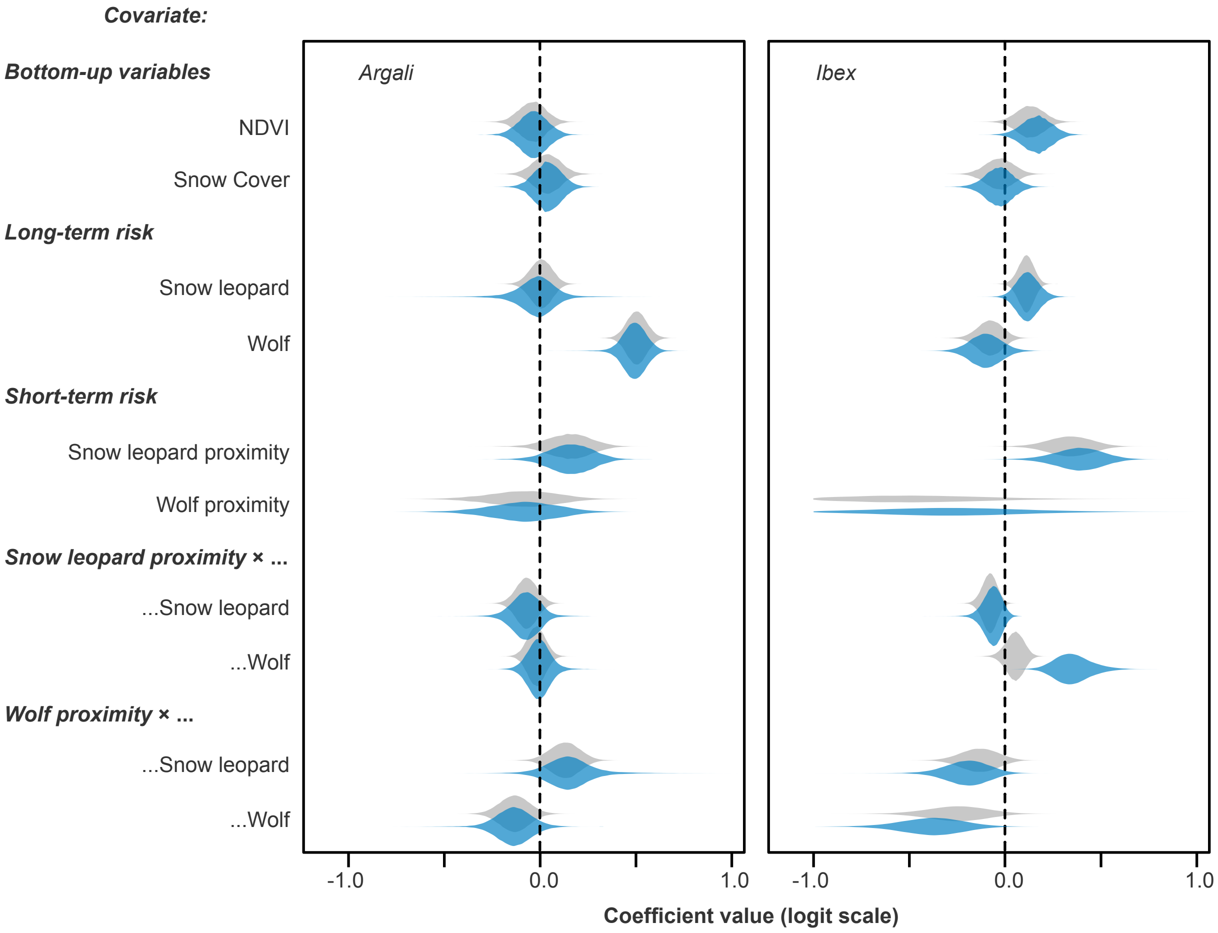

Figure 3. Comparison of selection coefficient posterior distributions for top models of ibex and argali resource selection with respect to wolf and snow leopard predation risk for models ignoring (gray) and incorporating (blue) estimation uncertainty associated with predation risk models.

Discussion

We found considerable evidence in support of the hypothesis that non-consumptive predator effects on ibex and argali behavior were driven by the interaction between long- and short-term risk (Lima and Bednekoff 1999), even after accounting for uncertainty in our model-based estimates of long-term risk. Ibex and argali responded differently to risk from snow leopards and wolves – with respect to each other and to each predator – in a manner that was predictable based on the relative compatibility of their respective escape tactics and predator hunting modes. Overall, observed habitat selection by ibex and argali suggested that both ungulates' spatial responses to contrasting predation risk may precipitate risk-enhancing multiple predator effects and mediate indirect interactions between wolves and snow leopards. In this respect, despite some uncertainty, the two ungulates' responses were nearly symmetrical. However, ibex responses to wolf proximity may precipitate a risk-reducing MPE and thus behaviorally mediated exploitation competition. Our results contribute to a more comprehensive understanding of the role of predators in ecosystems by highlighting how temporal patterns of risk and the interaction between hunting mode and prey escape tactics may shape non-consumptive effects, and multiple-predator effects in particular (Wirsing et al. 2021). Our findings also reinforce what is known about the relationship between snow leopards and wolves while offering novel insights into natural history and spatiotemporal predator-prey ecology in an ecosystem of significant conservation concern.

Our results add to the growing body of empirical evidence indicating that risk effects on prey behavior are driven by the interaction of short- and long-term risk (e.g., Ferrari et al. 2009, Dröge et al. 2017) as theorized by Lima and Bednekoff (1999). For both ungulate species, short-term risk modified patterns of selection with regard to long-term risk. The two ungulates avoided neither long-term risk wholesale, irrespective of predator identity, nor based solely on predator hunting mode. Instead, both species selected spaces where long-term risk from one predator or the other was higher, consistent with the risky contingencies/lethality hypothesis (Relyea 2003). Ibex generally favored the snow leopard habitat domain, and argali generally favored the wolf domain. Although our data were inappropriate for estimating predator-specific mortality rates, they suggest that for ibex, realized mortality from snow leopards outweighed that from wolves, and vice versa for argali (Table S1). Assuming this was the case, both ungulates generally selected space in a manner that increased their exposure to the predator responsible for most of their realized predation mortality, presumably because they were better able to manage post-encounter probability of death from this predator (Wirsing et al. 2010).

Ungulate responses were qualitatively similar regardless of which proxy we used for long-term predation risk. In part, this result comports with empirical findings elsewhere suggesting that predators preferentially select landscape features linked to hunting success (Decesare 2012). However, it may also reflect limitations in our data and our approach to characterizing realized risk. For example, neither of the risk proxies disentangled the *conditional* probability of a kill *given* an encounter (i.e., the intrinsic risk of a kill given the presence of predator *and* prey) – such a metric would theoretically be more cleanly distinct from marginal encounter risk and have a stronger theoretical basis as a driver of prey behavior (Moll et al. 2017, Wirsing et al. 2021). Additionally, the resolution of remotely-sensed covariate data determined the resolution at which we were able to estimate long-term predation risk. There is no clear means to determine the scale of the appropriate spatial window over which to evaluate prey responses to predation risk (Moll et al. 2017), in part because the relevant scale almost certainly varies with each encounter, and with individual heterogeneity in predator and prey. Similarly, we lacked the a priori information necessary to classify predation refugia, precluding explicit consideration of the spatial arrangement and proximity of refugia in shaping realized risk. Thus, our approach may have missed microhabitat features – but also large-scale features – key to enabling prey to manage kill risk independently of encounter risk.

The interactive effects of short- and long-term risk on both ungulates' space use were consistent with those predicted to precipitate MPEs and indirect interactions between snow leopards and wolves. Ibex avoided long-term wolf risk, except when short-term risk from snow leopards was high, in which case they selected for risky areas vis-à-vis wolves. This pattern suggests that the species' response to short-term snow leopard risk conflicted with its long-term strategy of wolf avoidance, and could therefore precipitate a risk-enhancing MPE (Sih et al. 1998) and mediate snow leopard facilitation of wolves by affording them additional hunting opportunity and prey (Charnov et al. 1976). Evidence that argali could mediate the reciprocal relationship (wolf facilitation of snow leopards) was less strong, but still apparent. Although similar dynamics have been observed among ungulates in multiple ecosystems (Creel et al. 2005, Atwood et al. 2009, Leblond et al. 2016, Gehr et al. 2018), the presence of conflicting responses to multiple predators alone does not demonstrate predator facilitation (or a risk-enhancing MPE, Sih et al. 1998), which ultimately predicts increased prey mortality and enhanced predator fitness. Furthermore, if predators partition time as well as space, prey may simply select for shifting temporal "vacancies" in risk in order to use otherwise risky places at safe times (Kohl et al. 2019). Although we did not explicitly account for diel variation in risk in our analysis (which was limited to daytime observations), approximations of that variation based on the likely timing of documented kills suggested that both predators were active and lethal to both ungulates throughout the day, with relatively little variation (Appendix Fig. S2). Likewise, estimates of snow leopard and wolf temporal overlap from other systems suggest substantial overlap in the temporal niches of the two predators (Kachel et al. *In press*, Salvatori et al. 2021). In addition to responses capable of precipitating risk-enhancing MPE's, for ibex the negative coefficients we estimated for interactions between short-term risk from wolves and long-term risk from snow leopards indicated that ibex selected less risky spaces with respect to *both* predators when short-term risk from the wolves was high – a risk-reducing MPE (Sih et al. 1998). The lack of correlation between our estimates of long- and short-term risk to ibex bolstered this interpretation. We did not find similar evidence for argali vis-à-vis snow leopards, but we could not dismiss the possibility either. Together, these findings suggest that MPEs, as with other NCEs, are contingent on the compatibility of predator hunting mode and prey escape tactics (Wirsing et al. 2021) and highlight how different prey may mediate different interactions between shared predators.

Though predictive rather than inferential, predator encounter models revealed contrasting patterns of snow leopard and wolf habitat use, as we expected based on their contrasting hunting modes. Namely, snow leopards used steeper slopes and more rugged features than wolves – consistent with findings elsewhere suggesting that the two predators coexist primarily via spatial partitioning along topographic dimensions (Kachel et al. *In press*). Yet, snow leopards and wolves co-occur positively at larger scales (Salvatori et al. 2021) and are sympatric throughout the snow leopard's geographic range. Considering that similar patterns of spatial differentiation but temporal and dietary overlap have been documented elsewhere, the MPEs and indirect prey-mediated relationships between the two carnivores that we infer may be widespread as well.

Given the relatively small number of collared snow leopards and wolves we used to estimate predator RSFs and to locate kill sites for estimating realized risk, we could not ignore the uncertainty associated with using those estimates as covariates in ungulate models, despite strong patterns of selection in both predators that likely reduced the total number of collared animals necessary to estimate consistent selection coefficients (Appendix Table S4; Street et al. 2021). Ignoring the uncertainty in estimated predation risk, and instead treating such estimates as known quantities, would have led us different levels of confidence in our interpretations of NCEs but not a qualitatively different understanding of the underlying ecology: the primary effect of accounting for estimation uncertainty was broader credible intervals on ungulate selection coefficients, but for most coefficients, the change was minor. Our confidence in the positive interactions between wolf proximity and snow leopard realized risk for argali, and between snow leopard proximity and wolf realized risk for ibex – effects of central interest in our investigation of the potential for predator facilitation – diminished somewhat from 90.5% to 85.6% in the first case, but increased dramatically in the second case, from 85.9% to >99.9%. Notably, we did not account for other sources of potential uncertainty such as measurement error in remotely sensed covariates (Dellaportas and Stephens 1995) and model choice uncertainty (Peters and Herrick 2004). Nonetheless, we expect that our approach, using a custom MCMC sampler to treat estimated covariates as random variables drawn from known distributions, should be transferable to other applications where researchers seek to treat derived quantities as predictor variables in subsequent analyses.

Conservation implications

Although Sarychat is somewhat unique among protected areas in Central Asia in that livestock are absent from the core of the reserve, the patterns of predator habitat use we described are consistent with evidence from comparable landscapes with significant livestock numbers (e.g., Karimov et al. 2018, Kachel et al. *In press*). Contrasting habitat use by wolves and snow leopards potentially imposes the same risk tradeoff on pastoralist communities as on wild prey. By implication, strategies that rely on shifting grazing areas out of snow leopard habitats in order to reduce and mitigate livestock depredation and the resultant retaliatory killing of snow leopards may, from the perspective of pastoralists, simply shift the problem from snow leopards to wolves, without meaningfully reducing livestock losses. Furthermore, the possibility of prey-mediated predator facilitation implied by our results suggests that neglecting wolves in snow leopard conservation efforts may be counterproductive over ecological timescales. The considerable conservation investment devoted to snow leopards has likely improved attitudes of local communities toward the species; despite perpetrating often comparable levels of livestock depredation, however, sympatric wolves remain poorly-perceived (Kusi et al. 2020) and highly persecuted across the high mountains of Asia, often with official sanction or bounties (Goldthorpe 2016, Kachel et al. 2021*b*). Indeed, even within strictly protected areas, rangers routinely target the wolves for lethal control (*personal observation*). Although we did not evaluate whether the potential for predator facilitation has realized foraging and fitness benefits for snow leopards (which are threatened in part by declining prey availability; McCarthy et al. 2017), the possibility highlights the potentially important interaction pathways that may be lost if conservation focuses too narrowly on single species. More broadly, carnivore conservation is justified in part because carnivores can shape ecosystem structure and function not only through density-mediated interactions, but behaviorally-mediated ones as well (Ripple et al. 2014). Whereas behaviorally-mediated interactions associated with NCEs that are triggered by long-term risk (such as ibex avoidance of long-term wolf risk) may persist even at low predator densities (Kuijper et al. 2016), NCEs that are triggered by short-term risk – as in the MPEs and indirect predator-predator interactions that we infer here – are likely attenuated at low predator densities, implying that the realized ecological role of large carnivores in low-density, human-dominated settings may fall short of its putative potential.

Conclusion

Although the importance of NCEs as ecosystem-structuring factors is widely recognized, multiple sources of contingency, of which predator hunting mode and prey escape tactics are but two, complicate the project of predicting their consequences in any particular community (Wirsing et al. 2021), particularly where prey contend with multiple predators. Our results demonstrate how consideration of interactions between various drivers of contingency, including the compatibility of hunting mode and escape tactics, may contribute to a more comprehensive and general understanding of the ecological role of predators: ibex and argali avoided or selected risk vis-à-vis their respective compatible and mismatched predators in a nearly identical fashion. Furthermore, these NCEs may propagate as multiple predator effects and indirect interactions between snow leopards and wolves. These insights were only possible because we investigated multiple predators and multiple prey in unison. In addition to further studies of multiple predator-prey systems capable of elucidating the interactive roles of contingencies in risk effects, those that explicitly measure if and how risk effects are transmitted as MPEs and indirect predator-predator interactions in terrestrial vertebrate systems, for example following the approach proposed by Ford and Goheen (2015), will shed valuable light on the ecological role of risk effects.

Literature Cited

Aarts, G., MacKenzie, M., McConnell, B., Fedak, M. and Matthiopoulos, J. (2008). Estimating space-use and habitat preference from wildlife telemetry data. *Ecography*, 31, 140–160.

Anderson, C.R. and Lindzey, F.G. (2003). Estimating Cougar Predation Rates from GPS Location Clusters. *J. Wildl. Manag.*, 67, 307.

Atwood, T.C., Gese, E.M. and Kunkel, K.E. (2009). Spatial Partitioning of Predation Risk in a Multiple Predator-Multiple Prey System. *J. Wildl. Manag.*, 73, 876–884.

Basille, M., Fortin, D., Dussault, C., Bastille-Rousseau, G., Ouellet, J.-P. and Courtois, R. (2015). Plastic response of fearful prey to the spatiotemporal dynamics of predator distribution. *Ecology*, 96, 2622–2631.

Boyce, M.S., Vernier, P.R., Nielsen, S.E. and Schmiegelow, F.K. (2002). Evaluating resource selection functions. *Ecol. Model.*, 157, 281–300.

Brown, J.S. and Kotler, B.P. (2004). Hazardous duty pay and the foraging cost of predation. *Ecol. Lett.*, 7, 999–1014.

Calabrese, J.M., Fleming, C.H. and Gurarie, E. (2016). ctmm: an r package for analyzing animal relocation data as a continuous-time stochastic process. *Methods Ecol. Evol.*, 7, 1124–1132.

Charnov, E.L., Orians, G.H. and Hyatt, K. (1976). Ecological Implications of Resource Depression. *Am. Nat.*, 110, 247–259.

Christianson, D., Becker, M.S., Brennan, A., Creel, S., Dröge, E., M'soka, J., *et al.* (2018). Foraging investment in a long-lived herbivore and vulnerability to coursing and stalking predators. *Ecol. Evol.*

Creel, S., Winnie, J., Maxwell, B., Hamlin, K. and Creel, M. (2005). Elk alter habitat selection as an antipredator response to wolves. *Ecology*, 86, 3387–3397.

Creel, S., Winnie, J.A. and Christianson, D. (2013). Underestimating the frequency, strength and cost of antipredator responses with data from GPS collars: an example with wolves and elk. *Ecol. Evol.*, 3, 5189–5200.

Creel, S., Winnie, J.A., Christianson, D. and Liley, S. (2008). Time and space in general models of antipredator response: tests with wolves and elk. *Anim. Behav.*, 76, 1139–1146.

Cresswell, W. and Quinn, J.L. (2013). Contrasting risks from different predators change the overall nonlethal effects of predation risk. *Behav. Ecol.*, 24, 871–876.

DeCesare, N.J. (2012). Separating spatial search and efficiency rates as components of predation risk. *Proc. R. Soc. B Biol. Sci.*, 279, 4626–4633.

Dellaportas, P. and Stephens, D.A. (1995). Bayesian Analysis of Errors-in-Variables Regression Models. *Biometrics*, 51, 1085–1095.

Dellinger, J.A., Shores, C.R., Craig, A., Heithaus, M.R., Ripple, W.J. and Wirsing, A.J. (2018). Habitat use of sympatric prey suggests divergent anti-predator responses to recolonizing gray wolves. *Oecologia*.

Dickson, B.G., Jenness, J.S. and Beier, P. (2005). Influence of Vegetation, Topography, and Roads on Cougar Movement in Southern California. *J. Wildl. Manag.*, 69, 264–276.

Dröge, E., Creel, S., Becker, M.S. and M'soka, J. (2017). Risky times and risky places interact to affect prey behaviour. *Nat. Ecol. Evol.*, 1, 1123–1128.

Eklöv, P. and VanKooten, T. (2001). Facilitation among piscivorous predators: effects of prey habitat use. *Ecology*, 82, 2486–2494.

Fedosenko, A.K. and Blank, D.A. (2001). Capra sibirica. *Mamm. Species*, 675, 1–13.

Fedosenko, A.K. and Blank, D.A. (2005). Ovis ammon. *Mamm. Species*, 773, 1–15.

Ferrari, M.C.O., Sih, A. and Chivers, D.P. (2009). The paradox of risk allocation: a review and prospectus. *Anim. Behav.*, 78, 579–585.

Fleming, C.H., Fagan, W.F., Mueller, T., Olson, K.A., Leimgruber, P. and Calabrese, J.M. (2015). Rigorous home range estimation with movement data: a new autocorrelated kernel density estimator. *Ecology*, 96, 1182–1188.

Ford, A.T. and Goheen, J.R. (2015). Trophic Cascades by Large Carnivores: A Case for Strong Inference and Mechanism. *Trends Ecol. Evol.*, 30, 725–735.

Gehr, B., Hofer, E.J., Pewsner, M., Ryser, A., Vimercati, E., Vogt, K., *et al.* (2018). Hunting-mediated predator facilitation and superadditive mortality in a European ungulate. *Ecol. Evol.*, 8, 109–119.

Gelman, A., Vehtari, A., Dunson, D.B., Rubin, D.B., Stern, H.S. and Carlin, J.B. (2014). *Bayesian data analysis*. Third Edition. Chapman and Hall.

Goldthorpe, G. (2016). *The wolf in Eurasia: a regional approach to the conservation and management of a top predator in Central Asia and the South Caucusus* (Technical Report). Flora and Fauna International.

Hall, D. and Riggs, G. (2016). MODIS/Terra Snow Cover 8-Day L3 Global 500m SIN Grid, Version 6 Boulder, Colorado USA. NASA National Snow and Ice Data Center Distributed Active Archive Center. DOI: 10.5067/MODIS/MOD10A2.006.

Hebblewhite, M., Merrill, E.H. and McDonald, T.L. (2005a). Spatial decomposition of predation risk using resource selection functions: an example in a wolf–elk predator–prey system. *Oikos*, 111, 101–111.

Hebblewhite, M., White, C.A., Nietvelt, C.G., McKenzie, J.A., Hurd, T.E., Fryxell, J.M., *et al.* (2005b). Human Activity Mediates a Trophic Cascade Caused by Wolves. *Ecology*, 86, 2135–2144.

Heithaus, M.R., Frid, A., Wirsing, A.J. and Worm, B. (2008). Predicting ecological consequences of marine top predator declines. *Trends Ecol. Evol.*, 23, 202–210.

Heithaus, M.R., Wirsing, A.J., Burkholder, D., Thomson, J. and Dill, L.M. (2009). Towards a predictive framework for predator risk effects: the interaction of landscape features and prey escape tactics. *J. Anim. Ecol.*, 78, 556–562.

Hooten, M.B. and Hobbs, N.T. (2015). A guide to Bayesian model selection for ecologists. *Ecol. Monogr.*, 85, 3–28.

Hooten, M.B., Johnson, D.S., McClintock, B.T. and Morales, J.M. (2017). *Animal Movement: Statistical Models for Telemetry Data*. 1 edition. CRC Press, Boca Raton.

JAXA EORC. (2020). *ALOS Global Digital Surface Model ALOS World 3D-30m (AW3D30) Version 3.1*. Japan Aerospace Exploration Agency.

Johansson, Ö., Rauset, G.R., Samelius, G., McCarthy, T., Andrén, H., Tumursukh, L., *et al.* (2016). Land sharing is essential for snow leopard conservation. *Biol. Conserv.*, 203, 1–7.

Jumabay-Uulu, K., Wegge, P., Mishra, C. and Sharma, K. (2013). Large carnivores and low diversity of optimal prey: a comparison of the diets of snow leopards Panthera uncia and wolves Canis lupus in Sarychat-Ertash Reserve in Kyrgyzstan. *Oryx*, 48, 529–535.

Kachel, S., Anderson, K., and Shokirov, Q. (2021). Predicting carnivore habitat use and livestock depredation risk with false-positive multi-state occupancy models. Submitted for publication.

Kachel, S., Karimov, K., and Wirsing, A. (*in press*). Predator niche overlap and partitioning and potential interactions in the mountains of Central Asia. J. Mammal.

Karimov, K., Kachel, S.M. and Hackländer, K. (2018). Responses of snow leopards, wolves and wild ungulates to livestock grazing in the Zorkul Strictly Protected Area, Tajikistan. *PLOS ONE*, 13, e0208329.

Knopff, K.H., Knopff, A.A., Warren, M.B. and Boyce, M.S. (2009). Evaluating Global Positioning System Telemetry Techniques for Estimating Cougar Predation Parameters. *J. Wildl. Manag.*, 73, 586–597.

Kohl, M.T., Ruth, T.K., Metz, M.C., Stahler, D.R., Smith, D.W., White, P.J., *et al.* (2019). Do prey select for vacant hunting domains to minimize a multi-predator threat? *Ecol. Lett.*, 22, 1724–1733.

Kotler, B.P., Blaustein, L. and Brown, J.S. (1992). Predator facilitation: the combined effect of snakes and owls on the foraging behavior of gerbils. *Ann. Zool. Fenn.*, 29, 199–206.

Kuijper, D.P.J., Sahlén, E., Elmhagen, B., Chamaillé-Jammes, S., Sand, H., Lone, K., *et al.* (2016). Paws without claws? Ecological effects of large carnivores in anthropogenic landscapes. *Proc. R. Soc. B Biol. Sci.*, 283, 20161625.

Kuijper, D.P.J., Schmidt, K., Behnke, R. and Wikenros, C. (2015). Behavioural responses of ungulates to indirect cues of an ambush predator. *Behaviour*, 152, 1019–1040.

Kusi, N., Sillero-Zubiri, C., Macdonald, D.W., Johnson, P.J. and Werhahn, G. (2020). Perspectives of traditional Himalayan communities on fostering coexistence with Himalayan wolf and snow leopard. *Conserv. Sci. Pract.*, 2, e165.

Leblond, M., Dussault, C., Ouellet, J.-P. and St-Laurent, M.-H. (2016). Caribou avoiding wolves face increased predation by bears - Caught between Scylla and Charybdis. *J. Appl. Ecol.*, 53, 1078–1087.

Lewis, J.S., Rachlow, J.L., Garton, E.O. and Vierling, L.A. (2007). Effects of habitat on GPS collar performance: using data screening to reduce location error. *J. Appl. Ecol.*, 44, 663–671.

Lima, S.L. (1992). Life in a multi-predator environment: some considerations for anti-predatory vigilance. *Ann. Zool. Fenn.*, 29, 217–226.

Lima, S.L. (1998). Nonlethal Effects in the Ecology of Predator-Prey Interactions. *BioScience*, 48, 25–34.

Lima, S.L. and Bednekoff, P.A. (1999). Temporal Variation in Danger Drives Antipredator Behavior: The Predation Risk Allocation Hypothesis. *Am. Nat.*, 153, 649–659.

Lima, S.L. and Dill, L.M. (1990). Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.*, 68, 619–640.

Lone, K., Loe, L.E., Gobakken, T., Linnell, J.D.C., Odden, J., Remmen, J., *et al.* (2014). Living and dying in a multi-predator landscape of fear: roe deer are squeezed by contrasting pattern of predation risk imposed by lynx and humans. *Oikos*, 123, 641–651.

Lone, K., Mysterud, A., Gobakken, T., Odden, J., Linnell, J. and Loe, L.E. (2017). Temporal variation in habitat selection breaks the catch-22 of spatially contrasting predation risk from multiple predators. *Oikos*, 126, 624–632.

Luttbeg, B., Hammond, J.I., Brodin, T. and Sih, A. (2020). Predator hunting modes and predator–prey space games. *Ethology*, 126, 476–485.

Manly, B.F.J., McDonald, L., Thomas, D., McDonald, T.L. and Erickson, W.P. (2002). *Resource selection by animals: statistical design and analysis for field studies*. Kluwer, Dordrecht.

McCarthy, J.L., McCarthy, K.P., Fuller, T.K. and McCarthy, T.M. (2010). Assessing Variation in Wildlife Biodiversity in the Tien Shan Mountains of Kyrgyzstan Using Ancillary Camera-trap Photos. Mt. Res. Dev., 30, 295–301.

McCarthy, T.M., Mallon, D.P., Jackson, R.M., Zahler, P. and McCarthy, K.P. (2017). Panthera uncia. The IUCN Red List of Threatened Species 2017: e.T22732A50664030.

McClintock, B.T. and Michelot, T. (2018). momentuHMM: R package for generalized hidden Markov models of animal movement. *Methods Ecol. Evol.*, 9, 1518–1530.

Meadows, A.J., Owen, J.P. and Snyder, W.E. (2017). Keystone nonconsumptive effects within a diverse predator community. *Ecol. Evol.*, 7, 10315–10325.

Moll, R.J., Redilla, K.M., Mudumba, T., Muneza, A.B., Gray, S.M., Abade, L., *et al.* (2017). The many faces of fear: a synthesis of the methodological variation in characterizing predation risk. *J. Anim. Ecol.*, 86, 749–765.

Montgomery, R.A., Moll, R.J., Say-Sallaz, E., Valeix, M. and Prugh, L.R. (2019). A tendency to simplify complex systems. *Biol. Conserv.*, 233, 1–11.

Muff, S., Signer, J. and Fieberg, J. (2020). Accounting for individual-specific variation in habitat-selection studies: Efficient estimation of mixed-effects models using Bayesian or frequentist computation. *J. Anim. Ecol.*, 89, 80–92.

Mumma, M.A., Gillingham, M.P., Johnson, C.J. and Parker, K.L. (2017). Understanding predation risk and individual variation in risk avoidance for threatened boreal caribou. *Ecol. Evol.*, 7, 10266–10277.

NASA LP DAAC. (2016). MODIS/Terra Vegetation Indices 16-Day L3 Global 250m SIN Grid NASA EOSDIS Land Processes DAAC.

Northrup, J.M. and Gerber, B.D. (2018). A comment on priors for Bayesian occupancy models. *PLoS ONE*, 13.

Nouvellet, P., Rasmussen, G.S.A., Macdonald, D.W. and Courchamp, F. (2012). Noisy clocks and silent sunrises: measurement methods of daily activity pattern: Measurement of activity pattern. *J. Zool.*, 286, 179–184.

Ogle, K. and Barber, J.J. (2020). Ensuring identifiability in hierarchical mixed effects Bayesian models. *Ecol. Appl.*, 30, e02159.

Peters, D.P.C. and Herrick, J.E. (2004). Strategies for ecological extrapolation. *Oikos*, 106, 627–636.

Preisser, E.L., Orrock, J.L. and Schmitz, O.J. (2007). Predator Hunting Mode and Habitat Domain Alter Nonconsumptive Effects in Predator–Prey Interactions. *Ecology*, 88, 2744–2751.

R Core Development Team. (2018). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Relyea, R.A. (2003). How Prey Respond to Combined Predators: A Review and an Empirical Test. *Ecology*, 84, 1827–1839.

Ripple, W.J. and Beschta, R.L. (2004). Wolves and the Ecology of Fear: Can Predation Risk Structure Ecosystems? *BioScience*, 54, 755.

Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., *et al.* (2014). Status and Ecological Effects of the World's Largest Carnivores. *Science*, 343, 1241484–1241484.

Sappington, J.M., Longshore, K.M. and Thompson, D.B. (2007). Quantifying Landscape Ruggedness for Animal Habitat Analysis: A Case Study Using Bighorn Sheep in the Mojave Desert. *J. Wildl. Manag.*, 71, 1419–1426.

Schmitz, O.J., Beckerman, A.P. and O'Brien, K.M. (1997). Behaviorally Mediated Trophic Cascades: Effects of Predation Risk on Food Web Interactions. *Ecology*, 78, 1388.

Sih, A., Englund, G. and Wooster, D. (1998). Emergent impacts of multiple predators on prey. *Trends Ecol. Evol.*, 13, 350–355.

Street, G.M., Potts, J.R., Börger, L., Beasley, J.C., Demarais, S., Fryxell, J.M., *et al.* (2021). Solving the sample size problem for resource selection functions. *Methods Ecol. Evol.*, 2041–210X.13701.

Thaker, M., Vanak, A.T., Owen, C.R., Ogden, M.B., Niemann, S.M. and Slotow, R. (2011). Minimizing predation risk in a landscape of multiple predators: effects on the spatial distribution of African ungulates. *Ecology*, 92, 398–407.

Tornberg, R., Helle, P. and Korpimäki, E. (2011). Vulnerability of black grouse hens to goshawk predation: result of food supply or predation facilitation? *Oecologia*, 166, 577–584.

Valeix, M., Loveridge, A.J., Chamaillé-Jammes, S., Davidson, Z., Murindagomo, F., Fritz, H., *et al.* (2009). Behavioral adjustments of African herbivores to predation risk by lions: spatiotemporal variations influence habitat use. *Ecology*, 90, 23–30.

de Valpine, P., Turek, D., Paciorek, C.J., Anderson-Bergman, C., Lang, D.T. and Bodik, R. (2017). Programming With Models: Writing Statistical Algorithms for General Model Structures With NIMBLE. *J. Comput. Graph. Stat.*, 26, 403–413.

Watanabe, S. (2010). Asymptotic Equivalence of Bayes Cross Validation and Widely Applicable Information Criterion in Singular Learning Theory. *Jounral Mach. Learn. Res.*, 11, 3571–3594.

Wiens, J.A. (1993). Fat times, lean times and competition among predators. *Trends Ecol. Evol.*, 8, 348–349.

Wirsing, A.J., Cameron, K.E. and Heithaus, M.R. (2010). Spatial responses to predators vary with prey escape mode. *Anim. Behav.*, 79, 531–537.

Wirsing, A.J., Heithaus, M.R., Brown, J.S., Kotler, B.P. and Schmitz, O.J. (2021). The context dependence of non-consumptive predator effects. *Ecol. Lett.*, 24, 113–129.

Appendix

Table S1. Summary of prey species identified via carcass searches at potential collared wolf and snow leopard winter kill sites in Sarychat-Ertash.

		Prey species found at investigated clusters						
Predator	Winter clusters investigated (# identified)	Argali	Ibex	Yak	Lynx	Fox	Himalayan Snowcock	Unknown
Wolf	173 (298)	65	9	3	1	0	1	4
Snow leopard	230 (397)	30	102	0	0	2	2	7

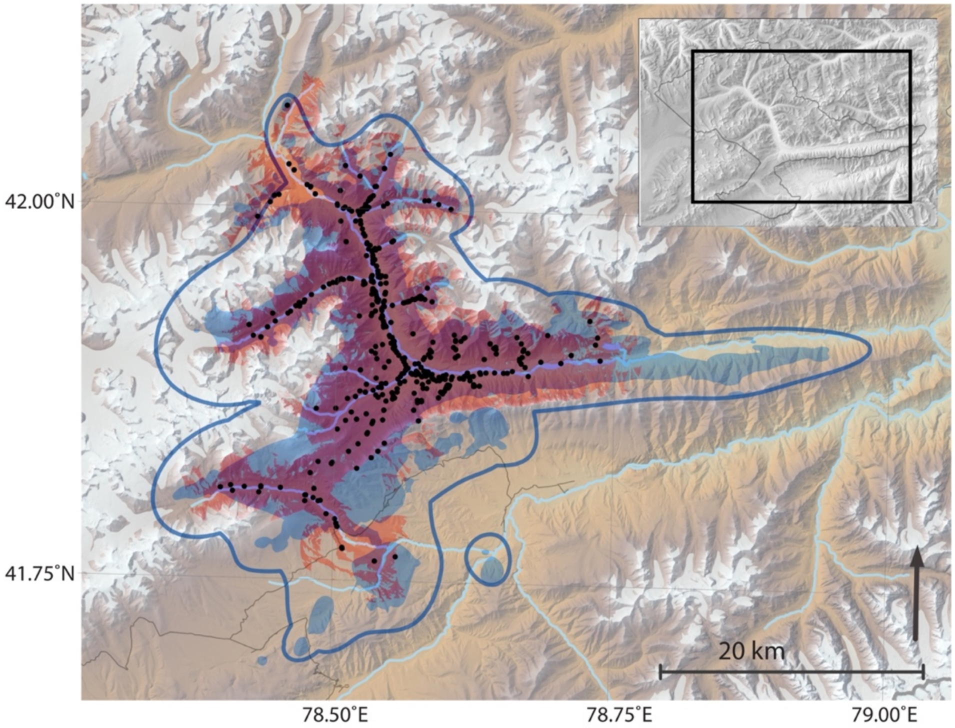

Figure S1. Ungulate observer locations (black points) and background area (red) used in ungulate RSF models. Blue outline and shading respectively indicate the combined 99% autocorrelated kernel density estimated “home ranges” (outline) and occurrence distributions (shading) of all collared predators. Points and sampled area shown only for points from which ungulates were detected, consistent with the nature of the data and modelling approach.

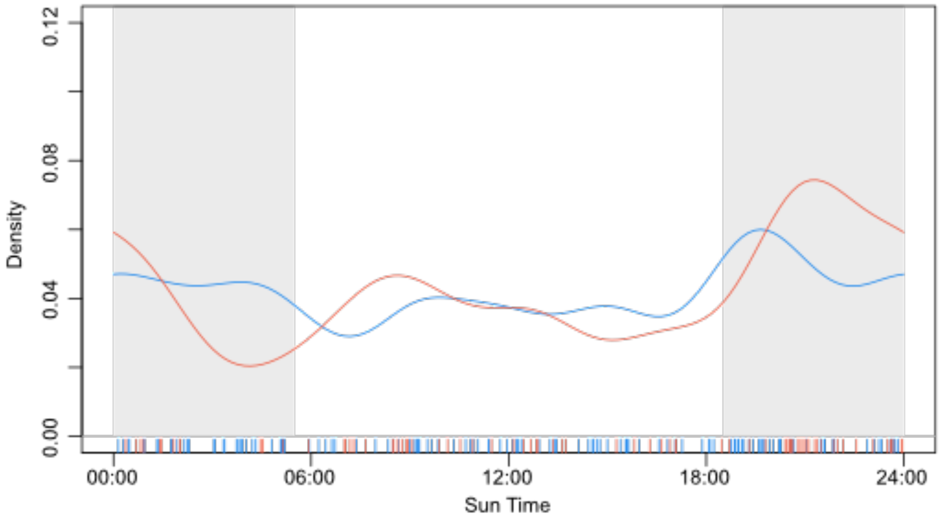

Figure S2. Approximate 24-hour kernel density of collared snow leopard (blue) and wolf (red) ibex and argali kills. We used the R package ‘overlap’ (Meredith and Ridout 2014) to estimate and visualize temporal overlap in the diel timing of ibex and argali kills by wolves and snow leopards. At best, GPS collar data supplied only coarse (4 or 5 hour) temporal resolution on the timing of when predators killed prey; for ~20% of recorded kills, missed GPS fixes meant that the fix interval preceding the first fix at a kill site was longer. We assigned each kill to the midpoint of the preceding interval, censoring kills for which this interval exceeded 24 hours. Mean overlap, on a scale from 0 to 1 (Δ_4; Ridout and Linkie, 2009), was 0.81 (95% Bootstrap CI: 0.71- 0.90), similar to estimates of temporal activity overlap between snow leopards and wolves based on camera trap detections elsewhere (0.74, Kachel et al. *In press*; 0.79, Salvatori et al. 2021). Assuming kills could have happened with uniform probability at any time in the preceding interval, 92.3% of snow leopard kills and 72.9% of wolf kills could plausibly have occurred during daylight hours.

Meredith, M., Ridout, M.S., 2014. Overlap: estimates of coefficient of overlapping for animal activity patterns. R package version 0.3.2.

Ridout, M.S., Linkie, M., 2009. Estimating overlap of daily activity patterns from camera trap data. Journal of Agricultural, Biological, and Environmental Statistics 14, 322–337.

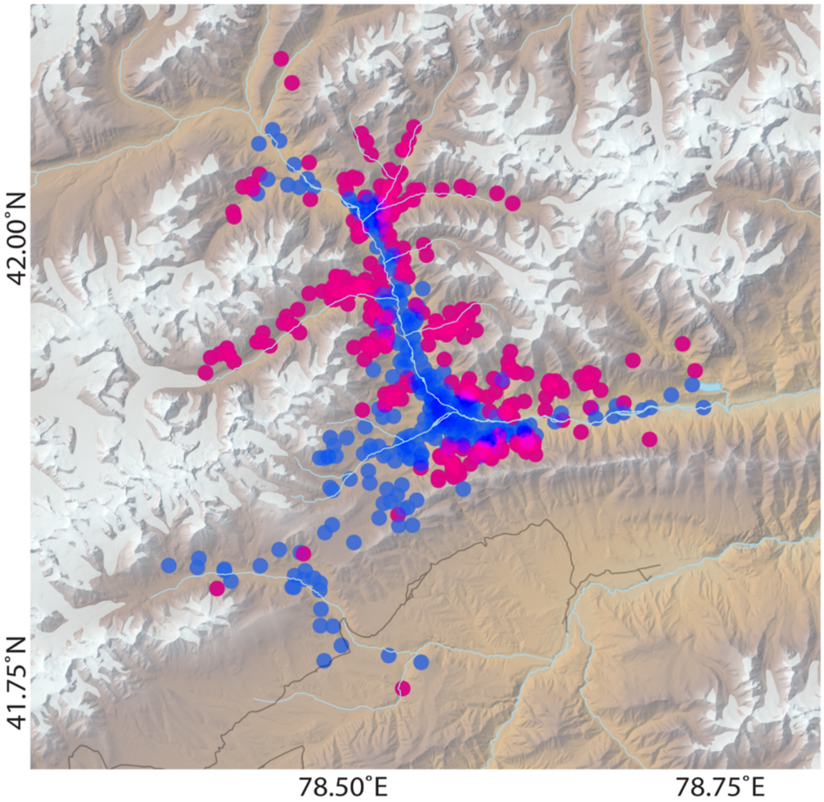

Figure S3. Observed winter locations of argali (blue) and ibex (pink) in Sarychat-Ertash.

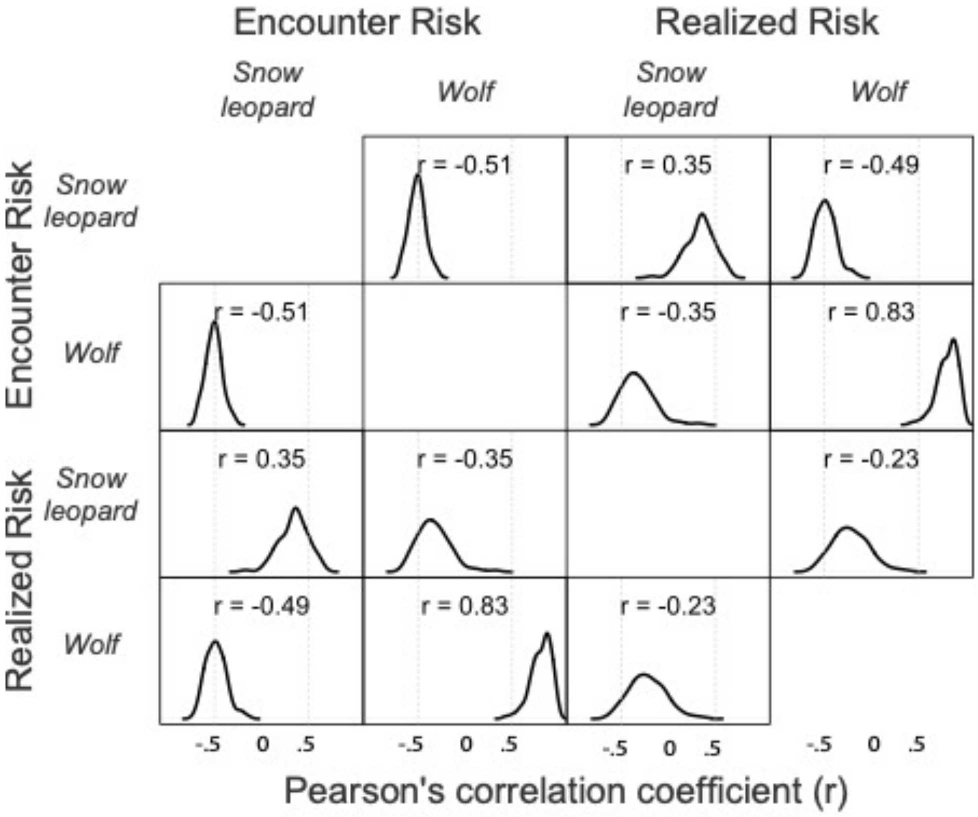

Figure S4. Median pairwise correlations and associated distributions arising from estimation uncertainty for components of estimated wolf and snow leopard predation risk in argali spatial response models.

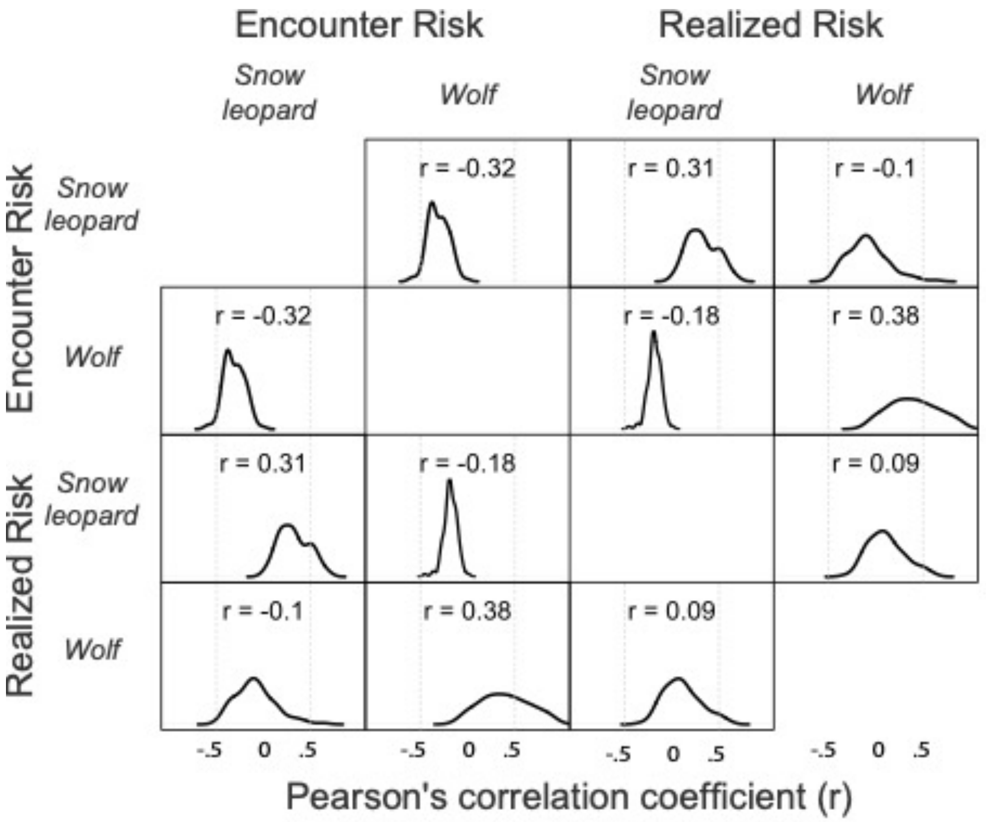

Figure S5. Median pairwise correlations and associated distributions arising from estimation uncertainty for components of estimated wolf and snow leopard predation risk in ibex spatial response models.

Table S2. Predicted coefficient effects (+/–) of short- and long-term predation risk on ungulate space use under models representing competing hypotheses of risk responses, and multiple-predator responses. Parentheses indicate responses predicted to be weak or unimportant, as wholesale avoidance of integrated or encounter risk obviates the need for fine-scale or reactive responses. Under the "bottom up" hypothesis, ungulates are predicted to use space only according to the distribution of vegetative resources and the limitations imposed by snow cover. The "risky times" hypothesis predicts responses only to short-term risk as measured by predator proximity. In both cases, prey are not predicted to display any particular strategy with respect to multiple predators, whereas multiple predator responses are expected under various formulations of the "risky places" and "risk allocation" hypotheses, which respectively predict responses to long-term risk, or to long-term risk and its interactions with short-term risk. Under the "gap hypothesis", both ungulates should consistently avoid both short- and long-term risk from both predators, whereas under the "hunting mode" hypothesis, both ungulates should select spaces with long-term wolf risk, setting up the possibility that short-term wolf risk may induce shifting responses to the interaction between short- and long-term risk. Alternatively, the "risky contingencies" hypothesis predicts that ibex will generally favor areas with greater long-term snow leopard risk, and argali will favor areas of greater wolf risk. Responses consistent with multiple predator effects precipitated by ungulate space use are evident only as interactions between short-term risk of one predator and long-term risk of the other. Specifically, negative coefficients on these multiple predator risk interactions are consistent with risk-reducing MPEs (and competitive indirect predator-predator interactions) as prey avoiding one predator simultaneously reduce their overall exposure to the other as well; positive coefficients alternatively signal the potential for risk-enhancing MPEs (and predator facilitation).

(Table S2)

			Bottom up Factors		Long-term Risk		Predator proximity		Predator proximity – long-term risk Interactions			
Species	Risk response hypothesis	Multi-predator response hypothesis	NDVI	Snow Cover	Snow leopard	Wolf	Snow leopard	Wolf	Snow leopard - Snow leopard	Snow leopard - Wolf	Wolf - Snow leopard	Wolf - Wolf
Both	*Bottom up*	*NA*	+	–								
Both	*Risky times*	*NA*	+	–			–	–				
Both	*Risky places*	*Gap*	+	–	–	–						
	Risk allocation		+	–	–	–	(–)	(–)	(–)	(–)	(–)	(–)
Both	*Risky places*	*Hunting mode*	+	–	–	+						
	Risk allocation		+	–	–	+	(–)	–	(–)	(–)	+	–
Argali	*Risky places*	*Risky contingencies*	+	–	–	+						
	Risk allocation		+	–	–	+	(–)	–	(–)	(+)	+	–
Ibex	*Risky places*	*Risky contingencies*	+	–	+	–						
	Risk allocation		+	–	+	–	–	(–)	–	+	(+)	(–)

Table S3. Ibex and argali spatial response selection coefficient estimates and credible intervals for naïve models that ignored estimation uncertainty in long-term predation risk estimates. Bold text highlights coefficients with 95% CRIs that do not overlap 0.

	β posterior mean (95% Credible Interval)			
Covariate	**Argali**		**Ibex**	
Vegetation & climate				
NDVI	-0.04	(-0.17 - 0.09)	0.13	(-0.01 - 0.27)
Snow cover	0.04	(-0.10 - 0.18)	-0.03	(-0.17 - 0.11)
Long-term predation risk				
Snow leopard	0.00	(-0.11 - 0.11)	0.11	(-0.03 - 0.18)
Wolf	0.50	(0.40 - 0.61)	-0.08	(-0.21 - 0.04)
Short-term predation risk				
Snow leopard	0.15	(-0.07 - 0.36)	0.34	(0.11 - 0.55)
Wolf	-0.09	(-0.45 - 0.23)	-0.51	(-1.26 – 0.21)
Interactions - Snow leopard distance...				
Snow leopard	-0.07	(-0.17 - 0.03)	-0.08	(-0.16 - -0.01)
Wolf	-0.02	(-0.11 - 0.07)	0.05	(-0.04 - 0.14)
Interactions - Wolf distance...				
Snow leopard	0.10	(-0.05- 0.25)	-0.13	(-0.32 - 0.04)
Wolf	-0.13	(-0.28 - 0.01)	-0.25	(-0.56 - 0.03)

Estimating M and N for predator encounter risk models

Wolf and snow leopard encounter models were potentially limited by the small number of collared animals of each species. Yet, there were both ecological and statistical justifications for using this small data set to characterize encounter risk with RSF models.

Ecologically, the large majority of our study area (with respect to ungulates) lay within the geographic territory of a single wolf pack, and indeed, both collared wolves were members of this pack. Fully 87% of all direct observations of ungulates fell within the 99% isopleths of aKDEs of these two animals (99% of observations fell within snow leopard aKDE isopleths). Although ungulates observed at the northern and eastern margins of the study area likely shared space with different wolf packs, for most of the ungulates that we observed, the wolves informing encounter risk models were the very same predators, or at least part of the same pack, with which the ungulates had to contend. In addition, investigations of the habitat associations of wolves elsewhere in the mountains of Central Asia (Karimov et al. 2018; Chapter Two) suggest that the patterns we observed in fact represent typical patterns of wolf habitat use in such landscapes.

Statistically, our intention for these data was to predict encounter risk to ungulates in our study area, rather than to conduct resource selection inference per se. Efforts to deal with the problem of estimating what numbers of collared animals (M) and relocations (N) of those individuals are sufficient to achieve stable, reliable inference in animal resource selection analyses have historically relied on heuristic rules (M>30, and N= "as many as possible"). Street et al. (2021) developed closed-form analytical expressions that demonstrate that in many cases, M may be an order of magnitude less than 30 (and as few as 2 individuals), and N less than 100. The required M and N necessary to reach consistent selection coefficients is entirely a function of the strength of population-level selection and complexity of the landscape with respect to the animal and a given resource covariate. Although their equations are more properly utilized in an *a priori* fashion, we calculated the predicted M and N necessary to estimate each selection coefficient in wolf and snow leopard RSF models (such that each coefficient's 95% confidence interval does not overlap zero, and assuming that our β-estimates represented the true population mean selection coefficients) as a *post hoc* metric (Street et al. 2021). For snow leopards, the hyperparameters of RSF selection coefficients were directly translatable to population level estimates of coefficients and their variances. For wolves, we calculated individual RSFs (results of which were entirely consistent with the individual random intercept model used) in order to arrive at the variances of selection coefficients among the two collared individuals as required to predict M. For both snow leopards and wolves, M_{Pred} and N_{Pred} were less than or equal to M_{Obs} and N_{Obs}, respectively, in every case except for 2000-m TPI for snow leopards, and vector ruggedness for wolves, covariates whose coefficients' posterior credible intervals overlapped zero in RSF models (i.e., coefficients for which we lacked clear evidence of an effect; Table S4). This post hoc assessment suggested that our observed βs were likely consistent with hypothetical βs estimated from more individuals.

Table S4. Post hoc calculation of the number of collared animals (M_{Pred}) and relocations (N_{Pred}) per animal necessary to estimate consistent selection coefficients (β) for each covariate in the global set used to estimate snow leopard and wolf RSFs (encounter models). Complexity is partly a function of the landscape and β, which together with β determines N and M.

	Snow leopards ($\bar{N}_{Obs}$=285.7, M_{Obs}=7)			Wolves ($\bar{N}_{Obs}$=486.5, M_{Obs}=2)		
Covariate	Complexity	N_{Pred}	M_{Pred}	Complexity	N_{Pred}	M_{Pred}
TPI2000	0.65	29.62	3	1.00	32.39	2
VRM	6.56	26.46	2	1.39	3806.12	3
Slope	0.75	66.68	2	0.47	21.68	2
TPI50	1.17	252.49	2	1.41	145.48	2
$TPI2K^2$	0.81	219.61	8	1.31	329.28	2
$Slope^2$	0.76	198.84	3	0.65	245.55	2

CHAPTER 4

PREDICTING CARNIVORE HABITAT USE AND LIVESTOCK DEPREDATION RISK WITH FALSE-POSITIVE MULTI-STATE OCCUPANCY MODELS

Abstract

Livestock depredation by large carnivores and subsequent human retaliation constitute a major threat to carnivores worldwide and impose considerable hardships on affected communities. Mitigation efforts are often undertaken with little knowledge of the spatial patterns and ecological underpinnings of depredation, limiting conservationists' ability to develop, prioritize, and evaluate solutions. Carnivore detection and depredation data from interviews in affected communities can help address this gap, but such data are often prone to false-positive uncertainty. To address these challenges in the Pamir Mountains of Tajikistan we collected snow leopard, lynx, wolf, and bear detection and depredation reports from local communities via semi-structured interviews. We used a novel hierarchical multi-species multi-state occupancy model that accounted for potential false-positives to investigate carnivore site use and depredation concurrently with respondents' apparent vulnerability to that risk. Estimated false-positive probabilities were small, but failure to account for them overstated site use probabilities and depredation risk for all species. Nonetheless, depredation was commonplace, but individual respondents' vulnerability was low. Carnivore site use was driven by clear habitat associations, but we did not identify any important large-scale spatial correlates of depredation risk despite considerable spatial variation in that risk. Respondents who sheltered livestock in household corrals reinforced with wire mesh were less likely to report snow leopard depredations. Reducing depredation and retaliation at adequately large scales in the Pamirs will likely require a portfolio

of species-specific strategies, including widespread proactive corral improvements. Our approach expanded inference on the often-cryptic processes surrounding human-carnivore conflict even though structured wildlife data were scarce.

Introduction

The cycle of human-carnivore conflict (HCC), in which carnivores kill livestock and humans retaliate by killing carnivores, threatens carnivore populations globally and the health and livelihoods of human communities (Woodroffe et al. 2005). Substantial prey requirements and wide-ranging behavior predispose large carnivores to kill livestock, while low densities and slow reproductive rates render their populations vulnerable to retaliation (Ripple et al. 2014). Simultaneously, pastoralist communities living alongside carnivores are often unable to absorb the impacts of livestock depredation (Dickman et al. 2011). Yet, as human populations and their effects on ecosystems grow, the viability of large carnivore populations may increasingly depend on human capacity for coexistence (Inskip and Zimmermann 2009). To ensure the long-term persistence of carnivores threatened by HCC, there is a clear need to understand ecological and anthropogenic underpinnings of depredation – the primary cause of conflict (Treves et al. 2011).

Spatial risk mapping is a practical tool for understanding geographic patterns of depredation risk (Treves et al. 2011), and for informing where to focus resources to reduce depredation and retaliation. Typically, such maps predict realized predation risk (Miller 2015) – the outcome of heterogeneity in the probability of predator-prey encounters and the conditional probability of predation given an encounter (Lima and Dill 1990) – and may thus conflate factors influencing carnivore presence with those influencing prey vulnerability (Hebblewhite et al. 2005). It may therefore be desirable to understand the spatial distribution of depredation in tandem with carnivore habitat use and distributions. Furthermore, understanding how the threat of retaliation, for which depredation risk is presumably an appropriate proxy (e.g., Ogada et al. 2003), maps onto species' distributions may help address the threat of HCC to vulnerable populations.

Occupancy models predict species distributions or site use from repeated sampling of detection/non-detection data in discrete sites, thereby explicitly quantifying imperfect detection (MacKenzie et al. 2002). However, popular tools for obtaining such data (e.g., camera traps) are not well-suited to rapid assessment across large areas. Alternatively, local knowledge, distilled from interviews, can be a practical source of detection/non-detection data (Karanth et al. 2009). Srivathsa et al. (2019) extended interview-based occupancy approaches to jointly estimate site use and depredation risk using multi-state occupancy models (Nichols et al. 2007), providing a potentially useful decomposition of realized depredation risk into probabilities of site use and conditional depredation risk. Disentagnling these underlying ecological processes from an individual respondent's probability of experiencing depredation may provide insight into individual vulnerability, with the potential to inform where, and how, to reduce depredation at respondent and landscape scales.

Unverified interview data may violate one of the assumptions of occupancy models, which is that data do not contain false-positives (Pillay et al. 2014). Whether from exaggeration, misidentification, faulty recall, or deception, false-positive errors can produce large positive biases in occupancy estimates (Royle and Link 2006). These errors may be particularly likely and problematic where conflict-prone carnivores of high conservation value are concerned. Yet, additional information is needed to probabilistically differentiate between true and false detections (Royle and Link 2006). One solution is to glean information about the true site-use state by integrating false-positive data with classic occupancy data free of false-positives, thereby establishing state certainty for at least some sites (Miller et al. 2011). Multi-species models may further enable estimation and inference for data-sparse species by treating species-specific parameters as sampled from shared distributions (Zipkin et al. 2009). A multi-species solution is appealing logistically and conceptually: communities coexisting with multiple carnivores experience depredation risk from each simultaneously; depredation by co-occurring species may be germane to understanding non-targeted retaliation; and false detections may be particularly likely in multi-carnivore landscapes.

Livestock depredation in the Pamir Mountains of Tajikistan is regularly attributed to snow leopards (*Panthera uncia*), lynx (*Lynx lynx*), brown bears (*Ursus arctos*) and wolves (*Canis lupus*), and retaliatory killing is thought to be commonplace. Previous research on social and ecological correlates of perceived depredation in the region suggests that patterns of depredation are context-dependent (e.g., Mishra 1997; Suryawanshi et al. 2013; Davie et al. 2014). Lacking foundational ecological knowledge, prevention efforts in the Pamirs have largely comprised reactive construction of predator-proof corrals, but the problem persists (Saidov et al. 2016). An incident in which two people were killed by wolves in 2019 led to coordinated lethal control efforts, with likely spillover consequences. Elsewhere in the high mountains of Asia, wolf-control efforts have precipitated indiscriminate trapping and poisoning (Li and Lu 2014), raising the prospect that human-driven mortality of snow leopards, a species of global conservation concern, may become an increasingly acute threat. Patterns of carnivore site use and depredation should be immediately relevant to disrupting the cycle of HCC in the region – a goal of conservation and humanitarian initiatives alike.

Here, we modelled interview-based detection and depredation data for Pamiri carnivores using a novel multi-species, multi-state false-positive occupancy model. This allowed us to investigate spatial variation in carnivore site use and depredation concurrently with individual vulnerability to that risk, within a unified framework that accounted for imperfect and uncertain data. Depredation is predation complicated by human dimensions (Gervasi et al. 2020). Thus, landscapes likely affect depredation patterns much as they affect predation – via influences on predator distributions, functional and numerical responses (Holling 1959), and encounter and kill rates between predators and prey (Hebblewhite et al. 2005) – but in a manner modulated by livestock husbandry practices (e.g., Ogada et al. 2003). Accordingly, we hypothesized that at local scales, husbandry practices exert more influence on patterns of depredation than do habitat characteristics. This hypothesis predicts that after accounting for large-scale variation in carnivore site use probability and depredation risk, variables linked to husbandry practices should be more important predictors of individual apparent vulnerability to depredation. Our goal was to understand the extent of the social and ecological challenges posed by HCC in the Pamirs and to provide foundational knowledge to enable Pamiri communities to coexist with threatened carnivores.

Methods

Study Area

Tajikistan's Gorno-Badakhshan Autonomous Oblast (Fig. 1) encompasses dramatic gradients in physical terrain and bioclimatic conditions, driven by extreme elevational variation (1000-7000+m). Livelihoods are typified by transhumance pastoralism and agropastoralism, centered around sheep (*Ovis aries*), goats (*Capra aegagrus*), cows (*Bos taurus*), and yaks (*B. grunniens*). May-October, livestock are moved to high elevation pastures, often under the care of professional herders, whereas heavy snows and cold temperatures confine people and livestock to villages and nearby pastures during winter (November-April), when livestock are kept in household corrals. Carnivore prey include markhor (*Capra falconeri*), ibex (*C. sibirica*), argali (*Ovis ammon*), wild boar (*Sus scrofa*), marmots (*Marmota longicauda*), hare (*Lepus tolai*), and porcupine (*Hystrix indica*).

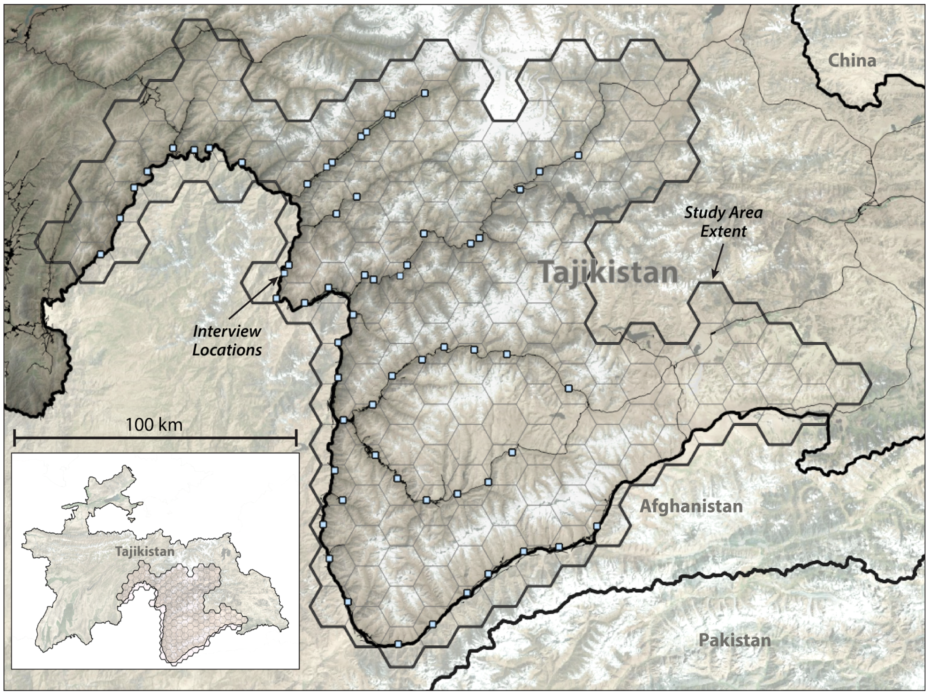

Figure 1. Study area in the western Pamir Mountains of Tajikistan, showing 225 km^2 hexagonal occupancy "sites" and interview locations/villages (light blue circles).

Interviews

This study (ID:00009580) was approved by the University of Washington IRB under FWA #00006878. We obtained reports of carnivore sighting and depredation between 1 December 2018 and 30 November 2019 through semi-structured interviews conducted November 2019 to February 2020. We divided the 38,700 km^2 study area into 172 discrete 225 km^2 sites (Ghoshal et al. 2017; Fig. 1). We conducted interviews in each site with permanent settlements, treating each interview as a replicate sample of one or more sites. The survey team approached community leaders who helped identify and recruit two sets of potential respondents: individuals regarded by the community as having expert knowledge of local wildlife (e.g., hunters, rangers, scientists, guides) and livestock owners (most people, as livestock ownership is ubiquitous outside of large towns). See Appendix S1 for further details.

Using 1:50,000 topographic maps, respondents defined an area of knowledge (AOK; Zeller et al. 2011) with which they were familiar in the course of the previous year's activities (typically spanning multiple sites) and marked locations of carnivore sightings and depredations. We documented age, livestock type and number, depredation details, husbandry infrastructure, and duration of activity in their AOK. We manually digitized hand-drawn map annotations (Fig. S1) in QGIS 2.18.9 (QGIS Development Team 2019) to link observations to discrete sites.

Multi-species multi-state occupancy model

We built a multi-species, multi-state occupancy model (Nichols et al. 2007) that explicitly accounted for false-positive uncertainty by extending Miller et al.'s (2011) "multiple-detection method" model to multiple states. The partially-observed latent variable $z_{i,k}$ was a categorical random variable,

$$z_{i,k} \sim categorical(\Phi_{i,k}) \qquad \text{(eqn. 1)}$$

taking values $z_{i,k}$ = 0,1,2 indicating the true state of site use (unused, used, or used with depredation) for species k in site i. The multinomial probability $\Phi_{i,k}$ of site use for each state (0,1,2) was

$$\Phi_{i,k} = [(1 - \Psi_{i,k}) \quad \Psi_{i,k}(1 - R_{i,k}) \quad \Psi_{i,k}(R_{i,k})] \qquad \text{(eqn. 2)}$$

where $\Psi_{i,k}$ and $R_{i,k}$ were the site-level probabilities of use and depredation conditional on use, respectively.

The data, $y_{i,j,k}$, taking values y = 0,1,2, were apparent site use and depredation states (species not detected, species detected, species detected via depredation) observed in site i by respondent j, which we modelled conditional on $z_{i,k}$ such that

$$y_{i,j,k} | z_{i,k} \sim categorical(\mathbf{\Omega}_{i,j,k}). \qquad \text{(eqn. 3)}$$

The observation process matrix $\mathbf{\Omega}_{i,j,k}$ describes the probabilities of observing state y=0,1,2 (columns) given z=0,1,2 (rows):

$$\mathbf{\Omega}_{i,j,k} = \begin{bmatrix} 1 - q_{01} & q_{01}(1 - q_{02}) & q_{01}(q_{02}) \\ 1 - p_1 - q_{12} & p_1 & q_{12} \\ 1 - p_2 & p_2(1 - \delta) & p_2\delta \end{bmatrix} \qquad \text{(eqn. 4)}$$

where p_1 was the probability of detecting the species given true state, z=1, p_2 was the probability of detecting the species given z=2, δ was the conditional probability of detecting depredation when z=2, and q_{zy} were the probabilities of falsely observing state y given z<y.

We modeled Ψ, R, p_1, p_2, and δ as logit-linear functions of covariates; e.g., $logit(\Psi_{i,k}) = \alpha_{\Psi,k} + \beta_{\Psi,k}\boldsymbol{X_i}$ and $logit(p_{1i,j,k,m}) = \alpha_{p1,k} + \beta_{p1,k}\boldsymbol{X_{i,j}} + \varepsilon_{p1,j}$ where the α terms were species intercepts (drawn from distributions shared across species for p_1, p_2, and δ), $\boldsymbol{X_{i,j}}$ was the design matrix, β's were parameter coefficients, and ε terms were respondent-specific random (intercept) effects on detection probabilities. We included these effects to account for respondents sampling multiple sites. We did not model covariate effects on false-positive probabilities because we expected false-positive detections to represent a small fraction of the observed data.

Detection terms (p's and q's) were essentially nuisance parameters of limited ecological interest. By contrast, δ encompasses imperfect detection of depredation *and* depredation vulnerability, and is ecologically relevant. Although covariates on δ may logically link to one or the other, we could not fully parse these two processes, so we interpret δ as *apparent* vulnerability: individual depredation risk confounded by detection.

In practice, false-positive models require extra information to parse ambiguities in the likelihood (Royle and Link 2006). To break these symmetries, we assumed observations reported by experts were free of false-positive errors, so the observation process matrix was:

$$\boldsymbol{\Omega}_{\boldsymbol{E}i,j,k} = \begin{bmatrix} 1 & 0 & 0 \\ 1 - r_1 & r_1 & 0 \\ 1 - r_2 & r_2(1 - \delta_E) & r_2\delta_E \end{bmatrix} \qquad \text{(eqn. 5)}$$

where r_1, r_2, and δ_E were the expert-respondent equivalents to p_1, p_2, and δ in eqn. 4. This approach integrates "classic" multi-state occupancy data with data exposed to false-positive uncertainty (Miller et al. 2011). The former establishes state certainty for some sites, providing a reference by which to evaluate uncertain observations in the latter.

Covariates

False-positive models can misconstrue unmodeled heterogeneity in true detections as false-positives (Royle and Link 2006). Thus, we parameterized p_1, p_2, δ, r_1, r_2, and δ_E submodels as fully as possible, modelling heterogeneity as functions of respondent age, days spend outside in AOK, within-site AOK area, a binary variable indicating residence in the site, and AOK habitat characteristics (road density, mean topographic position, and forest cover). We additionally considered five covariates on δ related to husbandry practices: numbers of small (sheep, goats) and large (cows, yaks) livestock and dogs owned by the respondent, site-specific binaries indicating skylights and/or windows on corrals (given residence), and corrals built with wire mesh or metal bar coverings; these covariate data were not documented for experts. We standardized non-binary covariates to mean zero and variance one.

Because we assumed that data were only spatially accurate to site scale (to accommodate anticipated spatial uncertainty among respondents), we could not explicitly account for the partial space-for-time substitution (respondents "sampled" overlapping but different portions of each unit) and the associated heterogeneity arising from within-site variation in habitat use (Kéry and Royle 2016). Instead, we accounted for this heterogeneity indirectly via covariates linked to within-site AOK habitat, described above.

Owing to extreme elevational gradients, "raw" site-level covariates (on Ψ and R) were highly correlated with one another, potentially confounding variable-selection and interpretation. We used principal component analysis (PCA; Legendre and Legendre 2012) to reduce covariate dimensionality to eight PCA scores drawn from the first two components of four separate PCA's of thematic groups of potential use and depredation predictors for our target species (e.g., Chundawat 1990; Davie et al. 2014; Dar et al. 2021) – terrain, anthropogenic, bioclimatic, and land cover (Table A1). By thematically grouping covariates we retained some interpretability while reducing the overall dimensionality.

Implementation

We used 'Nimble' (de Valpine et al. 2017), accessed through R (R Core Team 2018), to build two models, adapted from Sipe (2019): a false-positive model and a "naive" model assuming no false-positive uncertainty (see Appendix S1 for full false-positive Nimble model). For each model, we ran two MCMC chains of 930,000 iterations and 30,000 burn in iterations per chain, thinned by 6 to limit file size.

As insurance against overfitting, we adopted a Bayesian variable selection approach (Hooten and Hobbs 2015) using reversible-jump Markov-chain Monte-Carlo (RJMCMC; Green 1995) and species-level indicator variables (Kuo and Mallick 1998) to evaluate the strength of evidence for all covariates while efficiently sampling the posterior distributions even as the parameter space varied among iterations. We multiplied β-coefficients by binary indicator variables, $w_{\beta k}$, with priors $w_{\beta k} \sim Bernoulli(0.5)$. The posterior of a given parameter β_k was thus sampled when $w_{\beta k} = 1$, and held at 0 otherwise, inducing a regularizing spike at 0. The posterior inclusion probability (PIP) for each β_k was the posterior mean of $w_{\beta k}$, which we interpreted as evidence of a covariate's importance, where $PIP<0.25$ indicated clear unimportance; $0.25 \leq PIP < 0.5$ inconclusive unimportance; $0.5 \leq PIP < 0.75$ inconclusive importance; and $PIP \geq 0.75$, clear importance (Mutshinda et al. 2013). Because coefficients were conditional on the covariates included at each iteration, the implicitly model-averaged estimates for important covariates may nonetheless have credible intervals that overlap zero, and vice-versa (Mutshinda et al. 2013). We therefore looked to credible intervals for insight into direction of effects, but not their importance. By contrast, interpretations of p_1, p_2, δ, r_1, r_2, and δ_E were not conditional on included covariates, and were thus suitable for their intended predictive purpose (Hooten and Hefley 2019).

We used *Logistic*(*0,1*) priors – weakly informative on the logit scale, but essentially flat between 0 and 1 on the probability scale – on independent intercepts and covariate coefficients (Northrup and Gerber 2018). Species-level detection intercept parameters were drawn from shared distributions such that for each detection process, α_k~*Normal*(μ_α,σ_α), μ_α~*Logistic*(*0,1*), and σ_α~*Exponential*(*1*). The logistic prior for μ_α is consistent with independent coefficient priors, above, whereas the weakly informative exponential prior on σ_α allows for flexible variation among species, while nonetheless sharing strength among them. When investigating sensitivity to this specification compared to three alternatives, we found that *half-Cauchy*(*1*) and *Uniform*(*0,5*) – priors were too broad, resulting in bimodal posteriors with minimal information pooling across species, whereas a similarly informative *half-Normal*(*0,1*) prior resulted in comparable inference. In preliminary model runs, the conditional probability of false depredation in a truly occupied site (q_{12}) for wolves failed to converge to unimodal posterior; we thus constrained logit(q_{12}) to be less than the product logit(α_{p2})* logit(α_δ) (the baseline probability of reporting depredation in a site where z=2) to achieve convergence. This constraint imposes an assumption that on average, true positive depredations in sites where z=2 are more likely than false positive reports in sites where z=1. For true-positive detection submodels, we specified ε_j~Normal($0,\sigma_\varepsilon$) where σ_ε terms were assigned a half-Cauchy(A) prior centered at 0, with hyperprior A_σ ~*Uniform*(*0,5*) on the Cauchy scale parameter, shared among species and detection processes (Gelman 2006).

Model checking and validation

We inspected trace and density plots of all posterior chains to assess unimodality, mixing, and convergence, and calculated $\hat{R}$ convergence diagnostics (Gelman et al. 2014) for universal parameters (Sisson 2005). We checked goodness-of-fit with binned residual plots (Wright et al. 2019) and Bayesian P-values (Appendix S2) based on a chi-square discrepancy measure comparing the proportion of observed and simulated data in each state at each iteration (Gelman et al. 2014).

We used *K*-fold cross validation (Hooten and Hobbs 2015) with 12 folds to calculate Brier and log-scores to compare the predictive ability of false-positive and naive models (Broms et al. 2016). Thus, for each fold, we withheld 22 respondents (reflecting how the data were observed) selected randomly without replacement, fit the model, and calculated scores of the withheld data at each iteration (see Appendix S3). We regarded the model with the lowest mean scores as the best-predicting model.

Results

Of 271 respondents, including 45 locally-identified experts, 264 were able to identify species in verification photos and locate carnivore sightings and depredations on maps (see Appendix S1, Fig. S1). We interviewed 6.2 (SD=3.6) respondents per site, with an average cumulative within-site AOK of 105 km^2 (SD=67) (Appendix Fig. S2); 32% of respondents reported first-hand livestock depredation during the 12-month sampling period (Appendix Table S2, Fig. S3). Reported snow leopard depredations occurred more frequently inside corrals, and involved more livestock per event, yet wolves were putatively responsible for the majority of depredation events (Appendix Table S3). Seasonally, 80% of reported snow leopard depredations occurred late-autumn through early spring (November-April), compared to 49% for wolves, 33% for lynx, and 25% for bears.

Cross-validation indicated that the false-positive model produced superior predictions (Log-score=53.32; Brier score=12.04) compared to the naive model (Log-score=184.80; Brier score=41.46). Binned residual plots and Bayesian P-values indicated no major lack of fit (false-positive: 0.41; naive: 0.47). Density and trace plots and $\hat{R} < 1.1$ for universal model parameters indicated acceptable convergence (Appendix Tables S4-S8).

False-positive probabilities were low relative to true-positive observation probabilities (Fig. 2). Standard deviations on detection hyper-parameters as well-as species-specific parameters for false-positive probabilities had wide credible intervals (CRI) on the logit-scale (Appendix Tables S4-S8). For all species, false-depredation probabilities ($q_{02,}$ and q_{12}) were greater than false-detection probabilities (q_{01}). Although all false-positive observations were apparently rare in our data, failing to account for them led to consistently higher estimates of site use and depredation probabilities (Table 1).

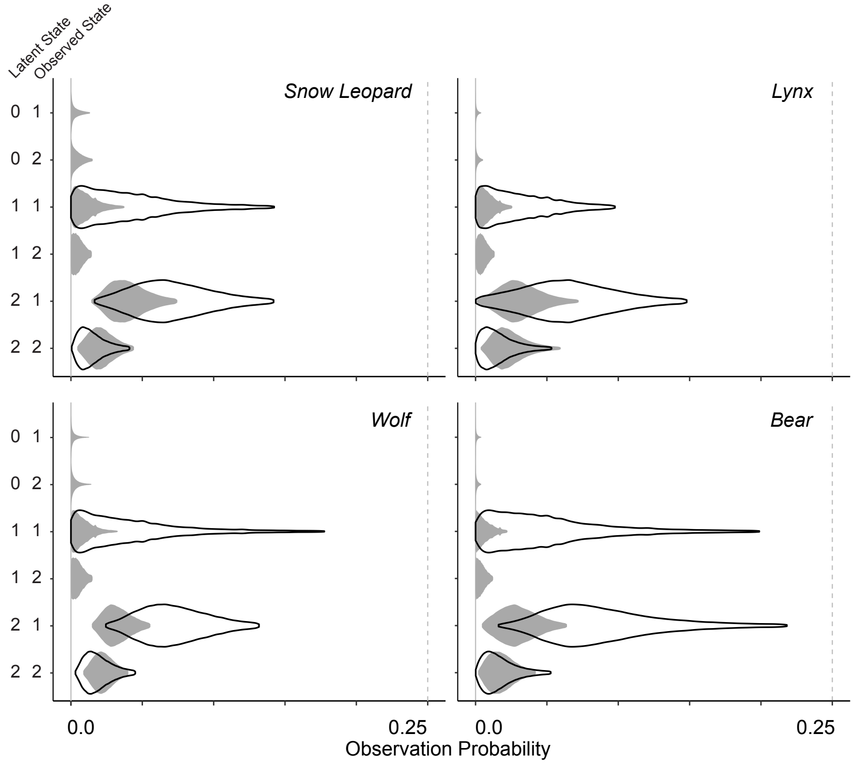

Figure 2. Posterior distributions (95% CRI) for baseline observation probabilities for experts (outlines) and all other respondents (solid gray) on the probability scale. Each row corresponds

to the baseline probability of a respondent reporting observed state, 1=detection and 2=depredation, given true (latent) state, 0=unused, 1=used, 2=used with depredation.

Table 1. Mean predicted site use and depredation probabilities (95% CRI in parentheses) and discrepancies between false-positive and naive models.

Species	**False-positive Model**		**Naive Model**		**Discrepancy**	
	Site Use	Depredation	Site Use	Depredation	Site Use	Depredation
Snow leopard	0.54 (0.31-0.79)	0.29 (0.12-0.49)	0.65 (0.44-0.90)	0.40 (0.19-0.60)	20.8%	35.3%
Lynx	0.40 (0.24-0.59)	0.11 (0.01-0.24)	0.48 (0.29-0.70)	0.25 (0.06-0.42)	20.5%	129.5%
Wolf	0.68 (0.48-0.95)	0.53 (0.37-0.71)	0.77 (0.58-0.99)	0.62 (0.43-0.81)	12.1%	14.9%
Bear	0.38 (0.19-0.58)	0.18 (0.09-0.29)	0.44 (0.22-0.68)	0.24 (0.10-0.39)	16.7%	29.6%

Important spatial covariates emerged for site use, but not for depredation risk (Fig. 3, Appendix Tables S5-S8). Snow leopard site use was importantly and positively associated with Terrain.1 (PIP=0.90), corresponding to steeper, more rugged sites (Appendix Table S1). For lynx, Terrain.2 (PIP=0.77), corresponding to increasing elevation and topographic position, had a clearly important negative effect on predicted site use, whereas a positive important relationship with Human.1 (PIP=0.75), corresponding to anthropogenic infrastructure and human and livestock densities. Wolf site use was similarly related to Human.1, although the importance of this relationship was less clear (PIP=0.71). Bear site use was importantly and positively affected by Land.1 (PIP=0.91), corresponding to greater herbaceous vegetation, tree, and cultivated land cover.

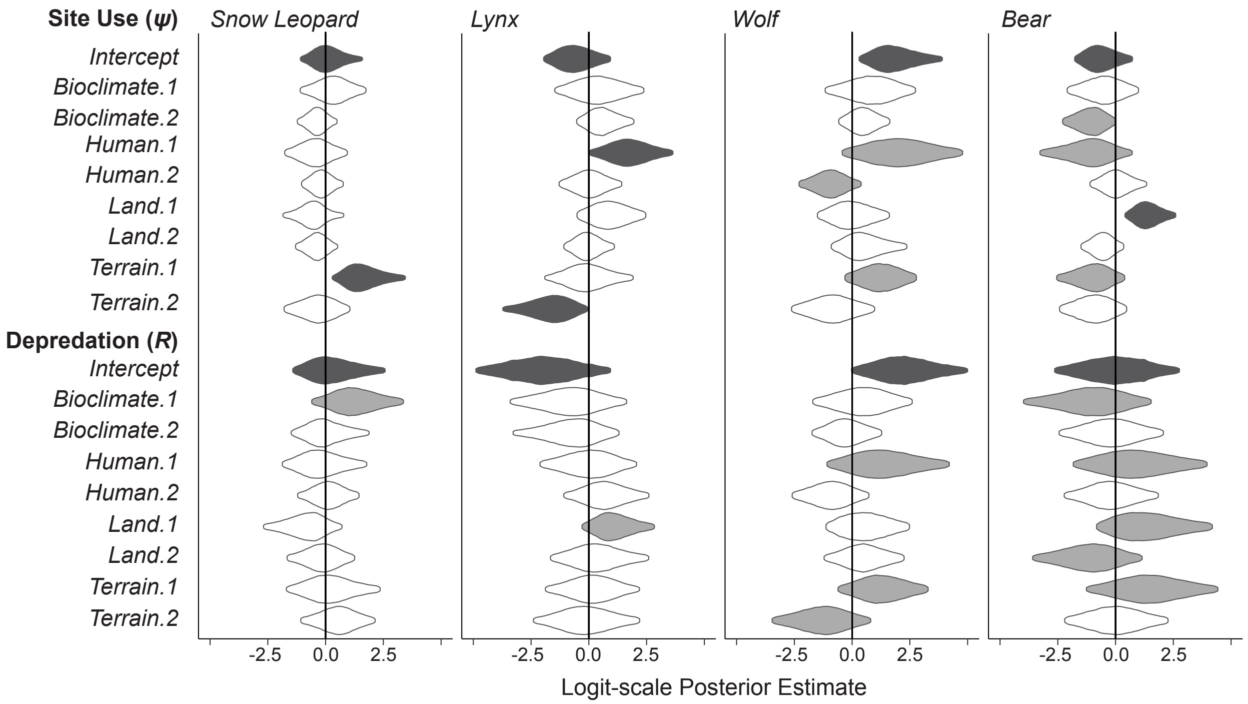

Figure 3. Logit-scale 95% CRI posterior distributions of site use and depredation submodel coefficients. Black indicates intercepts or covariates for which PIP≥0.75; grey 0.5≤PIP<0.75; hollow fill PIP<0.5. Listed covariates are the first and second PCA scores of four thematic PCAs of site level variables (Bioclimate = bioclimatic variables; Human = anthropogenic variables; Land = land cover variables; Terrain = topographic variables).

Although the impacts of spatial covariates on depredation were inconclusive, posterior predicted site use probability and depredation risk illuminated clear spatial patterns for each species (Figs. 4-5). For all species, depredation risk was greatest in valley bottom sites, where humans and livestock live year-round. Wolf conditional depredation risk was consistently greatest in sites with high site use probability, resulting in substantively similar maps for realized depredation risk and site use; this was not the case for other species (Fig. 5). Bear and lynx depredation risk, for example, was greatest in the more heavily vegetated northwestern region of the study area, but not in other regions with comparably high site use probabilities. Similarly, snow leopard depredation risk was concentrated along the middle and upper reaches of the deep river gorges typical of the Western Pamirs; high elevations sites had lower predicted depredation risk, despite comparable site use probabilities.

Heterogeneity in various species observation processes was importantly associated with the number of days respondents spent engaged in outdoor activities, site-level AOK area and forest cover, and whether a respondent lived in the sampling site (Tables S5-S8). Nearly all covariates on apparent vulnerability (δ_k and δ_{Ek}) were inconclusive or clearly not important (Fig. 6), with four exceptions: $\delta_{SnowLeopard}$ was negatively associated with the presence of wire mesh coverings corrals (PIP=0.82), $\delta_{E,SnowLeopard}$ with expert respondent age (PIP=0.78); $\delta_{E,Wolf}$ was positively associated with average site-level expert AOK forest cover (PIP=0.85); and δ_{Bear} was positively associated with the presence of windows or skylights on corrals (PIP=0.78).

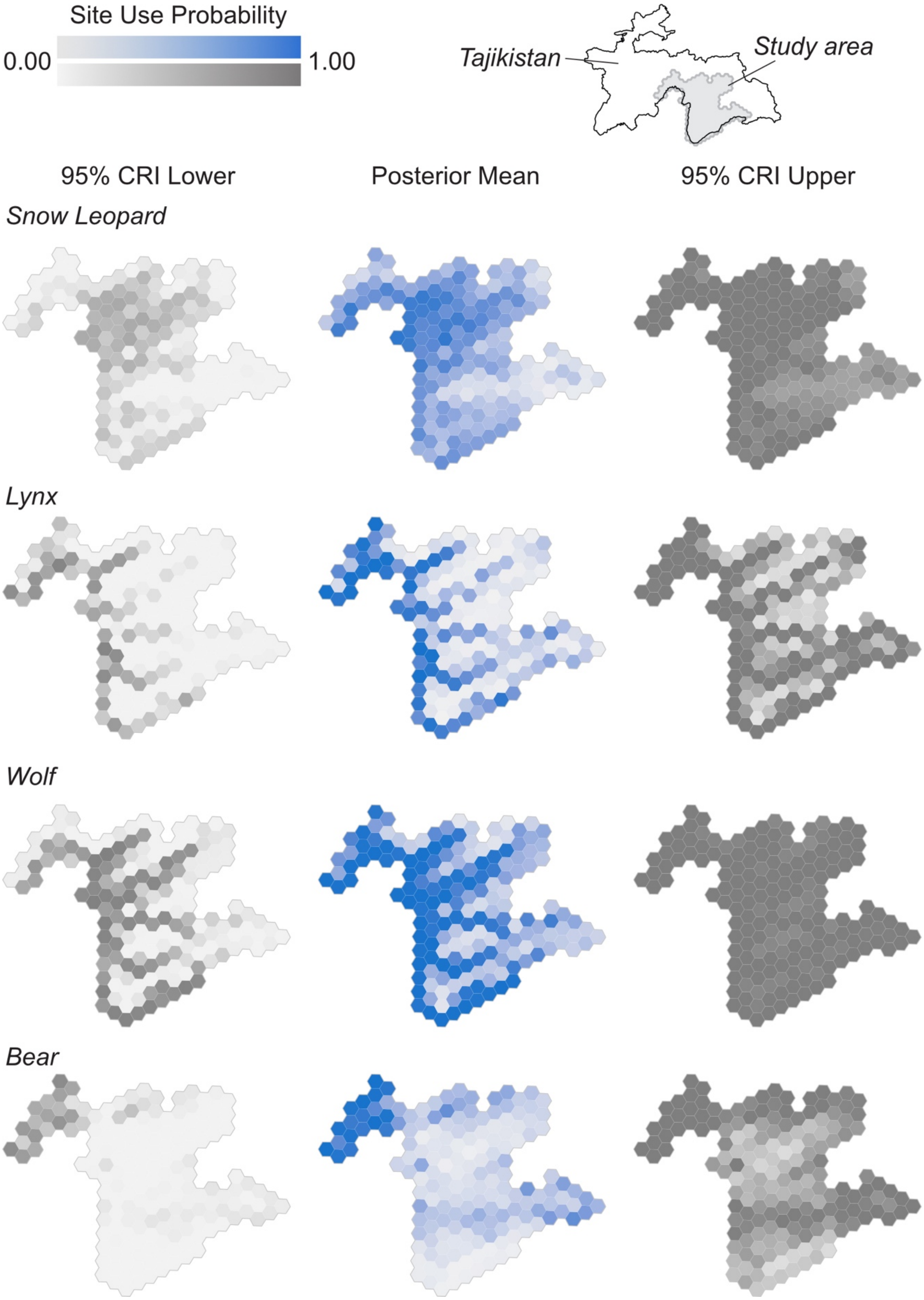

Figure 4. Predicted carnivore site use probability and 95% Credible Interval bounds.

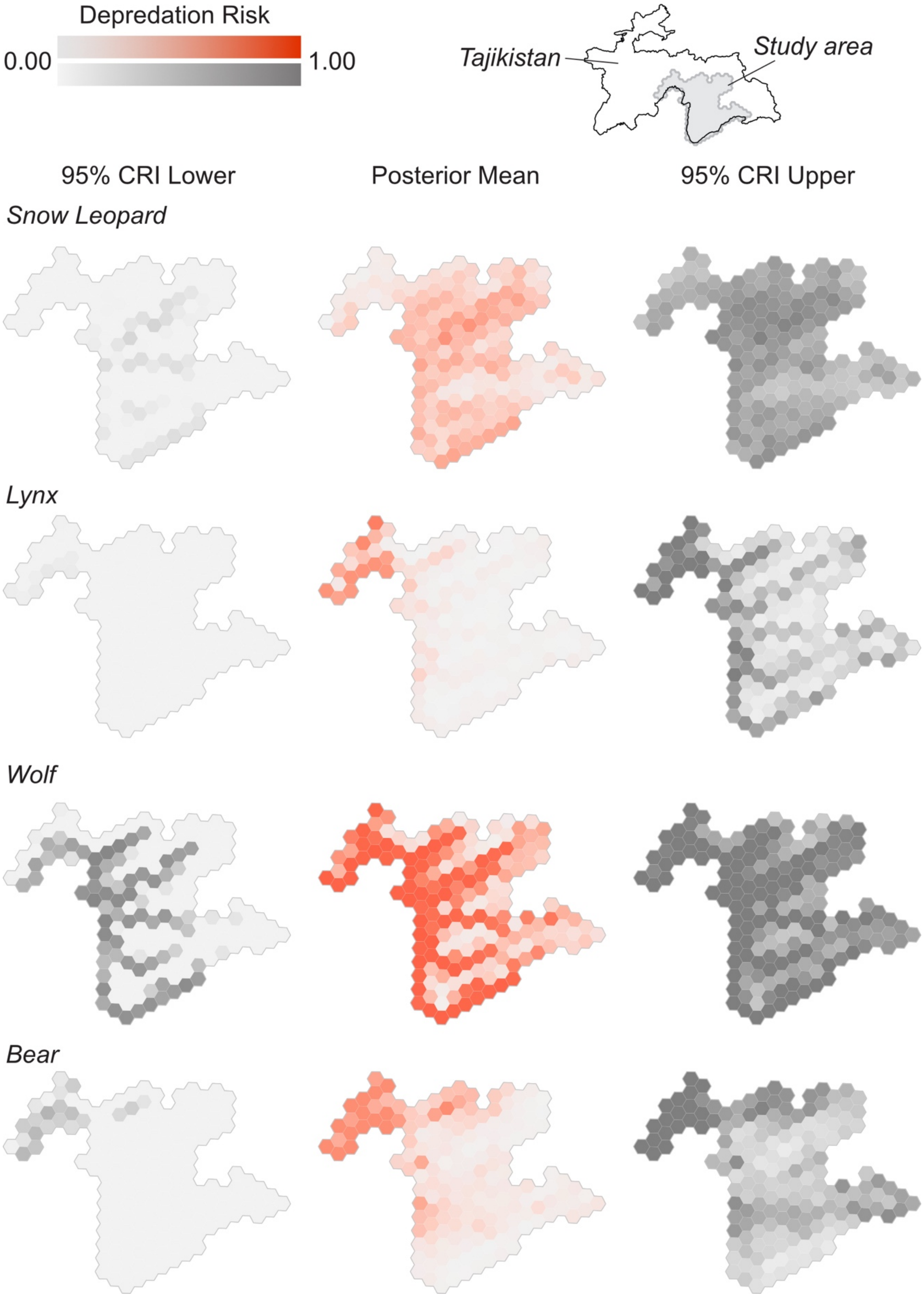

Figure 5. Predicted livestock depredation risk and 95% Credible Interval bounds.

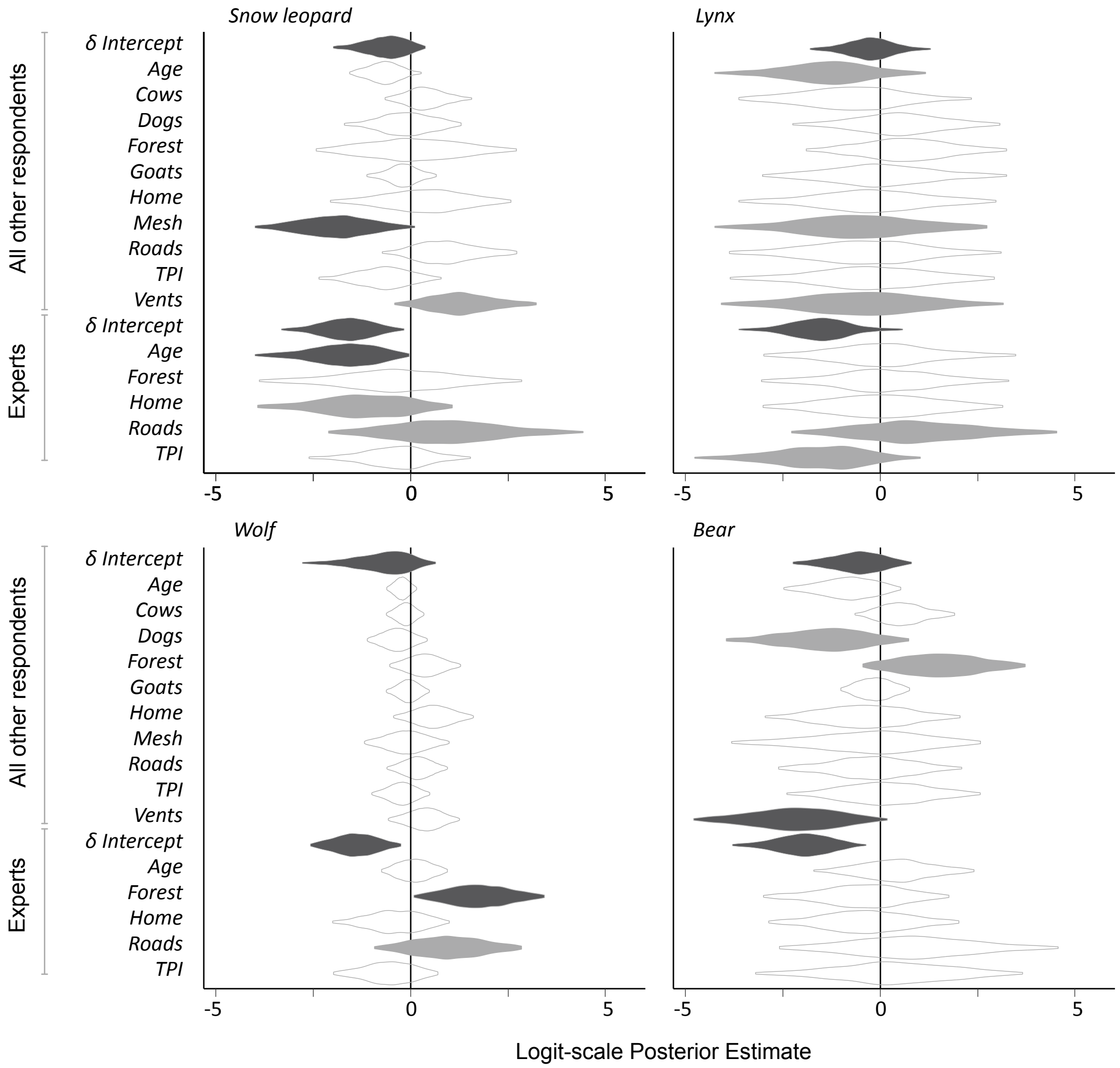

Figure 6. Logit-scale 95% CRI posterior distributions of expert and non-expert conditional depredation detection (δ, δ_E) submodel coefficients. Black indicates PIP≥0.75; grey 0.5≤PIP<0.75; and hollow PIP<0.5. Age = respondent age; Cows, Dogs, and Goats = respectively, number of cattle, dogs, and combined sheep and goats owned by respondent; Forest = percent forest cover of site-AOK; Home = binary indicating respondent residence; Mesh = binary indicating mesh-fortified corral, Vents = binary indicating presence of windows and skylights in corral; Roads = road density of site-AOK; TPI = average topographic position index of site-AOK.

Discussion

Even after accounting for suspected positive biases arising from ambiguous interview-based detection data, livestock depredation in the Pamirs was widespread. In partial support of our hypothesis, vulnerability to snow leopard depredation was reduced by livestock husbandry practices, but this was not the case for other species. Thus, our results suggest that differences in depredation ecology among carnivores preclude blanket solutions to preventing depredation from multiple carnivores simultaneously. Instead, meaningful conflict reduction will require a portfolio of species-specific interventions, enacted broadly to account for the difficulty of targeting future depredation that is predictable at large scales but stochastic from the perspective of individual pastoralists.

Our prediction that husbandry would be more important than habitat characteristics to individual vulnerability was supported for snow leopards, not conclusively resolved for lynx or bears, and contradicted for wolves, underscoring that depredation ecology is species- and scale-specific. Snow leopard vulnerability was importantly associated with husbandry at specific locations (corrals), but wolf vulnerability corresponded with broader habitat characteristics (forest cover). Abundance and overlap with livestock consistently predict wolf depredation elsewhere (e.g., Treves et al. 2011, DeCesare et al. 2018); this pattern appears to extend to our data, assuming site use is a reasonable proxy for abundance. For other species, dissimilarities between site use and depredation risk recapitulate Gervasi et al.'s (2020) finding that carnivore distributions alone can be a poor predictor of depredation risk, even as they provide necessary context.

False-positive observations, though rare, exerted outsized influence on naive model predictions. By implication, interview-based occupancy analyses that do not account for this potential bias are likely exaggerated. True bias in our estimates was unknowable, however. We assumed that the 17% of observations obtained from locally-identified experts were free of false-positive errors. Although this partial reliance on the classic occupancy assumption is common in studies using unverified interview data (e.g., Pillay et al. 2014, Ghodoussi et al. 2020), whenever possible future interview-based occupancy-type analyses should establish known-truth data for at least some sites (Miller et al. 2011).

Carnivore site use was heterogeneous across the region and among species. Unsurprisingly, snow leopard site use was positively associated with steep, rugged sites (Chundawat 1990). The topography of the Pamirs concentrates most human activity in narrow valley bottoms; even urban areas have only a small footprint in a matrix of undeveloped (but heavily-grazed) habitat. Thus, the positive relationship between anthropogenic landscape characteristics (Human.1) and wolf and lynx site use might be explained by shared preferences for valley bottom habitats. The negative influence of topographic position and elevation (Terrain.2) on lynx site use bolsters this interpretation. For wolves, the frequency of depredations suggests an additional explanation: anthropogenic facilitation (Mohammadi et al. 2019). The positive association between bear site use and herbaceous vegetation (i.e., high elevation grasslands), tree, and cultivated land cover (Land.1) comports with other regional investigations (Dar et al. 2021).

Although we did not identify any important site-level covariates on depredation, maps of posterior predicted risk suggested differences in species' responses to livestock. Predator functional responses (Holling 1959) may play an important role in explaining those differences. Suryawanshi et al. (2017) found that snow leopards switch from wild to domestic prey only when relative abundance of livestock exceeds some threshold. Here, seasonality in snow leopard depredations supports a similar interpretation, but we could not evaluate distributions of livestock and wild prey directly as both were reportedly present in every site. Neonate ungulates and marmots – important wild prey – are only available in spring and summer, meaning that livestock account for a greater proportion of available prey in winter, even as winter snows may facilitate encounters by constraining predators and livestock to valley bottoms. Wolves elsewhere consume alternative wild prey proportionately with their availability (Vucetich et al. 2002), a tendency that would explain the ubiquity and lack of seasonality in wolf depredation if it extended to livestock here. Conversely, multiple respondents noted bears and lynx were more abundant in the northwestern parts of the study area, where we predicted hotspots of depredation risk for both species, suggesting that density helps explain depredation for these species.

Despite high site-level risk, the probability that any given individual experienced depredation was small. Across species we identified four important covariates on apparent vulnerability. 1) Older experts, and 2) non-experts with mesh-fortified corrals were less likely to report snow leopard depredations, even as the majority of snow leopard depredations happened inside corrals. Interviewers did not collect data on livestock holdings for expert respondents, so it is unclear why older experts were less vulnerable. The apparent benefit of wire mesh construction suggests preventive measures that we discuss below. Mesh-fortified corrals may have reduced only detection of depredation, but we found no evidence of this relationship in other species, undermining this explanation. 3) Non-experts with corral skylights or windows were less likely to report bear depredation. We attribute this counterintuitive result to a single village where all four respondents had corrals without vents, and none reported bear depredation in an otherwise likely site for it – a sampling artifact. 4) Experts with greater forest cover in site-level AOK's were more likely to report wolf depredation, consistent with findings from

Mongolia and India, where vegetation and habitat structure predicted local-scale wolf depredation (Suryawanshi et al. 2013, Davie et al. 2014). This finding suggests that livestock should not be left to range freely in heavily-vegetated or forested areas.

Poorly-fortified corrals appear to facilitate the entire cycle of human conflict with snow leopards from depredation to retaliation. Pamiri corrals are built with wood, rocks, and mud, with solid roofs and vents for dropping feed inside. As multiple respondents explained, snow leopards enter corrals through these vents or by digging through the roof, typically kill multiple livestock once inside (Jackson et al. 2010), and are often unable to escape when discovered, leading to opportunistic retaliation. Proactive interventions to fortify as many corrals as possible could substantially and simultaneously reduce the risk of the most catastrophic depredation events for people and the opportunity for retaliation against snow leopards. This strategy has proven effective in Trans-Himalayan India: snow leopard depredations decreased by an order of magnitude following proactive predator-proofing programs (Jamwal et al. 2018).

Comprehensive reduction of HCC may require multi-pronged interventions tailored to all four carnivores. The ubiquity of wolf depredation, in particular, suggests that non-targeted retaliation is a pervasive threat for other species. Elsewhere, wolf depredation risk is well-predicted by recent depredation history (Karlsson and Johansson 2010; Decesare et al. 2018). Non-lethal reactive interventions may therefore be particularly important for reducing non-targeted retaliation. Yet, for reactive measures to protect predators as well as livestock, predators must survive the initial interaction; hence, reactive strategies alone are unlikely to meaningfully reduce the impact of HCC on snow leopards.

Future research is necessary to better understand how livestock grazing and husbandry practices may impact depredation rates. Interventions and incentives to limit depredation and retaliation abound, but rigorous experimentation is needed to understand what works (van Eeden et al. 2018); even without perfect understanding of local depredation ecology, such experimentation could benefit from the high background risk of depredation in the Pamirs, while also benefiting local communities.

In light of foreseeable global trends, preserving carnivores will require conservation strategies that promote coexistence between people and carnivores in shared landscapes (Woodroffe et al. 2005). Simultaneously, limited conservation resources dictate a need for evidence-based insight into where and how to do so, even where unambiguous data may be scarce. Our approach – accommodating ambiguous data in a multi-state occupancy model of site use and depredation risk – expands the possibilities for leveraging uncertain data to understand distributions and ecology of rare and elusive species.

Literature Cited

Broms, K., Hooten, M., and Fitzpatrick, R. (2016). Model selection and assessment for multi-species occupancy models. *Ecology*, *97*(7), 1759–1770. https://doi.org/10.1890/15-1471.1

Chundawat, R. (1990). Habitat selection by a snow leopard in Hemis National Park, India. In *International Pedigree Book of Snow Leopards* (Vol. 6, pp. 85–92).

Dar, S., Singh, S., Wan, H., Kumar, V., Cushman, S., and Sathyakumar, S. (2021). Projected climate change threatens Himalayan brown bear habitat more than human land use. *Animal Conservation*, acv.12671. https://doi.org/10.1111/acv.12671

de Valpine, P., Turek, D., Paciorek, C., Anderson-Bergman, C., Lang, D., and Bodik, R. (2017). Programming With Models: Writing Statistical Algorithms for General Model Structures With NIMBLE. *Journal of Computational and Graphical Statistics*, *26*(2), 403–413. https://doi.org/10.1080/10618600.2016.1172487

Decesare, N., Wilson, S., Bradley, E., Gude, J., Inman, R., Lance, N., Laudon, K., … Smucker, T., 2018. Wolf-livestock conflict and the effects of wolf management. *Journal of Wildlife Management 82*, 711–722. https://doi.org/10.1002/jwmg.21419

Dickman, A., Macdonald, E., and Macdonald, D. (2011). A review of financial instruments to pay for predator conservation and encourage human–carnivore coexistence. *PNAS*, *108*(34), 13937–13944. https://doi.org/10.1073/pnas.1012972108

Gervasi, V., Linnell, J.D.C., Berce, T., Boitani, L., Cerne, R., Cretois, B., Ciucci, P., … Gimenez, O. 2020. Ecological and anthropogenic drivers of large carnivore depredation on sheep in Europe. *bioRxiv* 2020.04.14.041160. https://doi.org/10.1101/2020.04.14.041160

Fick, S., Hijmans, R. (2017). WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology* 37, 4302–4315. https://doi.org/10.1002/joc.5086

Gelman, A. (2006). Prior distributions for variance parameters in hierarchical models. *Bayesian Analysis*, 1(3):515-533.

Gelman, A., Vehtari, A., Dunson, D., Rubin, D., Stern, H., and Carlin, J. (2014). *Bayesian data analysis*. Chapman and Hall

Ghoddousi, A., Bleyhl, B., Sichau, C., Ashayeri, D., Moghadas, P., Sepahvand, P., Hamidi, A., Soofi, M., and Kuemmerle, T. (2020). Mapping connectivity and conflict risk to identify safe corridors for the Persian leopard. *Landscape Ecology*. https://doi.org/10.1007/s10980-020-01062-0

Ghoshal, A., Bhatnagar, Y.V., Pandav, B., Sharma, K., Mishra, C., Raghunath, R., Suryawanshi, K.R. (2017). Assessing changes in distribution of the Endangered snow leopard Panthera uncia and its wild prey over 2 decades in the Indian Himalaya through interview-based occupancy surveys. *Oryx* 1–13. https://doi.org/10.1017/S0030605317001107

Gilbert, M., Nicolas, G., Cinardi, G., Van Boeckel, T.P., Vanwambeke, S.O., Wint, G.R.W., Robinson, T.P. (2018). Global distribution data for cattle, buffaloes, horses, sheep, goats, pigs, chickens and ducks in 2010. *Scientific Data* 5, 180227. https://doi.org/10.1038/sdata.2018.227

Green, P. (1995). Reversible jump Markov chain Monte Carlo computation and Bayesian model determination. *Biometrika*, *82*(4), 711–732. https://doi.org/10.1093/biomet/82.4.711

Gneiting, T., and Raftery, A.T. (2007). Strictly proper scoring rules, prediction, and estimation. *Journal of American Statistical Association*, *102*(477), 359-378.

Hebblewhite, M., Merrill, E., and McDonald, T. (2005). Spatial decomposition of predation risk using resource selection functions: An example in a wolf–elk predator–prey system. *Oikos*, *111*(1), 101–111.

Holling, C. (1959). Some characteristics of simple types of predation and parasitism. *Canadian Entomology*, *91*, 385–398.

Hooten, M., and Hefley, T. (2019). *Bringing Bayesian models to life*. CRC Press.

Hooten, M., and Hobbs, N. (2015). A guide to Bayesian model selection for ecologists. *Ecological Monographs*, *85*(1), 3–28.

Inskip, C., and Zimmermann, A. (2009). Human-felid conflict: A review of patterns and priorities worldwide. *Oryx*, *43*(1), 18–34. https://doi.org/10.1017/S003060530899030X

Jackson, R., Mishra, C., McCarthy, T., Ale. S. (2010). Snow leopards: conflict and conservation, in: Macdonald, D.W., Loveridge, A.J. (Eds.), *Biology and Conservation of Wild Felids* (pp. 417–430) Oxford University Press.

Jamwal, P.S., Takpa, J., Parsons, M.H. (2018). Factors contributing to a striking shift in human–wildlife dynamics in Hemis National Park, India: 22 years of reported snow leopard depredation. *Oryx* 1–5. https://doi.org/10.1017/S0030605317001892

JAXA EORC. (2020). ALOS Global Digital Surface Model ALOS World 3D-30m (AW3D30) Version 3.1. *Japan Aerospace Exploration Agency.*

Karanth, K., Nichols, J., Hines, J., Karanth, K., and Christensen, N. (2009). Patterns and determinants of mammal species occurrence in India. *Journal of Applied Ecology*, *46*(6), 1189–1200. https://doi.org/10.1111/j.1365-2664.2009.01710.x

Karlsson, J., and Johansson, Ö. (2010). Predictability of repeated carnivore attacks on livestock favours reactive use of mitigation measures. *Journal of Applied Ecology*, *47*(1), 166–171. https://doi.org/10.1111/j.1365-2664.2009.01747.x

Kennedy, C.M., Oakleaf, J.R., Theobald, D.M., Baruch-Mordo, S., Kiesecker, J. (2018). Managing the middle: A shift in conservation priorities based on the global human modification gradient. *Global Change Biology* 0. https://doi.org/10.1111/gcb.14549

Kéry, M., and Royle, J. (2016). *Applied hierarchical modeling in ecology: Analysis of distribution, abundance and species richness in R and BUGS*. Elsevier/AP.

Kuo, L., and Mallick, B. (1998). Variable Selection for Regression Models. *Sankhyā: The Indian Journal of Statistics, Series B (1960-2002)*, *60*(1), 65–81.

Legendre, P., and Legendre, L. (2012). *Numerical ecology*. Elsevier.

Li, J., and Lu, Z. (2014). Snow leopard poaching and trade in China 2000–2013. *Biological Conservation*, *176*, 207–211. https://doi.org/10.1016/j.biocon.2014.05.025

Lima, S., and Dill, L. (1990). Behavioral decisions made under the risk of predation: A review and prospectus. *Canadian Journal of Zoology*, *68*(4), 619–640. https://doi.org/10.1139/z90-092

MacKenzie, D., Nichols, J., Lachman, G., Droege, S., Royle, J., and Langtimm, C.(2002).

Estimating Site Occupancy Rates When Detection Probabilities Are Less Than One. *Ecology*, *83*(8), 2248. https://doi.org/10.2307/3072056

Miller, D., Nichols, J., McClintock, B., Grant, E., Bailey, L., and Weir, L. (2011). Improving occupancy estimation when two types of observational error occur: Non-detection and species misidentification. *Ecology*, *92*(7), 1422–1428. https://doi.org/10.1890/10-1396.1

Miller, J. (2015). Mapping attack hotspots to mitigate human–carnivore conflict: Approaches and applications of spatial predation risk modeling. *Biodiversity and Conservation*, *24*(12), 2887–2911. https://doi.org/10.1007/s10531-015-0993-6

Mishra, C. (1997). Livestock depredation by large carnivores in the Indian trans-Himalaya: Conflict perceptions and conservation prospects. *Environmental Conservation*, *24*(4), 338–343.

Mohammadi, A., Kaboli, M., Sazatornil, V., López-Bao, J. (2019). Anthropogenic food resources sustain wolves in conflict scenarios of Western Iran. *PLoS ONE 14*, e0218345. https://doi.org/10.1371/journal.pone.0218345

Mutshinda, C., Finkel, Z., and Irwin, A. (2013). Which environmental factors control phytoplankton populations? A Bayesian variable selection approach. *Ecological Modelling*, *269*, 1–8. https://doi.org/10.1016/j.ecolmodel.2013.07.025

Nichols, J., Hines, J., Mackenzie, D., Seamans, M., and Gutiérrez, R. (2007). Occupancy estimation and modeling with multiple states and state uncertainty. *Ecology*, *88*(6), 1395–1400. https://doi.org/10.1890/06-1474

Northrup, J., and Gerber, B. (2018). A comment on priors for Bayesian occupancy models. *PLoS ONE*, *13*(2). https://doi.org/10.1371/journal.pone.0192819

Ogada, M., Woodroffe, R., Oguge, N., Frank, L. (2003). Limiting depredation by african carnivores: the role of livestock husbandry. *Conservation Biology 17*, 1521–1530. https://doi.org/10.1111/j.1523-1739.2003.00061.x

OpenStreetMap Contributors. (2020). OpenStreetMap. https:://www.openstreetmap.org (accessed 6.10.20).

Petracca, L., Frair, J., Cohen, J., Calderón, A., Carazo-Salazar, J., Castañeda, F., ... Quigley, H. (2017). Robust inference on large-scale species habitat use with interview data: The status of jaguars outside protected areas in Central America. *Journal of Applied Ecology*. https://doi.org/10.1111/1365-2664.12972

Pillay, R., Miller, D., Hines, J., Joshi, A., and Madhusudan, M. (2014). Accounting for false positives improves estimates of occupancy from key informant interviews. *Diversity and Distributions*, *20*(2), 223–235. https://doi.org/10.1111/ddi.12151

Ripple, W., Estes, J., Beschta, R., Wilmers, C., Ritchie, E., Hebblewhite, M., Berger, J., … Wirsing, A. (2014). Status and Ecological Effects of the World's Largest Carnivores. *Science*, *343*(6167), 1241484–1241484. https://doi.org/10.1126/science.1241484

Royle, J., and Link, W. (2006). Generalized Site Occupancy Models Allowing for False Positive and False Negative Errors. *Ecology*, *87*(4), 835–841. https://doi.org/10.1890/0012-9658(2006)87[835:GSOMAF]2.0.CO;2

Saidov, A., Karimov, K., Amirov, Z., and Rosen, T. (2016). Central Asia: Tajikistan. In T. McCarthy and D. Mallon (Eds.), *Snow leopards* (pp. 433–437). Elsevier.

Sipe, H.A. (2019). Multi-state occupancy modeling and optimal allocation of survey resources for Common Loons in Washington State (Thesis). University of Washington, Seattle, WA, USA.

Sisson, S. A. (2005). Transdimensional Markov Chains: A Decade of Progress and Future Perspectives. *Journal of the American Statistical Association*, *100*, 1077–1089.

Srivathsa, A., Puri, M., Karanth, K. K., Patel, I., and Kumar, N. (2019). Examining human–carnivore interactions using a socio-ecological framework: Sympatric wild canids in India as a case study. *Royal Society Open Science*, *6*(5), 182008. https://doi.org/10.1098/rsos.182008

Suryawanshi, K., Bhatnagar, Y., Redpath, S., and Mishra, C. (2013). People, predators and perceptions: Patterns of livestock depredation by snow leopards and wolves. *Journal of Applied Ecology*, *50*(3), 550–560. https://doi.org/10.1111/1365-2664.12061

Suryawanshi, K., Redpath, S., Bhatnagar, Y., Ramakrishnan, U., Chaturvedi, V., Smout, S., and Mishra, C. (2017). Impact of wild prey availability on livestock predation by snow leopards. *Royal Society Open Science*, *4*(6), 170026. https://doi.org/10.1098/rsos.170026

Treves, A., Martin, K., Wydeven, A., and Wiedenhoeft, J. (2011). Forecasting environmental hazards and the application of risk maps to predator attacks on livestock. *BioScience*, *61*(6), 451–458. https://doi.org/10.1525/bio.2011.61.6.7

Tuanmu, M.-N., Jetz, W. (2014). A global 1-km consensus land-cover product for biodiversity and ecosystem modelling. *Global Ecology and Biogeography 23*, 1031–1045. https://doi.org/10.1111/geb.12182

van Eeden, L., Eklund, A., Miller, J., López-Bao, J., Chapron, G., Cejtin, M., Crowther, M., … Treves, A. (2018). Carnivore conservation needs evidence-based livestock protection. *PLOS Biology*, *16*(9), e2005577. https://doi.org/10.1371/journal.pbio.2005577

Vucetich, J., Peterson, R., Schaefer, C. (2002). The Effect of Prey and Predator Densities on Wolf Predation. *Ecology 83*, 3003–3013. https://doi.org/10.1890/0012-9658(2002)083[3003:TEOPAP]2.0.CO;2

Wright, W., Irvine, K., and Higgs, M. (2019). Identifying occupancy model inadequacies: Can residuals separately assess detection and presence? *Ecology*, *100*(6), e02703. https://doi.org/10.1002/ecy.2703

Zeller, K., Nijhawan, S., Salom-Pérez, R., Potosme, S., and Hines, J. (2011). Integrating occupancy modeling and interview data for corridor identification: A case study for jaguars in Nicaragua. *Biological Conservation*, *144*(2), 892–901. https://doi.org/10.1016/j.biocon.2010.12.003

Zipkin, E., DeWan, A., and Royle, J. (2009). Impacts of forest fragmentation on species richness: A hierarchical approach to community modelling. *Journal of Applied Ecology*, *46*(4), 815–822. https://doi.org/10.1111/j.1365-2664.2009.01664.x

Appendix

S1. Additional interview details

The interview team consisted of three men and five women, all of whom were Tajik nationals except for one American. Interviews were conducted in Tajik, Russian, and/or Shugni, according to the comfort of respondents. Pairs of surveyors presented each respondent with a set of verification photographs depicting local large and medium-sized mammal species as well as several species that are not present in the region, such as tigers and dholes. Respondents were asked if the species depicted were present in the region, and if so, to identify the species. Experts were additionally asked to identify photographs of tracks and sign (e.g., scats, scent marking posts, scrapes) of target species. All respondents considered in the analysis (264 of 271 total) correctly identified the local carnivores and ungulates and determined that other depicted species were absent from the region. All expert respondents correctly identified photos of tracks and signs of all four large carnivores of interest.

S2. Model checking with Bayesian P-values

To evaluate goodness-of-fit, we calculated Bayesian P-values (P_B) based on chi-square test statistics comparing observed data (y) and data simulated from model parameters (y_{new}) against model expectations (p), where

$$\chi^2_{new} = \sum_i \frac{(y_i - p_i)^2}{p_i}$$

and values of the expression $Pr(\chi^2_{new} \geq \chi^2_{data})$ outside of the interval 0.1-0.9 indicate a potential lack of fit, as estimated by the proportion of iterations where $\chi^2_{new} \geq \chi^2_{data}$ (Hooten and Hobbs 2015). Expected values, p, were calculated as

$$p_i = \sum_{z=0}^{2} \frac{\sum_{s=0}^{2}(\boldsymbol{\Omega}_{z,s} * s)}{3} * \Phi_s$$

where z's were the potential latent states and s's were the potential observed states. If lack of fit was indicated, we used binned residual plots (Wright et al. 2019) to identify problematic covariates, which were then removed from the models.

S3. Evaluating predictive performance via cross-validation

We used K-fold cross validation (Hooten and Hobbs, 2015) with 12 folds to calculate two proper scoring rules with which to compare the predictive ability of false positive and naive models for each species (Gneiting and Raftery 2007, Broms et al. 2016). Log-scores were calculated as the mean, across all iterations, of $-2\ log(Pr(y|\hat{\theta}))$, where $\hat{\theta}$ were parameter estimates in each iteration. Brier scores were calculated as the mean, across all iterations, of the expression

$$BS_i = \sum_{i=1}^{N} \sum_{s=0}^{2} (p_{s,i} - o_{s,i})^2$$

where s's were potential observed states for N withheld observations, $p_{s,i}$ was the probability of observing the sth state for each withheld observation and o_s was a binary indicating whether the observed state matched the sth state (Gneiting and Raftery 2007). In both cases, lower scores indicated better predictive performance.

S4. *Nimble modelling language code for multispecies multi-state false-positive occupancy model for carnivore site use and depredation in the Pamir Mountains, Tajikistan*

```
#  Nimble Model --------------------------------------------------------------
nimbleCode({

  ######## Priors
  # Community mean hyperpriors for detection intercepts
  mu.alpha.p1     ~ dlogis(0, 1) # Detection when z=1
  mu.alpha.p2     ~ dlogis(0, 1) # Detection when z=2
  mu.alpha.delta  ~ dlogis(0, 1) # Apparent Vulnerability when z=2
  mu.alpha.r1     ~ dlogis(0, 1) # Expert detection when z=1
  mu.alpha.r2     ~ dlogis(0, 1) # Expert detection when z=2
  mu.alpha.deltaE ~ dlogis(0, 1) # Expert apparent Vulnerability when z=2
  mu.alpha.q01    ~ dlogis(0, 1) # False positive detection when z=0
  mu.alpha.q02    ~ dlogis(0, 1) # False positive depredation when z=0
  mu.alpha.q12    ~ dlogis(0, 1) # False positive depredation when z=1
  # Regularizing exponential hyperprior for detection intercept sigmas
  sd.alpha.p1     ~ dexp(1)
  sd.alpha.p2     ~ dexp(1)
  sd.alpha.delta  ~ dexp(1)
  sd.alpha.r1     ~ dexp(1)
  sd.alpha.r2     ~ dexp(1)
  sd.alpha.deltaE ~ dexp(1)
  sd.alpha.fp     ~ dexp(1)
  sd.alpha.q02    ~ dexp(1)
  sd.alpha.q12    ~ dexp(1)

  # Uniform Hyperprior for (half)Cauchy scale Parameter
  A.sigma ~ dunif(0, 5)
  # Half-cauchy priors on random-effects sigmas
  s.p1     ~ dt(mu = 0, df = 1, sigma = A.sigma)
  s.p2     ~ dt(mu = 0, df = 1, sigma = A.sigma)
  s.delta  ~ dt(mu = 0, df = 1, sigma = A.sigma)
  s.r1     ~ dt(mu = 0, df = 1, sigma = A.sigma)
  s.r2     ~ dt(mu = 0, df = 1, sigma = A.sigma)
  s.deltaE ~ dt(mu = 0, df = 1, sigma = A.sigma)
  sigma.p1     <- abs(s.p1)
  sigma.p2     <- abs(s.p2)
  sigma.delta  <- abs(s.delta)
  sigma.r1     <- abs(s.r1)
  sigma.r2     <- abs(s.r2)
  sigma.deltaE <- abs(s.deltaE)
  # Individual effects
  for (l in 1:(nSurveyID - 1)) {
    epsilon.p1[l]     ~ dnorm(0, sd = sigma.p1)
    epsilon.p2[l]     ~ dnorm(0, sd = sigma.p2)
    epsilon.delta[l]  ~ dnorm(0, sd = sigma.delta)
    epsilon.r1[l]     ~ dnorm(0, sd = sigma.r1)
    epsilon.r2[l]     ~ dnorm(0, sd = sigma.r2)
    epsilon.deltaE[l] ~ dnorm(0, sd = sigma.deltaE)
  }
  # Sum-to-zero constraint on individual effects
```

```
  epsilon.p1[nSurveyID]     <- -sum(epsilon.p1[1:(nSurveyID - 1)])
  epsilon.p2[nSurveyID]     <- -sum(epsilon.p2[1:(nSurveyID - 1)])
  epsilon.delta[nSurveyID]  <- -sum(epsilon.delta[1:(nSurveyID - 1)])
  epsilon.r1[nSurveyID]     <- -sum(epsilon.r1[1:(nSurveyID - 1)])
  epsilon.r2[nSurveyID]     <- -sum(epsilon.r2[1:(nSurveyID - 1)])
  epsilon.deltaE[nSurveyID] <- -sum(epsilon.deltaE[1:(nSurveyID - 1)])

# Species-specific Priors
  for (k in 1:nSpecies) {
    alpha.psi[k]         ~ dlogis(0, 1) # Site Use
    alpha.HWC[k]         ~ dlogis(0, 1) # Depredation
    # Covariates given natural intuitive names that correspond to the
    # descriptions in main text
    beta.Terrain.1[k]    ~ dlogis(0, 1)
    beta.Terrain.2[k]    ~ dlogis(0, 1)
    beta.HumanPCA2[k]    ~ dlogis(0, 1)
    beta.HumanPCA[k]     ~ dlogis(0, 1)
    beta.Land.1[k]       ~ dlogis(0, 1)
    beta.Land.2[k]       ~ dlogis(0, 1)
    beta.BioPCA.1[k]     ~ dlogis(0, 1)
    beta.BioPCA.2[k]     ~ dlogis(0, 1)
    betaHWC.Terrain.1[k] ~ dlogis(0, 1)
    betaHWC.Terrain.2[k] ~ dlogis(0, 1)
    betaHWC.HumanPCA2[k] ~ dlogis(0, 1)
    betaHWC.HumanPCA[k]  ~ dlogis(0, 1)
    betaHWC.Land.1[k]    ~ dlogis(0, 1)
    betaHWC.Land.2[k]    ~ dlogis(0, 1)
    betaHWC.BioPCA.1[k]  ~ dlogis(0, 1)
    betaHWC.BioPCA.2[k]  ~ dlogis(0, 1)

    # State-dependent detection intercepts
    alpha.p1[k]     ~ dnorm(mu.alpha.p1,     sd = sd.alpha.p1)
    alpha.p2[k]     ~ dnorm(mu.alpha.p2,     sd = sd.alpha.p2)
    alpha.r1[k]     ~ dnorm(mu.alpha.r1,     sd = sd.alpha.r1)
    alpha.r2[k]     ~ dnorm(mu.alpha.r2,     sd = sd.alpha.r2)
    alpha.delta[k]  ~ dnorm(mu.alpha.delta,  sd = sd.alpha.delta)
    alpha.deltaE[k] ~ dnorm(mu.alpha.deltaE, sd = sd.alpha.deltaE)
    alpha.q01[k]    ~ dnorm(mu.alpha.q01,    sd = sd.alpha.q01)
    alpha.q02[k]    ~ dnorm(mu.alpha.q02,    sd = sd.alpha.q02)
    alpha.q12[k]    ~ dnorm(mu.alpha.q12,    sd = sd.alpha.q12)
    # Constraint to ensure that q12 < p2δ (on average)
    constraint1[k] ~
      dconstraint(ilogit(alpha.q12[k]) <= (ilogit(alpha.p2[k])) *
      ilogit(alpha.delta[k]))

    # Detection covariates
    b.home[k]         ~ dlogis(0, 1)
    b.effort1[k]      ~ dlogis(0, 1)
    b.age[k]          ~ dlogis(0, 1)
    b.days[k]         ~ dlogis(0, 1)
    b.Roads[k]        ~ dlogis(0, 1)
    b.Forest[k]       ~ dlogis(0, 1)
    b.TPI[k]          ~ dlogis(0, 1)
    br.Roads[k]       ~ dlogis(0, 1)
    br.home[k]        ~ dlogis(0, 1)
    br.effort1[k]     ~ dlogis(0, 1)
```

```
br.age[k]         ~ dlogis(0, 1)
br.days[k]        ~ dlogis(0, 1)
br.Forest[k]      ~ dlogis(0, 1)
br.TPI[k]         ~ dlogis(0, 1)

bp2.effort1[k]    ~ dlogis(0, 1)
bp2.home[k]       ~ dlogis(0, 1)
bp2.age[k]        ~ dlogis(0, 1)
bp2.days[k]       ~ dlogis(0, 1)
bp2.Roads[k]      ~ dlogis(0, 1)
bp2.Forest[k]     ~ dlogis(0, 1)
bp2.TPI[k]        ~ dlogis(0, 1)

br2.effort1[k]   ~ dlogis(0, 1)
br2.home[k]      ~ dlogis(0, 1)
br2.age[k]       ~ dlogis(0, 1)
br2.days[k]      ~ dlogis(0, 1)
br2.Roads[k]     ~ dlogis(0, 1)
br2.Forest[k]    ~ dlogis(0, 1)
br2.TPI[k]       ~ dlogis(0, 1)

bdelta.age[k]     ~ dlogis(0, 1)
bdelta.vents[k]   ~ dlogis(0, 1)
bdelta.dogs[k]    ~ dlogis(0, 1)
bdelta.mesh[k]    ~ dlogis(0, 1)
bdelta.cows[k]    ~ dlogis(0, 1)
bdelta.goats[k]   ~ dlogis(0, 1)
bdelta.home[k]    ~ dlogis(0, 1)
bdelta.TPI[k]     ~ dlogis(0, 1)
bdelta.Roads[k]   ~ dlogis(0, 1)
bdelta.Forest[k]  ~ dlogis(0, 1)

bdeltaE.home[k]   ~ dlogis(0, 1)
bdeltaE.age[k]    ~ dlogis(0, 1)
bdeltaE.Roads[k]  ~ dlogis(0, 1)
bdeltaE.Forest[k] ~ dlogis(0, 1)
bdeltaE.TPI[k]    ~ dlogis(0, 1)

# Indicators Variables (not strictly necessary given psi.ind=0.5)
z.beta.Terrain.1[k]    ~ dbern(psi.ind)
z.beta.Terrain.2[k]    ~ dbern(psi.ind)
z.beta.HumanPCA2[k]    ~ dbern(psi.ind)
z.beta.HumanPCA[k]     ~ dbern(psi.ind)
z.beta.Land.1[k]       ~ dbern(psi.ind)
z.beta.Land.2[k]       ~ dbern(psi.ind)
z.beta.BioPCA.1[k]     ~ dbern(psi.ind)
z.beta.BioPCA.2[k]     ~ dbern(psi.ind)
z.betaHWC.Terrain.1[k] ~ dbern(psi.ind)
z.betaHWC.Terrain.2[k] ~ dbern(psi.ind)
z.betaHWC.HumanPCA2[k] ~ dbern(psi.ind)
z.betaHWC.HumanPCA[k]  ~ dbern(psi.ind)
z.betaHWC.Land.1[k]    ~ dbern(psi.ind)
z.betaHWC.Land.2[k]    ~ dbern(psi.ind)
z.betaHWC.BioPCA.1[k]  ~ dbern(psi.ind)
z.betaHWC.BioPCA.2[k]  ~ dbern(psi.ind)
z.b.home[k]            ~ dbern(psi.ind)
```

```
  z.b.effort1[k]         ~ dbern(psi.ind)
  z.b.age[k]             ~ dbern(psi.ind)
  z.b.days[k]            ~ dbern(psi.ind)
  z.bp2.effort1[k]       ~ dbern(psi.ind)
  z.bp2.home[k]          ~ dbern(psi.ind)
  z.bp2.age[k]           ~ dbern(psi.ind)
  z.bp2.days[k]          ~ dbern(psi.ind)
  z.bdelta.age[k]        ~ dbern(psi.ind)
  z.bdelta.vents[k]      ~ dbern(psi.ind)
  z.bdelta.dogs[k]       ~ dbern(psi.ind)
  z.bdelta.mesh[k]       ~ dbern(psi.ind)
  z.bdelta.cows[k]       ~ dbern(psi.ind)
  z.bdelta.goats[k]      ~ dbern(psi.ind)
  z.bdelta.home[k]       ~ dbern(psi.ind)
  z.br.home[k]           ~ dbern(psi.ind)
  z.br.effort1[k]        ~ dbern(psi.ind)
  z.br.age[k]            ~ dbern(psi.ind)
  z.br.days[k]           ~ dbern(psi.ind)
  z.br2.effort1[k]       ~ dbern(psi.ind)
  z.br2.home[k]          ~ dbern(psi.ind)
  z.br2.age[k]           ~ dbern(psi.ind)
  z.br2.days[k]          ~ dbern(psi.ind)
  z.bdeltaE.age[k]       ~ dbern(psi.ind)
  z.bdeltaE.home[k]      ~ dbern(psi.ind)
  z.b.Roads[k]           ~ dbern(psi.ind)
  z.br.Roads[k]          ~ dbern(psi.ind)
  z.bp2.Roads[k]         ~ dbern(psi.ind)
  z.br2.Roads[k]         ~ dbern(psi.ind)
  z.bdelta.Roads[k]      ~ dbern(psi.ind)
  z.bdeltaE.Roads[k]     ~ dbern(psi.ind)
  z.b.Forest[k]          ~ dbern(psi.ind)
  z.br.Forest[k]         ~ dbern(psi.ind)
  z.b.TPI[k]             ~ dbern(psi.ind)
  z.br.TPI[k]            ~ dbern(psi.ind)
  z.bp2.Forest[k]        ~ dbern(psi.ind)
  z.br2.Forest[k]        ~ dbern(psi.ind)
  z.bp2.TPI[k]           ~ dbern(psi.ind)
  z.br2.TPI[k]           ~ dbern(psi.ind)
  z.bdelta.Forest[k]     ~ dbern(psi.ind)
  z.bdeltaE.Forest[k]    ~ dbern(psi.ind)
  z.bdeltaE.TPI[k]       ~ dbern(psi.ind)
  z.bdeltaE.TPI[k]       ~ dbern(psi.ind)
}
psi.ind <- 0.5 # Prior Inclusion Probability

########## Likelihood
# Site use and depredation state model
for (k in 1:nSpecies) {
  for (i in 1:nSites) {
    logit(psi[i, k]) <-
      alpha.psi[k] +
      z.beta.Terrain.1[k] * beta.Terrain.1[k] * Terrain.1[i] +
      z.beta.Terrain.2[k] * beta.Terrain.2[k] * Terrain.2[i] +
      z.beta.HumanPCA2[k] * beta.HumanPCA2[k] * HumanPCA2[i] +
      z.beta.HumanPCA[k]  * beta.HumanPCA[k]  * HumanPCA[i] +
      z.beta.Land.1[k]    * beta.Land.1[k]    * Land.1[i] +
```

```
    z.beta.Land.2[k]    * beta.Land.2[k]    * Land.2[i] +
    z.beta.BioPCA.1[k]  * beta.BioPCA.1[k]  * BioPCA.1[i] +
    z.beta.BioPCA.2[k]  * beta.BioPCA.2[k]  * BioPCA.2[i]
  logit(HWC[i, k]) <-
    alpha.HWC[k] +
    z.betaHWC.Terrain.1[k] * betaHWC.Terrain.1[k] * Terrain.1[i] +
    z.betaHWC.Terrain.2[k] * betaHWC.Terrain.2[k] * Terrain.2[i] +
    z.betaHWC.HumanPCA2[k] * betaHWC.HumanPCA2[k] * HumanPCA2[i] +
    z.betaHWC.HumanPCA[k]  * betaHWC.HumanPCA[k]  * HumanPCA[i] +
    z.betaHWC.Land.1[k]    * betaHWC.Land.1[k]    * Land.1[i] +
    z.betaHWC.Land.2[k]    * betaHWC.Land.2[k]    * Land.2[i] +
    z.betaHWC.BioPCA.1[k]  * betaHWC.BioPCA.1[k]  * BioPCA.1[i] +
    z.betaHWC.BioPCA.2[k]  * betaHWC.BioPCA.2[k]  * BioPCA.2[i]
}
# The multinomial ecological State
for (i in 1:nSites) {
  z[i, k] ~ dcat(phi[i, 1:3, k])
  phi[i, 1, k] <- 1 - psi[i, k]
  phi[i, 2, k] <- psi[i, k] * (1 - HWC[i, k])
  phi[i, 3, k] <- psi[i, k] * HWC[i, k]
}

# Observation Model
for (i in 1:nSites) {
  for (j in 1:nVisits[i]) {
    # Loop Expert/NonExpert
    for (m in 1:2) {
      # Detection when z==1
      logit(p1[i, j, k, m]) <-
        alpha.p1[k] +  epsilon.p1[SurveyID[i, j]] +
        z.b.home[k]    * b.home[k]    * home[i, j] +
        z.b.days[k]    * b.days[k]    * days[i, j] +
        z.b.effort1[k] * b.effort1[k] * effort1[i, j] +
        z.b.age[k]     * b.age[k]     * age[i, j] +
        z.b.Roads[k]   * b.Roads[k]   * Roads.P[i, j] +
        z.b.TPI[k]     * b.TPI[k]     * TPI[i, j] +
        z.b.Forest[k]  * b.Forest[k]  * Forest[i, j]
      # Expert detection when z==1
      logit(r1[i, j, k, m]) <-
        alpha.r1[k] + epsilon.r1[SurveyID[i, j]] +
        z.br.home[k]    * br.home[k]    * home[i, j] +
        z.br.days[k]    * br.days[k]    * days[i, j] +
        z.br.effort1[k] * br.effort1[k] * effort1[i, j] +
        z.br.age[k]     * br.age[k]     * age[i, j]  +
        z.br.Roads[k]   * br.Roads[k]   * Roads.P[i, j] +
        z.br.TPI[k]     * br.TPI[k]     * TPI[i, j] +
        z.br.Forest[k]  * br.Forest[k]  * Forest[i, j]
      # Detection when z==2
      logit(p2[i, j, k, m]) <-
        alpha.p2[k] + epsilon.p2[SurveyID[i, j]] +
        z.bp2.effort1[k] * bp2.effort1[k] * effort1[i, j] +
        z.bp2.days[k]    *  bp2.days[k]   * days[i, j] +
        z.bp2.home[k]    *  bp2.home[k]   * home[i, j] +
        z.bp2.age[k]     *  bp2.age[k]    * age[i, j] +
        z.bp2.Roads[k]   *  bp2.Roads[k]  * Roads.P[i, j] +
        z.bp2.TPI[k]     *  bp2.TPI[k]    * TPI[i, j] +
```

```
  z.bp2.Forest[k]  *  bp2.Forest[k] * Forest[i, j]
# Expert detection when z==2
logit(r2[i, j, k, m]) <-
  alpha.r2[k] + epsilon.r2[SurveyID[i, j]] +
  z.br2.effort1[k] * br2.effort1[k] * effort1[i, j] +
  z.br2.days[k]    * br2.days[k]    * days[i, j] +
  z.br2.home[k]    * br2.home[k]    * home[i, j] +
  z.br2.age[k]     * br2.age[k]     * age[i, j]  +
  z.br2.Roads[k]   * br2.Roads[k]   * Roads.P[i, j] +
  z.br2.TPI[k]     * br2.TPI[k]     * TPI[i, j] +
  z.br2.Forest[k]  * br2.Forest[k]  * Forest[i, j]
# Conditional Vulnerability when z==2
logit(deltao[i, j, k, m]) <-
  alpha.delta[k] + epsilon.delta[SurveyID[i, j]] +
  z.bdelta.vents[k]  * bdelta.vents[k]  * Vents[i, j] +
  z.bdelta.dogs[k]   * bdelta.dogs[k]   * Dogs[i, j] +
  z.bdelta.mesh[k]   * bdelta.mesh[k]   * Mesh[i, j] +
  z.bdelta.age[k]    * bdelta.age[k]    * age[i, j] +
  z.bdelta.cows[k]   * bdelta.cows[k]   * Cows[i, j] +
  z.bdelta.goats[k]  * bdelta.goats[k]  * Goats[i, j] +
  z.bdelta.home[k]   * bdelta.home[k]   * home[i, j] +
  z.bdelta.Roads[k]  * bdelta.Roads[k]  * Roads.P[i, j] +
  z.bdelta.TPI[k]    * bdelta.TPI[k]    * TPI[i, j] +
  z.bdelta.Forest[k] * bdelta.Forest[k] * Forest[i, j]
# Expert Conditional Vulnerability when z==2
logit(deltaoE[i, j, k, m]) <-
  alpha.deltaE[k] + epsilon.deltaE[SurveyID[i, j]] +
  z.bdeltaE.age[k]    * bdeltaE.age[k]    * age[i, j] +
  z.bdeltaE.home[k]   * bdeltaE.home[k]   * home[i, j] +
  z.bdeltaE.Roads[k]  * bdeltaE.Roads[k]  * Roads.P[i, j] +
  z.bdeltaE.TPI[k]    * bdeltaE.TPI[k]    * TPI[i, j] +
  z.bdeltaE.Forest[k] * bdeltaE.Forest[k] * Forest[i, j]
# False Positive Submodels (Could put covariates here)
logit(q01[i, j, k, m]) <- alpha.q01[k]
logit(q02[i, j, k, m]) <- alpha.q02[k]
logit(q12[i, j, k, m]) <- alpha.q12[k]
# Objects for observation matrix
p11[i, j, k, m]     <- p1[i, j, k, m]
p22[i, j, k, m]     <- p2[i, j, k, m]
delta1[i, j, k, m]  <- deltao[i, j, k, m]
r11[i, j, k, m]     <- r1[i, j, k, m]
r22[i, j, k, m]     <- r2[i, j, k, m]
deltaE1[i, j, k, m] <- deltaoE[i, j, k, m]
Q.01[i, j, k, m]    <- q01[i, j, k, m]
Q.02[i, j, k, m]    <- q02[i, j, k, m]
Q.12[i, j, k, m]    <- q12[i, j, k, m]
# Call Observation Probability Matrix function to
# Get state-specific Observation Probability Vector
pvec[i, j, k, m, 1:3] <- obsFun(
  p1      = p11[i, j, k, m],
  p2      = p22[i, j, k, m],
  q.01    = Q.01[i, j, k, m],
  q.02    = Q.02[i, j, k, m],
  q.12    = Q.12[i, j, k, m],
  delta   = delta1[i, j, k, m],
  r1      = r11[i, j, k, m],
```

```
          r2      = r22[i, j, k, m],
          deltaE  = deltaE1[i, j, k, m],
          z       = z[i, k],
          ID      = Expert[i, j]
        )
        # At long last, the Observation Model
        # (In this case the funky switch in index ordering
        # reflects the data structure and is accurate)
        y[i, j, m, k] ~ dcat(pvec[i, j, k, m, 1:3])
      }
    }
  }
  #Derived Quantities of interest (Predicted Use and Conflict state):
  for (i in 1:nSites) {
    PredZ[i, k]   <- psi[i, k]
    PredHWC[i, k] <- HWC[i, k]
  }
}})# End of the model!

## Also need a function to go along with the model
## for the detection probability matrix split by "experts/non-experts"
obsFun <- nimbleFunction(
  run = function(p1 = double(),
                 p2 = double(),
                 r1 = double(),
                 r2 = double(),
                 delta = double(),
                 deltaE = double(),
                 q.01 = double(),
                 q.02= double(),
                 q.12 = double(),
                 ID = integer(),
                 z = integer()) {
    p <- matrix(nrow = 3, ncol = 3)
    if (ID == 1) {
      p[1, 1:3] <- c(1 - q.01        , q.01 * (1 - q.02) , q.01 * q.02 )
      p[2, 1:3] <- c((1 - p1 - q.12) , p1                , q.12        )
      p[3, 1:3] <- c((1 - p2)        , p2 * (1 - delta)  , p2 * delta  )
    } else {
      p[1, 1:3] <- c( 1      , 0                , 0           )
      p[2, 1:3] <- c((1 - r1), r1               , 0           )
      p[3, 1:3] <- c((1 - r2), r2 * (1 - deltaE), r2 * deltaE )
    }
    pvec <- p[z, 1:3]
    return(pvec[1:3])
    returnType(double(1))
  }
)
```

Table S1. Principal component (PC) loadings of raw spatial covariates on the first two principal components (PC1 and PC2) of four thematically grouped PC analyses of spatial habitat covariates.

Theme (Sources)	**Covariate**	**PC1**	**PC2**
Bioclimatic	Mean temperature of the coldest quarter	0.41	0.55
(Fick and Hijmans, 2017)	Mean diurnal temperature range	0.34	-0.53
	Max temperature of coldest month	0.51	0.38
	Precipitation in the warmest quarter	-0.54	0.04
	Precipitation in the coldest quarter	-0.41	0.52
	Proportion of variance explained	0.55	0.34
Terrain	Terrain Ruggedness	0.61	0.32
(JAXA EORC 2020)	Slope	0.62	0.31
	Multiscale Topographic Position Index (500mX5km)	-0.23	0.72
	Elevation	-0.43	0.52
	Proportion of variance explained	0.56	0.34
Human	Sheep and goat density	0.40	0.48
(Gilbert et al. 2018, OpenStreetMap Contributors 2020, FCL and CIESIN 2016, Kennedy et al. 2018)	Cattle density	0.42	0.34
	Road density	0.40	-0.36
	Permanent settlement	0.38	-0.53
	Population	0.42	-0.34
	Global Human Modification	0.42	0.36
	Proportion of variance explained	0.72	0.13
Land Cover	Evergreen/deciduous needleleaf trees	0.37	0.16
(Tuanmu and Jetz 2014)	Deciduous broadleaf trees	0.35	0.11
	Mixed/other trees	0.41	0.06
	Shrubs	-0.05	-0.37
	Herbaceous vegetation	0.42	-0.28
	Cultivated/managed land	0.50	0.09
	Snow/ice	-0.24	-0.50
	Barren	-0.28	0.69
	Proportion of variance explained	0.42	0.18

Table S2. Summaries of reported carnivore detections and depredations across 172 sites and 264 respondents. Multiple detections or depredation events reported within a single site by the same respondent are counted only once.

Species	**Respondents**		**Sites**		**Proportion**		
	Detection only	Depredation	Detection only	Depredation	Sites with any detection	Sites with depredation	Detection sites with depredation
Snow leopard	53	25	25	17	0.24	0.10	0.40
Lynx	21	6	19	5	0.14	0.03	0.21
Wolf	88	67	23	40	0.37	0.23	0.63
Bear	32	8	14	6	0.12	0.03	0.30

Table S3. Summary of reported livestock losses to carnivore depredation, malnutrition, disease, or accidents (e.g., exposure, falls, avalanche, and drowning).

				Proportion in Corrals	
Predator/Cause	**Total Depredations**	**Total Livestock Killed/Lost**	**Mean Livestock Killed (±SD)**	**Depredations**	**Livestock Killed**
Lynx	6	14	2.3 (±1.0)	0.33	0.21
Bear	8	12	1.5 (±0.8)	0.25	0.17
Snow Leopard	25	130	5.9 (±6.5)	0.60	0.78
Wolf	67	141	2.0 (±1.9)	0.10	0.07
Unknown Predator	7	7	1.0	0.00	0.00
Disease	--	243	--	--	--
Malnutrition	--	56	--	--	--
Accidents	--	54	--	--	--

Table S4. Posterior distribution summaries, convergence diagnostics (Rhat), and effective sample size (ESS) for the shared observation intercept means (μ_α terms) and standard deviations (σ_α terms) and individual-level observation process random effects (σ_ε terms).

				Posterior Quantiles				
Parameter	Hyperparameter	Mean	SD	2.50%	50%	97.50%	Rhat	ESS
	A_σ	0.24	0.30	0.01	0.14	1.03	1.02	368
p_1	μ_α	-4.76	1.28	-7.99	-4.69	-2.20	<1.01	931
	σ_α	0.91	0.97	0.03	0.61	3.64	<1.01	3765
$\sigma_{\varepsilon p1}$		0.24	0.44	0.00	0.09	1.61	1.01	101
p_2	μ_α	-2.77	0.42	-3.53	-2.78	-1.93	1.02	1920
	σ_α	0.42	0.42	0.01	0.30	1.52	1.01	5128
$\sigma_{\varepsilon p2}$		0.12	0.12	0.01	0.09	0.44	1.01	409
δ	μ_α	-0.42	0.52	-1.47	-0.40	0.58	<1.01	2641
	σ_α	0.54	0.50	0.02	0.40	1.87	<1.01	10430
$\sigma_{\varepsilon\delta}$		0.13	0.16	0.00	0.08	0.59	1.08	280
r_1	μ_α	-3.16	1.16	-5.68	-3.07	-1.03	1.01	2870
	σ_α	0.80	0.81	0.02	0.56	2.99	<1.01	10189
$\sigma_{\varepsilon r1}$		0.66	1.02	0.00	0.17	3.53	1.03	175
r_2	μ_α	-2.22	0.50	-3.17	-2.24	-1.17	<1.01	16607
	σ_α	0.49	0.50	0.02	0.34	1.79	<1.01	13481
$\sigma_{\varepsilon r2}$		0.20	0.23	0.01	0.11	0.87	1.03	267
δ_E	μ_α	-1.48	0.67	-2.79	-1.49	-0.15	<1.01	14595
	σ_α	0.64	0.60	0.03	0.47	2.24	<1.01	17565
$\sigma_{\varepsilon\delta E}$		0.24	0.30	0.01	0.12	1.10	1.01	231
q_{01}	μ_α	-5.31	1.49	-8.19	-5.38	-1.75	<1.01	12785
	σ_α	1.44	1.27	0.04	1.11	4.83	<1.01	13211
q_{02}	μ_α	0.36	1.44	-2.36	0.29	3.54	<1.01	7077
	σ_α	0.89	0.91	0.02	0.62	3.33	<1.01	11941
q_{12}	μ_α	-5.41	1.09	-7.78	-5.30	-3.46	1.01	1518
	σ_α	0.76	0.84	0.02	0.49	3.09	1.02	5087

Table S5. Snow leopard false-positive posterior parameter estimates and summary statistics. Refer to main text and Table A1 for explanations of covariates.

					Highest Posterior Density Interval				
Process (Submodel)	Parameter	PIP	Mean	SD	2.5%	50%	97.5%	Rhat	ESS
Site Use (ψ)	Intercept	–	0.28	0.94	-1.33	0.13	2.15	<1.01	1887
	Terrain.1	0.90	1.84	1.05	0.14	1.65	4.13		3048
	Terrain.2	0.35	-0.36	0.88	-2.15	-0.33	1.36		1655
	Human.1	0.37	-0.40	0.84	-2.11	-0.42	1.26		2262
	Human.2	0.26	-0.17	0.56	-1.27	-0.18	0.97		3999
	LandCover.1	0.41	-0.54	0.81	-2.26	-0.55	1.13		1515
	LandCover.2	0.30	-0.37	0.58	-1.52	-0.37	0.82		2354
	Bioclimatic.1	0.35	0.32	0.88	-1.45	0.33	2.08		1924
	Bioclimatic.2	0.29	-0.36	0.54	-1.49	-0.36	0.71		3735
Depredation (R)	Intercept	–	0.54	1.29	-1.83	0.40	3.26	1.01	517
	Terrain.1	0.41	0.37	1.28	-1.97	0.24	3.10		974
	Terrain.2	0.42	0.51	1.00	-1.50	0.54	2.50		2714
	Human.1	0.40	-0.11	1.13	-2.24	-0.20	2.26		2101
	Human.2	0.31	0.12	0.84	-1.52	0.12	1.78		2001
	LandCover.1	0.46	-0.93	1.05	-3.24	-0.83	1.02		2536
	LandCover.2	0.34	-0.18	0.90	-2.02	-0.15	1.59		1558
	Bioclimatic.1	0.59	1.38	1.23	-0.97	1.28	3.94		2582
	Bioclimatic.2	0.36	0.12	1.05	-1.79	-0.01	2.41		1513
Detection ($p1$)	Intercept	–	-4.82	1.18	-7.27	-4.65	-2.82	<1.01	1448
	Age	0.41	0.43	1.03	-1.72	0.45	2.42		2822
	Home	0.44	-0.16	1.43	-3.11	-0.02	2.50		8150
	Effort	0.36	0.28	0.98	-1.90	0.33	2.10		4819
	Days	0.58	1.09	1.28	-1.63	1.13	3.62		2416
	Roads	0.49	-1.21	1.23	-3.81	-1.07	1.00		7071
	Forest	0.42	-0.44	1.31	-3.17	-0.33	2.03		12371
	TPI	0.28	-0.13	0.77	-1.71	-0.14	1.36		8832
Expert Detection (r_1)	Intercept	–	-3.47	1.28	-6.16	-3.26	-1.23	1.02	1305
	Age	0.65	-1.05	0.83	-2.82	-1.03	0.58		8407
	Home	0.48	0.38	1.43	-2.70	0.52	2.97		2876
	Effort	0.66	0.95	0.97	-1.24	0.92	3.05		1818
	Days	0.37	0.50	0.96	-1.42	0.47	2.59		2138
	Roads	0.66	-1.92	1.67	-5.39	-1.82	1.23		4273
	Forest	0.46	0.61	1.24	-1.98	0.65	2.95		6639
	TPI	0.40	-0.48	1.09	-2.71	-0.48	1.73		9684

(Table S5 continued)

Detection (p_2)	Intercept	–	-2.72	0.34	-3.37	-2.73	-2.03	1.01	3400
	Age	0.67	-0.57	0.27	-1.10	-0.56	-0.05		4163
	Home	1	2.51	0.47	1.61	2.50	3.44		7530
	Effort	0.45	0.51	0.32	-0.11	0.50	1.15		6797
	Days	0.19	0.16	0.33	-0.48	0.17	0.80		4147
	Roads	0.18	-0.11	0.37	-0.87	-0.09	0.60		6868
	Forest	0.83	-1.60	0.76	-3.14	-1.59	-0.13		7223
	TPI	0.27	-0.39	0.35	-1.10	-0.37	0.25		6779
Expert Detection (r_2)	Intercept	–	-2.39	0.49	-3.40	-2.37	-1.45	<1.01	4874
	Age	0.59	-0.75	0.43	-1.61	-0.75	0.12		11693
	Home	0.98	2.26	0.78	0.75	2.24	3.81		11233
	Effort	0.64	0.69	0.36	-0.07	0.69	1.39		3751
	Days	0.26	0.29	0.43	-0.61	0.30	1.13		1868
	Roads	0.33	-0.25	0.84	-1.96	-0.26	1.46		5012
	Forest	0.40	-0.30	1.13	-2.67	-0.24	1.83		8141
	TPI	0.26	0.30	0.47	-0.60	0.30	1.23		8432
Detection (δ)	Intercept	–	-0.64	0.60	-1.93	-0.56	0.42	<1.01	2683
	Age	0.46	-0.63	0.41	-1.47	-0.62	0.16		14004
	Home	0.42	0.05	1.10	-2.23	0.15	2.07		2981
	Vents	0.66	1.37	0.92	-0.39	1.31	3.22		5737
	Dogs	0.31	-0.12	0.75	-1.62	-0.12	1.35		9968
	Mesh	0.82	-1.94	1.04	-4.01	-1.88	0.06		35527
	Cows	0.30	0.45	0.53	-0.56	0.42	1.50		8218
	Sheep & Goats	0.21	-0.21	0.41	-1.03	-0.20	0.62		12110
	Roads	0.47	0.99	0.81	-0.47	0.90	2.66		15249
	Forest	0.42	0.07	1.22	-2.30	0.09	2.54		10160
	TPI	0.41	-0.69	0.65	-2.06	-0.66	0.51		18704
Expert Detection (δ_E)	Intercept	–	-1.66	0.76	-3.21	-1.63	-0.16	<1.01	5601
	Age	0.78	-1.69	1.02	-3.79	-1.57	0.12		8917
	Home	0.52	-1.21	1.21	-3.64	-1.12	1.08		16510
	Roads	0.52	1.04	1.55	-1.95	0.97	4.19		12345
	Forest	0.50	-0.48	1.68	-3.87	-0.46	2.89		8589
	TPI	0.35	-0.40	0.90	-2.22	-0.35	1.27		12243
False Positive (q_{01})	Intercept	–	-5.26	1.41	-7.97	-4.96	-3.19	1.02	2540
False Positive (q_{02})	Intercept	–	0.52	1.78	-2.76	0.38	4.43	<1.01	3359
False Positive (q_{12})	Intercept	–	-5.54	1.17	-7.82	-5.30	-3.79	<1.01	1833

Table S6. Lynx false-positive posterior parameter estimates and summary statistics. Refer to main text and Table A1 for explanations of covariates.

					Highest Posterior Density Interval				
Process (Submodel)	Parameter	PIP	Mean	SD	2.5%	50%	97.5%	Rhat	ESS
Site Use (ψ)	Intercept	–	-0.48	0.93	-2.17	-0.56	1.41	<1.01	3510
	Terrain.1	0.38	0.04	1.20	-2.29	-0.05	2.56		1867
	Terrain.2	0.77	-1.86	1.20	-4.32	-1.69	0.31		4025
	Human.1	0.75	1.82	1.14	-0.38	1.76	4.17		5552
	Human.2	0.32	0.00	0.84	-1.63	0.01	1.73		3313
	LandCover.1	0.48	0.98	0.93	-0.74	0.93	2.87		2726
	LandCover.2	0.27	0.03	0.68	-1.26	-0.03	1.48		2336
	Bioclimatic.1	0.42	0.50	1.21	-1.77	0.43	2.98		1831
	Bioclimatic.2	0.38	0.70	0.78	-0.73	0.62	2.35		3976
Depredation (R)	Intercept	–	-2.09	1.80	-5.60	-2.03	1.64	<1.01	624
	Terrain.1	0.41	0.16	1.28	-2.45	0.15	2.68		2889
	Terrain.2	0.45	-0.10	1.43	-2.94	-0.14	2.81		2372
	Human.1	0.43	-0.02	1.31	-2.75	0.02	2.44		2041
	Human.2	0.44	0.76	1.14	-1.49	0.70	3.09		3901
	LandCover.1	0.57	1.24	1.01	-0.57	1.11	3.36		2891
	LandCover.2	0.43	0.40	1.31	-2.18	0.34	3.10		2127
	Bioclimatic.1	0.50	-0.92	1.56	-4.07	-0.83	2.17		3634
	Bioclimatic.2	0.46	-0.87	1.44	-3.95	-0.74	1.78		3318
Detection ($p1$)	Intercept	–	-4.96	0.95	-6.85	-4.85	-3.23	<1.01	1486
	Age	0.25	0.24	0.50	-0.78	0.26	1.17		6257
	Home	0.93	2.21	0.98	0.37	2.20	4.13		2958
	Effort	0.28	0.15	0.67	-1.24	0.20	1.41		5027
	Days	0.93	1.43	0.69	0.23	1.36	2.87		6650
	Roads	0.23	-0.04	0.71	-1.50	0.01	1.33		4280
	Forest	0.42	-0.60	1.12	-2.89	-0.54	1.54		12048
	TPI	0.28	-0.27	0.63	-1.51	-0.26	0.90		6001
Expert Detection (r_1)	Intercept	–	-3.78	1.22	-6.33	-3.55	-1.81	1.01	1421
	Age	0.33	0.35	0.85	-1.25	0.29	2.16		6128
	Home	0.46	0.56	1.19	-1.84	0.62	2.86		4597
	Effort	0.70	0.88	0.60	-0.12	0.81	2.17		2458
	Days	0.36	0.19	0.96	-1.96	0.30	1.99		2048
	Roads	0.44	-0.91	1.18	-3.39	-0.81	1.29		17106
	Forest	0.43	0.03	1.35	-2.79	0.16	2.52		4561
	TPI	0.38	0.48	0.99	-1.52	0.46	2.51		8703

(Table S6 continued)

Detection (p_2)	Intercept	–	-2.82	0.50	-3.86	-2.82	-1.79	<1.01	3634
	Age	0.29	0.43	0.74	-0.90	0.33	2.01		5030
	Home	0.45	-0.76	1.36	-3.53	-0.60	1.64		4406
	Effort	0.63	1.31	1.01	-0.52	1.16	3.48		5944
	Days	0.38	-0.23	0.97	-2.20	-0.21	1.54		2642
	Roads	0.47	-1.29	1.15	-3.80	-1.10	0.44		10361
	Forest	0.43	0.73	1.11	-1.26	0.68	3.15		4895
	TPI	0.24	-0.10	0.68	-1.53	-0.06	1.27		8312
Expert Detection (r_2)	Intercept	–	-2.47	0.71	-4.00	-2.39	-1.15	<1.01	5693
	Age	0.43	-0.68	1.13	-3.04	-0.64	1.53		8553
	Home	0.55	1.10	1.27	-1.52	1.11	3.54		10638
	Effort	0.44	-0.29	1.26	-3.06	-0.10	1.74		4246
	Days	0.46	0.61	1.16	-1.75	0.61	2.92		5615
	Roads	0.42	0.46	1.42	-2.18	0.29	3.48		9644
	Forest	0.43	0.40	1.18	-2.04	0.44	2.74		9116
	TPI	0.41	-0.83	1.04	-3.00	-0.71	1.07		7348
Detection (δ)	Intercept	–	-0.23	0.79	-1.75	-0.29	1.43	<1.01	3706
	Age	0.61	-1.52	1.36	-4.30	-1.40	1.10		20655
	Home	0.49	-0.33	1.68	-3.76	-0.32	3.04		15626
	Vents	0.51	-0.60	1.76	-4.21	-0.56	2.90		18260
	Dogs	0.45	0.38	1.39	-2.34	0.36	3.20		13934
	Mesh	0.51	-0.68	1.80	-4.37	-0.62	2.88		23437
	Cows	0.48	-0.58	1.55	-3.83	-0.51	2.36		11533
	Sheep & Goats	0.46	0.01	1.59	-3.14	-0.04	3.27		20608
	Roads	0.49	-0.47	1.67	-3.83	-0.43	2.88		28000
	Forest	0.46	0.59	1.35	-2.05	0.57	3.31		16110
	TPI	0.48	-0.30	1.65	-3.66	-0.24	2.98		21477
Expert Detection (δ_E)	Intercept	–	-1.52	0.97	-3.52	-1.52	0.47	<1.01	8833
	Age	0.47	0.12	1.60	-3.04	0.11	3.41		24716
	Home	0.47	0.10	1.57	-3.00	0.08	3.29		16430
	Roads	0.53	0.97	1.80	-2.52	0.86	4.65		33607
	Forest	0.46	-0.02	1.52	-3.09	-0.05	2.99		13875
	TPI	0.66	-1.77	1.41	-4.64	-1.61	0.83		35399
False Positive (q_{01})	Intercept	–	-6.62	1.60	-9.83	-6.27	-4.33	<1.01	5933
False Positive (q_{02})	Intercept	–	0.50	1.91	-3.26	0.40	4.63	<1.01	3927
False Positive (q_{12})	Intercept	–	-5.52	1.05	-7.60	-5.32	-3.93	1.01	1727

Table S7. Wolf false-positive posterior parameter estimates and summary statistics. Refer to main text and Table A1 for explanations of covariates.

					Highest Posterior Density Interval				
Process (Submodel)	Parameter	PIP	Mean	SD	2.5%	50%	97.5%	Rhat	ESS
Site Use (ψ)	Intercept	–	2.09	1.20	0.07	1.90	4.56	<1.01	2779
	Terrain.1	0.59	1.25	0.95	-0.60	1.24	3.15		3266
	Terrain.2	0.49	-0.87	1.10	-3.06	-0.86	1.33		2380
	Human.1	0.71	2.15	1.60	-1.01	2.07	5.31		2186
	Human.2	0.53	-0.96	0.82	-2.64	-0.95	0.68		4647
	LandCover.1	0.37	0.06	0.97	-1.72	0.00	2.09		1431
	LandCover.2	0.37	0.65	1.01	-1.18	0.52	2.83		1930
	Bioclimatic.1	0.49	0.81	1.20	-1.59	0.84	3.15		2029
	Bioclimatic.2	0.34	0.52	0.68	-0.76	0.49	1.93		5786
Depredation (R)	Intercept	–	2.53	1.60	-0.28	2.34	5.92	1.03	568
	Terrain.1	0.58	1.35	1.20	-0.92	1.29	3.82		3105
	Terrain.2	0.58	-1.38	1.32	-4.05	-1.30	1.17		3386
	Human.1	0.58	1.56	1.66	-1.48	1.41	4.99		2603
	Human.2	0.49	-0.94	1.02	-2.99	-0.91	1.08		3017
	LandCover.1	0.43	0.66	1.12	-1.44	0.59	2.91		2504
	LandCover.2	0.41	0.57	1.06	-1.47	0.52	2.75		3837
	Bioclimatic.1	0.46	0.46	1.31	-2.11	0.47	3.12		3528
	Bioclimatic.2	0.37	-0.18	0.93	-1.92	-0.23	1.80		4758
Detection ($p1$)	Intercept	–	-5.09	1.36	-7.87	-4.91	-2.80	<1.01	2288
	Age	0.43	-0.23	1.23	-2.54	-0.30	2.28		8108
	Home	0.50	-0.14	1.77	-3.62	-0.12	3.49		18878
	Effort	0.46	0.23	1.28	-2.40	0.36	2.66		8331
	Days	0.47	0.54	1.34	-2.20	0.56	3.19		11328
	Roads	0.46	-0.08	1.52	-3.22	-0.06	2.92		18920
	Forest	0.48	0.02	1.66	-3.41	0.09	3.26		24613
	TPI	0.39	-0.07	1.26	-2.74	-0.06	2.48		18109
Expert Detection (r_1)	Intercept	–	-3.50	1.44	-6.58	-3.34	-0.86	<1.01	1949
	Age	0.50	-0.72	1.35	-3.44	-0.76	1.98		8258
	Home	0.53	0.69	1.96	-3.06	0.59	4.85		12139
	Effort	0.71	1.50	1.47	-1.53	1.37	4.76		5697
	Days	0.41	-0.33	1.37	-3.18	-0.27	2.38		11607
	Roads	0.47	0.27	1.63	-2.97	0.24	3.62		21713
	Forest	0.50	-0.35	1.77	-4.01	-0.31	3.08		30077
	TPI	0.45	0.38	1.48	-2.58	0.36	3.39		21967

(Table S7 continued)

Detection (p_2)	Intercept	–	-2.84	0.29	-3.41	-2.84	-2.27	<1.01	3004
	Age	0.08	-0.05	0.13	-0.29	-0.05	0.20		18533
	Home	1	2.26	0.31	1.66	2.26	2.87		5850
	Effort	1	0.77	0.16	0.45	0.76	1.09		20572
	Days	0.38	0.34	0.19	-0.03	0.34	0.70		17069
	Roads	0.13	-0.16	0.20	-0.54	-0.14	0.22		13309
	Forest	0.67	0.68	0.31	0.07	0.68	1.29		10994
	TPI	0.10	0.05	0.17	-0.31	0.05	0.38		12610
Expert Detection (r_2)	Intercept	–	-2.30	0.39	-3.08	-2.30	-1.52	<1.01	4370
	Age	0.35	-0.42	0.28	-0.97	-0.41	0.13		14011
	Home	1	2.98	0.52	1.96	2.97	4.01		8559
	Effort	0.43	0.36	0.19	-0.01	0.36	0.74		9122
	Days	0.14	0.11	0.23	-0.35	0.11	0.55		7503
	Roads	0.25	-0.35	0.48	-1.34	-0.32	0.53		13696
	Forest	0.34	-0.50	0.61	-1.72	-0.49	0.68		8989
	TPI	0.54	0.65	0.36	-0.04	0.64	1.38		17692
Detection (δ)	Intercept	–	-0.36	0.41	-1.24	-0.30	0.37	<1.01	2603
	Age	0.20	-0.24	0.20	-0.62	-0.23	0.14		20709
	Home	0.39	0.58	0.52	-0.45	0.58	1.60		2060
	Vents	0.29	0.34	0.46	-0.58	0.36	1.25		4712
	Dogs	0.27	-0.35	0.40	-1.12	-0.35	0.42		11603
	Mesh	0.26	-0.12	0.55	-1.20	-0.12	0.98		19108
	Cows	0.15	-0.15	0.25	-0.63	-0.14	0.33		11483
	Sheep & Goats	0.15	-0.07	0.28	-0.63	-0.07	0.47		15224
	Roads	0.21	0.17	0.39	-0.62	0.17	0.94		13961
	Forest	0.28	0.35	0.47	-0.55	0.35	1.28		8220
	TPI	0.22	-0.24	0.38	-1.01	-0.24	0.48		13115
Expert Detection (δ_E)	Intercept	–	-1.37	0.58	-2.49	-1.38	-0.19	1.01	5028
	Age	0.21	0.07	0.43	-0.76	0.07	0.93		16638
	Home	0.34	-0.36	0.76	-1.91	-0.35	1.08		5160
	Roads	0.51	1.01	0.98	-0.92	0.98	2.94		28150
	Forest	0.85	1.76	0.83	0.13	1.72	3.41		13730
	TPI	0.35	-0.58	0.71	-2.01	-0.53	0.77		15405
False Positive (q_{01})	Intercept	–	-5.76	1.66	-9.14	-5.51	-3.04	1.01	4592
False Positive (q_{02})	Intercept	–	0.38	1.88	-3.24	0.29	4.45	<1.01	3657
False Positive (q_{12})	Intercept	–	-5.53	1.16	-7.83	-5.30	-3.75	<1.01	2022

Table S8. Bear false-positive posterior parameter estimates and summary statistics. Refer to main text and Table A1 for explanations of covariates.

					Highest Posterior Density Interval				
Process (Submodel)	Parameter	PIP	Mean	SD	2.5%	50%	97.5%	Rhat	ESS
Site Use (ψ)	Intercept	–	-0.49	0.86	-1.98	-0.60	1.17	1.00	2170
	Terrain.1	0.52	-1.04	0.92	-2.92	-0.98	0.71		2529
	Terrain.2	0.48	-1.01	0.92	-2.85	-0.95	0.67		2406
	Human.1	0.56	-1.17	1.24	-3.77	-1.12	1.20		1679
	Human.2	0.29	0.12	0.76	-1.34	0.07	1.73		1842
	LandCover.1	0.91	1.51	0.73	0.21	1.42	3.03		4275
	LandCover.2	0.38	-0.57	0.58	-1.76	-0.56	0.54		3474
	Bioclimatic.1	0.40	-0.54	0.94	-2.41	-0.51	1.33		1778
	Bioclimatic.2	0.64	-1.13	0.72	-2.56	-1.08	0.25		7004
Depredation (*R*)	Intercept	–	0.12	1.71	-3.27	0.05	3.37	1.01	701
	Terrain.1	0.61	1.65	1.77	-1.74	1.55	5.27		2940
	Terrain.2	0.44	-0.01	1.38	-2.73	-0.01	2.77		4369
	Human.1	0.54	1.05	1.79	-2.37	0.92	4.69		3237
	Human.2	0.42	-0.18	1.25	-2.76	-0.20	2.30		4178
	LandCover.1	0.55	1.67	1.62	-1.11	1.45	4.94		2665
	LandCover.2	0.53	-1.19	1.48	-4.23	-1.11	1.64		3168
	Bioclimatic.1	0.54	-1.24	1.73	-4.86	-1.10	1.96		2414
	Bioclimatic.2	0.45	-0.17	1.39	-2.95	-0.17	2.65		3598
Detection (*p1*)	Intercept	–	-5.43	1.38	-8.22	-5.18	-3.21	1.00	2130
	Age	0.33	-0.09	0.89	-1.86	-0.08	1.68		17858
	Home	0.51	0.33	1.78	-3.20	0.35	3.88		5313
	Effort	0.49	0.53	1.05	-1.70	0.68	2.46		4010
	Days	0.42	0.13	1.20	-2.25	0.16	2.48		6630
	Roads	0.43	-0.36	1.37	-3.11	-0.33	2.39		12943
	Forest	0.49	0.00	1.72	-3.44	0.01	3.51		22545
	TPI	0.40	-0.40	1.10	-2.66	-0.38	1.75		14763
Expert Detection (r_1)	Intercept	–	-3.21	1.28	-6.03	-3.09	-0.85	1.01	1783
	Age	0.37	-0.05	1.13	-2.24	-0.05	2.30		9541
	Home	0.67	1.72	2.20	-2.67	1.76	6.07		4075
	Effort	0.44	0.67	0.91	-1.21	0.67	2.54		4171
	Days	0.43	-0.82	1.07	-3.13	-0.74	1.17		5834
	Roads	0.40	0.08	1.24	-2.45	0.11	2.52		14996
	Forest	0.51	-0.66	1.78	-4.30	-0.57	2.83		13456
	TPI	0.44	0.46	1.42	-2.37	0.42	3.37		11748

(Table S8 continued)

Detection (p_2)	Intercept	–	-3.00	0.51	-4.13	-2.95	-2.08	1.01	2562
	Age	0.19	0.24	0.29	-0.32	0.23	0.79		11386
	Home	0.86	1.43	0.63	0.21	1.41	2.67		8818
	Effort	0.99	1.25	0.43	0.46	1.19	2.14		5366
	Days	0.41	-0.73	0.61	-1.98	-0.67	0.39		2762
	Roads	0.26	-0.46	0.52	-1.52	-0.39	0.40		8441
	Forest	0.76	1.19	0.59	0.03	1.19	2.35		4568
	TPI	0.20	-0.24	0.39	-1.03	-0.21	0.49		7006
Expert Detection (r_2)	Intercept	–	-2.14	0.60	-3.30	-2.18	-0.86	1.00	5642
	Age	0.43	-0.79	0.71	-2.21	-0.75	0.58		9100
	Home	0.83	1.99	1.00	0.04	1.99	3.97		8412
	Effort	0.84	1.22	0.61	0.12	1.16	2.42		12475
	Days	0.48	-0.92	0.75	-2.40	-0.88	0.52		9643
	Roads	0.47	-1.02	1.14	-3.45	-0.92	1.00		14912
	Forest	0.37	0.34	0.87	-1.36	0.35	2.07		6101
	TPI	0.35	-0.28	0.96	-2.23	-0.23	1.59		7525
Detection (δ)	Intercept	–	-0.50	0.67	-1.94	-0.45	0.78	1.00	3205
	Age	0.43	-0.75	0.67	-2.10	-0.73	0.51		15363
	Home	0.44	-0.40	1.22	-2.81	-0.41	1.97		6264
	Vents	0.78	-1.94	1.12	-4.24	-1.88	0.14		17218
	Dogs	0.58	-1.39	1.11	-3.63	-1.31	0.71		10603
	Mesh	0.48	-0.37	1.64	-3.65	-0.30	2.87		41185
	Cows	0.35	0.57	0.58	-0.50	0.53	1.77		9514
	Sheep & Goats	0.22	-0.04	0.48	-1.00	-0.02	0.88		10603
	Roads	0.40	-0.20	1.12	-2.39	-0.18	2.04		18249
	Forest	0.62	1.39	0.98	-0.48	1.34	3.35		7769
	TPI	0.42	0.16	1.19	-2.22	0.17	2.49		12581
Expert Detection (δ_E)	Intercept	–	-1.80	0.84	-3.58	-1.72	-0.25	1.00	7080
	Age	0.40	0.48	1.01	-1.45	0.45	2.50		24473
	Home	0.42	-0.32	1.18	-2.70	-0.29	2.00		15582
	Roads	0.50	0.79	1.54	-2.23	0.73	3.88		38374
	Forest	0.42	-0.46	1.18	-2.84	-0.43	1.84		13484
	TPI	0.46	0.16	1.47	-2.76	0.13	3.10		22709
False Positive (q_{01})	Intercept	–	-6.87	1.67	-10.18	-6.51	-4.47	1.00	6400
False Positive (q_{02})	Intercept	–	0.26	1.96	-3.69	0.23	4.44	1.00	4336
False Positive (q_{12})	Intercept	–	-5.80	1.23	-8.27	-5.54	-4.01	1.00	2008

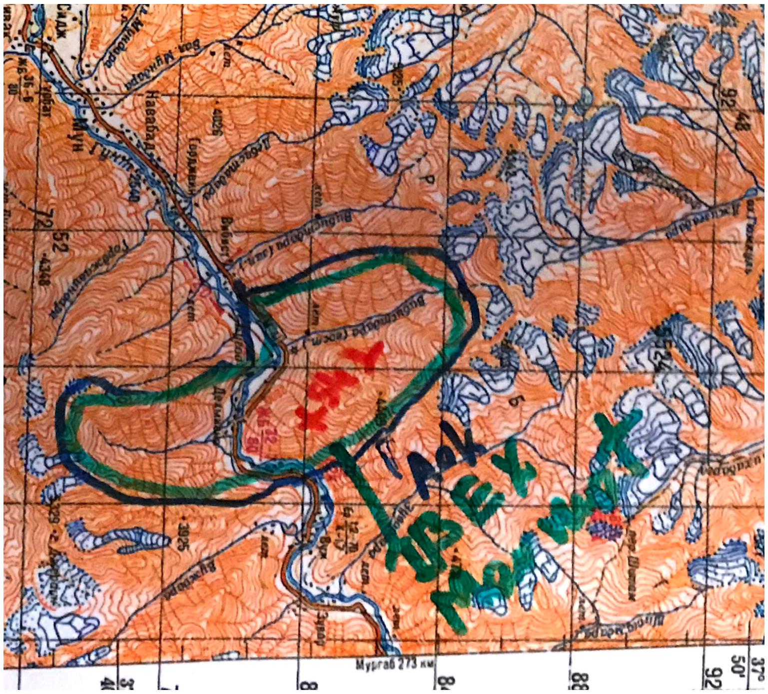

Figure S1. Example of annotated topographic map, showing one respondent's area of knowledge (AOK; dark blue outline), within which ibex and marmot were reportedly present throughout (green outline), and a single snow leopard sighting was reported (red "X" marked "SL1").

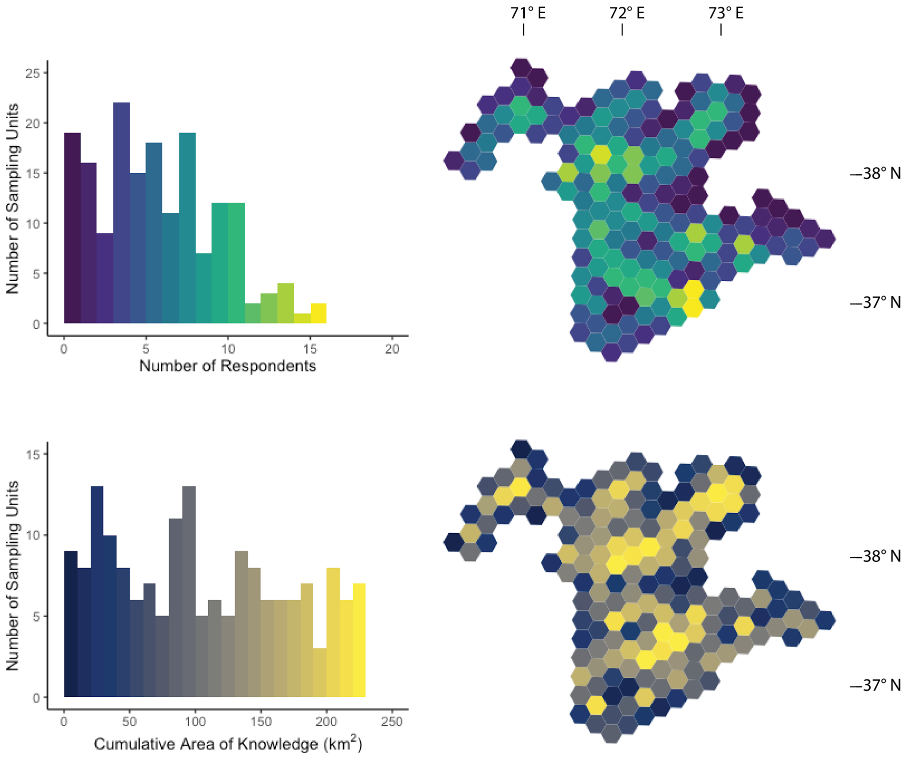

Figure S2. Frequency and geographic distribution of two measures of interview sampling effort across the study area. The top row is number of respondents in each sampling unit. The bottom row is the cumulative area of each hexagonal sampling unit (225 km^2) known to the respondents.

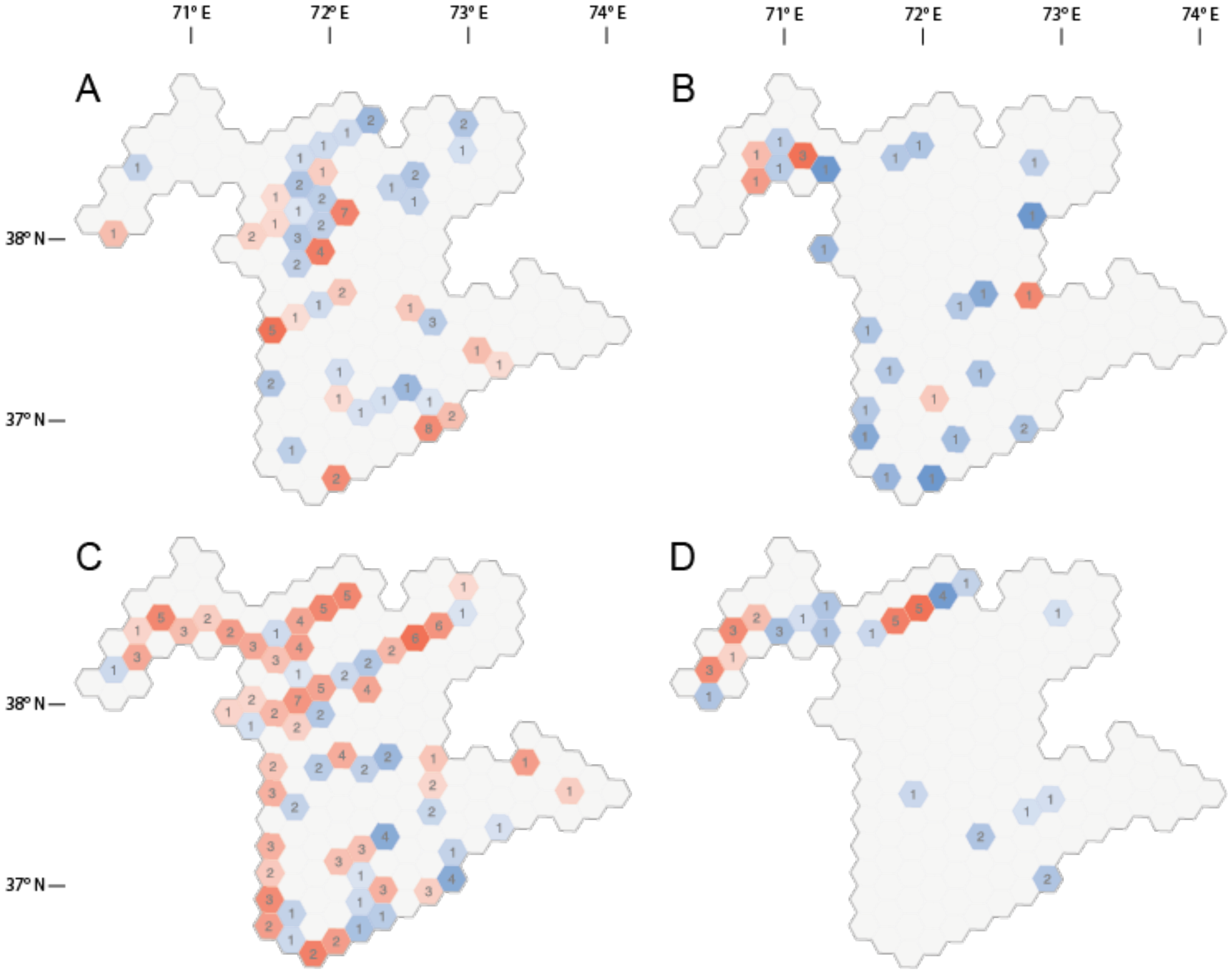

Figure S3. Observed site use and depredation and frequency of total detections for (A) snow leopards, (B) lynx, (C) wolves, and (D) bears. Red indicates sites with depredations and detections, blue indicates sites with detections but not depredations, numbers indicate absolute number of respondents reporting detections of either type, and color saturation indicates site-level proportion of respondents reporting any detection.