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Effects of wolf and grizzly bear recovery on cougars in the Southern Greater Yellowstone Ecosystem

Jennifer A. Feltner

Wildlife Biology Program, University of Montana, Missoula, Montana, jennifer.feltner@umontana.edu

Abstract Within the large carnivore guild, competitively dominant species can limit the population sizes and alter the behavior of subordinate competitors. However, the mechanisms by which dominant competitors affect subordinates are complex and challenging to disentangle, particularly for free ranging large mammals. For my dissertation, I took advantage of a natural experiment and sixteen years of location data from a subordinate carnivore (cougars), two dominant competitors (wolves and grizzly bears), and a shared prey species (elk), as well as kill site data from cougars in the Southern Greater Yellowstone Ecosystem (SGYE), a multi-use landscape with numerous anthropogenic impacts. My dissertation was an investigation of three mechanisms, both direct and indirect, by which competition from recovering wolves and grizzly bears affected subordinate cougars in a system where human impacts also play strong roles in shaping dynamics. Specifically, I evaluated 1) whether cougar habitat selection changed as wolf and grizzly bear populations recovered and whether these changes could be attributed to cougars actively avoiding dominant competitors; 2) how cougar access to the habitat of its primary prey species was affected by wolf and grizzly bear recovery; and 3) how kleptoparasitism from recovering wolves and grizzly bears – as well as black bears –may have affected the SGYE cougar population.

Introduction

Across North America and Europe, populations of top carnivores such as wolves and grizzly bears are recovering and expanding throughout portions of their range where they had previously been extirpated (Ordiz et al., 2015; White and Gunther, 2017; Ruth et al., 2019). Research on changes in species interactions and broader ecosystem effects resulting from large carnivore recovery has exploded in recent years as heterogeneous recovery patterns have provided natural experiments and opportunities for researchers to observe dynamic ecosystems (Bartnick et al., 2013; Morell, 2015). There has been special emphasis on predator-prey interactions and trophic cascades related to recovering predators (e.g., Sand et al., 2006; Seddon et al., 2007; Ripple et al., 2014). However, recovering large carnivores also affect subordinate carnivores through intraguild competition, which can strongly affect the distribution, population dynamics and behavior of subordinate species, with community and ecosystem wide cascading effects (Dill et al., 2003; Hopcraft et al., 2005; Vanak et al., 2013; Elbroch et al., 2015). Despite an impressive body of work on community dynamics following large predator recovery, relatively few of these studies have explored intraguild competition in depth (Riley et al., 2004), and there are still many gaps in our understanding of how large carnivore recovery affects subordinate carnivore behavior and population sizes, the competitive mechanisms driving possible changes, as well as how humans may influence dynamics. Additional research efforts are needed to clarify responses of subordinate carnivores following large carnivore recovery and resultant impacts to subordinates and prey.

Due to their top-down effects on shared prey species, large carnivore species fill similar ecological roles and are therefore expected to compete strongly (Morin, 2011). Competition most commonly takes two forms within the large carnivore guild: interference and exploitation competition (Ballard et al., 2003). Interference competition involves direct aggressive interactions that are typically asymmetrical and include kleptoparasitism, harassment, and intraguild killing, as well as avoidance of dominant competitors by subordinate species (Goss-Custard et al., 1982; Holt and Polis, 1997; Palomares and Caro, 1999; Durant, 2000; Creel et al., 2001; Creel and Christianson, 2008; Swanson et al., 2014). Although avoidance behaviors by subordinates may not have immediate negative fitness impacts, they may limit prey availability for subordinate carnivores (Vanak et al., 2013), and ultimately reduce subordinate competitor fitness (Lima and Dill, 1990; Durant, 1998, 2000; Creel et al., 2001; Gigliotti et al., 2020). In contrast, exploitation competition is a form of indirect competition that involves the reduction of shared resources such as prey (Schoener, 1974; Krebs, 1994). If shared prey species shift their own behavior in response to predation risk from dominant competitors (Heithaus and Dill, 2002; Dill et al., 2003), the spatio-temporal availability of prey may also be altered for sympatric predators (Atwood et al., 2007, 2009; Northfield et al., 2017; Schmitz et al., 2017). These behavioral shifts by prey have the potential to both facilitate predation by subordinate carnivores (Dill et al., 2003; Atwood et al., 2007), or limit access, particularly if prey shift their habitat selection or grouping behavior in a way that makes it more difficult for subordinates to hunt them (Sinclair, 1985; Hopcraft et al., 2005; Mao et al., 2005; White et al., 2009; Ruth et al., 2019).

Measuring the degree to which species compete has remained difficult outside of manipulative experiments with small species in small, controlled spaces (Morin, 2011). This is logistically challenging to do with highly mobile animals in large, open landscapes, and in particular for cryptic species that exist at low densities such as carnivores (Kortello et al., 2007; Schmitz et al., 2017). Thus, natural experiments such as large carnivore reintroductions and recovery efforts provide unique opportunities for researchers to examine evidence for competition, explore competitive dynamics and test hypotheses about mechanisms driving behavioral changes – and possible population declines – in subordinate carnivore species (Kortello et al., 2007; Ruth et al., 2019).

In the northwestern United States and southwestern Canada, the recovery of wolf and grizzly bear populations have provided researchers more than twenty-five years to observe dynamic ecosystems and study the effects of recovering dominant carnivores on competitors such as cougars (e.g., Murphy et al., 1998; Kunkel et al., 1999; Husseman et al., 2003; Kortello et al., 2007; Bartnick et al., 2013; Elbroch et al., 2018, 2020; Kohl et al., 2019; Orning, 2019; Ruth et al., 2019). The findings of these studies generally indicate that while cougars are formidable predators, they are typically subordinate to both wolves and grizzly bears (Elbroch et al., 2018), as wolves are advantaged by their pack social structure (Ruth et al., 2019), and grizzly bears by size and aggressiveness (Murphy et al., 1998; Gunther and Smith, 2004; Van Manen et al., 2017; Jimenez et al., 2008). However, most of these studies have been conducted over relatively short time spans (Orning, 2019; Ruth et al., 2019, but see) or been limited to a single season (e.g. winter) of inference, and all of these studies have been restricted to primarily examining competitive dynamics between pairs of carnivore species, with the vast majority of studies focusing on wolf-cougar interactions. Without more complete information on the influence of grizzly bears on cougars in addition to wolves – as well as how the strongly seasonal dynamics of prey availability, weather patterns, and human activities in much of the Northern Rockies outside the bounds of national parks – influence species interactions, our ability to untangle the specific mechanisms by which increasing populations of dominant competitors affect the behavior and population sizes of subordinate cougars have been limited.

In the multi-use Southern Greater Yellowstone Ecosystem (SGYE) north of Jackson, Wyoming, management and monitoring of large carnivores and ungulates is complex. Multiple federal and state agencies, and non-profit organizations collect data on these species, and anthropogenic impacts range from motorized and non-motorized dispersed recreation to hunting and supplemental feeding of elk. Although separate long-term datasets exist on the locations, population dynamics and food habits of cougars, wolves, grizzly bears, and their primary prey species, elk, these single species datasets have not been merged or examined comprehensively to date. As such, the SGYE offers a challenging but unique opportunity to study competitive dynamics between top carnivores and cascading impacts to subordinate carnivores and shared prey species. In 2015 I began working with Panthera's Puma Program as a graduate student researcher for the Teton Cougar Project to develop a PhD project focusing on cougar interactions with competitors and shared prey species. In addition to Panthera, Craighead Berignia South, the National Park Service, U.S. Fish and Wildlife Service, the U.S. Geological Survey and Wyoming Game and Fish Department agreed to collaborate on my PhD research and share data with me. Collectively these organizations shared location data from Very High Frequency (VHF) and Global Positioning System (GPS) collared cougars, wolves, grizzly bears and elk and kill site data from cougars collected over the course of sixteen years (2001-2016) in the SGYE for this project.

For my PhD project, I investigated three mechanisms, both direct and indirect, by which competition from recovering wolves and grizzly bears may have affected subordinate cougars in the SGYE; possible cascading effects to prey species were also explored in each chapter.

In Chapter 2, I investigated one of the direct impacts of competition from recovering wolves and grizzly bears on cougars by examining the influence of dominant competitor avoidance on cougar habitat selection in the SGYE. I sought to evaluate whether: 1) cougars shifted their seasonal habitat and kill site selection as wolf and grizzly bear populations increased in the SGYE from 2001-2016; and 2) whether changes in cougar habitat selection were driven by cougar avoidance of wolves and grizzly bears. Subordinate carnivore habitat selection is hypothesized to be driven by both prey availability and risk of dominant competitor encounter (Lima and Dill, 1990; Durant, 1998; Vanak et al., 2013; Elbroch and Kusler, 2018; Ruth et al., 2019). In this chapter I focused specifically on the role of dominant competitor avoidance as a driving mechanism behind changes in cougar habitat selection. To address my first objective, I estimated seasonal resource selection functions (RSFs; Manly et al., 2002) for cougars at three spatial scales, and examined changes in cougar selection for key environmental and anthropogenic habitat parameters over time.

In Chapter 3, I shifted my focus to prey availability, and employed the same data set as Chapter 2 to investigate the effects of recovering wolves and grizzly bears on cougar's spatio-temporal access to elk habitat in the SGYE. I explored two possible mechanisms by which cougar access to elk habitat may have been reduced: the indirect effects of elk shifting their own habitat selection in the presence of increasing wolf and grizzly bear populations; and the direct effects of wolf and grizzly bear spatial monopolization of elk habitat. Elk are the primary prey of not only cougars, but also wolves and grizzly bears in the SGYE (Smith et al., 2006; Interagency Grizzly Bear Study Team, 2013; Elbroch et al., 2016; Woodruff et al., 2018). In this chapter my objectives were to 1) investigate whether elk shifted their own seasonal habitat selection in response to increasing wolf and grizzly bear populations in the SGYE from 2001-2016; and 2) evaluate how cougar access to elk was affected by changing elk habitat selection and possible wolf and grizzly bear monopolization of elk habitat. Finally, to determine whether cougars were increasing the proportion of mule deer in their diets as their access to elk habitat was potentially declining, I examined the seasonal composition of ungulate prey in cougar diets over time.

In Chapter 4, I examined another dimension of interference competition from recovering wolves and grizzly bears– as well as black bears – on cougars by quantifying kleptoparasitism of cougar kills in the SGYE. In this final chapter, my objectives were to 1) characterize the temporal and competitor-specific patterns of kleptoparasitism of cougar kills in the SGYE from 2001-2016; 2) examine the factors affecting the seasonal likelihood that cougars would be displaced from their kills; and 3) evaluate possible negative impacts to the SGYE cougar population.

Methods

My study area (Figure 1) was defined by the 100% Minimum Convex Polygon (MCP) for all species location data, an area of 36,000 km^2 in the GYE, ranging from southern Yellowstone National Park (YNP), eastern Caribou-Targhee National Forest, western Shoshone National Forest and Bridger-Teton National Forest (BTNF) north of Pinedale, WY. Our core cougar study area (Figure 1, black bounding box) included Grand Teton National Park (GTNP), the National Elk Refuge (NER), large portions of BTNF and the city of Jackson, Wyoming.

For Chapter 2, I first estimated seasonal resource selection functions (RSFs; Manly et al., 2002) for cougars at three spatial scales, and examined changes in cougar selection for key environmental and anthropogenic habitat parameters over time. Next, I estimated RSFs for concurrently collared wolves and grizzly bears as well as elk. Then I modeled cougar habitat selection as a function of wolf, grizzly bear or elk habitat selection and assessed model fit and predictive power for each competitor or prey species. Finally, I quantified the impact of interference competition from wolves and grizzly bears on cougars by estimating the magnitude and direction (positive or negative) of cougar selection of competitor habitats, and competitor selection of cougar habitats, as well as any changes over time.

For Chapter 3, I first estimated seasonal RSFs for elk at two spatial scales, and examined changes in elk selection for key habitat parameters over time. To address my second objective for this chapter, I first quantified the impact of predation risk from cougars, wolves and grizzly bears on elk habitat selection by estimating the magnitude and direction (positive or negative) of elk selection of predator habitats, as well as any changes over time. Finally, to assess whether wolf and grizzly bear monopolization of elk habitat played a role in reducing cougar access to elk habitat, I estimated the magnitude and direction of predator selection of elk habitats, as well as any changes over time.

For Chapter 4 I first determined the frequency that cougars were displaced from their kills by all competitors and by each dominant competitor species (i.e., wolves, grizzly bears and black bears), documenting seasonal and monthly trends in displacement. For my second objective, I assessed the effects of biotic, environmental and anthropogenic factors on the likelihood that cougars would be displaced from their kills within four seasons (winter, spring, summer, fall). I also tested whether cougars were more likely to be displaced from their kills over time as wolf and grizzly bear populations increased in the SGYE. Finally, I investigated whether kleptoparasitism negatively affected the SGYE cougar population by testing the effects of annual rates of kleptoparasitism on cougar population densities.

Preliminary results

In Chapter 2, I found that cougar habitat selection changed significantly over time as wolves and grizzly bears recovered, and that spatial overlap with the habitat of both dominant carnivores induced increased refuge seeking by cougars in more densely forested, steep and rugged terrain across seasons, as well as higher elevation areas in the winter.

In Chapter 3, I found that elk habitat selection also changed significantly following wolf and grizzly bear recovery, that elk avoided cougar habitat more than either dominant competitor's habitat, and that wolves and grizzly bears selected elk habitat across seasons, while cougar selection of elk habitat sharply declined as wolves and grizzly bears recovered. Both mechanisms appeared to contribute to a reduction in cougar access to elk habitat. Additionally, supplemental feeding of elk in the winter appeared to magnify negative effects to cougars.

In Chapter 4, I documented significant rates of kleptoparasitism from not only wolves and grizzly bears, but also black bears. Cougar kills were more likely to be kleptoparasited as wolf and grizzly bear popula-

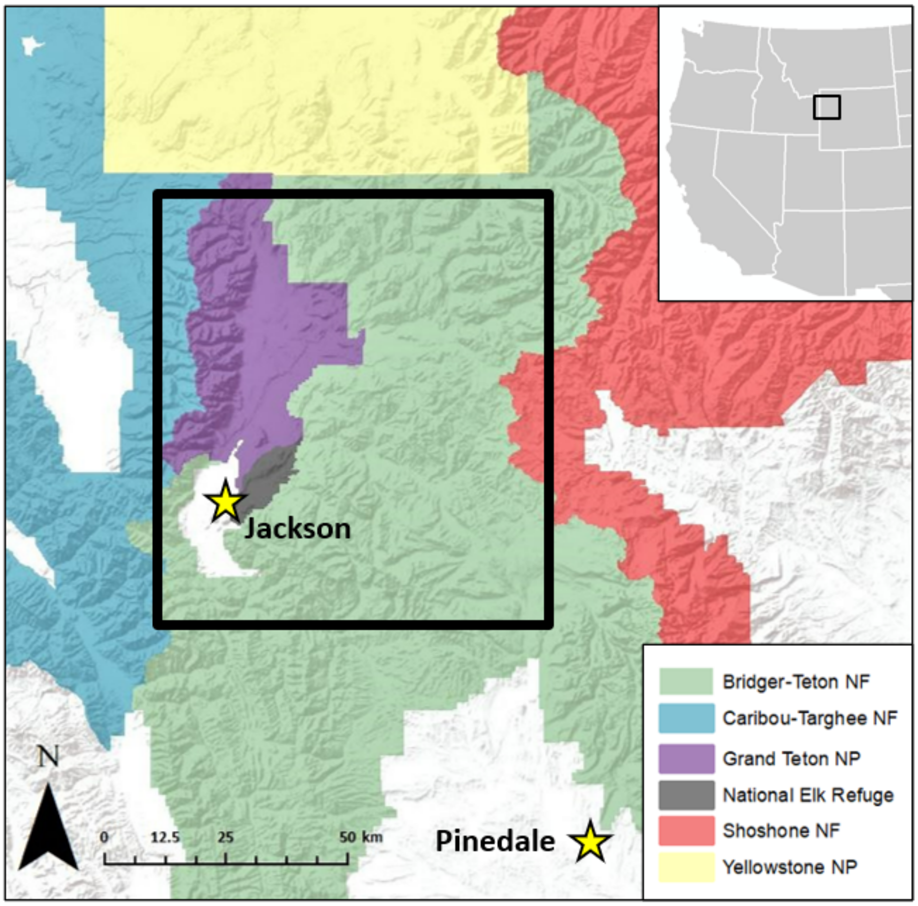

Figure 1. The study area in northwest Wyoming USA. The core cougar study area is encompassed by a black bounding box.

tions increased, and densities of adult cougars and dependent offspring were lower in years with higher rates of kleptoparasitism.

Conclusions

Competition from both recovering wolves and grizzly bears as well as black bears had strong, year-round effects on cougars, and these effects may be strongest in the winter. The declines observed in the SGYE cougar population in previous studies (Elbroch et al., 2018, 2020) are most likely attributed to both reduced spatio-temporal access to elk habitat and heighted interference competition from wolves and bears species. Elk feed grounds may amplify these effects in the winter. Subordinate carnivore densities will likely be reduced in presence of recovering dominant competitors and human activities and management practices may further contribute to declines. A community /multi-species approach is necessary for making informed and effective decisions in species conservation and wildlife management

Future work

My dissertation is currently embargoed until June 2023 while I work with my dissertation collaborators to revise and publish each chapter as journal articles.

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References

Atwood, T. C., E. M. Gese, and K. E. Kunkel. 2007. Comparative patterns of predation by cougars and recolonizing wolves in Montana's Madison Range. The Journal of Wildlife Management **71**:1098–1106.

Atwood, T. C., E. M. Gese, and K. E. Kunkel. 2009. Spatial partitioning of predation risk in a multiple predator-multiple prey system. The Journal of Wildlife Management **73**:876–884.

Ballard, W. B., L. N. Carbyn, and D. W. Smith, 2003. Wolf interactions with non-prey. Pages 259–271 *in* Wolves: Behavior, ecology, and conservation. Chicago Press: Chicago, IL, USA.

Bartnick, T., T. Van Deelen, H. Quigley, and D. Craighead. 2013. Variation in cougar (*Puma concolor*) predation habits during wolf (*Canis lupus*) recovery in the southern Greater Yellowstone Ecosystem. Canadian Journal of Zoology **91**:82–93.

Creel, S., and D. Christianson. 2008. Relationships between direct predation and risk effects. Trends in ecology & evolution **23**:194–201.

Creel, S., G. Spong, and N. Creel, 2001. Interspecific competition and the population biology of extinction-prone carnivores. Pages 35–60 *in* Carnivore conservation. Cambridge University Press Cambridge.

Dill, L. M., M. R. Heithaus, and C. J. Walters. 2003. Behaviorally mediated indirect interactions in marine communities and their conservation implications. Ecology **84**:1151–1157.

Durant, S. M. 1998. Competition refuges and coexistence: An example from Serengeti carnivores. Journal of Animal Ecology **67**:370–386.

Durant, S. M. 2000. Living with the enemy: Avoidance of hyenas and lions by cheetahs in the Serengeti. Behavioral ecology **11**:624–632.

Elbroch, L. M., J. M. Ferguson, H. Quigley, D. Craighead, D. J. Thompson, and H. U. Wittmer. 2020. Reintroduced wolves and hunting limit the abundance of a subordinate apex predator in a multi-use landscape. Proceedings of the Royal Society B: Biological Sciences **287**:20202202. https://royalsocietypublishing.org/doi/10.1098/rspb.2020.2202.

Elbroch, L. M., and A. Kusler. 2018. Are pumas subordinate carnivores, and does it matter? PeerJ **6**:e4293. https://peerj.com/articles/4293.pdf.

Elbroch, L. M., P. E. Lendrum, J. Newby, H. Quigley, and D. J. Thompson. 2015. Recolonizing wolves influence the realized niche of resident cougars. Zoological Studies **54**:41.

Elbroch, L. M., P. E. Lendrum, H. Robinson, and H. B. Quigley. 2016. Population-and individual-level prey selection by a solitary predator as determined with two estimates of prey availability. Canadian Journal of Zoology **94**:275–282.

Elbroch, L. M., L. Marescot, H. Quigley, D. Craighead, and H. U. Wittmer. 2018. Multiple anthropogenic interventions drive puma survival following wolf recovery in the Greater Yellowstone Ecosystem. Ecology and evolution **8**:7236–7245. https://onlinelibrary.wiley.com/doi/10.1002/ece3.4264.

Gigliotti, L. C., R. Slotow, L. T. Hunter, J. Fattebert, C. Sholto-Douglas, and D. S. Jachowski. 2020. Habitat complexity and lifetime predation risk influence mesopredator survival in a multi-predator system. Scientific reports **10**:1–10. https://www.nature.com/articles/s41598-020-73318-3.

Goss-Custard, J., S. L. V. D. Durell, and B. Ens. 1982. Individual differences in aggressiveness and food stealing among wintering oystercatchers, Haematopus ostralegus L. Animal Behaviour **30**:917–928.

Gunther, K. A., and D. W. Smith. 2004. Interactions between wolves and female grizzly bears with cubs in Yellowstone National Park. Ursus pages 232–238.

Heithaus, M. R., and L. M. Dill. 2002. Food availability and tiger shark predation risk influence bottlenose dolphin habitat use. Ecology **83**:480–491.

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

Hopcraft, J. G. C., A. R. Sinclair, and C. Packer. 2005. Planning for success: Serengeti lions seek prey accessibility rather than abundance. Journal of Animal Ecology **74**:559–566.

Husseman, J. S., D. L. Murray, G. Power, C. Mack, C. Wenger, and H. Quigley. 2003. Assessing differential prey selection patterns between two sympatric large carnivores. Oikos **101**:591–601.

Interagency Grizzly Bear Study Team, 2013. Response of Yellowstone grizzly bears to changes in food resources: A synthesis. Final report to the Interagency Grizzly Bear Committee and Yellowstone Ecosystem Subcommittee. Technical report, US Geological Survey, Norhern Rocky Mountain Science Center, ozeman, Montana, USA. https://pubs.er.usgs.gov/publication/70131502.

Jimenez, M. D., V. J. Asher, C. Bergman, E. E. Bangs, and S. P. Woodruff. 2008. Gray wolves, Canis lupus, killed by cougars, Puma concolor, and a grizzly bear, Ursus arctos, in Montana, Alberta, and Wyoming. The Canadian field-naturalist **122**:76–78.

Kohl, M. T., T. K. Ruth, M. C. Metz, D. R. Stahler, D. W. Smith, P. White, and D. R. MacNulty. 2019. Do prey select for vacant hunting domains to minimize a multi-predator threat? Ecology letters **22**:1724–1733. https://onlinelibrary.wiley.com/doi/abs/10.1111/ele.13319.

Kortello, A. D., T. E. Hurd, and D. L. Murray. 2007. Interactions between cougars (Puma concolor) and gray wolves (Canis lupus) in Banff National Park, Alberta. Ecoscience **14**:214–222.

Krebs, C. J., 1994. Ecology: The experimental analysis of distribution and abundance. Technical report.

Kunkel, K. E., T. K. Ruth, D. H. Pletscher, and M. G. Hornocker. 1999. Winter prey selection by wolves and cougars in and near Glacier National Park Montana. The Journal of Wildlife Management pages 901–910.

Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: A review and prospectus. Canadian Journal of Zoology **68**:619–640.

Manly, B., L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. Resource selection by animals: Statistical design and analysis for field studies. 2nd edition. Kluwer Academic Publishers.

Mao, J. S., M. S. Boyce, D. W. Smith, F. J. Singer, D. J. Vales, J. M. Vore, and E. H. Merrill. 2005. Habitat selection by elk before and after wolf reintroduction in Yellowstone National Park. The Journal of Wildlife Management **69**:1691–1707.

Morell, V. 2015. Lessons from the wild lab. Science **347**:1302–1307.

Morin, P. J. 2011. Community Ecology, 2nd Edition. Wiley-Blackwell: Oxford, UK.

Murphy, K. M., G. S. Felzien, M. G. Hornocker, and T. K. Ruth. 1998. Encounter competition between bears and cougars: Some ecological implications. Ursus **10**:55–60.

Northfield, T. D., B. T. Barton, and O. J. Schmitz. 2017. A spatial theory for emergent multiple predator–prey interactions in food webs. Ecology and Evolution **7**:6935–6948. https://www.ncbi.nlm.nih.gov/pmc/articles/PMC5587500/.

Ordiz, A., C. Milleret, J. Kindberg, J. Mnsson, P. Wabakken, J. E. Swenson, and H. Sand. 2015. Wolves, people, and brown bears influence the expansion of the recolonizing wolf population in Scandinavia. Ecosphere **6**:1–14. https://esajournals.onlinelibrary.wiley.com/doi/full/10.1890/ES15-00243.1.

Orning, E. K., 2019. Carnivore competition: Spatial and dietary implications of gray wolf recolonization for cougars in northeast Oregon. Ph.D. dissertation, Oregon State University, Corvallis, OR. https://ir.library.oregonstate.edu/concern/graduate_thesis_or_dissertations/m900p119m.

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

Riley, S. J., G. M. Nesslage, and B. A. Maurer. 2004. Dynamics of early wolf and cougar eradication efforts in Montana: Implications for conservation. Biological Conservation **119**:575–579.

Ripple, W. J., R. L. Beschta, J. K. Fortin, and C. T. Robbins. 2014. Trophic cascades from wolves to grizzly bears in Yellowstone. Journal of Animal Ecology **83**:223–233.

Ruth, T. K., P. C. Buotte, and M. G. Hornocker. 2019. Yellowstone cougars: Ecology before and during wolf restoration. University Press of Colorado.

Sand, H., C. Wikenros, P. Wabakken, and O. Liberg. 2006. Cross-continental differences in patterns of predation: Will naive moose in Scandinavia ever learn? Proceedings of the Royal Society B: Biological Sciences **273**:1421–1427.

Schmitz, O. J., J. R. Miller, A. M. Trainor, and B. Abrahms. 2017. Toward a community ecology of landscapes: Predicting multiple predator-prey interactions across geographic space. Ecology **98**:2281–2292. https://esajournals.onlinelibrary.wiley.com/doi/abs/10.1002/ecy.1916.

Schoener, T. W. 1974. Resource partitioning in ecological communities: Research on how similar species divide resources helps reveal the natural regulation of species diversity. Science **185**:27–39.

Seddon, P. J., D. P. Armstrong, and R. F. Maloney. 2007. Developing the science of reintroduction biology. Conservation biology **21**:303–312.

Sinclair, A. R. 1985. Does interspecific competition or predation shape the African ungulate community? The Journal of Animal Ecology pages 899–918.

Smith, B., E. Williams, K. McFarland, T. McDonald, G. Wang, and T. Moore, 2006. Neonatal mortality of elk in Wyoming: Environmental, population, and predator effects. Biological Technical Publication. Technical report, BTP-R6007-2006. US Department of Interior, US Fish and Wildlife Services . . . .

Swanson, A., T. Caro, H. Davies-Mostert, M. G. Mills, D. W. Macdonald, M. Borner, E. Masenga, and C. Packer. 2014. Cheetahs and wild dogs show contrasting patterns of suppression by lions. Journal of animal ecology **83**:1418–1427. https://pubmed.ncbi.nlm.nih.gov/24724917/.

Van Manen, F. T., M. A. Haroldson, and K. A. Gunther, 2017. Historical perspective – from protection to food dependency to recovery as wildlife. Pages 13–27 *in* P. J. White, K. A. Gunther, and F. T. Van Manen, editors. Yellowstone grizzly bears: Ecology and conservation of an icon of wildness. Yellowstone Forever, Yellowstone National Park, Gardiner, MT USA and U.S. Geological Survey, Northern Rocky Mountain Science Center, Bozeman, MT.

Vanak, A. T., D. Fortin, M. Thaker, M. Ogden, C. Owen, S. Greatwood, and R. Slotow. 2013. Moving to stay in place: Behavioral mechanisms for coexistence of African large carnivores. Ecology **94**:2619–2631. https://esajournals.onlinelibrary.wiley.com/doi/10.1890/13-0217.1.

White, P., R. A. Garrott, S. Cherry, F. G. Watson, C. N. Gower, M. S. Becker, and E. Meredith, 2009. Changes in elk resource selection and distribution with the reestablishment of wolf predation risk. Pages 451–476 *in* R. A. Garrott, P. J. White, and F. G. Watson, editors. The ecology of large mammals in central Yellowstone: Sixteen years of integrated field studies. Academic Press: San Diego, California.

White, P. J., and K. A. Gunther, 2017. Historical perspective – from protection to food dependency to recovery as wildlife. Pages 13–27 *in* P. J. White, K. A. Gunther, and F. T. Van Manen, editors. Yellowstone grizzly bears: Ecology and conservation of an icon of wildness. Yellowstone Forever, Yellowstone National Park, Gardiner, MT USA and U.S. Geological Survey, Northern Rocky Mountain Science Center, Bozeman, MT.

Woodruff, S. P., M. D. Jimenez, and T. R. Johnson. 2018. Characteristics of winter wolf kill sites in the southern Yellowstone ecosystem. Journal of Fish and Wildlife Management **9**:155–167. https://meridian.allenpress.com/jfwm/article/9/1/155/210504/Characteristics-of-Winter-Wolf-Kill-Sites-in-the.