

Impacts of recolonizing gray wolves (*Canis lupus*) on survival and mortality in two sympatric ungulates

J.A. Dellinger, C.R. Shores, M. Marsh, M.R. Heithaus, W.J. Ripple, and A.J. Wirsing

Abstract: There is growing recognition that humans may mediate the strength and nature of the ecological effects of large predators. We took advantage of ongoing gray wolf (*Canis lupus* Linnaeus, 1758) recolonization in Washington, USA, to contrast adult survival rates and sources of mortality for mule deer (*Odocoileus hemionus* (Rafinesque, 1817)) and white-tailed deer (*Odocoileus virginianus* (Zimmermann, 1780)) in areas with and without wolf packs in a managed landscape dominated by multiple human uses. We tested the hypothesis that the addition of wolves to the existing predator guild would augment predator-induced mortality rates for both ungulates. Source of mortality data from adult mule deer and white-tailed deer, respectively, revealed that wolf-related mortality was low compared with that inflicted by other predators or humans. Predator-caused mortality was largely confined to winter. There was little effect of wolf presence on adult deer mortality rates, and there was no difference in mortality between the two deer species relative to wolf-free or wolf-occupied sites. Although this study occurred early in wolf recovery in Washington, our results differ from those demonstrated for gray wolves in protected areas. Thus, we encourage further investigation of effects of direct predation by recolonizing large carnivores on prey in human-dominated landscapes.

Key words: *Canis lupus*, consumptive effects, gray wolf, managed landscapes, mule deer, *Odocoileus hemionus*, *Odocoileus virginianus*, top-down effects, white-tailed deer.

Résumé : Il est de plus en plus reconnu que les humains pourraient moduler l'intensité et le caractère des effets écologiques de grands prédateurs. Nous avons tiré parti de la recolonisation par le loup gris (*Canis lupus* Linnaeus, 1758) en cours dans Washington (États-Unis) pour comparer les taux de survie d'adultes et les sources de mortalité pour le cerf mulet (*Odocoileus hemionus* (Rafinesque, 1817)) et le cerf de Virginie (*Odocoileus virginianus* (Zimmermann, 1780)) dans des secteurs avec ou sans meutes de loups dans un paysage aménagé dominé par divers usages humains. Nous avons vérifié l'hypothèse selon laquelle l'ajout de loups à la guildes de prédateurs existante augmenterait les taux de mortalité induite par les prédateurs pour les deux ongulés. Des données sur les sources de mortalité pour des cerfs muets et cerfs de Virginie adultes, respectivement, révèlent que la mortalité associée aux loups est faible par rapport à celle associée à d'autres prédateurs ou aux humains. La mortalité causée par les prédateurs est en bonne partie limitée à l'hiver. La présence de loups a peu d'effet sur les taux de mortalité des cerfs adultes, et il n'y a aucune différence de mortalité entre les deux espèces de cerfs pour les sites exempts de loups ou occupés par des loups. Bien que l'étude ait été menée au début du rétablissement des loups dans l'État de Washington, ses résultats diffèrent de résultats obtenus pour des loups gris dans des aires protégées. Nous recommandons donc de poursuivre l'étude des effets de la prédation directe par de grands carnivores en recolonisation sur les proies dans des paysages dominés par les humains. [Traduit par la Rédaction]

Mots-clés : *Canis lupus*, effets associés à la consommation, loup gris, paysages aménagés, cerf mulet, *Odocoileus hemionus*, *Odocoileus virginianus*, effets descendants, cerf de Virginie.

Introduction

The potential for top-down effects initiated by large predators is widely recognized (Terborgh et al. 2001; Estes et al. 2011; Ripple et al. 2014). Consequently, there is growing concern about the ecosystem impacts of ongoing global declines in these species (Estes et al. 2011; Ripple et al. 2014, 2016). Despite evidence that humans can attenuate the effects of large predators (e.g., Hebblewhite et al. 2005; Rogala et al. 2011; Kuijper et al. 2016; Haswell et al. 2017), most terrestrial studies of top-down forcing to date have occurred where the anthropogenic footprint is minimal (i.e., protected ar-

eas and wilderness that still contain adequate predator populations; Newsome and Ripple 2015). Thus, questions remain about the extent to which our current understanding of the ecological roles of large predators applies to managed landscapes that have been modified by human activity and, importantly, cover the majority of the Earth's terrestrial surface (Vucetich et al. 2005; Hamlin et al. 2008; Newsome and Ripple 2015).

Over the past few decades, some large predator species have begun to recolonize portions of their historical ranges, including many areas that are shared by humans (Chapron et al. 2014; Ripple

Received 5 October 2017. Accepted 7 February 2018.

J.A. Dellinger,* C.R. Shores, and A.J. Wirsing. School of Environment and Forest Sciences, University of Washington, Box 352100, Seattle, WA 98195-2100, USA.

M. Marsh. United States Forest Service, Okanogan–Wenatchee National Forest, Tonasket Ranger District, Tonasket, WA 98855, USA.

M.R. Heithaus. Department of Biological Sciences, Florida International University, North Miami, FL 33181, USA.

W.J. Ripple. Department of Forest Ecosystems and Society, Oregon State University, Corvallis, OR 97331, USA.

Corresponding author: Justin Dellinger (email: Justin.dellinger@wildlife.ca.gov).

*Present address: Wildlife Investigations Laboratory, California Department of Fish and Wildlife, Rancho Cordova, CA 95670, USA.

This work is free of all copyright and may be freely built upon, enhanced, and reused for any lawful purpose without restriction under copyright or database law. The work is made available under the [Creative Commons CC0 1.0 Universal Public Domain Dedication](https://creativecommons.org/licenses/by/4.0/) (CC0 1.0).

et al. 2014). This trend facilitates natural experiments along recolonization fronts that quantify the impacts of large predator recovery on ecosystems through spatial and (or) temporal comparison of areas where predators are and are not present. For example, the recovery of Eurasian lynx (*Lynx lynx* (Linnaeus, 1758)) in parts of Scandinavia has enabled comparative studies revealing impacts on both prey species (roe deer, *Capreolus capreolus* (Linnaeus, 1758); Melis et al. 2009) and smaller mesocarnivores (red fox, *Vulpes vulpes* (Linnaeus, 1758); Pasanen-Mortensen et al. 2013). The recent eastward recovery of puma (*Puma concolor* (Linnaeus, 1771)) populations in North America (LaRue et al. 2012; Mallory et al. 2012) offers a similar opportunity to perform natural experiments examining the ability of this large predator to affect hyperabundant prey (e.g., deer) populations and, in turn, influence plant recruitment, nutrient dynamics, and habitat succession (Côté et al. 2004; Ripple and Beschta 2008; Ripple et al. 2014).

The gray wolf (*Canis lupus* Linnaeus, 1758) is currently recolonizing large portions of western North America, and numerous studies have capitalized on this process to explore interactions between these canid predators and prey species (Metz et al. 2016). Results from these investigations are mixed, rendering it difficult to generalize about the impacts of recolonizing wolves on prey population dynamics (Messier 1994; Ballard et al. 2001; Mech and Peterson 2003; Garrott et al. 2005; Evans et al. 2006; Hamlin et al. 2008; Brodie et al. 2013, Christianson and Creel 2014). In Yellowstone National Park, for example, White and Garrott (2005) concluded that predation by wolves on adult elk (*Cervus elaphus* Linnaeus, 1758) was additive because it led to marked decreases in adult survival and subsequent elk population declines. By contrast, Vucetich et al. (2005) found that gray wolf predation on adult elk in the same system was largely compensatory and that human harvest and winter weather were largely responsible for observed changes in adult elk survival. In Minnesota (USA), factors such as winter severity were linked to decreased body condition in white-tailed deer (*Odocoileus virginianus* (Zimmermann, 1780)), suggesting that at least some of the mortalities attributed to recolonizing gray wolves were compensatory (Nelson and Mech 1991). Finally, long-term research on Isle Royale has led to the conclusion that food influences moose (*Alces alces* (Linnaeus, 1758)) demography more than predation from gray wolves in the absence of other large carnivores (Vucetich and Peterson 2004). Most of these studies, however, have occurred in protected rather than managed landscapes, leaving open the question of whether the top-down effects of wolf predation that have been observed also manifest in areas subject to more extensive human modification. (Hebblewhite et al. 2005; Hurley et al. 2011; Brodie et al. 2013).

In 2008, gray wolves began naturally recolonizing Washington (USA) from northern Idaho (USA) and southern British Columbia (Canada), and there are now 18 confirmed packs in the state (Jimenez and Becker 2016; Maletzke et al. 2016). In areas of Washington colonized by gray wolves, mean home-range size, mean pack size, and pack density are similar to other managed landscapes in neighboring states (Jimenez and Becker 2016; Maletzke et al. 2016), but pack size and pack density in these managed areas is low relative to protected areas (Jimenez and Becker 2016). At present, these packs are distributed heterogeneously across eastern Washington, setting the stage for natural experiments examining the effects of wolf recovery on native prey populations. In this region, mule deer (*Odocoileus hemionus* (Rafinesque, 1817)) and white-tailed deer dominate the ungulate prey guild (Robinson et al. 2002). Gray wolves are known to readily take both species (Nelson and Mech 1991; McNay and Voller 1995). Mule deer and white-tailed deer may differ in their vulnerability to predation by gray wolves, however, because of inherent differences in their resource selection patterns. Namely, mule deer use rocky uneven terrain, whereas white-tailed deer use more rolling riparian habitat (Lingle and Pellis 2002). As coursing predators, gray wolves generally tend to select for relatively gentle terrain while hunting

(Mech and Peterson 2003; Oakleaf et al. 2006; J.A. Dellinger, unpublished data). Thus, gray wolves could exert larger consumptive effects on white-tailed deer compared with mule deer because of greater overlap in habitat use patterns.

In this study, we investigated effects of gray wolves on sympatric mule deer and white-tailed deer in a managed landscape in eastern Washington affected by multiple human activities such as hunting, logging, and ranching. Specifically, taking advantage of spatial heterogeneity in wolf presence, we contrasted survival rates and sources of mortality for adult mule deer and white-tailed deer in areas with and without established wolf packs. Under the hypothesis that the extent to which gray wolves influence prey survival is mediated by habitat overlap, we predicted that any observed differences in prey mortality rates and overall survival between wolf-occupied and wolf-free areas would be exhibited by white-tailed deer to a greater extent than by mule deer. Alternatively, gray wolf predation could have little impact on ungulate survival in managed landscapes if wolf density and (or) predation efficiency are limited by anthropogenic activity (Pimlott 1967; Messier 1994; Vucetich et al. 2005; Kuijper et al. 2016). Under this latter scenario, the presence of wolves would not be expected to correlate with differences in rates of predator-induced mortality and overall survival in prey populations.

Materials and methods

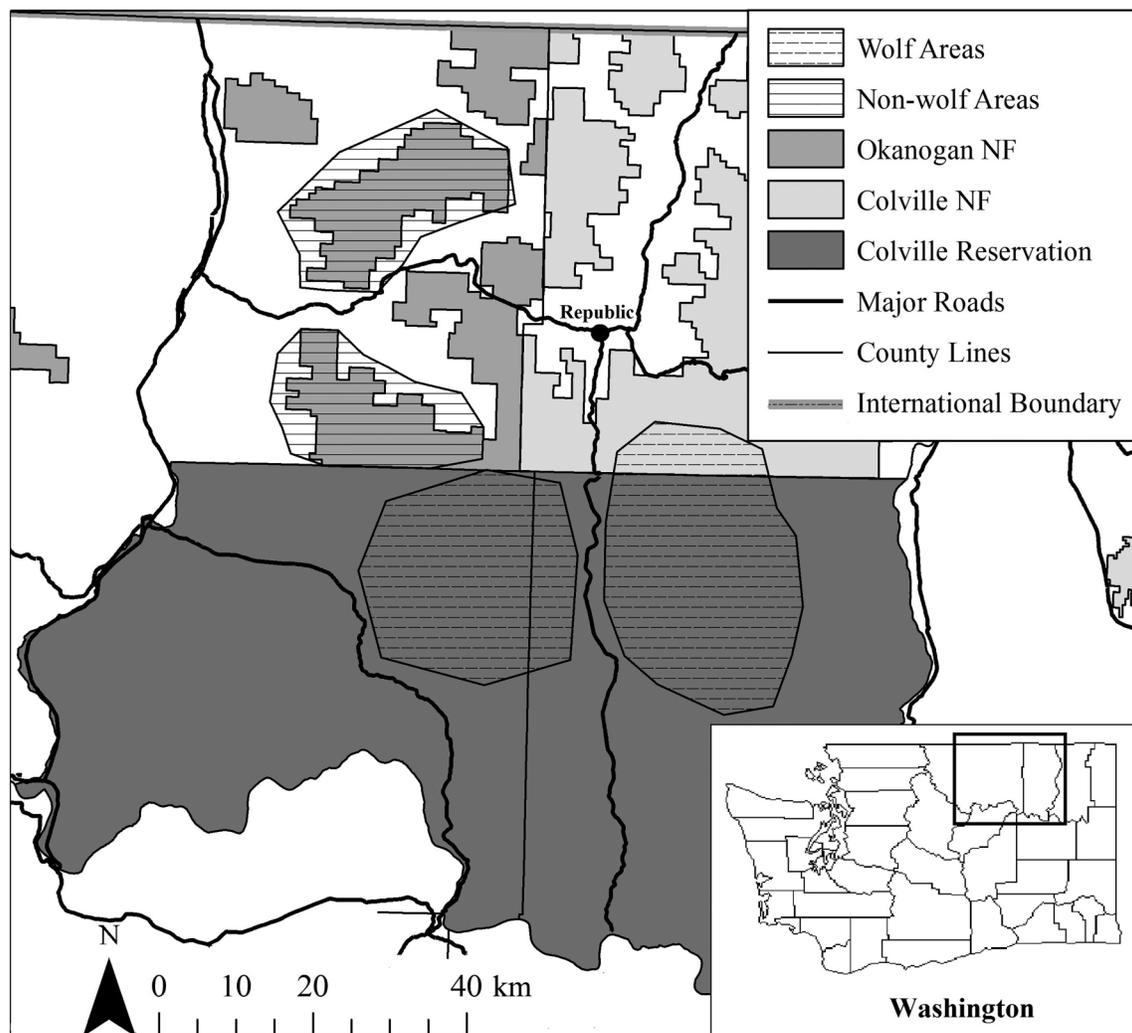
Study area

The study took place from 2013 to 2016 in an area of eastern Washington, USA, spanning Okanogan and Ferry counties and including portions of the Okanogan–Wenatchee and Colville National Forests and the Colville Reservation (Fig. 1). National Forest and Colville Reservation lands cover 3282 km² (28%) and 5657 km² (47%), respectively, with the remaining 2993 km² (25%) being privately owned. Human density averaged 2.25/km² (range: 0–179/km²) over the entirety of the study area (U.S. Census Bureau 2016). Road density averaged 1.12 km/km² (range: 0–3.76 km/km²) for primary and secondary roads combined (U.S. Census Bureau 2016).

The study area contains the Okanogan Highlands and Kettle River Range, which create a topography composed of predominantly moderate slopes on mountainous and hilly terrain with broad round summits. The Okanogan Highlands and Kettle River Range are bisected by the Sanpoil River. Elevations range from 300 to 2065 m. Mean temperatures range from 28 °C during summer to –8 °C in winter. Mean precipitation ranges from 21 cm in summer in the form of rain to 105 cm in winter in the form of snow. Habitat types range from shrub–steppe composed primarily of sagebrush (*Artemisia tridentata* Nutt.) and bitterbrush (*Purshia tridentata* (Pursh) DC.) at lower elevations to ponderosa pine (*Pinus ponderosa* Douglas ex. P. Lawson & C. Lawson), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) forest at higher elevations. Riparian areas, dominated by poplars (genus *Populus* L.), are regularly dispersed along drainages that flow into the Okanogan and Sanpoil River valleys, respectively (Clausnitzer and Zamora 1987). Mule deer, white-tailed deer, elk, and moose comprise the resident ungulate community, though each deer species was ~20 and 50 times more abundant than moose and elk, respectively (Spence 2017). Coyotes (*Canis latrans* Say, 1823), bobcats (*Lynx rufus* (Schreber, 1777)), American black bears (*Ursus americanus* Pallas, 1780), and cougars represented the mammalian predators present at all four sites, whereas gray wolves were only present in the “wolf” sites.

The study area was broken up into four sites, two occupied by gray wolf packs and two lacking wolves. The four sites encompassed a mean of 613 km² (range = 550–680 km²). The two “wolf” sites were defined by an amalgamated 95% kernel density home range from multiple adult radio-collared wolves in each pack. The two “non-wolf” sites were defined based on National Forest boundaries. Wolf packs first colonized the region in summer of

Fig. 1. Location of the study area (11N 372208 E, 5389786 N) in Washington, USA, which included two areas occupied by gray wolves (*Canis lupus*) that fell primarily within the Colville Reservation and two wolf-free areas in the Okanogan–Wenatchee National Forest.



2010 and, over the course of the investigation, used the Colville National Forest and Colville Reservation but not the adjacent Okanogan–Wenatchee National Forest (Fig. 1). Specifically, wolf-occupied areas occurred on either side of the Sanpoil River. One non-wolf site was immediately south of Aeneas Valley and north of the Colville Reservation. The other non-wolf site was located north of the other non-wolf area near Bonaparte Lake (Fig. 1). All four sites consisted of similar topography and habitat types, and experience similar levels of human use in the form of cattle ranching, logging, and hunting. Cattle were present on the landscape in each year of the investigation from mid-June to mid-October. Logging occurred year-round.

Hunting of both deer species on the National Forests occurs in autumn and length of season varies depending on game management unit and weapon type. Generally, no game management unit is hunted more than two full months in a year. During the study period, 844 (range: 648–966) deer were harvested each year with >80% being antlered individuals. Furthermore, a mean of 4 (range: 1–7) cougars and 116 (range: 103–147) American black bears were harvested each year. Note that these cougar and bear data come from game management units that are larger than our study area (harvest data obtained from <https://wdfw.wa.gov/hunting/harvest/>). Hunting of both species on the Colville Reservation occurs from 1 June to 31 December each year. There was no reporting of harvest of any kind on reservation lands. It is possible that

overall harvest is comparable with off-reservation lands given that less people hunted the reservation but did so for a longer period of time, but we cannot be certain.

Field data collection

We monitored gray wolf activity in all four sites within the study area in three ways. First, we deployed 16 motion-activated game cameras (M880 by Moultrie®, Calera, Alabama, USA) year-round as a grid along logging roads and game trails (1 per 5 km²) at each site and checked the cameras every 3 months. Game cameras were deployed for a mean of 18 173 trap nights (range: 16 409 – 19 564 trap nights) over all four sites. Second, we conducted weekly track surveys along logging roads and game trails during winter months (mid-December to mid-March) using snowmobiles. Specifically, track surveys covered a minimum of 60 km each week in each site. The surveys did not always cover the same roads and trails each week; rather, we surveyed the same general area each week and the same roads and trails every 2 weeks. Third, global positioning system (GPS) radio collars deployed on at least one member of each wolf pack occupying the designated wolf areas by the Colville Confederated Tribes Fish and Wildlife Department aided in monitoring wolf presence and movements. Wolves were captured using aerial net gunning in winter and #7 double long spring rubber jawed foothold traps in summer. Foothold traps were checked mid-morning and early afternoon.

Captured wolves were outfitted with GPS radio collars (Globalstar Survey Collars, Vectronic Aerospace GmbH, Berlin, Germany), sexed, and weighed. To ensure only adults were collared, we did not trap <400 m from a den or rendezvous site with pups <6 months of age. The GPS collars were programmed to obtain a location every 5 h. Combined, these three methods enabled continuous and intensive monitoring of presence or absence and the overall number of wolves present in each site. Neither non-wolf site had any documented gray wolf activity during this study. Both the wolf sites were occupied continuously by individual packs, each ranging in size from 3 to 8 individuals throughout the study with a mean of 5 individuals for each pack for a mean wolf density of 8.6/1000 km². This mean pack size and wolf density is similar to that of wolves in other managed landscapes in the northwestern United States where mean pack size is ~5.7 and density is 6.3/1000 km² (Jimenez and Becker 2016).

To determine survival rates and sources of mortality of mule deer and white-tailed deer, we captured individuals of each species over four winters (December–March) using aerial net gunning and baited clover trapping (Haulton et al. 2001). We outfitted clover traps with trap transmitters to alert us to captures. Trap transmitter signals were checked in the early morning and late afternoon. Captured deer were outfitted with GPS radio collars (Globalstar Survey Collars, Vectronic Aerospace GmbH, Berlin, Germany), ear tagged, aged, sexed, and weighed. To ensure only adults were collared, we did not collar any individual weighing <30 kg. The GPS collars were programmed to obtain a location every 12 h and switch to mortality mode if the deer wearing the collar exhibited no movement for a 12 h period. GPS collars had the potential to last 4–5 years with this location fix rate but 3 years was the longest any deer was monitored. An individual deer was assigned to the wolf present treatment if its 95% kernel home range was completely contained within the 95% kernel home range of a wolf pack, otherwise deer were assigned to the non-wolf treatment. Given most trapping in the wolf present areas occurred within the core home range of the wolf packs (as determined from GPS collars, cameras, and track surveys), very few ($n = 4$) deer only partially overlapped with a wolf pack home range. After 12 consecutive hours of inactivity, GPS collars sent a mortality notification via email detailing the location of the likely mortality. We attempted to get to GPS-collared deer within 24 h after receiving mortality notification to aid in identifying the proximate cause of death. We used the most recent GPS fix and VHF telemetry equipment to navigate to the site where a potential mortality took place. We used puncture marks, scat, tracks, and other signs to determine cause of death and, if predation, the species of predator (Barber-Meyer et al. 2008; Hurley et al. 2011). None of the deer that partially overlapped with wolf pack home ranges were killed by wolves. Human-related mortality included take from firearm and archery seasons, as well as tribal hunts and illegal harvest. Other causes of death included accidents (e.g., falls), injury, and disease. If death could not be attributed to a specific cause, then it was categorized as unknown. Individuals were censored from survival analyses following emigration from a given study site (>10 km), collar failure, or termination of the study. All animal captures and collar deployments were conducted under the University of Washington Institutional Animal Care and Use Committee (IACUC) protocol number 4226-01 and wildlife collection permits from the Washington Department of Fish and Wildlife and the Colville Tribes Fish and Wildlife Department.

Analyses

We recorded time to mortality events or loss of contact such that the date the animal was collared was zero and every day after was additive. Accordingly, an animal monitored for exactly 1 year would have a monitoring period of 365 days. We used Kaplan–Meier estimates of annual survival and nonparametric cumula-

tive incidence functions to estimate cause-specific mortality rates of both deer species in areas with and without wolf packs (Murray 2006). We estimated cumulative incidence functions using a competing risks framework, whereby mortality from one source precluded mortality from other sources, to characterize the impacts of non-human predators on adult deer survival while separately accounting for the influence of human hunters (Heisey and Patterson 2006).

We also evaluated a variety of factors potentially affecting deer survival using Cox proportional hazards regression. This approach enables rigorous evaluation of covariate effects on the instantaneous rate of death experienced by individuals due to two or more mutually exclusive sources of mortality, and can incorporate time-varying explanatory variables including time itself (Murray 2006; Hosmer et al. 2008; Murray et al. 2010). Our analysis compared hazard ratios from two competing sources of mortality, human and non-human predators, and focused on adult deer. We created multiple records for each adult deer monitored such that the number of records matched the number of competing risks. Causes of death not accounted for in the competing risks of interests were censored (Murray et al. 2010). We derived regression coefficient estimates for the competing risks based on explanatory variables considered likely to influence survival patterns: wolf presence, deer species, and season. We treated wolf presence, species, and season as binary variables. We expressed season as binary variables for autumn and winter, respectively, whereby it was 1 or 0 for autumn versus the rest of the year and likewise for winter. Seasonal variation was expressed this way because human-caused mortality was confined to autumn (i.e., September–November, during the hunting season) and predator-caused mortality was primarily confined to late autumn and winter ($n = 17$; 77.3%; November–March).

Following multiple regression, we built global Cox proportional hazards models for each competing risk based on all of the variables above, and all potential interactions therein, with foremost interest in the main effect of wolf presence. We were also particularly interested in the interaction between wolf treatment and deer species as evidence for the hypothesis that predation by wolves would be more pronounced in white-tailed deer than mule deer. Specifically, because mule deer were assigned a “1”, whereas white-tailed deer were assigned a “0”, a negative coefficient for the deer \times wolf interaction would support this hypothesis. Furthermore, significant interactions between wolf treatment and season would indicate that wolf impacts on deer survival were confined largely to a particular time of year for one or both prey species. We initially included individual site variables to test for differences between sites within a wolf treatment type; however, preliminary analyses revealed no significant difference between sites nested within wolf treatment types so sites within wolf treatment types were pooled. Causes of death not accounted for when individually assessing each competing risk of interest were censored. Global models initially included variables for wolf treatment, deer species, autumn, winter, and interactions between wolf treatment and deer species and all other variables, respectively. We used Akaike’s information criteria corrected for small sample size (AIC_c) to select the most parsimonious model (Heisey and Patterson 2006) for each competing risk, and restricted consideration of the most parsimonious models to those with a $\Delta AIC_c \leq 2$ relative to the top model (Hosmer et al. 2008). Sample sizes for AIC_c calculations were based on the number of related mortalities. Finally, we verified the proportional hazards assumption for all top models by first calculating Schoenfeld residuals and then performing a χ^2 test to check for correlation ($\alpha \leq 0.05$; Therneau and Grambsch 2000).

Table 1. Sample sizes of adult mule deer (*Odocoileus hemionus*) and white-tailed deer (*Odocoileus virginianus*) that were GPS-collared and deer dying from different causes.

Treatment	Species	Sex	Collared	Cause of mortality					
				Cougar	Coyote	Black bear	Gray wolf	Human	Unknown
Wolf	White-tailed deer	Male	6	0	0	0	0	2	0
Wolf	White-tailed deer	Female	19	1	0	0	2	0	0
Wolf	Mule deer	Male	9	1	0	0	0	2	1
Wolf	Mule deer	Female	18	3	2	0	0	0	0
Non-wolf	White-tailed deer	Male	13	1	0	1	0	6	0
Non-wolf	White-tailed deer	Female	21	2	3	0	0	2	1
Non-wolf	Mule deer	Male	12	0	1	0	0	3	0
Non-wolf	Mule deer	Female	22	4	1	0	0	1	1

Note: Adult deer sample sizes (numbers collared and succumbing to specific forms of mortality) are stratified by wolf (*Canis lupus*) treatment (presence and absence), deer sex, and deer species.

Table 2. Overall annual survival rates (mean \pm SE) and cause-specific mortality rates (mean \pm SE) for mule deer (*Odocoileus hemionus*) and white-tailed deer (*Odocoileus virginianus*), derived from Kaplan–Meier analyses and cumulative incidence functions.

Treatment	Species	Overall survival	Mortality	
			Predator-related	Human-related
Both	Both	0.69 \pm 0.04	0.16 \pm 0.03	0.15 \pm 0.03
Wolf	Both	0.78 \pm 0.05	0.16 \pm 0.04	0.06 \pm 0.03
Wolf	White-tailed deer	0.83 \pm 0.07	0.08 \pm 0.05	0.09 \pm 0.06
Wolf	Mule deer	0.74 \pm 0.07	0.19 \pm 0.06	0.07 \pm 0.04
Non-wolf	Both	0.60 \pm 0.06	0.16 \pm 0.04	0.24 \pm 0.05
Non-wolf	White-tailed deer	0.53 \pm 0.09	0.17 \pm 0.06	0.30 \pm 0.08
Non-wolf	Mule deer	0.67 \pm 0.08	0.17 \pm 0.07	0.16 \pm 0.06

Note: Survival and cause-specific mortality rates are broken out by treatment and species.

Results

Across our four study sites over the course of 3 years, we collared 120 individual adult mule deer ($n = 61$) and white-tailed deer ($n = 59$). We based survival analyses on a total of 38 mortalities out of the 120 individuals (Table 1). The largest mortality factor was predation ($n = 22$; 53.7%), followed by hunting ($n = 16$; 39.0%) and unknown causes ($n = 3$; 7.3%). Of the 22 mortalities due to predation, cougars were the predominant predator ($n = 12$; 54.5%), followed by coyotes ($n = 7$; 31.8%), gray wolves ($n = 2$; 9.2%), and American black bears ($n = 1$; 4.5%).

Overall annual survival probability from Kaplan–Meier analysis was 0.69 (SE = 0.04; Table 2). Annual survival for adults of both deer species was greater in the areas with versus without wolves (Table 2). Deer mortality rates due to predators were more than twice as high as human-related mortality in areas with wolves. Mortality rates due to humans were four times higher in areas without wolves compared with areas with wolves (Table 2). Cumulative incidence functions revealed that human-related mortality was greater than predator-related mortality for all deer species and treatment combinations except for mule deer in the non-wolf areas (Fig. 2A, 2B). We acknowledge that the large standard errors in these and subsequent analyses potentially indicate a lack of power which could be due to low occurrence of deer being eaten by wolves.

Multiple regression coefficient estimates derived using a competing risks framework revealed that there was no significant difference in hazard ratios due to predation between wolf and non-wolf areas (Table 3). Hazard ratios due to human predation were significantly higher in autumn compared with spring and summer, whereas hazard ratios due to non-human predation were significantly higher in winter compared with all other seasons. Cox proportional hazards modeling for each competing risk demonstrated that the most parsimonious model for determining the overall and relative influences of factors driving white-tailed deer and mule deer mortality for each risk type were different

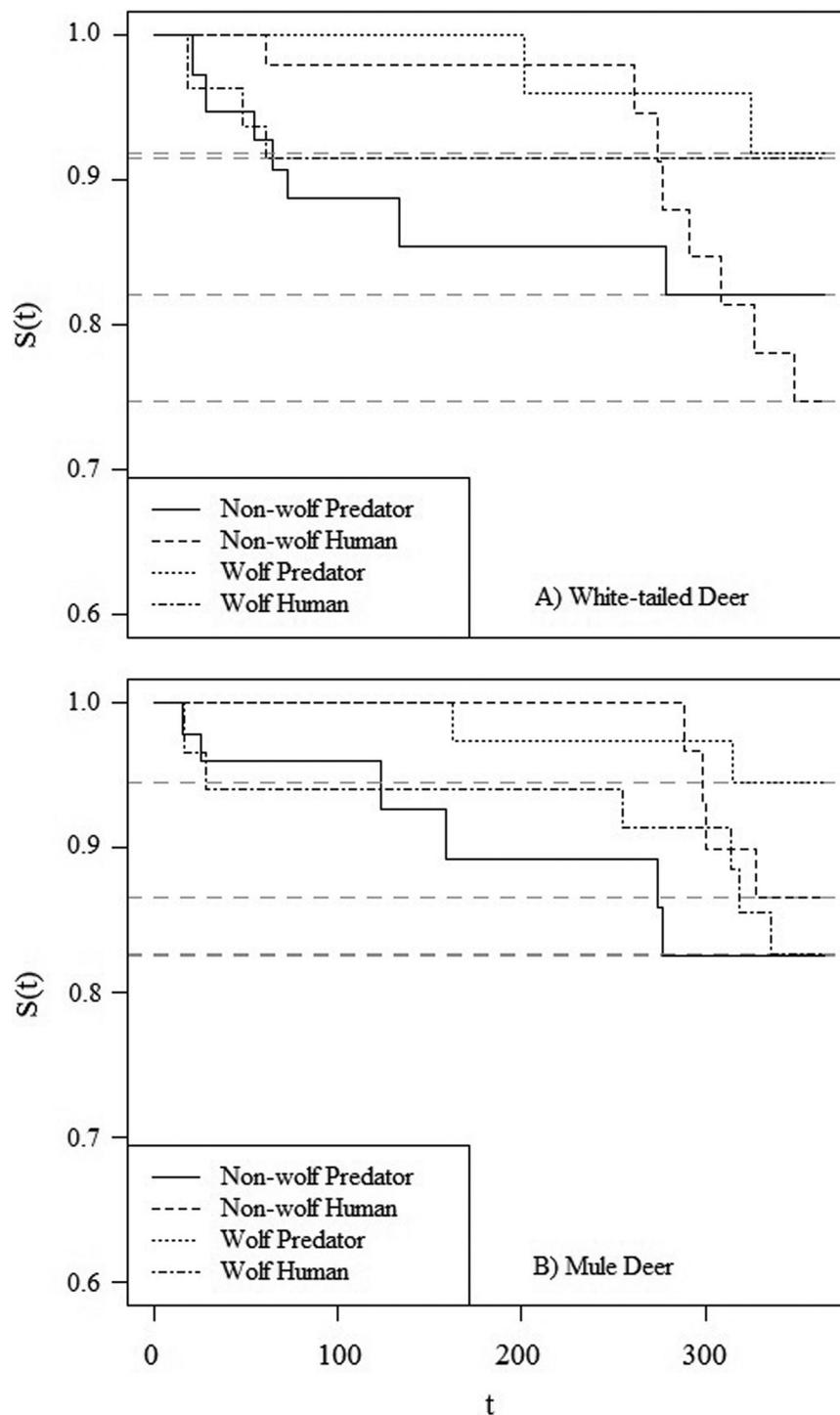
(Table 4). Namely, the winter season was the main factor driving risk to deer dying because of non-human predation (coefficient estimate = 2.90, SE = 0.412, $P < 0.001$). Support for this model was nearly six times greater than the next best model based on comparison of AIC_c weights (Table 4). By implication, deer were more at risk from non-human predation in winter than any other season. It is important to note that deer species did not show up in any of the top predator models, indicating that adults of both species experienced similar levels of risk for predator-caused mortality.

Discussion

In terrestrial ecosystems, the top-down impacts of large predators are now widely recognized and yet have received relatively little attention in managed landscapes where human modification is pervasive (Vucetich et al. 2005; White and Garrott 2005; Hamlin et al. 2008; Dorresteijn et al. 2015). Accordingly, questions remain about the extent to which our understanding of the consumptive impacts of large predators in wilderness and protected areas applies to areas with a deeper human footprint (Kuijper et al. 2016). Our results are not consistent with the idea that wolves exert strong effects on prey survival in managed landscapes, at least during the early phases of recolonization, nor do they support the hypothesis that wolves in these systems alter patterns of adult deer mortality to a degree that coincides with species-specific habitat use patterns. Rather, non-human predation hazard rates for adult mule and white-tailed deer were primarily influenced by season, with both sexes of both deer species experiencing elevated predator-caused mortality in winter irrespective of wolf treatment (Tables 3 and 4).

Why was the impact of wolf predation on adult deer survival so weak in our study system? One possible answer is that, in managed landscapes, gray wolves tend to be sparsely distributed relative to conspecifics in protected areas because of low pack size and (or) some territories not being occupied (Borg et al. 2015;

Fig. 2. Cumulative incidence functions estimating cause-specific mortality rates for (A) white-tailed deer (*Odocoileus virginianus*) and (B) mule deer (*Odocoileus hemionus*) in wolf (*Canis lupus*) and non-wolf areas. The y axis presents time in Julian days within a year and the x axis depicts survival over time.



Jimenez and Becker 2016). This disparity in wolf distribution could arise from wolves avoiding anthropogenic features (e.g., roads, trails, livestock grazing allotments; Muhly et al. 2011). As a result, human-modified landscapes may offer greater amounts of wolf-free, or at least low-risk, space for prey to occupy (Mech et al. 1980; Haight et al. 1998; Kuijper et al. 2016). Indeed, recent research has demonstrated support for the predator shelter hypothesis, under which prey take refuge from predators in areas of increased hu-

man activity (Shannon et al. 2014). Another possible answer is that, despite overall habitat similarity between the study sites, it is possible that subtle habitat differences between sites may have contributed to differences in survival. We also acknowledge that low power owing to the small number ($n = 2$) of deer killed by wolves over the course of the investigation may have hindered our ability to detect an effect of wolves on deer survival. Importantly, however, the paucity of wolf predation

Table 3. Cause-specific hazard coefficient estimates for the two primary (competing) sources of mortality influencing mule deer (*Odocoileus hemionus*) and white-tailed deer (*Odocoileus virginianus*) mortality in northeastern Washington: non-human predators and humans.

Variable	Predator			Human		
	Estimate	SE	P	Estimate	SE	P
Wolf	-0.36	0.65	0.58	0.10	0.64	0.88
Species	0.14	0.56	0.80	-1.13	0.53	0.03
Fall	1.22	0.65	0.06	3.16	0.76	<0.01
Winter	3.29	0.55	<0.01	0.43	1.08	0.69

Note: All variables were binomial: the Wolf variable distinguished between wolf (*Canis lupus*; 1) and non-wolf (0) areas; the Species variable contrasted mule deer (1) and white-tailed deer (0); and the Winter and Fall variables identified mortalities in those seasons, respectively.

events in our study is itself evidence of the weak impact of these predators on deer demography.

The wolf packs in our study region did not suffer any anthropogenic mortalities over the course of the investigation as determined from regular and close monitoring of each pack. For managed landscapes in general, however, humans are the primary driver of wolf mortality, and the combination of anthropogenic and natural mortality in these areas can result in lower overall survival than would be observed in systems where humans are not a major cause of death (Murray et al. 2010). Accordingly, another non-mutually exclusive driver of attenuated wolf impact might be increased rates of breeder loss in managed landscapes due to potentially increased likelihood of human-related mortality (e.g., vehicle strike, hunting, poaching). Such losses can fracture pack dynamics and reduce denning and recruitment rates, which are key for population growth (Brainerd et al. 2008), and may also affect pack hunting success (Borg et al. 2015).

Mule deer and white-tailed deer were not the only ungulates in the study area. Moose and elk were also present but in relatively small numbers (Washington Department of Fish and Wildlife 2014). It is therefore also possible that gray wolves selected for moose and elk given their larger body size and greater nutritional payout relative to either deer species (Griffiths 1980), rendering additive effects of wolf predation on our focal prey species less likely. However, given their generalist diet (Newsome et al. 2016), wolves would not be expected to preferentially target prey species whose relative availability is low (Huggard 1993). Furthermore, past research has shown that gray wolves often target smaller species where sympatric ungulates exist (Potvin et al. 1988; Paquet 1992; Dale et al. 1994). Indeed, a contemporary investigation of gray wolf foraging behavior using GPS clusters from collared individuals in our study system found deer at over 50% of gray wolf kill sites compared with 36% for moose and elk combined (Spence 2017).

Gray wolves in British Columbia were shown to subsist primarily on moose and secondarily on caribou (*Rangifer tarandus* (Linnaeus, 1758)), with which they had reduced spatial overlap relative to moose (Seip 2001). Furthermore, previous studies have revealed that patterns of predator-prey spatial overlap explain why mule deer and white-tailed deer exhibit differing levels of susceptibility to another coursing canid, the coyote (Lingle 2002; Atwood et al. 2009). Accordingly, we predicted that wolves would affect the survival of sympatric mule deer and white-tailed deer differentially (Lingle 2002; Gervasi et al. 2012). Specifically, we expected that white-tailed deer, which favor escape terrain that is shared by wolves and which are disproportionately preyed on by wolves in other systems (Nelson and Mech 1991; Lingle and Pellis 2002), would be more susceptible to wolf predation than mule deer. Instead, the presence of gray wolves did not result in a significant difference in mortality rates due to predation between the two deer species, either within or between treatments (Table 3). By implication, the intensity of wolf predation in man-

Table 4. Comparison of ΔAIC_c , AIC_c weights, and concordance (a measure of fit) of top Cox proportional hazards models for the two primary sources of mortality influencing mule deer (*Odocoileus hemionus*) and white-tailed deer (*Odocoileus virginianus*) survival in northeastern Washington: non-human predators and humans.

Source	Model	ΔAIC_c	AIC_c weights	Concordance
Predator	Winter	0.00	0.77	0.81
	Winter \times Wolf	3.63	0.13	0.85
	Null	4.25	0.09	0.66
	Wolf	8.85	0.01	0.58
Human	Fall	0.00	0.93	0.76
	Fall \times Species	6.08	0.04	0.75
	Wolf	7.85	0.02	0.61
	Null	10.35	0.01	0.30

Note: All variables were binomial: the Wolf variable distinguished between wolf (*Canis lupus*; 1) and non-wolf (0) areas; the Species variable contrasted mule deer (1) and white-tailed deer (0); and the Winter and Fall variables identified mortalities in those seasons, respectively. AIC_c is Akaike's information criteria corrected for small sample size.

aged landscapes may need to reach a certain density threshold beyond that found in our study area (8.6 wolves/1000 km²) and other managed landscapes (6.3 wolves/1000 km² in areas of Idaho and Montana; Jimenez and Becker 2016) before manifesting differentially across prey species. By comparison, wolf densities in protected areas can exceed 40 wolves/1000 km² (Smith et al. 2003). In our system, then, diminished wolf effectiveness and (or) widespread low-risk gaps may have enabled white-tailed deer to avoid heavy predation in areas occupied by wolf packs despite similar habitat use patterns (Lingle and Pellis 2002; Mech and Peterson 2003; Oakleaf et al. 2006).

In our system, it is interesting to note that overall deer mortality from predators and humans was nearly equal and that human-caused mortality was greater than that caused by predators for each species in each treatment with the exception of mule deer in wolf areas (Table 2). Accordingly, our results add to a growing literature implying that human-caused mortality may rival or even exceed wolf predation as a driver of ungulate survival and population trends in landscapes where human activities include hunting (White and Garrott 2005; Wright et al. 2006; Brodie et al. 2013; Dorresteijn et al. 2015). Notably, for example, a recent review of ecosystems in the western United States found that human-related factors were the primary influence on adult elk mortality, regardless of predator assemblage (Brodie et al. 2013). The relative influence of human and non-human predation on ungulate dynamics in any particular situation, however, is likely to depend on myriad factors including human density, interactions between predator species, predator and ungulate management, and landscape configuration (Kuijper et al. 2016). Thus, a more comprehensive understanding of how ungulate populations are shaped by predation in human-dominated ecosystems will require studies that rigorously address these drivers of context dependency.

Seasonal patterns of adult deer mortality, especially in relation to large carnivores, are well documented (Ballard et al. 2001; DeLGiudice et al. 2002; White and Garrott 2005; Wright et al. 2006). During summer, adult deer tend to be in relatively good condition because of access to high-quality forage and are not impeded by snow accumulation, making them hard for predators to catch and bring down. As winter approaches, however, adult deer are rendered easier to catch and bring down because their body condition decreases along with forage quality and availability and snow accumulates (Mech et al. 2001). Accordingly, wolves in the Greater Yellowstone Ecosystem were found to primarily take juvenile and older elk (Mech et al. 2001; Wright et al. 2006), but as winter severity increased, this pattern attenuated and reliance on prime-aged individuals increased (Mech et al. 2001). By inference, severe winter conditions could compound the effects of humans and wolves on ungulate populations by allowing wolves

to increasingly rely on the healthy and prime-aged individuals that are typically harvested by human hunters (Brodie et al. 2013). Our study occurred over a 3 year period during which winters were relatively mild. Thus, the effects of wolf predation on deer populations in our study area could grow in concert with increasing winter severity.

Collectively, our findings suggest that direct wolf predation on adult deer in ecosystems where human activity is pervasive may be too weak to markedly affect ungulate population dynamics (Gervasi et al. 2012; Kuijper et al. 2016). Accordingly, they raise questions about the extent to which results from studies of wolf-prey interactions in wilderness and protected areas apply to managed landscapes with an extensive human footprint (Hebblewhite et al. 2005; Hamlin et al. 2008; Dorresteijn et al. 2015). Other studies of wolf recolonization have revealed large and immediate impacts of wolves on prey survival and numbers (Hebblewhite et al. 2002, 2005; Christianson and Creel 2014). Given our work started several years after wolves appeared on the landscape in our study area, these studies suggest that had wolves had an impact on ungulate demography, we should have been able to detect it.

We would caution, however, that we did not investigate the impacts of gray wolves on neonate survival, which can greatly impact ungulate population dynamics (Nelson and Mech 1986). Furthermore, predator-prey interactions can vary markedly over time (Gaillard et al. 1998; Owen-Smith et al. 2005; Vucetich et al. 2005), partly because they are modified by a suite of dynamic environmental factors including catastrophic wildfires, severe winters, and drought (Vucetich et al. 2005; Barber-Meyer et al. 2008). For example, severe winters have been shown to exacerbate the effects of wolf predation on both white-tailed deer (Fuller 1991) and elk (Brodie et al. 2013). Lastly, given the brevity of our investigation, small sample size may have limited the scope of our inference and, moreover, top-down impacts on prey in our system could strengthen as wolves become more established. Thus, there remains need for longitudinal studies of consumptive predator-prey interactions in managed landscapes in general and studies capable of exploring relationships between variability in predator-prey population dynamics and abiotic and biotic conditions (Vucetich et al. 2005; Nelson et al. 2011; Brodie et al. 2013).

Acknowledgements

This project was carried out under National Science Foundation grants DEB1145902 to A.J. Wirsing and DEB1145522 to M.R. Heithaus. Additional funding was provided by the Safari Club International Foundation, Conservation Northwest, the Washington Department of Fish and Wildlife (Aquatic Lands Enhancement Account (ALEA)), and the University of Washington Student Technology Fee (STF) program. We are grateful to the Colville Tribes Fish and Wildlife Department, and especially E. Krausz and R. Whitney, for permission to access their lands, guidance, and logistical support. We also thank the Okanogan-Wenatchee National Forest for logistical support. Field assistance was provided by M. Bianco, K. Ebenhoch, J. Fournier, A. Smethurst, K. Perenovich, S. Stark, C. Montgomerie, B. Woodruff, I. Hull, C. Whitney, T.C. Walker, C. Shores, and A. Craig. Valuable field training was provided by W. Myers and J. Kujala.

References

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. Manage.* **73**: 876-884. doi:10.2193/2008-325.

Ballard, W.B., Lutz, D., Keegan, T.W., Carpenter, L.H., and deVos, J.C., Jr. 2001. Deer-predator relationships: a review of recent North American studies with emphasis on mule and black-tailed deer. *Wildl. Soc. Bull.* **29**: 99-115.

Barber-Meyer, S., Mech, L.D., and White, P.J. 2008. Elk calf survival and mortality following wolf restoration to Yellowstone National Park. *Wildl. Monogr.* **169**: 1-30. doi:10.2193/2008-004.

Borg, B.L., Brainerd, S.M., Meier, T.J., and Prugh, L.R. 2015. Impacts of breeder

loss on social structure, reproduction and population growth in a social canid. *J. Anim. Ecol.* **84**: 177-187. doi:10.1111/1365-2656.12256. PMID:25041127.

Brainerd, S.M., Andr n, H., Bangs, E.E., Bradley, E.H., Fontaine, J.A., Hall, W., Iliopoulos, Y., Jiminez, M.D., Jozwiak, E.A., Liberg, O., Mack, C.M., et al. 2008. The effects of breeder loss on wolves. *J. Wildl. Manage.* **72**: 89-98. doi:10.2193/2006-305.

Brodie, J., Johnson, H., Mitchell, M., Zager, P., Proffitt, K., Hebblewhite, M., Kauffman, M., Johnson, B., Bissonette, J., Bishop, C., Gude, J., et al. 2013. Relative influence of human harvest, carnivores, and weather on adult female elk survival across western North America. *J. Appl. Ecol.* **50**: 295-305. doi:10.1111/1365-2664.12044.

Chapron, G., Kaczensky, P., Linnell, J.D.C., von Arx, M., Huber, D., Andr n, H., L pez-Bao, J.V., Adamec, M.,  lvares, F., Anders, O., Bal auskas, L., et al. 2014. Recovery of large carnivores in Europe's modern human-dominated landscapes. *Science*, **346**: 1517-1519. doi:10.1126/science.1257553. PMID:25525247.

Christianson, D., and Creel, S. 2014. Ecosystem scale declines in elk recruitment and population growth with wolf colonization: a before-after-control-impact approach. *PLoS ONE*, **9**(7): e102330. doi:10.1371/journal.pone.0102330. PMID:25028933.

Clausnitzer, R.R., and Zamora, B.A. 1987. Forest habitat types of the Colville Indian Reservation. Department of Forestry and Range Management, Washington State University, Pullman.

C t , S.D., Rooney, T.P., Tremblay, J.-P., Dussault, C., and Waller, D.M. 2004. Ecological impacts of deer overabundance. *Annu. Rev. Ecol. Syst.* **35**: 113-147. doi:10.1146/annurev.ecolsys.35.021103.105725.

Dale, B.W., Adams, L.G., and Bowyer, R.T. 1994. Functional response of wolves preying on barren-ground caribou in a multiple-prey ecosystem. *J. Anim. Ecol.* **63**: 644-652. doi:10.2307/5230.

DelGiudice, G.D., Riggs, M.R., Joly, P., and Pan, W. 2002. Winter severity, survival, and cause-specific mortality of female white-tailed deer in north-central Minnesota. *J. Wildl. Manage.* **66**: 698-717. doi:10.2307/3803136.

Dorresteijn, I., Schultner, J., Nimmo, D.G., Fischer, J., Hanspach, J., Kuemmerle, T., Kehoe, L., and Ritchie, E.G. 2015. Incorporating anthropogenic effects into trophic ecology: predator-prey interactions in a human-dominated landscape. *Proc. R. Soc. B Biol. Sci.* **282**: 20151602. doi:10.1098/rspb.2015.1602.

Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J., Carpenter, S.R., Essington, T.E., Holt, R.D., Jackson, J.B.C., Marquis, R.J., et al. 2011. Trophic downgrading of planet earth. *Science*, **333**: 301-306. doi:10.1126/science.1205106. PMID:21764740.

Evans, S.B., Mech, L.D., White, P.J., and Sargeant, G.A. 2006. Survival of adult female elk in Yellowstone following wolf restoration. *J. Wildl. Manage.* **70**: 1372-1378. doi:10.2193/0022-541X(2006)70[1372:SOAFEL]2.0.CO;2.

Fuller, T.K. 1991. Effect of snow depth on wolf activity and prey selection in north central Minnesota. *Can. J. Zool.* **69**(2): 283-287. doi:10.1139/z91-044.

Gaillard, J., Festa-Bianchet, M., and Yoccoz, N. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. *Trends Ecol. Evol.* **13**: 58-63. doi:10.1016/S0169-5347(97)01237-8. PMID:21238201.

Garrott, R.A., Gude, J.A., Bergman, E.J., Gower, C., White, P.J., and Hamlin, K.L. 2005. Generalizing wolf effects across the Greater Yellowstone Area: a cautionary note. *Wildl. Soc. Bull.* **33**: 1245-1255. doi:10.2193/0091-7648(2005)33[1245:GWEATG]2.0.CO;2.

Gervasi, V., Nilsen, E.B., Sand, H., Panzacchi, M., Rauset, G.R., Pedersen, H.C., Kindberg, J., Wabakken, P., Zimmermann, B., Odden, J., Liberg, O., et al. 2012. Predicting the potential demographic impact of predators on their prey: a comparative analysis of two carnivore-ungulate systems in Scandinavia. *J. Anim. Ecol.* **81**: 443-454. doi:10.1111/j.1365-2656.2011.01928.x. PMID:22077484.

Griffiths, D. 1980. Foraging costs and relative prey size. *Am. Nat.* **116**: 743-752. doi:10.1086/283666.

Haight, R.G., Mladenoff, D.J., and Wydeven, A.P. 1998. Modeling disjunct gray wolf populations in semi-wild landscapes. *Conserv. Biol.* **12**: 879-888. doi:10.1046/j.1523-1739.1998.97103.x.

Hamlin, K.L., Garrott, R.A., White, P.J., and Cunningham, J.A. 2008. Contrasting wolf-ungulate interactions in the Greater Yellowstone Ecosystem. *Terr. Ecol.* **3**: 541-577. doi:10.1016/S1936-7961(08)00225-X.

Haswell, P.M., Kusak, J., and Hayward, M.W. 2017. Large carnivore impacts are context-dependent. *Food Webs*, **12**(Sept.): 3-13. doi:10.1016/j.fooweb.2016.02.005.

Haulton, S.M., Porter, W.F., and Rudolph, B.A. 2001. Evaluating 4 methods to capture white-tailed deer. *Wildl. Soc. Bull.* **29**: 255-264.

Hebblewhite, M., Pletscher, D.H., and Paquet, P.C. 2002. Elk population dynamics in areas with and without predation by recolonizing wolves in Banff National Park, Alberta. *Can. J. Zool.* **80**(5): 789-799. doi:10.1139/z02-058.

Hebblewhite, M., White, C.A., Nietvelt, C.G., McKenzie, J.A., Hurd, T.E., Fryxell, J.M., Bayley, S.E., and Paquet, P.C. 2005. Human activity mediates a trophic cascade caused by wolves. *Ecology*, **86**: 2135-2144. doi:10.1890/04-1269.

Heisey, D.M., and Patterson, B.R. 2006. A review of methods to estimate cause-specific mortality in presence of competing risks. *J. Wildl. Manage.* **70**: 1544-1555. doi:10.2193/0022-541X(2006)70[1544:AROMTE]2.0.CO;2.

Hosmer, D.W., Jr., Lemeshow, S., and May, S. 2008. Applied survival analysis: regression modeling of time-to-event data. Wiley Publishing, Hoboken, N.J.

Huggard, D.J. 1993. Prey selectivity of wolves in Banff National Park. I. Prey species. *Can. J. Zool.* **71**(1): 130-139. doi:10.1139/z93-019.

- Hurley, M.A., Unsworth, J.W., Zager, P., Hebblewhite, M., Garton, E.O., Montgomery, D.M., Skalski, J.R., and Maycock, C.L. 2011. Demographic response of mule deer to experimental reduction of coyotes and mountain lions in southeastern Idaho. *Wildl. Monogr.* **178**: 1–33. doi:10.1002/wmon.4.
- Jimenez, M.D., and Becker, S.A. 2016. Northern Rocky Mountain Wolf Recovery Program 2015 Interagency Annual Report. U.S. Fish and Wildlife Service, Ecological Services, 585 Shepard Way, Helena, MT 59601, USA.
- Kuijper, D.P.J., Sahlen, E., Elmhagen, B., Chamaille-Jammes, S., Sand, H., Lone, K., and Cromsigt, J.P.G.M. 2016. Paws without claws? Ecological effects of large carnivores in anthropogenic landscapes. *Proc. R. Soc. B Biol. Sci.* **283**: 20161625. doi:10.1098/rspb.2016.1625.
- LaRue, M.A., Nielsen, C.K., Dowling, M., Miller, K., Wilson, B., Shaw, H., and Anderson, C.R. 2012. Cougars are recolonizing the Midwest: analysis of cougar confirmations during 1990–2008. *J. Wildl. Manage.* **76**: 1364–1369. doi:10.1002/jwmg.396.
- Lingle, S. 2002. Coyote predation and habitat segregation of white-tailed deer and mule deer. *Ecology*, **83**: 2037–2048. doi:10.1890/0012-9658(2002)083[2037:CPAHSO]2.0.CO;2.
- Lingle, S., and Pellis, S. 2002. Fight or flight? Antipredator behavior and the escalation of coyote encounters with deer. *Oecologia*, **131**: 154–164. PMID: 28547505.
- Maletzke, B.T., Wielgus, R.B., Pierce, D.J., Martorello, D.A., and Stinson, D.W. 2016. A meta-population model to predict occurrence and recovery of wolves. *J. Wildl. Manage.* **80**: 368–376. doi:10.1002/jwmg.1008.
- Mallory, F.F., Carter, R.A., Fortier, J.L., Kenn, I.S., Weis, L., and White, B.N. 2012. Pumas, *Puma concolor*, in Ontario: additional evidence. *Can. Field-Nat.* **126**: 320–323. doi:10.22621/cfn.v126i4.1377.
- McNay, R.S., and Voller, J.M. 1995. Mortality causes and survival estimates for adult female Columbian black-tailed deer. *J. Wildl. Manage.* **59**: 138–146. doi:10.2307/3809126.
- Mech, L.D., and Peterson, R.O. 2003. Wolf–prey relations. In *Wolves: behavior, ecology, and conservation*. Edited by L.D. Mech and L. Boitani. University of Chicago Press, Chicago, Ill. pp. 131–160.
- Mech, L.D., Dawson, D.K., Peek, J.M., Korb, M., and Rogers, L.L. 1980. Deer distribution in relation to wolf pack territory edges. *J. Wildl. Manage.* **44**: 253–258. doi:10.2307/3808381.
- Mech, L.D., Smith, D.W., Murphy, K.M., and MacNulty, D.R. 2001. Winter severity and wolf predation on a formerly wolf-free elk herd. *J. Wildl. Manage.* **65**: 998–1003. doi:10.2307/3803048.
- Melis, C., Jędrzejewska, B., Apollonio, M., Bartoń, K.A., Jędrzejewski, W., Linnell, J.D.C., Kojola, I., Kusak, J., Adamic, M., Ciuti, S., Delehan, I., et al. 2009. Predation has a greater impact in less productive environments: variation in roe deer, *Capreolus capreolus*, population density across Europe. *Global Ecol. Biogeogr.* **18**: 724–734. doi:10.1111/j.1466-8238.2009.00480.x.
- Messier, F. 1994. Ungulate population models with predation: a case study with the North American moose. *Ecology*, **75**: 478–488. doi:10.2307/1939551.
- Metz, M.C., Smith, D.W., Hebblewhite, M., and Stahler, D.R. 2016. Temporal variation in wolf predation dynamics in the multi-prey system of northern Yellowstone National Park. In *Predator–Prey Dynamics: From Theory to Management conference*, Revelstoke, B.C., 5–7 April 2016. Columbia Mountains Institute of Applied Ecology, Revelstoke, B.C. PeerJ Preprints, **4**: e1963v1. doi:10.7287/peerj.preprints.1963v1.
- Muhly, T.B., Semeniuk, C., Massolo, A., Hickman, L., and Musiani, M. 2011. Human activity helps prey win the predator–prey space race. *PLoS ONE*, **6**: e17050. doi:10.1371/journal.pone.0017050. PMID:21399682.
- Murray, D.L. 2006. On improving telemetry-based survival estimation. *J. Wildl. Manage.* **70**: 1530–1543. doi:10.2193/0022-541X(2006)70[1530:OITSE]2.0.CO;2.
- Murray, D.L., Smith, D.W., Bangs, E.E., Mack, C., Oakleaf, J.K., Fontaine, J., Boyd, D., Jimenez, M., Niemeyer, C., Meier, T.J., Stahler, D., Holyan, J., and Asher, V.J. 2010. Death from anthropogenic causes is partially compensatory in recovering wolf populations. *Biol. Conserv.* **143**: 2514–2524. doi:10.1016/j.biocon.2010.06.018.
- Nelson, M.E., and Mech, L.D. 1986. Mortality of white-tailed deer in northeastern Minnesota. *J. Wildl. Manage.* **50**: 691–698. doi:10.2307/3800983.
- Nelson, M.E., and Mech, L.D. 1991. Wolf predation risk associated with white-tailed deer movements. *Can. J. Zool.* **69**(10): 2696–2699. doi:10.1139/z91-379.
- Nelson, M.P., Vucetich, J.A., Peterson, R.O., and Vucetich, L.M. 2011. The Isle Royale wolf–moose project (1958–present) and the wonder of long-term ecological research. *Endeavour*, **35**: 31–39. doi:10.1016/j.endeavour.2010.09.002. PMID:21310487.
- Newsome, T.M., and Ripple, W.J. 2015. Carnivore coexistence: trophic cascades. *Science*, **347**(6220): 383. doi:10.1126/science.347.6220.383-a. PMID:25613882.
- Newsome, T.M., Boitani, L., Chapron, G., Ciucci, P., Dickman, C.R., Dellinger, J.A., López-Bao, J.V., Peterson, R.O., Shores, C.R., Wirsing, A.J., and Ripple, W.J. 2016. Food habits of the world's grey wolves. *Mamm. Rev.* **46**: 255–269. doi:10.1111/mam.12067.
- Oakleaf, J.K., Murray, D.L., Oakleaf, J.R., Bangs, E.E., Mack, C.M., Smith, D.W., Fontaine, J.A., Jimenez, M.D., Meier, T.J., and Niemeyer, C.C. 2006. Habitat selection by recolonizing wolves in the northern Rocky Mountains of the United States. *J. Wildl. Manage.* **70**: 554–563. doi:10.2193/0022-541X(2006)70[554:HSBRWJ]2.0.CO;2.
- Owen-Smith, N., Mason, D.R., and Ogutu, J.O. 2005. Correlates of survival rates for 10 African ungulate populations: density, rainfall, and predation. *J. Anim. Ecol.* **74**: 774–788. doi:10.1111/j.1365-2656.2005.00974.x.
- Paquet, P.C. 1992. Prey use strategies of sympatric wolves and coyotes in Riding Mountain National Park, Manitoba. *J. Mammal.* **73**: 337–343. doi:10.2307/1382067.
- Pasanen-Mortensen, M., Pyykönen, M., and Elmhagen, B. 2013. Where lynx prevail, foxes will fail — limitation of a mesopredator in Eurasia. *Global Ecol. Biogeogr.* **22**: 868–877. doi:10.1111/geb.12051.
- Pimlott, D.H. 1967. Wolf predation and ungulate populations. *Am. Zool.* **7**: 267–278. doi:10.1093/icb/7.2.267.
- Potvin, F., Jolicoeur, H., and Huot, J. 1988. Wolf diet and prey selectivity during two periods for deer in Quebec: decline versus expansion. *Can. J. Zool.* **66**(6): 1274–1279. doi:10.1139/z88-186.
- Ripple, W.J., and Beschta, R.L. 2008. Trophic cascades involving cougar, mule deer, and black oaks in Yosemite National Park. *Biol. Conserv.* **141**: 1249–1256. doi:10.1016/j.biocon.2008.02.028.
- Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M.P., Schmitz, O.J., et al. 2014. Status and ecological effects of the world's largest carnivores. *Science*, **343**: 1241484. doi:10.1126/science.1241484. PMID:24408439.
- Ripple, W.J., Chapron, G., López-Bao, J.V., Durant, S.M., Macdonald, D.W., Lindsey, P.A., Bennett, E.L., Beschta, R.L., Bruskotter, J.T., Campos-Arceiz, A., Corlett, R.T., et al. 2016. Saving the world's terrestrial megafauna. *Bioscience*, **66**: 807–812. doi:10.1093/biosci/biw092. PMID:28533560.
- Robinson, H.S., Wielgus, R.B., and Gwilliam, J.C. 2002. Cougar predation and population growth of sympatric mule deer and white-tailed deer. *Can. J. Zool.* **80**(3): 556–568. doi:10.1139/z02-025.
- Rogala, J.K., Hebblewhite, M., Whittington, J., White, C.A., Coleshill, J., and Musiani, M. 2011. Human activity differentially redistributes large mammals in the Canadian Rockies national parks. *Ecol. Soc.* **16**: 24. doi:10.5751/ES-04251-160316.
- Seip, D.R. 2001. Wolf predation, wolf control and the management of ungulate populations. In *Wildlife 2001: populations*. Edited by D.R. McCullough and R.H. Barrett. Elsevier Applied Science, London, U.K. pp. 331–340.
- Shannon, G., Cordes, L.S., Hardy, A.R., Angeloni, L.M., and Crooks, K.R. 2014. Behavioral responses associated with a human-mediated predator shelter. *PLoS ONE*, **9**: e94630. doi:10.1371/journal.pone.0094630. PMID:24718624.
- Smith, D.W., Peterson, R.O., and Houston, D.B. 2003. Yellowstone after wolves. *Bioscience*, **53**: 330–340. doi:10.1641/0006-3568(2003)053[0330:YAWJ]2.0.CO;2.
- Spence, G. 2017. Wolf predation on livestock in Washington. Ph.D. thesis, Washington State University, Pullman.
- Terborgh, J., Lopez, L., Nuñez, P., Rao, M., Shahabuddin, G., Orihuela, G., Riveros, M., Ascanio, R., Adler, G.H., Lambert, T.D., and Balbas, L. 2001. Ecological meltdown in predator-free forest fragments. *Science*, **294**: 1923–1926. doi:10.1126/science.1064397. PMID:11729317.
- Therneau, T.M., and Grambsch, P.M. 2000. Modeling survival data: extending the Cox model. Springer-Verlag, New York.
- United States Census Bureau. 2016. TIGER/Line Shapefiles. Available from <https://www.census.gov/cgi-bin/geo/shapefiles/index.php>.
- Vucetich, J.A., and Peterson, R.O. 2004. The influence of top-down, bottom-up and abiotic factors on the moose (*Alces alces*) population of Isle Royale. *Proc. R. Soc. B Biol. Sci.* **271**: 183–189. doi:10.1098/rspb.2003.2589.
- Vucetich, J.A., Smith, D.W., and Stahler, D.R. 2005. Influence of harvest, climate and wolf predation on Yellowstone elk, 1961–2004. *Oikos*, **111**: 259–270. doi:10.1111/j.0030-1299.2005.14180.x.
- Washington Department of Fish and Wildlife. 2014. 2014 Game status and trend report. Wildlife Program, Washington Department of Fish and Wildlife, Olympia.
- White, P.J., and Garrott, R.A. 2005. Northern Yellowstone elk after wolf restoration. *Wildl. Soc. Bull.* **33**: 942–955. doi:10.2193/0091-7648(2005)33[942:NYEAWR]2.0.CO;2.
- Wright, G.J., Peterson, R.O., Smith, D.W., and Lemke, T.O. 2006. Selection of northern Yellowstone elk by gray wolves and hunters. *J. Wildl. Manage.* **70**: 1070–1078. doi:10.2193/0022-541X(2006)70[1070:SONYEB]2.0.CO;2.