

OIKOS

Research

Predator control alters wolf interactions with prey and competitor species over the diel cycle

Sandra Frey, Daniel Tejero, Katherine Baillie-David, A. Cole Burton and Jason T. Fisher

S. Frey (<https://orcid.org/0000-0001-9847-835X>)  (safrey@uvic.ca), K. Baillie-David and J. T. Fisher (<https://orcid.org/0000-0002-9020-6509>), School of Environmental Studies, Univ. of Victoria, Victoria, BC, Canada. – D. Tejero, Univ. de Alcalá de Henares, Alcalá de Henares, Madrid, Spain. – A. C. Burton, Dept of Forest Resources Management, Univ. of British Columbia, Vancouver, BC, Canada.

Oikos

2022: e08821

doi: 10.1111/oik.08821

Subject Editor: James D. Roth

Editor-in-Chief: Dries Bonte

Accepted 16 March 2022

Predator control remains one of the most common strategies for the conservation of threatened prey species. Despite significant and ongoing efforts to reduce predator populations, little is known about the impacts on the behaviour and interactions of target and non-target species following numerical and potentially behavioural suppression of predators. We used camera-trap data collected before and after an intensive wolf control program in northeastern Alberta's boreal forest to evaluate changes in activity patterns and overlap in wolves, competitors and prey. We hypothesized wolves would shift their activity toward increased nocturnality to avoid diurnal control efforts, and thereby cause a behavioural cascade where other species shift activity to maintain temporal segregation from wolves. Wolves shifted activity into the nighttime following predator control, reducing temporal overlap with the other, mostly diurnal, members of the community. Decreases in activity overlap between wolves and other species indicates reduced potential for wolf interactions with ungulate prey and large competitor species. Predator control may therefore not only release species from top to down regulation and competition following numerical suppression of top predators, but also through de-coupling of temporal overlap, with potential effects on species interactions. Understanding the indirect impacts of conservation strategies such as predator control on both target and non-target species provides insight into potential disruptions to top-down regulation and the associated species interactions that shape community structure.

Keywords: activity patterns, camera trap, population management, predator control, species' interactions, wolf cull

Introduction

Predators play a critical role within the ecological community, and their conservation and management are essential components of maintaining ecosystem health and biodiversity (Schmitz 2007, Schmitz et al. 2010). Despite their well-established role in shaping both ecosystem properties and function (Soulé et al. 1988), the wildlife management of reducing populations of predatory species (predator control), continues to



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be a widespread strategy for conserving threatened prey species throughout the world (Boertje et al. 1996, Hayes et al. 2003, Hervieux et al. 2014, Lennox et al. 2018). While many studies have explored distributional changes and numerical release of mid-sized (meso-) carnivore and prey populations following predator control (Polis et al. 1989, Palomares and Caro 1999, Ritchie and Johnson 2009) – often the outcome of behaviour changes – there is less research directly addressing behavioural changes among heterospecifics. Cascading behavioural shifts throughout the ecological community have the potential to impact species interactions and coexistence mechanisms, potentially compromising important processes shaping community structure (Brook et al. 2012). Understanding how predator control may elicit subtle changes to species' ecology and interactions across the larger ecological community is a critical component of assessing conservation strategies aimed at maintaining species diversity and ecosystem function.

Top-down regulation by predators is an important process shaping ecological communities (Sergio et al. 2005, Post et al. 2008). Predator regulation of sub-dominant carnivores and prey species manifests through both direct and indirect processes (Polis et al. 1989). Inter- and intra-guild predation directly suppresses prey and mesocarnivore populations (Fedriani et al. 2000, Wikenros et al. 2014), while predation risks and the 'landscape of fear' may incur behavioural and physiological costs manifesting as reduced survival and fecundity (Sivy et al. 2017, Kohl et al. 2018). In the absence of predators, mesopredator and prey 'release' may manifest in altered species' abundances, space-use and behaviours, with potentially cascading effects throughout the rest of the community (Terborgh et al. 2001, Berger and Conner 2008, Berger et al. 2008, Prugh et al. 2009, Prugh and Arthur 2015).

Sympatric species may mitigate risk from negative interactions by avoiding competitors and predators across space or time. Spatial avoidance can lead to spatial segregation, whereby species avoid habitats or areas regularly accessed by dominant predators (James et al. 2004, Fisher et al. 2014). Alternatively, species can maintain access to shared habitats by avoiding predators over time through temporal niche partitioning (Kronfeld-Schor and Dayan 2003, Bischof et al. 2014, Frey et al. 2017). While temporal niche partitioning has in the past been deemed the least important mechanism by which species segregate (Schoener 1974), more recent evidence has revealed that activity partitioning over the circadian period may provide important mechanisms for species to reduce costly interactions with dominant predators and competitors (Cozzi et al. 2012, Lewis et al. 2015, Frey et al. 2020). Human-driven changes to species' behaviours such as activity times over the diel period may alter how species temporally segregate to reduce competition or mitigate predation risk (Wang et al. 2015, Gaynor et al. 2018, Suraci et al. 2019). Following reduction of an apex or dominant predator, any subsequent changes to that species' diel activity may lead to behavioural changes in diel activity of competing predators species, with indirect and

potentially cascading impacts on the remainder of the ecological community.

Despite the potential for cascading impacts throughout the rest of the community, predator control remains a common strategy to mitigate livestock loss, and one of the most common strategies towards the conservation of threatened prey species (Boertje et al. 1996, Hayes et al. 2003, Hervieux et al. 2014, Lennox et al. 2018). In the northwestern Nearctic, wolf *Canis lupus* populations are reduced to conserve woodland caribou *Rangifer tarandus caribou*. Caribou are one of the most threatened circumboreal large prey species and globally their populations show persistent declines due to anthropogenic climate and landscape change (Vors and Boyce 2009). In the boreal forests of western Canada, woodland caribou populations have suffered substantial reductions, with anthropogenic landscape change the ultimate cause (Boutin et al. 2012, Hebblewhite 2017). Wolf predation is a proximate cause: linear features such as roads and petroleum exploration lines facilitate wolf travel (Dickie et al. 2017) and hence encounter rate (McKenzie et al. 2012) for caribou (DeCesare et al. 2010, Whittington et al. 2011). Moreover, wolf populations have been bolstered by invading white-tailed deer *Odocoileus virginianus* (Latham et al. 2011c), which are sustained by the landscape change stemming from those resource extraction activities (Fisher and Burton 2020, Fisher et al. 2020). Government-mandated control programs were approved as a necessary measure to protect remaining woodland caribou herds (Bridger et al. 2019). These programs have had some positive effects for conserving caribou, with caveats (Hervieux et al. 2014, Serrouya et al. 2019). The cascading effects of wolf control on the predator community has yet to be elucidated.

We hypothesized three behavioural consequences of wolf control. First, we hypothesized that predator control alters target species' (i.e. wolf) activity patterns (hypothesis 1). We predicted that wolves would shift activity into the nighttime following predator control as a direct response to increased persecution risk during daytime. Second, we hypothesized that activity patterns of competing predator and prey species would shift in response to reduced wolf abundance and/or altered wolf activity patterns following predator control (hypothesis 2). We predicted species competing with wolves, and wolves' prey species, would shift activity into the daytime (if not already diurnal) to reduce competition and predation risk. Third, we hypothesized that temporal niche partitioning between wolves and non-target species would differ before and after predator control. We predicted reduced activity overlap between wolves and diurnal species following predator control, indicating a reduced potential for top-down regulation. Our null hypothesis predicted no change in target and non-target species' activity patterns and partitioning following predator control. We tested these hypotheses using images collected by camera-traps before and after wolf control.

Camera traps are extensively used in conservation ecology for examining species populations, distribution patterns and behaviours (O'Connell et al. 2010, Burton et al. 2015,

Caravaggi et al. 2017, Steenweg et al. 2017). Time-stamped camera trap images enable researchers to evaluate species' behaviour over the 24-h period, including diel activity patterns and activity overlap (O'Connell et al. 2010, Frey et al. 2017). These data provide insight into the temporal niche of species and how co-occurring species may partition along this niche axis to reduce competition and avoid antagonistic encounters with competitors and predators (Schoener 1974). Evaluation of species' activity patterns and interactions over the 24-h cycle provides important insights into how human-driven disturbances may impacts species' behaviour and interactions, and the potential impacts to niche partitioning and community structure (Wang et al. 2015, Frey et al. 2020). Investigating changes to predator behaviour and potentially cascading behavioural responses of both prey and competitor species can provide important insight into the sublethal, indirect effects of predator control across the mammal community.

Methods

Study area

We studied activity patterns of the mid- to large-sized mammal community across a 3500 km² landscape in the western Canadian boreal forest of Alberta (Fig. 1). Natural vegetation is predominantly forests of white spruce *Picea glauca* and black spruce *Picea mariana*, aspen *Populus tremuloides*, jack pine *Pinus banksiana*, as well as muskeg. This boreal landscape supports a large diversity of mid-sized and large mammalian species including grey wolf and black bear *Ursus americanus* as top predators, and various mesocarnivore species such as coyote *Canis latrans*, lynx *Lynx canadensis*, fisher *Pekania pennanti*, marten *Martes americana* and other mustelids *Mustela* spp. Prey species include white-tailed deer, moose *Alces alces*, woodland caribou and snowshoe hare *Lepus americanus*. This landscape has been a focal area for multiple studies of the effects of landscape development on mammal communities (Fisher and Burton 2018, 2020, Burgar et al. 2019, Wittische et al. 2021); this research builds on that work.

Since the 1990s forest harvest (Fisher et al. 2005) and oil and gas extraction have spread across this landscape (Cenovus 2021, MEG 2021). Petroleum exploration and extraction features (seismic lines, well-sites, pipelines), roads, off-highway vehicle trails and production processing facilities are widespread (Pickell et al. 2015).

Following drastic population declines in local caribou herds proximately linked to wolf depredation (but ultimately caused by landscape change) (Latham et al. 2011b, Whittington et al. 2011, DeCesare 2012), the government of Alberta implemented an intensive wolf control program in the area, with 92 wolves removed between 2017 and 2020 (30, 9, 20 and 33 in each year, respectively). Removals spanned the entire study area and were conducted via aerial gunning during the daylight hours.

Data analysis and collection

Our camera-trap study adopted a constrained stratified random design intended to distribute efforts among different forest types across the landscape. Using ArcGIS ver. 10.2 Spatial Analyst, we reclassified Alberta Vegetation Index data (Government of Alberta; Supporting information) into four strata based on deciduous or conifer forest cover, and mesic or hydric moisture regimes. Across the 3500 km² study area we imposed a 1 × 1 km² grid and randomly selected candidate cells equally allotted to each stratum. We added a constraint of access and a minimum 2-km distance between cameras to maintain independence among sampling units, as in Fisher and Burton (2018). Within each of the final 62 cells, we deployed one unbaited Reconyx PC900 Hyperfire infrared remote digital camera on an active game trail to maximize probability of detecting a species given presence (Bailey et al. 2007, MacKenzie et al. 2017).

The camera array (n=62) was active before wolf-control between October 2011 and October 2014 and after wolf-control (n=60) at nearly the exact same locations October 2017–October 2020. From each image we recorded camera site, date, time and species present in Timelapse ver. 2.0 (Greenberg et al. 2019). Temporal activity analysis does not account for potential missed detections, as in MacKenzie et al. (2002), and we assumed any missed detections were distributed similarly in time before and after wolf control (i.e. no directional bias).

To reduce temporal autocorrelation from individuals detected multiple times during a single event, we filtered for independent species detection events by applying a minimum elapsed time of 30 min from the previous event of the same species at the same site and day (Bischof et al. 2014, Frey et al. 2020). To account for the considerable seasonal variation in sunset and sunrise times at these latitudes we converted clock-time observations to solar time sensu Nouvellet et al. (2012). To resolve issues of variable daylength across the year, we expressed detection time relative to the length of day, anchoring to a sunrise and sunset time of 6:00 and 18:00, respectively (Vazquez et al. 2019, Frey et al. 2020).

Activity shifts in response to predator control

To test our hypotheses on behavioural shifts in target and non-target species (hypothesis 1 and 2), we compared species' diel activity patterns before and after wolf control. We applied kernel density estimation techniques developed by Ridout and Linkie (2009) to generate species' activity curves over the 24-h cycle. This approach treats the time of detection as a random variable from an underlying continuous distribution (Ridout and Linkie 2009). Using the package overlap (Meredith and Ridout 2014) in R (<www.r-project.org>) we created species' pre-control and post-control activity curves for wolves, competitor species (black bear and mesocarnivores) and prey species (ungulates and hare). To reduce bias from low sample sizes (Lashley et al. 2018), we compared activity patterns and overlap for which we had a

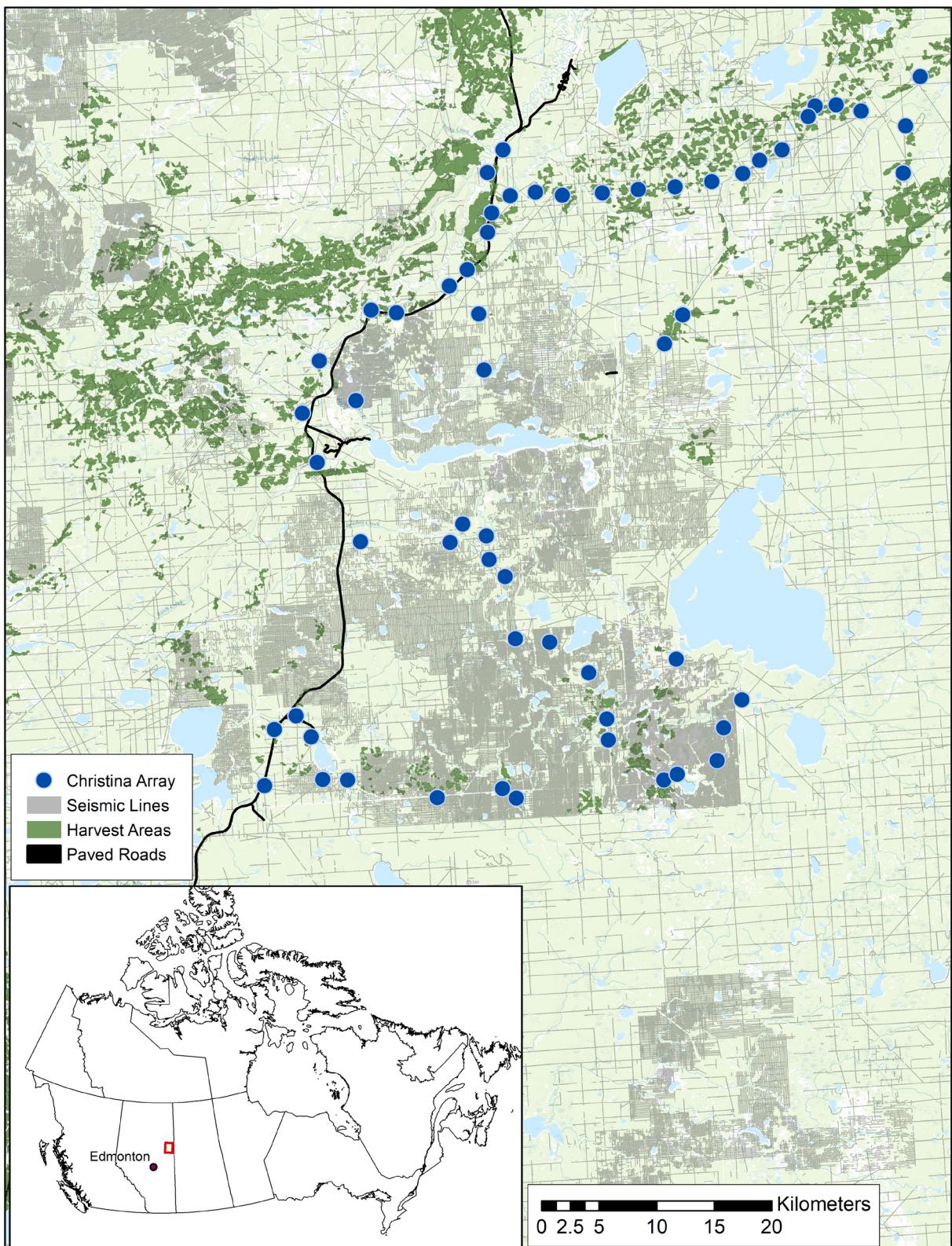


Figure 1. Christina Lake region of the Canadian oil sands region in northeastern Alberta. Camera traps of the Christina Lake array (blue dots) were distributed among landscape features such as seismic lines (grey), roads (black) and timber harvest (dark green).

minimum of 50 independent detections (with the exception of caribou, which are less frequently detected). To determine whether observed changes to activity curves represented statistically significant shifts, we applied the Mardia–Watson–Wheeler (MWW) test for circular data (Batschelet 1981, Zar 1999). This test looks at both the circular mean and circular variance to determine whether two datasets originated from statistically different distributions (Batschelet 1981).

Altered patterns of species' activity partitioning following predator control

We compared wolf activity overlap with prey (moose, woodland caribou, white-tailed deer and snowshoe hare) and competitor species (black bear, coyote and lynx) before and after wolf control to test for changes to wolf-heterospecific activity partitioning and interactions. Ridout and Linkie's (2009) density estimation techniques enable direct evaluation of activity overlap through calculation of an overlap coefficient (Δ). This coefficient is determined by calculating the shared area under two activity curves, with values ranging from 0 (no overlap) to 1 (complete overlap). We applied the Δ_4 estimator if the smaller sample had more than 75 observations and applied a smoothing parameter of 1, otherwise we used the Δ_1 estimator and a 0.8 smoothing parameter recommended for smaller sample sizes (Ridout and Linkie 2009, Meredith and Ridout 2014). We calculated 95% confidence intervals around each overlap index using a smoothed bootstrap with

10 000 resamples (Meredith and Ridout 2014). If confidence intervals around the pre- versus post-control overlap index were non-overlapping, we deemed the change to wolf-heterospecific activity overlap to be statistically significant and indicative of altered wolf-heterospecific activity partitioning following wolf control.

Results

We collected 141 140 images over 62 327 camera trap days during the pre-control sampling period and 270 264 images over 62 270 camera trap days during the post-control period, including multiple detections for wolves, competing predators and prey species (Fig. 2).

Wolf activity shifts in response to predator control

Wolves statistically significantly shifted their activity into the nighttime following predator control (MWW test, $\chi^2 = 30.2$, df = 2, $p < 0.001$), supporting our first hypothesis on behavioural changes in target species. Before predator control, wolves showed highest activity during the daylight hours, with one activity peak after sunrise and a second activity peak at sunset (Fig. 3). Following predator control, wolves shifted activity into the nighttime with a sharp activity peak after sunset and a second activity peak before sunrise (Fig. 3).

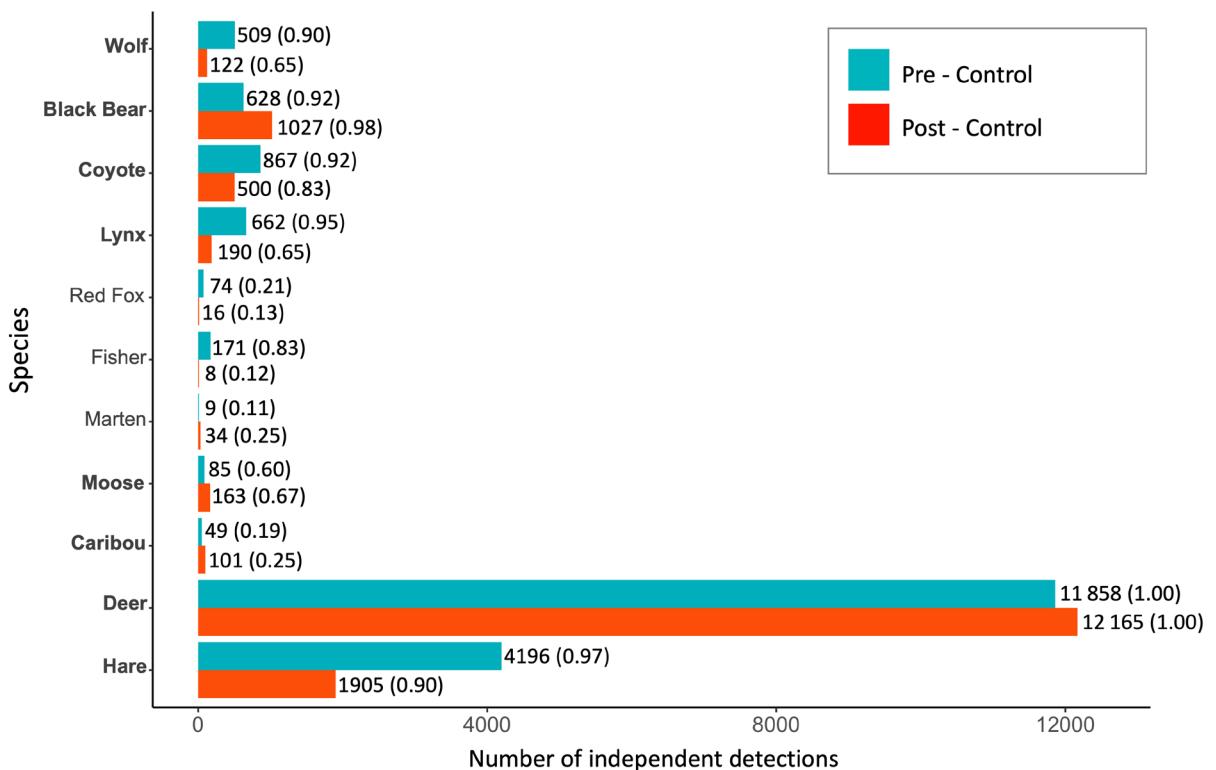


Figure 2. Number of independent detections (and proportion of sites with at least 1 detection in parentheses) for commonly detected mammalian species before (blue) and after (red) wolf-control. Focal species included in activity analyses shown in bold.

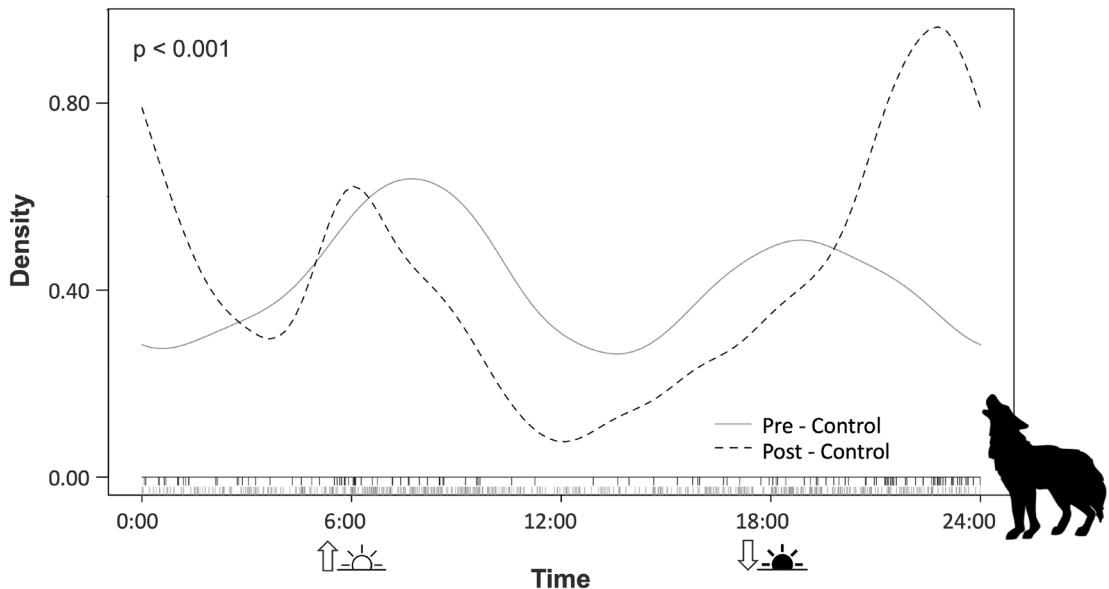


Figure 3. Wolf activity patterns across the 24-h cycle before (solid line) and after (dashed line) wolf – control in the oil sands landscape of Christina Lake, northeastern Alberta. Tick marks on the x-axis represent activity samples for before (bottom) and after (top) wolf-control.

Competitor and prey species' activity shifts following predator control

We observed only minor activity shifts in competing carnivore and prey species after wolf control, with little support for our second hypothesis of behavioural changes in non-target species following predator control. While black bear activity showed a statistically significant difference before and after wolf-control (MWW test, $\chi^2 = 6.8$, df = 2, $p = 0.03$), this did not manifest as any obvious behavioural change (Fig. 4a). Coyote and lynx activity showed no obvious or statistically significant changes to diel activity patterns (Fig. 4b–c).

Prey species likewise did not show marked change in activity patterns over the diel cycle. Moose, caribou and snowshoe hare activity showed no significant shifts between before and after wolf-control (Fig. 4d, e, g). White-tailed deer behaviour shifted statistically significantly after wolf control. However, deer activity curves before and after wolf-control showed a very similar bimodal distribution save for a more pronounced pre-sunset activity peak in the post-control period (Fig. 4f). We suggest that the observed statistical differences may have been the result of a large sample size of deer detections ($n = 11\,858$ and $n = 12\,165$) acting on a small effect size.

Altered patterns of wolf-heterospecific activity partitioning following predator control

Wolf activity shifts into the nighttime following predator control resulted in a marked reduction in wolf–ungulate and wolf–bear activity overlap, as well as increased activity overlap with snowshoe hare (Fig. 5). Species' activity partitioning with wolf changed statistically significantly for black bear, moose, white-tailed deer and snowshoe hare after wolf control (as determined by non-overlapping confidence intervals;

Fig. 6). Increased nocturnality in wolves resulted in an only marginal and non-significant activity overlap decrease with coyote and lynx (Fig. 6).

Wolf–caribou activity overlap decreased substantially after wolf control, but with large confidence intervals (Fig. 6). This does not necessarily indicate non-significance (Schenker and Gentleman 2001), it does signal that low simple size for caribou meant we had low statistical power; with a larger sample size this difference may be more apparent.

Discussion

Predator control changes wolf behaviour and temporal overlap with sympatric species, altering the likelihood of encounter and hence the potential for lethal and nonlethal interactions between wolves, competing predators and prey. Following an extensive wolf control program using daytime aerial gunning, wolves shifted their activity into the night. This decreased temporal activity overlap with diurnal ungulate prey, reducing the potential for top–down regulation of the ungulate community. Likewise, diurnal black bears overlapped less with activity times of wolves after predator control, and hence likely reduced encounter opportunities. Predator control may therefore contribute to the release of prey and competing predator populations not only through the numerical suppression of apex predator populations, but also through de-coupling of wolf–prey activity times and decreased competition with sympatric predators during the day.

Following predator control, surviving wolves became more nocturnal, likely in response to persecution risks during the daytime. Grey wolves have been extensively persecuted across the Northern Hemisphere, and exhibit a consistent

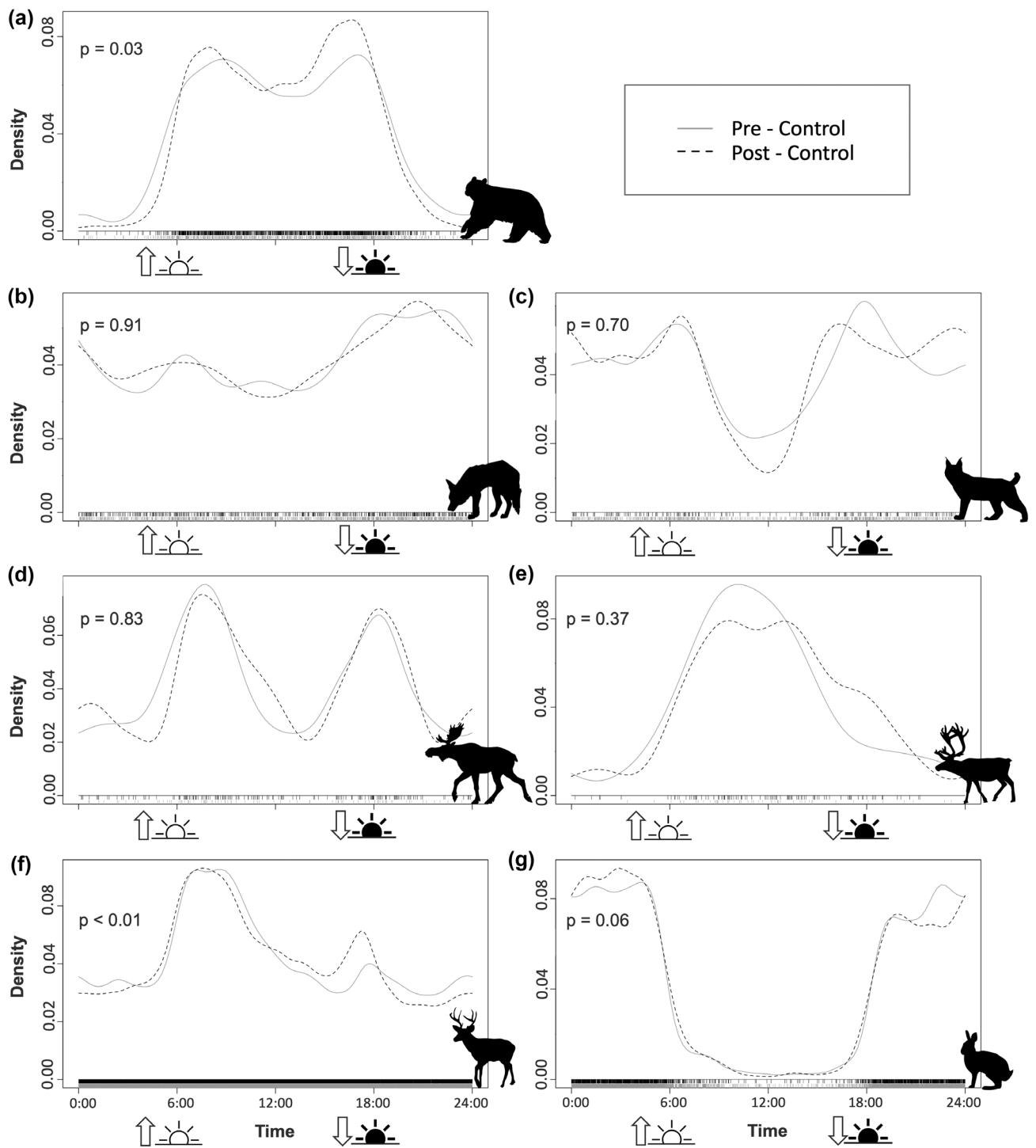


Figure 4. Competitor and prey species' activity patterns across the 24-h cycle before (solid line) and after (dashed line) wolf-control in the oil sands landscape of Christina Lake, northeastern Alberta. Tick marks on the x-axis represent activity samples for each species before (bottom) and after (top) wolf control. Note varying range in y-axis representing kernel density. Represented species include black bear (a), coyote (b) and lynx (c), moose (d), caribou (e), white-tailed deer (f) and snowshoe hare (g).

strategy for human avoidance: adopting nocturnality (Vilà 1995, Ciucci et al. 1997, Merrill and Mech 2003, Wam et al. 2012). Similarly, predator control of Australian dingoes *Canis lupus dingo* pushed that species to nocturnal and early

morning activity, which subsequently led the competing subordinate predator *Felis catus* to alter its diel activity to avoid that time-period (Brook et al. 2012). Similar plasticity in diel activity was observed in European predator communities

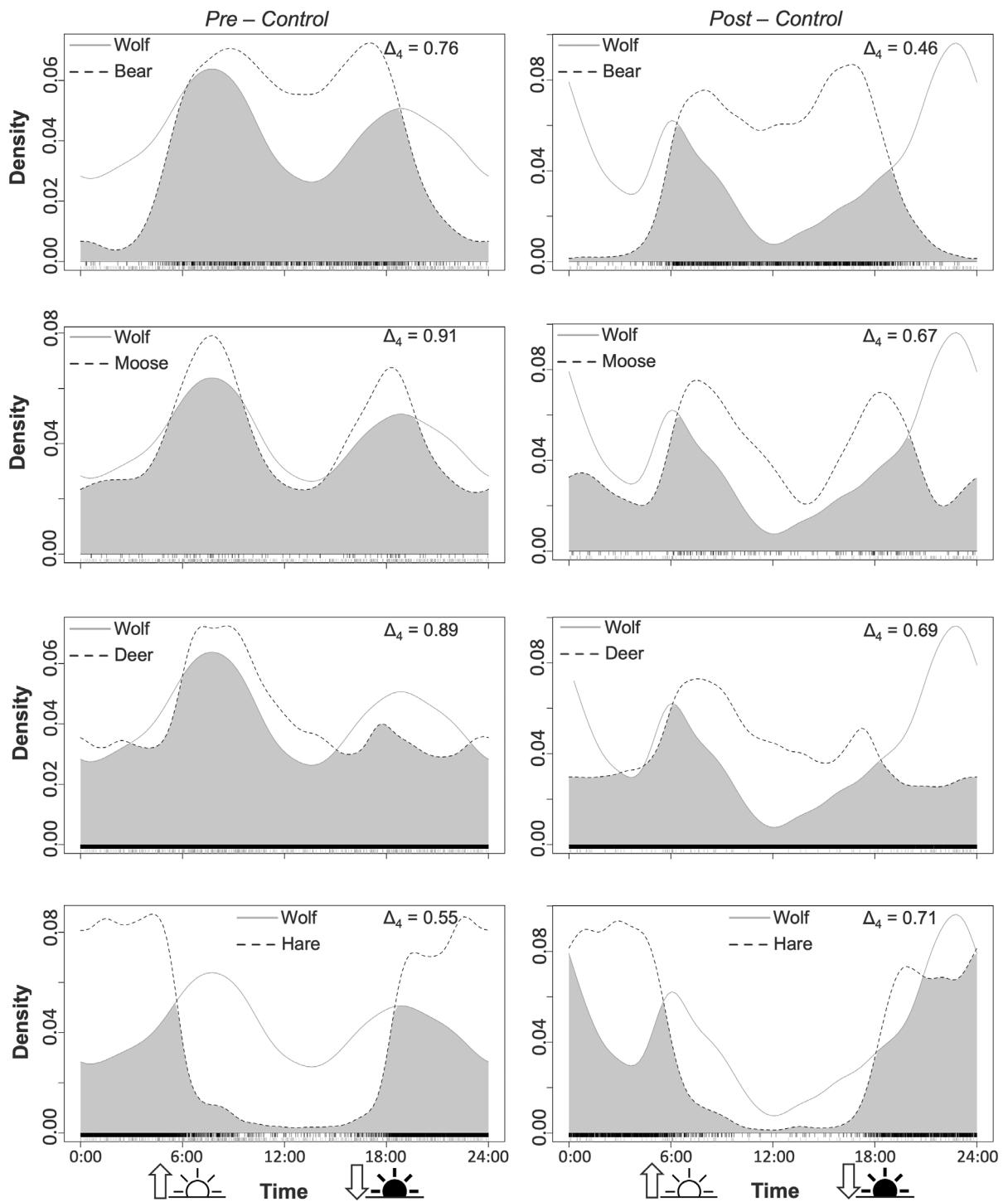


Figure 5. Wolf-heterospecific activity overlap before wolf-control (left panels) and after wolf-control (right panels). Shaded area represents periods of activity overlap between wolf and heterospecifics. Tick marks on the x-axis represent activity samples for wolf (grey ticks, bottom) and non-target species (black ticks, top). Note varying range in y-axis representing kernel density. Represented species include those for which we observed a significant change to wolf-heterospecific activity overlap following predator control.

(Monterroso et al. 2014). In other boreal Nearctic systems, increased daytime activity in coyote was observed in response to greater wolf nocturnality (Shores et al. 2019).

However, contrary to these studies and our hypotheses, boreal subordinate competitors showed no marked shifts

in activity patterns following wolves' shift to nocturnality (Fig. 4). For lynx and coyote, tradeoffs between overlapping with primarily nocturnal prey such as snowshoe hare (Fig. 5) and avoiding wolf during the nighttime may favour maintaining access to an important prey source (Todd et al. 1981,

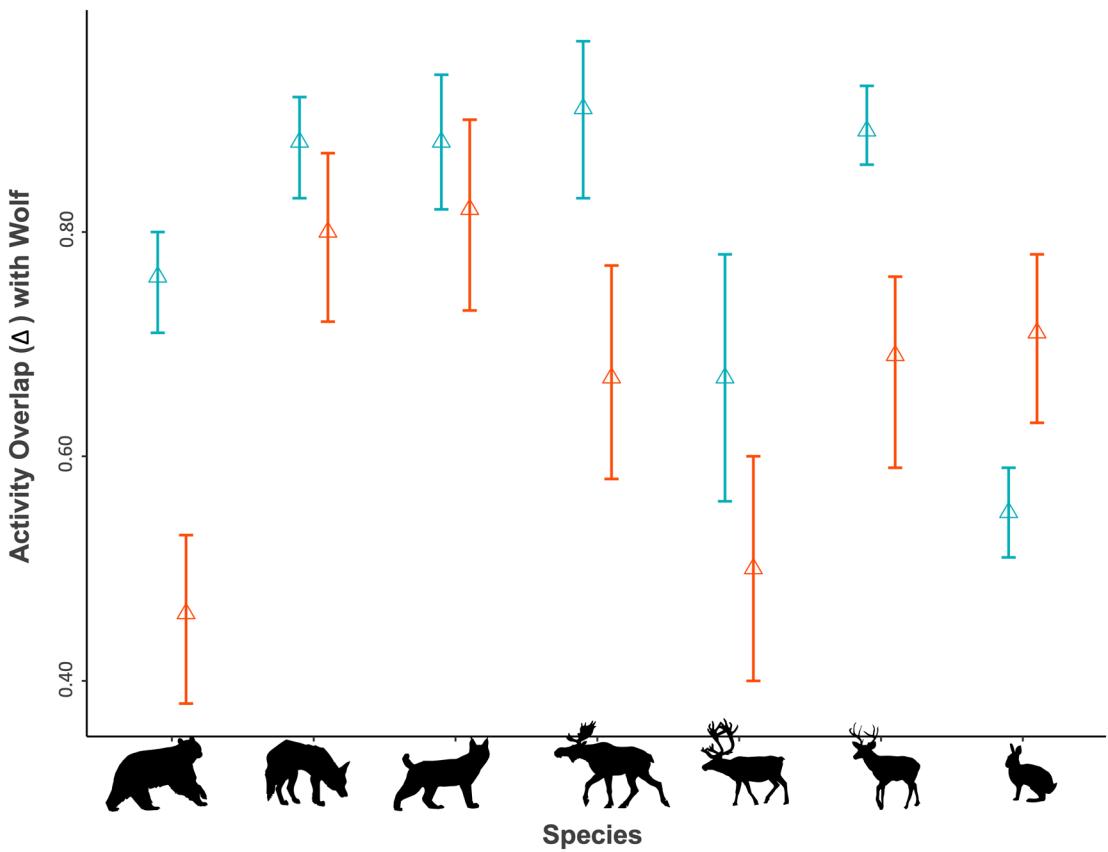


Figure 6. Wolf-heterospecific activity overlap (Δ) before (blue) and after (red) wolf-control. 95% confidence intervals (CIs) were estimated using smoothed bootstrapping with 10 000 re-samples. Non-overlapping CIs indicate a significant change in wolf-heterospecific activity overlap before versus after wolf-control. Species (from left to right): black bear, coyote, lynx, moose, caribou, white-tailed deer and snowshoe hare. Raw values of wolf-heterospecific Δ and 95% CIs available in the Supporting information.

O'Donoghue et al. 1997). However, despite the increase in nighttime wolf activity, we observed no significant increase in wolf–coyote or wolf–lynx activity overlap following wolf control. We contend the behavioural response to predators' shift to nocturnality is likely density-dependent, and mitigated by the numerical suppression of the predator population. In sum, predators are less relevant to mesopredators at low densities.

While mesopredator diel activity appeared unaffected by wolves' shift to nocturnality, opportunities for interference competition (Case and Gilpin 1974) between wolves and black bear were reduced following wolf control. Bear selected daylight hours, with very minor change to their bimodal activity pattern before and after wolf control (Fig. 5). However, the potential for wolf–bear interactions is greatly limited through a significant reduction in activity overlap following increased nocturnality in wolves. Wolf–black bear interactions can be lethal or kleptoparasitic, with wolf packs observed to prey on black bear and driving them off carcasses (Ballard et al. 2003). Bears may therefore experience a release from competition and predation with wolves through both numerical suppression of wolf as well as segregation of their temporal niche space.

Similar to black bears, prey species showed no marked change in diel activity following wolf control. Snowshoe

hares, which can comprise ca 10–30% of a wolf's diet (Urton and Hobson 2005, Gable et al. 2018, O'Donovan et al. 2018) remained nocturnal throughout, with wolf–hare activity overlap increasing markedly following wolves' switch to nocturnality. White-tailed deer and caribou activity remained largely diurnal, while moose remained crepuscular, so increased wolf nocturnality markedly reduced wolf–moose and wolf–deer activity overlap. There was reduction of overlap in wolf–caribou activity with overlapping confidence intervals, as the power to detect differences in overlap decreases steeply when sample size is below 100 (with a concomitant increase in overlap error; Lashley et al. 2018). Caribou are a threatened species with only 49 (pre-control) and 101 (post-control) independent detections. Wolf–caribou activity overlap was therefore likely underestimated in the pre-control period, with caribou potentially experiencing a much larger reduction in temporal niche overlap with wolf than we can detect.

The wolf control program was implemented to mitigate caribou population declines attributed to wolf predation (Hervieux et al. 2014, Serrouya et al. 2019). We observed a five-fold reduction in wolf detection frequency following predator control with a concomitant doubling in caribou detection frequency (Fig. 2). If detection frequency is indeed

correlated to abundance, an increase in caribou numbers may be driven by decreased wolf abundance on the landscape, but may be also supported by the decoupling of wolf–caribou interactions through segregation of their temporal niches. We could not test this hypothesis due to low caribou sample sizes but it is worth more research. We also note that anthropogenic disturbances are also often negatively correlated with wolf presence (Theuerkauf et al. 2003, Whittington et al. 2005, Hebblewhite and Merrill 2008, Musiani et al. 2010), and the interacting effects of intensive disturbance and predator control on wolf distribution merits further research.

We observed unintended consequences of wolf removal. Black bears also prey upon caribou (Latham et al. 2011a, Lewis et al. 2017, Frenette et al. 2020), and became temporally decoupled from the dominant predator; the consequent effect on bear predation rates on caribou merits research. Moreover, white-tailed deer are now also temporally decoupled from wolves. Deer are invasive in this landscape, with range expansions sustained by climate and landscape change (Dawe et al. 2014, Fisher and Burton 2020, Fisher et al. 2020). Invasive deer populations (Fig. 1) bolster wolf populations, contributing to caribou declines (Latham et al. 2011c) through apparent competition (DeCesare et al. 2010). Reduced wolf populations are expected to release predation pressure on white-tailed deer; consequences for the invasive deer population is likewise worth explicit examination. It might be expected that deer populations will increase, providing ample prey for a recovering wolf population post-control.

As wolves are notable prey-switchers (Garrott et al. 2007, Latham et al. 2013) it is possible that reduced numbers rob wolves of their ability to pack-hunt and compete with larger bears and much more numerous coyotes, potentially leading to the shift toward nocturnality to ‘trade down’ to easier prey (snowshoe hare). This intriguing hypothesis is suggested by the increased wolf–hare overlap, and warrants closer examination.

Research into the potential effects of altered wolf temporal overlap with the broader mammalian community may also yield insights into the indirect effects of predator control. Following wolf control, we observed an increase in detection frequencies for prey and predators with reduced wolf activity overlap, and vice versa: moose, white-tailed deer and black bear detections increased, while snowshoe hare detections decreased (Fig. 2). Again assuming detection frequencies correlate to abundance, it is unknown whether hare decreases are due to natural cycling or altered wolf interactions. Investigating interactions between species density and species behaviour would provide valuable insights into the indirect but additive effects of predator control on predator populations, but would require much greater sample sizes and spatial replication, likely across multiple landscapes. Conservation biologists and wildlife managers should implement more coordinated approaches to predator control ‘experiments’, where they are deemed necessary, and should consider not only numerical targets but also potential behavioural shifts that may alter species’ interactions across the broader ecological community.

Conclusions

Lethal predator control changes how wolves – a dominant predator in boreal ecosystems – use the day, which in turn alters opportunities for interactions between surviving wolves and their prey and competing predators. Activity segregation suggests the potential for de-coupling of wolf–prey interactions, releasing ungulates from top to down regulation via both numerical suppression and behavioural changes in wolves. Most predator control programs have had little monitoring of their impacts, leading some to call them a ‘shot in the dark’ (Treves et al. 2016). Our study highlights the importance of researching the behavioural responses of multiple species to predator control, including the potential impacts on interspecific interactions. We conclude that although wolves did exhibit a clear shift from diurnality to nocturnality – and a behavioural shift to avoid daytime mortality seems the most likely explanation (Theuerkauf 2009) – in contrast heterospecifics did not shift their diel activity to avoid wolves, suggesting an insufficient threat to warrant the change.

It is logical to assume the greatest impact of predator control on mammal communities is a numerical response to reduced wolf numbers. However, the behavioural response may not be trivial, and future research might consider parsing apart the relative contributions of the two, to anticipate and plan for unintended consequences of predator control (Brook et al. 2012, Curveira-Santos et al. 2019). If predators are pushed into sharing a temporal niche with the threatened species, this may counter the desired effect of predator control. Here, wolf control reduced activity overlap with threatened woodland caribou, potentially rendering a synergistic reduction of wolf–caribou interactions through numerical and behavioural suppression of wolves. However, if the new temporal segregation releases black bears and coyotes – alternate caribou predators – then gains in caribou population growth may not be seen.

As predator control remains a conservation tool employed worldwide (Reynolds and Tapper 1996, Packer et al. 2009, Treves et al. 2016), ecological research on the consequences of this significant action can reveal much about interspecific interactions, from both a behavioural and population perspective. Research on the direct and indirect effects of predator control is needed to better understand how altered patterns of species interactions shape community structure and species persistence on human-impacted landscapes.

Funding – Funding was provided by the University of Victoria, Mitacs Canada, and InnoTech Alberta.

Author contributions

Daniel Tejero and **Sandra Frey** share first authorship. **Sandra Frey**: Conceptualization (equal); Formal analysis (equal); Writing – original draft (equal); Writing – review and editing (equal). **Daniel Tejero**: Data curation (equal); Formal analysis

(equal); Writing – original draft (equal); Writing – review and editing (equal). **Katherine Baillie-David:** Data curation (lead); Project administration (supporting); Writing – review and editing (supporting). **A. Cole Burton:** Funding acquisition (supporting); Project administration (supporting); Resources (supporting); Writing – review and editing (supporting). **Jason T. Fisher:** Conceptualization (equal); Funding acquisition (lead); Project administration (lead); Resources (equal); Supervision (lead); Writing – review and editing (equal).

Data availability statement

Data are available from the University of Victoria's DataVerse repository: <<https://doi.org/10.5683/SP3/3W6SPK>> (Frey 2022).

Supporting information

The supporting information associated with this article is available from the online version.

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