Received: 22 June 2023 | Accepted: 23 December 2023

DOI: 10.1111/1365-2664.14589

Journal of Applied Ecology

RESEARCH ARTICLE

Humans drive spatial variation in mortality risk for a threatened wolf population in a *Canis* hybrid zone

John F. Benson[1] | Peter J. Mahoney[1] | Tyler J. Wheeldon[2] | Connor A. Thompson[3] | Mariah E. Ward[3] | Ashley A. D. McLaren[2] | Glenn E. Desy[4] | John M. Fryxell[4] | Brent R. Patterson[2,3]

[1]School of Natural Resources, University of Nebraska-Lincoln, Lincoln, Nebraska, USA

[2]Ministry of Natural Resources and Forestry, Wildlife Research and Monitoring Section, Peterborough, Ontario, Canada

[3]Environmental and Life Sciences Graduate Program, Trent University, Peterborough, Ontario, Canada

[4]Department of Integrative Biology, University of Guelph, Guelph, Ontario, Canada

Correspondence
John F. Benson
Email: jbenson22@unl.edu

Funding information
Science and Research Branch of the Ontario Ministry of Natural Resources and Forestry (OMNRF); Ontario Parks; Trent University through D. Murray; World Wildlife Fund Canada; OMNRF-Species at Risk; Wildlife Conservation Society Canada; W. Garfield Weston Foundation; Earthroots; Natural Sciences and Engineering Research Council of Canada Collaborative Research Opportunities Grant and Discovery Grant; National Science Foundation Integrated Research Challenges in Environmental Biology

Handling Editor: Ying-Chi Chan

Abstract

1. Large carnivores often exhibit high survival rates in protected areas, whereas intentional and unintentional human-caused mortality may be greater in adjacent areas. These patterns can result in source-sink dynamics and limit population expansion beyond protected areas.
2. We used telemetry data from 438 canids in 141 packs collected from 2002 to 2020 to evaluate mortality risk for wolves, coyotes, and admixed canids in a 3-species hybrid zone in and adjacent to a large protected area in Ontario, Canada. The hybrid zone is occupied by most of the remaining eastern wolves (*Canis lycaon*), a rare, threatened species that hybridizes with sympatric eastern coyotes (*C. latrans*) and Great Lakes grey wolves (*C. lupus*).
3. Within Algonquin Provincial Park (APP), annual human-caused mortality from harvest and vehicles was low (0.06, 95% CI [0.03, 0.08]), whereas annual human-caused mortality was higher in adjacent areas (0.31, 95% CI [0.25, 0.37]). Smaller protected areas implemented to help protect eastern wolves did not significantly reduce mortality. Eastern wolves survived poorly relative to other canids and dispersing canids survived poorly relative to residents. Mortality risk was greater when canids were closer to roads. Mortality risk was also increased or reduced by the strength of individual-level selection or avoidance of roads relative to their availability, respectively.
4. Our results provide a comprehensive evaluation of factors influencing spatial variation in mortality risk for canids to inform eastern wolf recovery efforts. Additionally, we developed a novel modelling approach for investigating the influence of resource selection on mortality risk, which highlighted that individual-level responses to risk can strongly influence population-level mortality patterns.
5. *Synthesis and applications*. Despite being listed as 'threatened' under the Ontario Endangered Species Act, eastern wolves are still legally trapped and shot outside

---

John F. Benson and Peter J. Mahoney contributed equally to this work.

protected areas in central Ontario. Eastern wolves and dispersing canids survive poorly outside of APP, primarily from human-caused mortality. These results, along with the apparent inadequacy of the smaller protected areas, suggest that expanding the threatened eastern wolf population outside APP is unlikely under current management conditions. Protecting eastern wolves from human-caused mortality is complicated as it would require a harvest ban for all canids, including coyotes.

KEYWORDS
coyote, eastern wolf, grey wolf, human-caused mortality, hybridization, resource selection, source-sink, spatial mortality risk

1 | INTRODUCTION

Vital rates of wild animals can vary dramatically in relation to spatial variation in human disturbance across the landscape (Hansen & DeFries, 2007; Novaro et al., 2005). For instance, wide-ranging large carnivores often exhibit high survival rates in protected areas, whereas human-caused mortality associated with conflict, persecution, and vehicles is higher in adjacent landscapes (Loveridge et al., 2017). These scenarios can result in source-sink dynamics as protected areas provide refuge, but high mortality in the surrounding matrix limits population expansion (Balme et al., 2009; Carroll et al., 2004). Critically, protected areas are rarely large enough to ensure long-term persistence of threatened carnivores meaning that understanding factors limiting survival in adjacent areas is needed to inform sustainable management of human-caused mortality (Carroll & Miquelle, 2006; Woodroffe & Ginsberg, 1998).

Large carnivores require large spaces and exist at low densities, which makes obtaining sample sizes needed for robust inference on mortality patterns challenging (e.g. Hebblewhite & Whittington, 2020). These limitations are exacerbated because detailed studies of mortality for elusive species are expensive and time-intensive, which generally results in short-term studies of limited geographic scope (Krebs et al., 2004; Murray, 2006). A compounding problem is that survival studies are rarely replicated such that the original snapshot of mortality risk in time and space is often not validated or built upon with additional data (Robinson et al., 2015). Importantly, environmental conditions and management policies change over time and may result in different patterns of survival and mortality than those documented during previously published research (Martinez Cano et al., 2016). Thus, managers are often forced to develop conservation strategies without knowing if the best available information is still relevant.

Understanding relationships between resource selection and mortality risk has been a long-standing challenge for ecologists and most approaches come with conceptual and statistical limitations. McLoughlin et al. (2005) pioneered a novel approach using individual-level resource selection coefficients as covariates in known-fate mortality risk models to relate predation mortality to multivariate habitat selection. This approach explicitly links the ecological processes of interest, but involves a 2-step modelling approach where the considerable uncertainty in resource selection coefficients is usually ignored. Others have fit interactions between mortality status and resource variables directly within resource selection functions (e.g. Benson et al., 2015; Dussault et al., 2012). This approach is effective at identifying resource selection strategies associated with mortality or survival, but fails to account for variation in monitoring times in the survival data. DeCesare et al. (2014) developed a novel approach linking population-level, multi-scale resource selection values derived for landscape pixels to location data for animals included in mortality risk models. This technique results in valuable inference at the population-level, but does not explicitly link resource selection behaviour of individual animals to their mortality data. Global Positioning System (GPS) telemetry simultaneously tracks resource selection and mortality risk, such that linking these processes explicitly for individual animals within a single model is possible and appropriate. Matching individual-level strategies with fate is essential for understanding fitness consequences of resource selection and these patterns could be scaled-up within known-fate models to provide population-level inference on behaviorally mediated mortality risk.

Carnivores can persist in landscapes dominated by humans if the prey base is sufficient and human-caused mortality is minimised (e.g. Bleyhl et al., 2021). However, hybridization of rare species complicates conservation and is a threat to several species of carnivores around the world (Allendorf et al., 2001; Wayne & Shaffer, 2016). Indeed, the three-species hybrid zone between eastern wolves (*Canis lycaon*), eastern coyotes (*Canis latrans*), and Great Lakes grey wolves (hereafter, Great Lakes wolves; *Canis lupus*) in central Ontario, Canada presents a daunting challenge for conservation of eastern wolves, which are listed as threatened in Ontario (Benson et al., 2012, 2014; COSSARO, 2016). Eastern wolves are also designated as threatened federally by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC, 2015). Most remaining eastern wolves are within the large protected area of Algonquin Provincial Park (APP) where trapping and shooting of canids is prohibited, coyotes are rare, and hybridization is minimal compared to adjacent areas (Benson et al., 2012). Previous work showed that eastern wolves survive well inside APP but were an estimated 3.5 times more likely to be harvested by trapping or shooting outside APP relative to sympatric coyotes and admixed canids (Benson et al., 2014). For all canids, harvest was the leading cause of death outside APP, dispersing canids survived poorly, and mortality was greater in areas of higher road density (Benson et al., 2014; *n* = 139 radiocollared canids). Combined, these results suggested interactions between human-caused mortality and hybridization limit numerical and geographic expansion of eastern wolves (Benson et al., 2014). However, subsequent research has identified new areas occupied by eastern wolves outside APP and three new areas of harvest protection for canids were implemented in 2016 following their listing as a threatened species in Ontario (Rutledge et al., 2017; Figure 1). Intensive telemetry-based research on canids has continued in this region such that survival and mortality risk should be re-evaluated to inform eastern wolf conservation with the much larger dataset collected across broader spatial and temporal extents now available.

We estimated survival and cause-specific mortality rates, and modelled factors influencing mortality risk for wolves, coyotes, and admixed canids throughout the proposed recovery zone for eastern wolves in central Ontario (Beacon Environmental Limited and Wildlife Consulting, 2018). We used all available telemetry data (*n* = 438 canids in 141 packs) collected from 2002 to 2020 to test multiple hypotheses. First, we hypothesised that humans drive differences in mortality risk of large carnivores across heterogeneous landscapes. To evaluate previous findings with a larger dataset of broader spatial and temporal scope, we predicted that harvest is the leading cause of death outside APP (prediction 1 [P1]), eastern wolves are at greater risk than other canids in harvested portions of the recovery zone (P2), and that non-resident (dispersing) canids are at higher risk than residents (P3; Benson et al., 2014). We also predicted that all canids are at greater risk when in areas of high road density and when they are closer to roads because these features increase access for harvest and result in vehicle collisions (P4). Second, we hypothesised that individual animals mitigate or exacerbate risk with behavioural responses to anthropogenic risk. We predicted that canids that avoid roads are at lower risk, whereas those that select roads are at higher risk (P5), which we evaluated by estimating resource selection directly within known-fate mortality risk models. Third, we hypothesised that only large protected areas reduce mortality risk for large carnivores when persecution is high in adjacent areas, because of the large spaces used by these animals (e.g. Larivière et al., 2000; Woodroffe & Ginsberg, 1998). Specifically, we predicted that mortality risk is reduced in the large protected area of APP, but not in smaller protected areas adjacent to the park

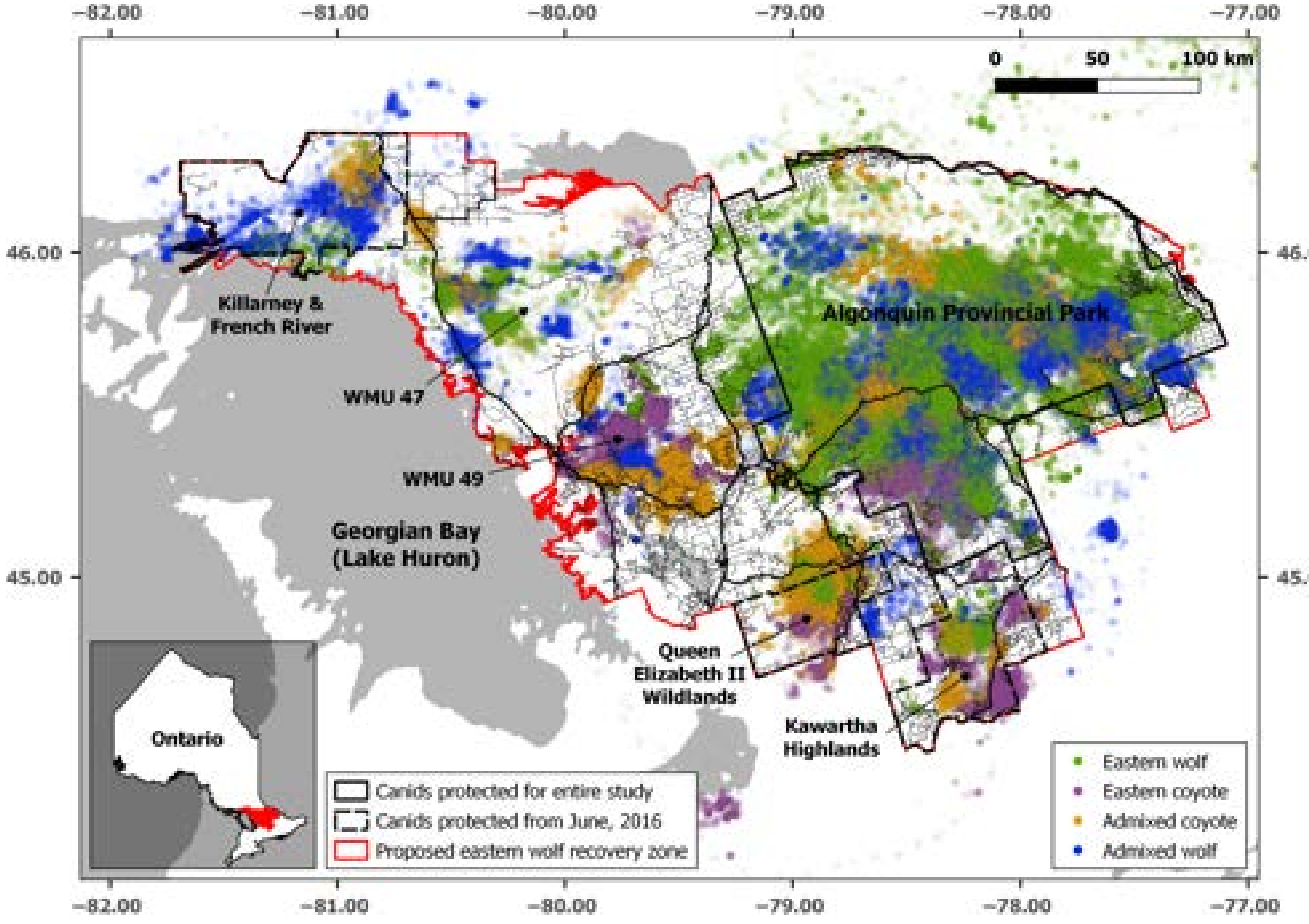


FIGURE 1 Proposed recovery zone for eastern wolves where we studied survival and mortality of canids in central Ontario, 2002–2020. Shown are telemetry locations for eastern wolves and other canids collected across the study area, major roads and boundaries of areas where canids were protected from harvest.

implemented in 2016 (P6). We also evaluated temporal trends in mortality across time, something not possible with the smaller dataset used by Benson et al. (2014). Our work provides a comprehensive evaluation of survival and mortality with all available data to inform eastern wolf conservation efforts in Ontario. More broadly, our work advances understanding of the influence of large protected areas, human-caused mortality, and behavioural responses to risk for large carnivores navigating heterogeneous landscapes.

2 | MATERIALS AND METHODS

2.1 | Study system

We studied survival and mortality of wolves, coyotes, and admixed canids from 2002 to 2020 across the proposed recovery zone for eastern wolves in central Ontario (Figure 1; Beacon Environmental Limited and Wildlife Consulting, 2018). From the beginning of our study (December 2002) to June 2016 canids were fully protected from harvest in the large protected area of APP and surrounding harvest ban area (7780 km^2; Figure 1). In June 2016, full harvest protection was implemented in 3 additional areas that included Kawartha Highlands (2076 km^2), Queen Elizabeth II Wildlands (1260 km^2), and Killarney (2562 km^2) Provincial Parks and surrounding areas (Figure 1). Canid harvest by trapping and shooting was allowed on a seasonal or year-round basis in virtually all other portions of the study area for the duration of the study. Benson et al. (2014) evaluated mortality of canids in portions of our current study area from 2004 to 2011 (APP, WMU49, WMU47 and the Kawartha Highlands; Figure 1; $n=139$ canids from 55 packs). Here, we re-evaluated mortality for canids with those and additional data collected across the entire proposed eastern wolf recovery zone (including Queen Elizabeth II Wildlands and Killarney Provincial Parks; Figure 1; $n=438$ canids from 141 packs; 2002–2020). Eastern wolves are the numerically dominant canid within APP where coyotes are rare and hybridization is minimal compared to adjacent areas (Benson et al., 2012; Rutledge et al., 2010). Outside APP, within the proposed eastern wolf recovery area (Figure 1), eastern wolves are rare and patchily distributed, whereas eastern coyotes and admixed canids are abundant and hybridization is common (Benson et al., 2012; Rutledge et al., 2017).

2.2 | Field methods

We captured canids with padded foothold traps, modified neck snares, or with nets fired from helicopters from 2002–2011 and 2014–2020. We estimated age classes of captured animals as pups, yearlings, and adults with tooth characteristics (Gipson et al., 2000). We deployed very high frequency (VHF; 38%) or GPS (62%) collars equipped with mortality sensors and obtained DNA samples at capture. We captured and handled animals in accordance with protocols approved by Trent University (08039, 24219) and Ontario Ministry of Natural Resources and Forestry (2-75 to 11-75 and 14-75 to 20-75) Animal Care Committees. We only included radiocollared adult and yearling canids in our analyses. We monitored survival at least once per week (VHF) and often daily (GPS) for the duration of the study. We investigated mortalities promptly and evaluated cause of death with field evidence and necropsy by experienced veterinarians when remains were sufficient (details in Appendix S1). We received authorisation to conduct research within the various provincial parks by Ontario Parks. We did not need permission to conduct research on other public lands as our project was carried out by biologists employed by or affiliated with the Ontario government. We received permission from landowners for any research conducted on private land.

2.3 | Genetic analyses

We amplified 12 autosomal microsatellite loci for each sample using markers and laboratory methods described in detail by Benson et al. (2012). We used a Bayesian approach, implemented in the program Structure (v.2.3.4, Pritchard et al., 2000) to estimate genetic ancestry of individuals using microsatellite allele frequencies (details in Appendix S1). We considered canids with ≥80% of their ancestry assigned to eastern wolves, eastern coyotes, or Great Lakes wolves to be highly assigned to that group, whereas we considered canids with <80% of ancestry assigned to any one of the 3 species to be admixed (Benson et al., 2012). We classified admixed canids as either admixed wolves or admixed coyotes depending on whether they had greater wolf (eastern and Great Lakes combined) or coyote ancestry.

2.4 | Survival and cause-specific mortality estimation

We estimated annual survival rates using the nonparametric Kaplan Meier product limit estimator with an annual recurrent timescale (Fieberg & DelGiudice, 2009). We entered canids into the analysis on the day they were radiocollared and removed them upon death (coded 1) or right-censored them if the monitoring ended prior to death (coded 0). We also censored canids due to collar failure, timed release of collars, emigration from the study area (VHF only), or at the end of the study. Canids in the Algonquin region give birth to pups in late April or early May (Benson et al., 2013), so we used a biological year from 1 May–30 April. We censored all living animals with an active collar on the last day of each biological year and re-entered them on the first day the following year. We clustered data from multiple years for the same individuals and estimated robust standard errors (Therneau & Grambsch, 2000). We used the nonparametric cumulative incidence function estimator (CIF) to estimate annual rates of different causes of mortality separately for canids inside and outside APP (Heisey & Patterson, 2006). Human-caused mortality in our study included harvest (trapping and shooting) and vehicle collisions. Natural mortality included intraspecific strife, mange, starvation, and other natural causes. Within APP, we estimated mortality rates from intraspecific strife, mange, starvation, other natural causes, vehicles, harvest, and unknown causes. Outside APP, we estimated mortality rates from harvest, vehicles, all natural mortality pooled (because sample sizes of individual causes were small), and unknown causes.

2.5 | Mortality risk modelling

We investigated factors hypothesised to influence mortality risk with semiparametric Cox proportional hazards regression models with a daily time-step using the annual recurrent model structure described above (Therneau & Grambsch, 2000). We investigated the potential influences of age-class, residency status, protected areas, and eastern wolf ancestry in several model sets with discrete, dummy-coded predictor variables. For spatial variables (protection status and road density), we estimated annual home ranges for packs of resident canids using GPS or VHF location data (≥30 locations) from individuals within the pack using 100% adaptive convex hulls (Getz et al., 2007). Residents were territorial canids in packs, whereas non-residents were solitary animals that were dispersing or otherwise not exhibiting home ranging behaviour (P3). We investigated potential differences in mortality risk between highly assigned eastern wolves (coded 1) and all other canids (coded 0; P3). For data collected prior to June 2016, we coded the protection status for each animal as a binary variable indicating whether they were inside or outside the large protected area of APP. Following June 2016, we considered 3 levels: APP, smaller protected areas, or unprotected (details in Appendix S1). We also included a binary, temporal variable that separated data before and after June 2016 to provide a simple test of whether mortality risk differed for canids following the implementation of the new protected areas (P6). Finally, to evaluate broader temporal trends, we included a continuous variable of year to investigate whether mortality risk increased or decreased from 2002 to 2020.

Previous research showed mortality risk for canids increased in areas with higher secondary road density (Benson et al., 2014). Secondary roads were mostly paved roads classified as local, arterial, or collector roads in the Ontario Road Network spatial layer. Here, we considered the influence of secondary roads on mortality risk in several ways. First, we included the density of secondary roads within seasonal home ranges of the packs of individual resident canids, as in Benson et al. (2014; P4). Additionally, in models using only data from canids tracked with GPS telemetry, we investigated the influence of distance to and selection of roads averaged across each day. The distance variable was simply the mean daily distance of each canid from the nearest secondary road (P4). We also created selection ratios in a use-availability framework to evaluate daily, distance-based selection and avoidance of secondary roads directly within our Cox models (P5). First, we estimated the local availability of roads at each time step with distributions of step-lengths and turning angles specific to each individual along their movement paths using the 'amt' package in R, similar to availability estimated in step-selection functions (Thurfjell et al., 2014). We used these movement distributions to generate 30 available steps from the animal's location at time *t* and paired locations at the end of these available steps with the location used by the animal at time $t+1$. Thus, we created ratios where the numerator was the mean daily distance from the animal to roads (use) and the denominator was the mean distance from all available locations to roads for that animal during the same day (availability). We then took the natural log of the daily selection ratio to rescale values and fit it as a time varying covariate in our Cox models using the following formula:

$$S_t = \ln\left(\frac{\text{used}_t}{\text{avail}_t}\right)$$

S_t = the selection ratio at day *t*, used_t = mean distance from canid telemetry locations to secondary roads at day *t*, and avail_t = mean distance from available locations at day *t*. We predicted that relationships between distance to and selection of roads with mortality risk might be non-linear if risk weakened when animals were farther from roads. Thus, we included second order polynomials for both daily distance and daily selection of secondary roads. We also considered a natural log transformation of daily distance to secondary roads. When no data were collected on a given day for an individual due to missed fixes or collar performance (<7% of data), we used the mean distance from secondary roads over the past 7 days to fill in these missing values.

We conducted our mortality risk modelling in a hierarchical manner with 6 model sets to isolate important factors influencing risk and avoid the complexity of multiple interactions in our models (Table 1). We started with all radiocollared resident and non-resident canids across the recovery zone (model set 1), inside APP (model set 2), and outside APP (model set 3). We also modelled risk for residents-only across the recovery zone (model set 4) given the predicted differences in risk for residents, because it allowed us to estimate road densities within home ranges, and because of the importance of understanding mortality of residents as the breeding animals in canid populations. Finally, we created two model sets restricted to data from GPS-collared canids across the recovery zone (model set 5) and outside APP (model set 6) to investigate mortality risk for canids associated with proximity to roads and selection of roads on a daily basis. The telemetry data (GPS or VHF), areas (APP, outside APP), animals (residents or non-residents), and predictor variables included in each model set are explained in Table 1. We did not include residency status and age-class in the same model sets to avoid redundancy because many yearlings were non-residents. We also kept the binary and continuous temporal variables out of the same models to avoid redundancy. Continuous predictor variables included in our models were not highly correlated. Specifically, we only included a single continuous predictor variable in model sets 1–4 (Table 1), whereas pairs of continuous variables in model sets 5 (all $r < 0.44$) and 6 (all $r < 0.53$) were not strongly correlated. The number of individuals of each canid type in each model set are provided in Table S1.

We centered and scaled all continuous variables by subtracting the mean and dividing by the standard deviation. We compared relative fit of models within each model set with all combinations of variables using Akaike's Information Criterion corrected for small samples (AICc;

TABLE 1 Description of the data (GPS and/or VHF telemetry), areas (entire recovery area, APP, or outside of APP), and animals (all = residents and non-residents), and predictor variables included in each of the six model sets (Set) used to evaluate mortality risk of canids in Ontario, Canada, 2002–2020.

Set	Data	Area	Animals	Predictor variables
1	GPS, VHF	Recovery area	All	APP[a], small protected[b], residency[c], eastern wolf[d], post-2016[e], year[f]
2	GPS, VHF	APP	All	Residency, eastern wolf, year
3	GPS, VHF	Outside APP	All	Small protected, residency, eastern wolf, post-2016, year
4	GPS, VHF	Recovery area	Residents only	APP, small protected, eastern wolf, post-2016, year
5	GPS	Recovery area	All	APP, small protected, residency, eastern wolf, distance to roads[g], selection of roads[h]
6	GPS	Outside APP	All	Small protected, residency, eastern wolf, distance to roads, selection of roads

[a] Algonquin Provincial Park (in APP = 1, outside = 0).

[b] Smaller protected areas where canid harvest was banned outside of APP in 2016 (in small protected area = 1, outside = 0).

[c] Residency status (residents = 1, non-residents = 0).

[d] Canid ancestry (eastern wolves = 1, all other canids = 0).

[e] Data before and after the new protections were implemented outside of APP in 2016 (post-2016 = 1, pre-2016 = 0).

[f] Continuous effect of year (2002–2020).

[g] Mean daily distance of canids to secondary roads.

[h] Daily selection or avoidance of secondary roads by canids.

with n = number of events; Burnham & Anderson, 2002). We considered models to be strongly supported if the difference in AICc from the top model (ΔAICc) < 2 (Burnham & Anderson, 2002). Measures of the proportion of variation explained or overall model performance can be inconsistent and difficult to interpret for Cox proportional hazards models, particularly in the presence of censoring (e.g. Hartman et al., 2023). Instead, we provide ΔAICc values from the null models for each model set to evaluate degree of separation (and thus information gain) from the top model. Models with stronger separation from the top model indicate more substantial information gain from the predictor variables retained (Burnham & Anderson, 2002). We verified the proportional hazards assumption of Cox models by examining the distribution of Schoenfeld residuals with a chi-square test using the cox.zph function in the 'survival' package (Therneau & Grambsch, 2000). We examined parameter estimates for strongly supported models (ΔAICc < 2) and present exponentiated beta coefficients (hazard ratios) with 95% confidence intervals. We considered variables with 95% confidence intervals that did not overlap 1 to have significantly increased or decreased mortality risk. We conducted analyses using the 'survival' and 'AICcmodavg' packages in R version 4.1.2.

3 | RESULTS

3.1 | Mortality risk and annual survival

We identified 220 eastern wolves, 47 eastern coyotes, 9 Great Lakes wolves, 87 admixed coyotes, and 75 admixed wolves in our telemetry dataset (details in Table S1). Across the recovery zone with data from both residents and non-residents, the model with the strongest support retained the influences of APP, residency status, and eastern wolf ancestry (model set 1; n = 438 animals in 141 packs, n = 165 mortalities; Table S2). Mortality risk was lower in APP (hazard ratio = 0.41, 95% CI [0.30, 0.57]) and for residents (hazard ratio = 0.48, 95% CI [0.36, 0.66], estimates from top model; Figure 2). Annual survival was highest for residents in APP ($\hat{s}$ = 0.83, 95% CI [0.80, 0.87]) and lowest for non-residents outside APP ($\hat{s}$ = 0.44, 95% CI [0.35, 0.56]). Annual survival was intermediate and similar for non-residents in APP ($\hat{s}$ = 0.68, 95% CI [0.60, 0.76]) and residents outside APP ($\hat{s}$ = 0.68, 95% CI [0.62, 0.74]).

In APP, the top model retained only residency status and indicated that mortality risk was lower for residents (model set 2; hazard ratio = 0.57, 95% CI [0.35, 0.92], n = 288 animals in 71 packs; Table S3). Outside APP, the top model also retained residency status and indicated that mortality risk was lower for residents (model set 3; hazard ratio = 0.40, 95% CI [0.26, 0.60], n = 237 animals in 101 packs; Table S3). Ancestry-specific survival rates outside APP are shown in Figure 3. With data for residents only across the recovery zone, the top model retained APP and eastern wolf ancestry (model set 4; n = 310 animals in 116 packs, n = 88 mortalities; Table S3). Mortality risk was lower for resident canids in APP (0.44, 95 CI [0.29, 0.69]) and greater for resident eastern wolves (hazard ratio = 1.56, 95% CI [1.01, 2.42], estimates from top model; n = 155 eastern wolves; Figure 2). Hazard ratios and confidence intervals from all plausible competing models (ΔAICc < 2) from model sets 1–4 provided in Tables S5–S7.

3.2 | Influence of proximity to and selection of roads

Across the recovery zone, the model for mortality risk of GPS collared canids with the strongest support retained the influences of APP,

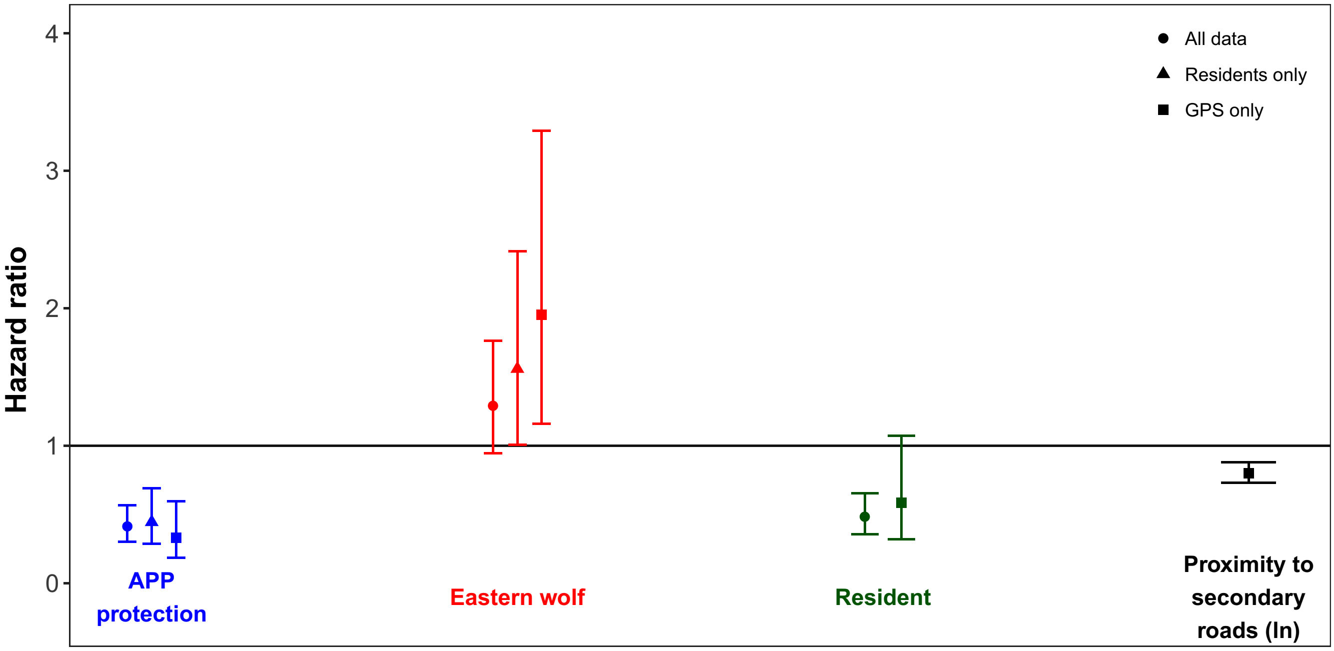


FIGURE 2 Hazard-ratios and 95% confidence intervals for predictor variables retained in models with strongest support for factors influencing instantaneous mortality risk of canids in central Ontario 2002–2020 for models sets with all data, resident canids only and GPS telemetry only.

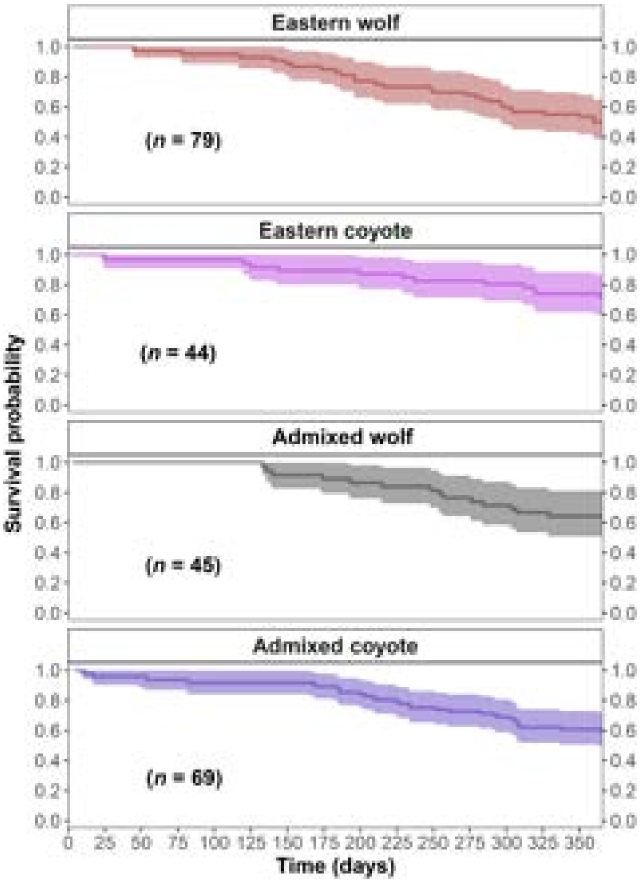


FIGURE 3 Ancestry-specific annual survival probability curves for radio-collared canids tracked outside of the large protected area of Algonquin Provincial Park, Ontario, 2002–2020. We combined Great Lakes wolves (n=7) with admixed wolves due to small sample sizes.

distance to secondary roads (log), eastern wolf ancestry, and residency status (model set 5; n=268 animals, 49 mortalities; Table S4). Mortality risk was lower in APP (hazard ratio=0.33, 95% CI [0.18, 0.60]) and for canids that were farther from secondary roads (log transformed, hazard ratio=0.80, 95% CI [0.73, 0.88], estimates from top model; Figures 2, 4a and 5). Mortality risk was greater for eastern wolves relative to all other canids (hazard=1.95, 95% CI [1.16, 3.29], estimate from top model; n=125 eastern wolves; Figure 2). Outside APP, the model with the strongest support for mortality risk of GPS-collared canids retained eastern wolf ancestry and the second-order polynomial for daily selection of secondary roads (model set 6; n=187, mortalities=35; Table S4). Mortality risk was greater for eastern wolves relative to all other canids (hazard=1.84, 95% CI [1.03, 3.33], estimate from top model; n=69 eastern wolves). Mortality risk was lower for animals that avoided secondary roads and higher for those that selected secondary roads (hazard=0.21, 95% CI [0.11, 0.40], second-order polynomial: hazard=0.81, 95% CI [0.70, 0.94], estimates from top model; Figure 4b). Hazard ratios and confidence intervals for all variables retained in plausible competing models (ΔAICc <2) for model sets 5 and 6 provided in Tables S8 and S9.

3.3 | Cause-specific mortality

In APP, the annual rate of natural mortality (0.13, 95% CI [0.10, 0.16], n=54) was greater than the annual rates of human-caused (0.06, 95% CI [0.03, 0.08], n=22) or unknown mortality (0.02, 95% CI [0.01, 0.03], n=8; Figure 6). Intraspecific strife was the most common known cause of natural mortality in APP (n=19), followed by

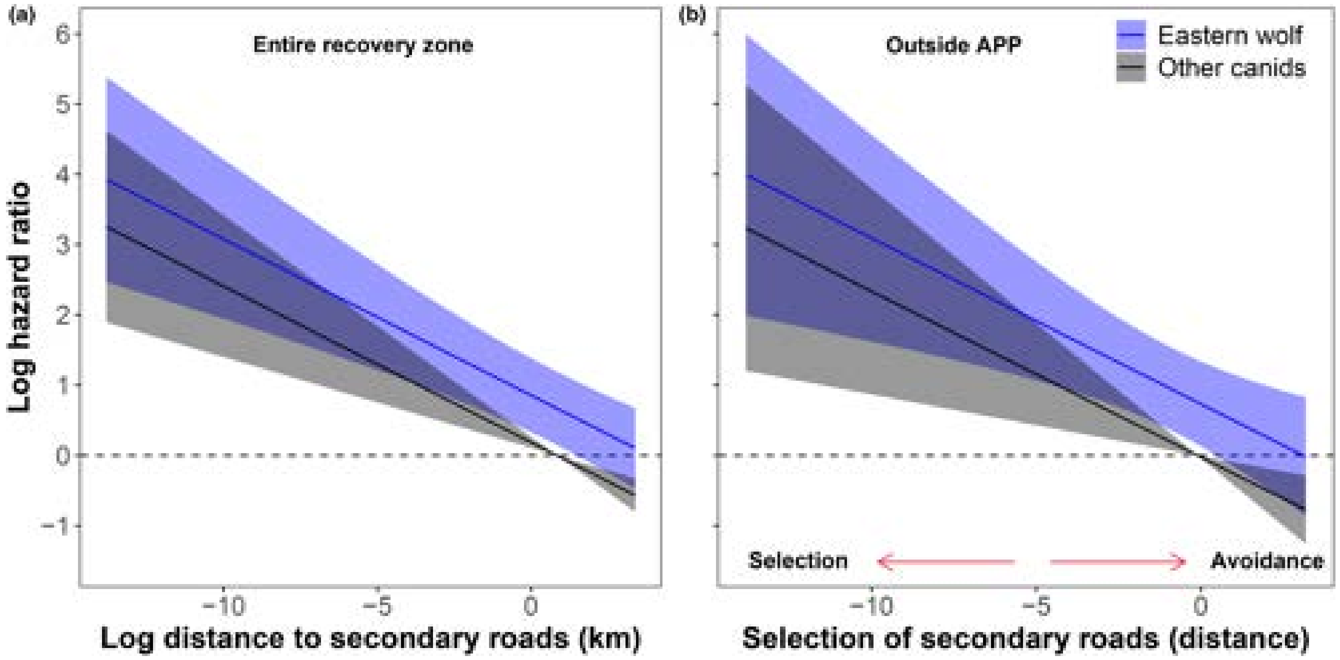


FIGURE 4 Log-transformed hazard ratios for canids relative to (a) distance to secondary roads (log-transformed; across all protected and unprotected areas of proposed eastern wolf recovery zone), and (b) selection of secondary roads (outside of Algonquin Provincial Park) from best mortality risk models with GPS telemetry data only, 2002–2020. We estimated distance-based selection of roads (use/availability) such that lower values indicate selection (canids closer than expected to roads) and higher values indicate avoidance (canids farther than expected from roads).

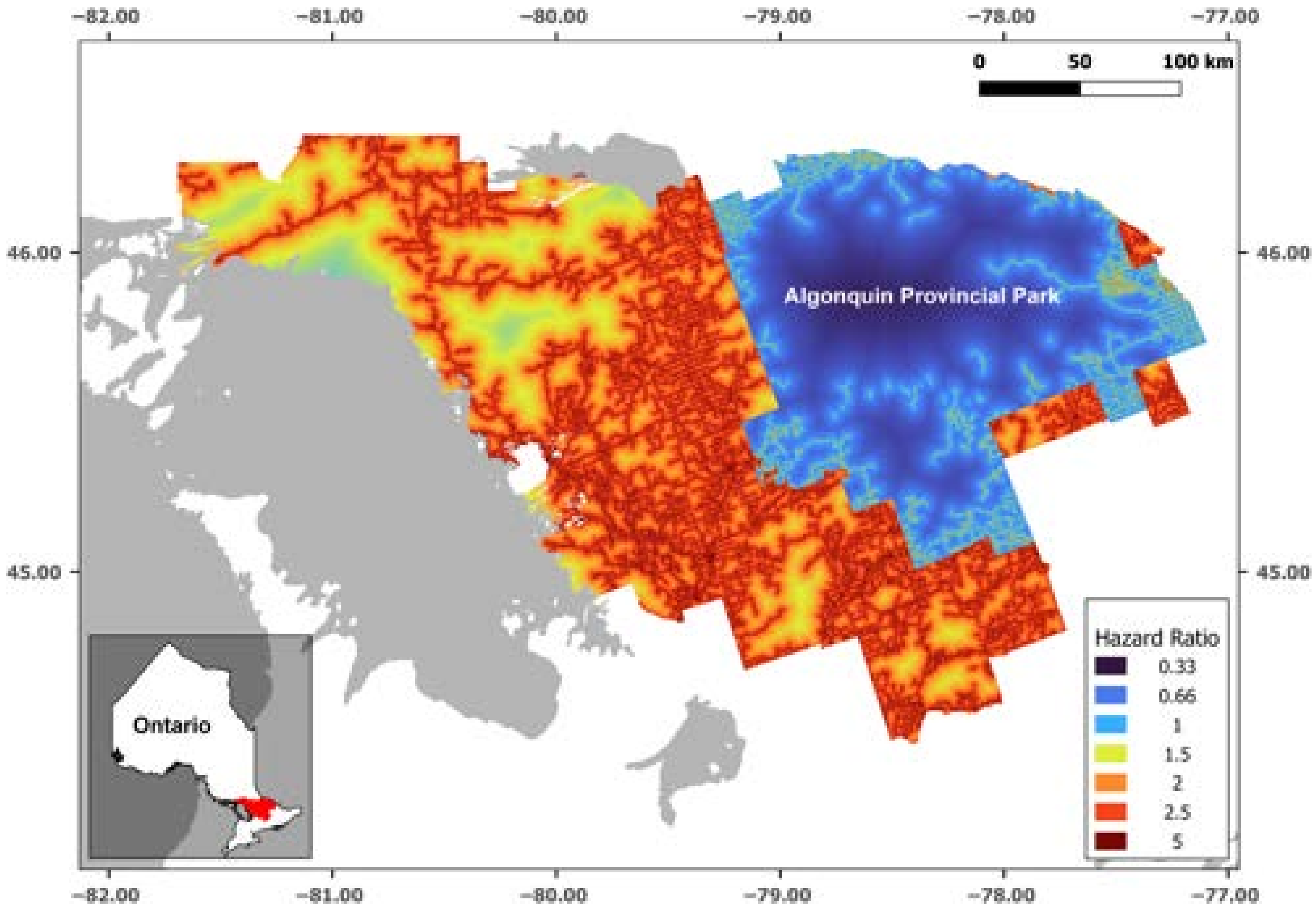
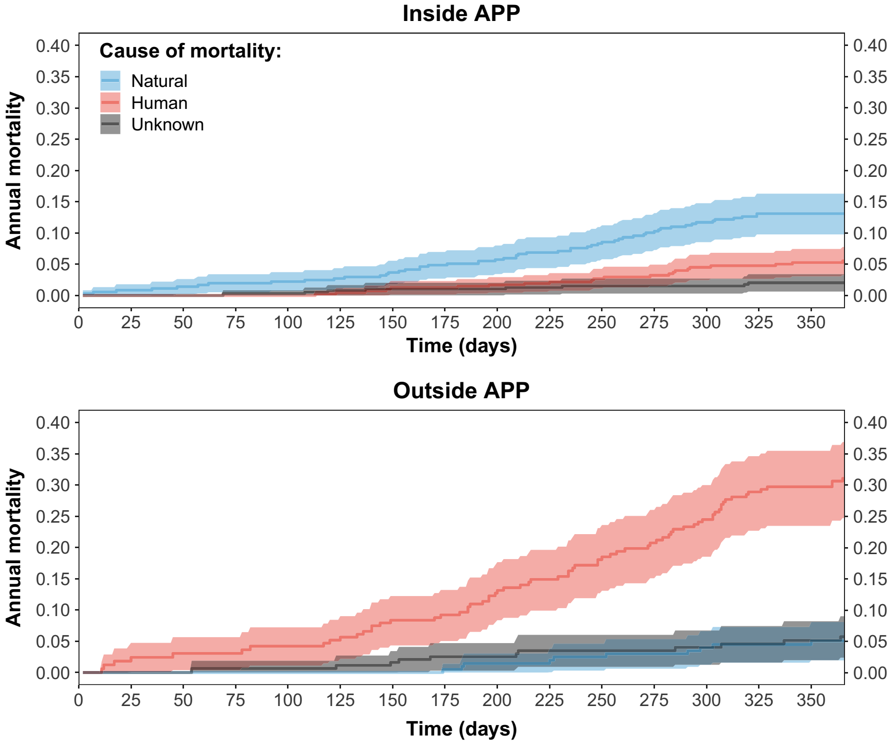


FIGURE 5 Spatial mortality risk map for canids in proposed eastern wolf recovery showing variation in hazard ratio relative to proximity to secondary roads and the large protected area of Algonquin Provincial Park from the best model with GPS telemetry only, 2002–2020.

FIGURE 6 Annual-cause specific mortality curves for radiocollared wolves, coyotes, and admixed canids inside and outside of Algonquin Provincial Park (APP; 2002–2020).



mange ($n=10$), and starvation ($n=8$). Outside APP, annual human-caused mortality (0.31, 95% CI [0.25, 0.37], $n=69$) was greater than natural mortality (0.05, 95% CI [0.02, 0.08], $n=10$) or unknown mortality (0.06, 95% CI [0.02, 0.09], $n=11$; Figure 6). Outside APP, the annual rate of harvest (0.24, 95% CI [0.18, 0.30], $n=51$) was greater than the annual rates of vehicle (0.09, 95% CI [0.05, 0.13], $n=18$), natural (0.05, 95% CI [0.02, 0.08], $n=10$), and unknown (0.06, 95% CI [0.02, 0.09], $n=11$) mortality. The estimated annual rate of human-caused mortality indicated that approximately half of non-residents were killed by harvest or vehicles annually (0.52, 95% CI [0.36, 0.63], $n=28$). The estimated annual rate of human-caused mortality for residents was approximately half of the non-residency rate (0.25, 95% CI [0.18, 0.31], $n=40$).

4 | DISCUSSION

Despite the importance of understanding mortality risk for threatened species, managers are often forced to develop conservation strategies with information from short-term studies characterised by small sample sizes and results that are rarely validated (Hebblewhite & Whittington, 2020; Robinson et al., 2015). Benson et al. (2014) tracked 139 canids from 55 packs during 2004–2011 across portions of the proposed recovery zone for eastern wolves, whereas our current analyses included 438 canids from 141 packs across the entire recovery zone during 2002–2020 (Figure 1). Importantly, we were able to include 220 eastern wolves (including 79 tracked outside APP), compared with 54 eastern wolves (15 outside APP) in Benson et al. (2014). Thus, our work represents an updated, comprehensive evaluation of survival and mortality risk for canids in the Ontario *Canis* hybrid zone to inform conservation of eastern wolves. We confirmed earlier findings by showing that within APP, the population core of eastern wolves, human-caused mortality was relatively low (6% annually) and resident survival was relatively high (83% annually). Outside APP, where proposed recovery efforts are intended to increase eastern wolves numerically and geographically (Beacon Environmental Limited and Wildlife Consulting, 2018), an estimated 24% of canids were shot or trapped annually and vehicular collisions increased the overall estimated annual human-caused mortality rate to 31%. However, we also provide important new information as there was no detectable temporal trend in mortality risk over time from 2002 to 2020 and the smaller protected areas implemented in 2016 did not significantly influence mortality risk. Our results suggest that the proposed recovery goal of eastern wolf expansion outside APP, the only remaining source population for the species, will be challenging under the management conditions present during our study.

Our first hypothesis was supported as humans drove spatial variation in mortality risk for canids. The large protected area of APP strongly reduced risk for canids, whereas we estimated human-caused mortality to be more than 6 times greater than natural mortality outside APP. Harvest by trapping and shooting was the leading source of mortality outside APP and was greater than any other cause of death (supporting P1). Our current results generally validated previous findings of greater mortality risk for eastern wolves relative to sympatric canids outside APP (Benson et al., 2014), although the strength of this finding varied across our analyses (partially supporting P2). A negative influence of eastern wolf ancestry on mortality risk was retained in strongly supported models for all model sets that included data from outside APP, although uncertainty around the influence of eastern wolf ancestry on mortality risk was high in the models that included both GPS and VHF data for residents and non-residents. High mortality of non-residents may have contributed to greater variation in the ancestry-specific comparisons in these models. Regardless, mortality risk was significantly greater for eastern wolves in the residents-only model across the recovery zone, as well as in both models with only GPS data.

It remains unclear why eastern wolf mortality is higher than that of other canids in the hybrid zone, but a plausible explanation is that they are more naïve to risks associated with humans, because most eastern wolves originate from the protected area of APP (Benson et al., 2012, 2014; Rutledge et al., 2010). Higher mortality of resident eastern wolves likely has negative consequences for achieving recovery given that resident canids are the breeding segment of the population and adult survival is the parameter that most strongly influences eastern wolf population growth (Patterson & Murray, 2008). Despite being listed as 'threatened' under the Ontario Endangered Species Act, eastern wolves can still be legally trapped and shot outside APP and the smaller protected areas implemented in 2016. The Ontario ESA specifies that no person shall kill, harm, or take a threatened species. However, the similar size and appearance of eastern wolves, eastern coyotes, Great Lakes wolves, and admixed canids, as well as the indiscriminate nature of trapping, makes it difficult to protect eastern wolves in this region without protecting all sympatric canids. Thus, effective protection for eastern wolves would require banning harvest of coyotes, Great Lakes wolves, and admixed canids, which presents sociopolitical challenges.

We estimated mortality risk to be greater than 2 times higher for non-resident canids relative to residents (supporting P3). For APP to act as an effective source population, eastern wolves must survive and reproduce well within the park and offspring must successfully disperse and breed in areas outside the park. Reduced survival of non-resident, dispersing animals is common for large carnivores, especially when human-caused mortality is high (e.g. Goodrich et al., 2008; Smith et al., 2010). Ecologists and managers often focus mainly on survival of breeding adults and reproduction for wolves and other large carnivores when evaluating viability, given the strong influence of these parameters on population dynamics (e.g. Fuller et al., 2003; Patterson & Murray, 2008). However, when recovery requires geographic expansion of a small source population and relies on effective source-sink dynamics, the importance of survival of younger, dispersing animals is magnified. Indeed, high mortality of dispersing wolves and other large carnivores can negatively impact metapopulation dynamics by preventing successful dispersal from potential source populations into adjacent areas (sinks) that might otherwise compensate for high rates of human-caused mortality (Morales-González et al., 2022; Newby et al., 2013).

There has been a lack of consistency in the investigation of spatial variation in mortality risk for wildlife. Previous researchers have considered risk associated with landscape features at the home range level or at individual animal locations (e.g. Andrén et al., 2022; Benson et al., 2014, 2023), and also whether resource selection influences risk (DeCesare et al., 2014; Dussault et al., 2012; McLoughlin et al., 2005). We are unaware of previous studies quantifying the relative risk associated with risky landscape features themselves (e.g. roads) and behavioural responses of animals to those features (selection and avoidance) in the same models. We found that the mean daily distance of canids to secondary roads significantly increased their mortality risk (supporting P4). Additionally, our second hypothesis was supported as individual-level behavioural responses, in terms of selection or avoidance of secondary roads, appear to exacerbate or mitigate mortality risk (supporting P5). In fact, outside APP where mortality is higher, selection or avoidance of roads influenced risk more strongly than proximity to roads. Roads provide access for trapping and hunting and result in vehicle collisions for wolves (Person & Russell, 2008; Suutarinen & Kojola, 2018). However, roads also provide benefits to canids because they can facilitate easier travel conditions, increase predation success, and are associated with road-killed carcasses and other anthropogenic food (Benson et al., 2017; Hill et al., 2021). Thus, roads and humans present risk–reward trade-offs for large carnivores (e.g. Blecha et al., 2018; Penjor et al., 2022). Our results highlight that variation in individual responses to these trade-offs can mediate population-level mortality patterns in harvested landscapes. Our modelling approach provides straightforward methodology for incorporating resource selection behaviour into mortality risk models and addresses some of the limitations of previous approaches. Specifically, we quantified resource selection and mortality risk in a single model, rather than requiring a resource selection model followed by a mortality risk model (e.g. McLoughlin et al., 2005; Palumbo et al., 2022). Our approach also appropriately links selection behaviour of individual animals directly to mortality of the same individuals, rather than evaluating the influence of population-level resource selection patterns to mortality of individuals (DeCesare et al., 2014).

Our third hypothesis was supported as the large protected area APP strongly influenced mortality risk, whereas the smaller protected areas implemented in 2016 did not (consistent with P6). These smaller protected areas were temporally restricted (June 2016–October 2020) within our larger dataset, resulting in a relatively modest number of canids tracked within them that likely limited statistical power. We tracked 23 resident animals using these areas and 12 (52%) had home ranges that extended beyond the protected area boundaries. All mortality of animals using these areas was human-caused ($n = 6$, four harvested, two hit by vehicles), although three of the four harvested canids were killed illegally. Thus, our current data suggest that these areas were not sufficient to reduce mortality for canids, both due to disregard for the regulations and movement of canids beyond the boundaries of protected areas. Our results are consistent with the limited efficacy of smaller protected areas for large carnivores around the world (Balme et al., 2010; Larivière et al., 2000; Loveridge et al., 2017; Woodroffe & Ginsberg, 1998). Although not feasible because of the difficulty of distinguishing between the different canids, protecting eastern wolves without protecting other canids would be consistent with traditional, 'whole-animal' species conservation. However, protection for all canids, including highly assigned eastern wolves and admixed canids with varying levels of eastern wolf ancestry, could also contribute to conservation of biodiversity at the molecular level and might help to maintain adaptive potential of canids (Seehausen, 2004; Heppenheimer et al., 2018). Ultimately, decisions about protection of canids within the Algonquin region will be considered alongside perceptions regarding abundant coyotes and admixed canids that are viewed as a nuisance or source of conflict by some stakeholders.

Our current work generally confirms previous findings of Benson et al. (2014) with a larger sample of canids monitored over a broader spatial and temporal extent. However, we also provide new information to inform management of canids in Ontario, as well as a provincial and federal conservation strategy for eastern wolves. First, we show that the newer areas of harvest protection implemented following the elevation of eastern wolves to 'threatened' status have not significantly reduced mortality risk for canids in the landscape outside of APP. Second, the larger sample size of our current study had sufficient power to investigate temporal trends and we found no evidence that mortality risk has changed appreciably since 2002. Combined, these results suggest that the current strategy of implementing buffers around small-protected areas occupied by eastern wolves adjacent to APP is insufficient to reduce mortality. Finally, we build on the relatively coarse approach used by Benson et al. (2014) that indicated mortality risk was greater within annual home ranges with higher road densities. Here, we exploited the fine-scale temporal and spatial resolution of GPS telemetry data to show that canids were at greater risk on a daily basis when they were closer to roads. We also found that selection or avoidance of roads by canids influences mortality risk. These results highlight that (a) mortality for canids is likely to be high in areas where trappers and hunters have increased road access, and (b) individual variation in behaviour plays an important role in influencing population-level survival.

Across their range, the distribution, density, and viability of wolves are most strongly influenced by prey availability and human-caused mortality (Bleyhl et al., 2021; Fuller et al., 2003). Hybridization in the Algonquin region further complicates eastern wolf recovery because it interacts with human-caused mortality and appears to limit eastern wolf distribution, density, and population growth outside APP (Benson et al., 2012, 2014). Dispersing eastern wolves face high mortality and those that survive have difficulty finding conspecific mates outside APP given the low density of eastern wolves within a landscape saturated with territorial, hybridizing canids (Benson et al., 2012, 2014; Benson & Patterson, 2013). Interactions between human-caused mortality and hybridization also appear to threaten red wolves (*C. rufus*) in North Carolina, USA that hybridize with coyotes (Hinton et al., 2017). A key difference between the two hybrid zones is the presence of the large protected area (APP), which is almost certainly responsible for the persistence of eastern wolves in central Ontario. APP provides a continuous source of dispersing wolves, but these animals rarely establish to breed with other eastern wolves outside APP given the high rates of human-caused mortality and hybridization. Our work highlights that hybridization further increases the difficulty of achieving endangered species recovery in landscapes shared with humans.

AUTHOR CONTRIBUTIONS

John F. Benson, Peter J. Mahoney and Brent R. Patterson designed the research. John F. Benson, Peter J. Mahoney, Tyler J. Wheeldon, Connor A. Thompson, Mariah E. Ward, Ashley A. D. McLaren, Glenn E. Desy, John M. Fryxell and Brent R. Patterson conducted fieldwork. Peter J. Mahoney (design, coding) and John F. Benson (design, consultation) conducted the analyses. John F. Benson wrote the manuscript. All authors contributed to revising the manuscript.

ACKNOWLEDGEMENTS

Major funding for this research was provided by the Science and Research Branch of the Ontario Ministry of Natural Resources and Forestry (OMNRF). Additional funding was provided by Ontario Parks, Trent University through D. Murray, World Wildlife Fund Canada, OMNRF-Species at Risk, Wildlife Conservation Society Canada, the W. Garfield Weston Foundation, Earthroots, Natural Sciences and Engineering Research Council of Canada Collaborative Research Opportunities Grant and Discovery Grant, and the National Science Foundation Integrated Research Challenges in Environmental Biology Grant 0078130. We thank Ken Mills, Karen Loveless, Andrew Silver, Scott Taylor, Mike Allan and many others for help with fieldwork. We thank Linda Rutledge, Emily Walker, Kaela Beauclerc, Emily Kerr, Jen Dart and Chris Kyle for contributions to genetic lab work.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository: https://doi.org/10.5061/dryad.brv15dvgm (Benson et al., 2024).

ORCID

John F. Benson https://orcid.org/0000-0002-3993-4340
Peter J. Mahoney https://orcid.org/0000-0003-2857-1975
John M. Fryxell https://orcid.org/0000-0002-5278-8747

REFERENCES

Allendorf, F. W., Leary, R. F., Spruell, P., & Wenburg, J. K. (2001). The problems with hybrids: Setting conservation guidelines. *Trends in Ecology & Evolution*, *16*, 613–622.

Andrén, H., Aronsson, M., López-Bao, J. V., Samelius, G., Chapron, G., Rauset, G. R., Hemmingmoore, H., & Persson, J. (2022). Season rather than habitat affects lynx survival and risk of mortality in the human-dominated landscape of southern Sweden. *Wildlife Biology*, *2022*, e01008.

Balme, G. A., Slotow, R., & Hunter, L. T. (2009). Impact of conservation interventions on the dynamics and persistence of a persecuted leopard (*Panthera pardus*) population. *Biological Conservation*, *142*, 2681–2690.

Balme, G. A., Slotow, R., & Hunter, L. T. B. (2010). Edge effects and the impact of non-protected areas in carnivore conservation: Leopards in the Phinda-Mkhuze Complex, South Africa. *Animal Conservation*, *13*, 315–323.

Beacon Environmental Limited and Wildlife Consulting. (2018). DRAFT recovery strategy for the algonquin wolf (*Canis* sp.) in Ontario.

Ontario Recovery Strategy Series. Prepared for the Ontario Ministry of Natural Resources and Forestry. 62 pp.

Benson, J. F., Dougherty, K. D., Beier, P., Boyce, W. M., Cristescu, B., Gammons, D. J., Garcelon, D. K., Higley, J. M., Martins, Q. E., Nisi, A. C., Riley, S. P. D., Sikich, J. A., Stephenson, T. R., Vickers, T. W., Wengert, G. M., Wilmers, C. C., Wittmer, H. U., & Dellinger, J. A. (2023). The ecology of human-caused mortality for a protected large carnivore. *Proceedings of the National Academy of Sciences of the United States of America*, *120*, e2220030120.

Benson, J. F., Loveless, K. M., Rutledge, L. Y., & Patterson, B. R. (2017). Ungulate predation and ecological roles of wolves and coyotes in eastern North America. *Ecological Applications*, *27*, 718–733.

Benson, J. F., Mahoney, P. J., Wheeldon, T. J., Thompson, C. A., Ward, M. E., McLaren, A. A. D., Desy, G. E., Fryxell, J. M., & Patterson, B. R. (2024). Data from: Humans drive spatial variation in mortality risk for a threatened wolf population in a *Canis* hybrid zone. *Dryad Digital Repository* https://doi.org/10.5061/dryad.brv15dvgm

Benson, J. F., Mills, K. J., Loveless, K. M., & Patterson, B. R. (2013). Genetic and environmental influences on pup mortality risk for wolves and coyotes within a *Canis* hybrid zone. *Biological Conservation*, *166*, 133–141.

Benson, J. F., Mills, K. J., & Patterson, B. R. (2015). Resource selection by wolves at dens and rendezvous sites in Algonquin park, Canada. *Biological Conservation*, *182*, 223–232.

Benson, J. F., & Patterson, B. R. (2013). Inter-specific territoriality in a *Canis* hybrid zone: Spatial segregation between wolves, coyotes, and hybrids. *Oecologia*, *173*, 1539–1550.

Benson, J. F., Patterson, B. R., & Mahoney, P. J. (2014). A protected area influences genotype-specific survival and the structure of a *Canis* hybrid zone. *Ecology*, *95*, 254–264.

Benson, J. F., Patterson, B. R., & Wheeldon, T. J. (2012). Spatial genetic and morphologic structure of wolves and coyotes in relation to environmental heterogeneity in a Canis hybrid zone. *Molecular Ecology*, *21*, 5934–5954.

Blecha, K. A., Boone, R. B., & Alldredge, M. W. (2018). Hunger mediates apex predator's risk avoidance response in wildland–urban interface. *Journal of Animal Ecology*, *87*, 609–622.

Bleyhl, B., Ghoddousi, A., Askerov, E., Bocedi, G., Breitenmoser, U., Manvelyan, K., Palmer, S. C. F., Soofi, M., Weinberg, P., Zazanashvili, N., Shmunk, V., Zurell, D., & Kuemmerle, T. (2021). Reducing persecution is more effective for restoring large carnivores than restoring their prey. *Ecological Applications*, *31*, e02338.

Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach* (2nd ed.). Springer-Verlag.

Carroll, C., & Miquelle, D. G. (2006). Spatial viability analysis of Amur tiger *Panthera tigris altaica* in the Russian Far East: The role of protected areas and landscape matrix in population persistence. *Journal of Applied Ecology*, *43*, 1056–1068.

Carroll, C., Noss, R. F., Paquet, P. C., & Schumaker, N. H. (2004). Extinction debt of protected areas in developing landscapes. *Conservation Biology*, *18*, 1110–1120.

COSEWIC. (2015). COSEWIC assessment and status report on the Eastern Wolf *Canis* sp. cf. *lycaon* in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. xii + 67 pp.

COSSARO. (2016). Ontario species a risk evaluation report for Algonquin wolf (Canis sp.), an evolutionarily significant unit and distinct hybrid with *Canis lycaon*, *C. latrans*, and *C. lupus ancestry*. http://cossaroagency.ca/wp-content/uploads/2017/06/Accessible_COSSARO-evaluation-Algonquin-Wolf.pdf

DeCesare, N. J., Hebblewhite, M., Bradley, M., Hervieux, D., Neufeld, L., & Musiani, M. (2014). Linking habitat selection and predation risk to spatial variation in survival. *Journal of Animal Ecology*, *83*, 343–352.

Dussault, C., Pinard, V., Ouellet, J. P., Courtois, R., & Fortin, D. (2012). Avoidance of roads and selection for recent cutovers by threatened caribou: Fitness-rewarding or maladaptive behaviour? *Proceedings of the Royal Society B: Biological Sciences*, *279*, 4481–4488.

Fieberg, J., & DelGiudice, G. D. (2009). What time is it? Choice of time origin and scale in extended proportional hazards models. *Ecology*, *90*, 1687–1697.

Fuller, T. K., Mech, L. D., & Cochrane, J. F. (2003). Wolf population dynamics. In L. D. Mech & L. Boitani (Eds.), *Wolves: Behaviour, ecology, and conservation* (pp. 161–191). University of Chicago Press.

Getz, W. M., Fortmann-Roe, S., Cross, P. C., Lyons, A. J., Ryan, S. J., & Wilmers, C. C. (2007). LoCoH: Nonparameteric kernel methods for constructing home ranges and utilization distributions. *PLoS One*, *2*, e207.

Gipson, P. S., Ballard, W. B., Nowak, R. M., & Mech, L. D. (2000). Accuracy and precision of estimating age of gray wolves by tooth wear. *Journal of Wildlife Management*, *64*, 752–758.

Goodrich, J. M., Kerley, L. L., Smirnov, E. N., Miquelle, D. G., McDonald, L., Quigley, H. B., Hornocker, M. G., & McDonald, T. (2008). Survival rates and causes of mortality of Amur tigers on and near the Sikhote-Alin Biosphere Zapovednik. *Journal of Zoology*, *276*, 323–329.

Hansen, A. J., & DeFries, R. (2007). Ecological mechanisms linking protected areas to surrounding lands. *Ecological Applications*, *17*, 974–988.

Hartman, N., Kim, S., He, K., & Kalbfleisch, J. D. (2023). Pitfalls of the concordance index for survival outcomes. *Statistics in Medicine*, *42*, 2179–2190.

Hebblewhite, M., & Whittington, J. (2020). Wolves without borders: Transboundary survival of wolves in Banff National Park over three decades. *Global Ecology and Conservation*, *24*, e01293.

Heisey, D. M., & Patterson, B. R. (2006). A review of methods to estimate cause-specific mortality in presence of competing risks. *Journal of Wildlife Management*, *70*, 1544–1555.

Heppenheimer, E., Harrigan, R. J., Rutledge, L. Y., Koepfli, K. P., DeCandia, A. L., Brzeski, K. E., Benson, J. F., Wheeldon, T., Patterson, B. R., Kays, R., Hohenlohe, P. A., & Von Holdt, B. M. (2018). Population genomic analysis of North American eastern wolves (*Canis lycaon*) supports their conservation priority status. *Genes*, *9*, 606.

Hill, J. E., DeVault, T. L., & Belant, J. L. (2021). A review of ecological factors promoting road use by mammals. *Mammal Review*, *51*, 214–227.

Hinton, J. W., White, G. C., Rabon, D. R., Jr., & Chamberlain, M. J. (2017). Survival and population size estimates of the red wolf. *The Journal of Wildlife Management*, *81*, 417–428.

Krebs, J., Lofroth, E., Copeland, J., Banci, V., Cooley, D., Golden, H., Magoun, A., Mulders, R., & Shults, B. (2004). Synthesis of survival rates and causes of mortality in North American wolverines. *The Journal of Wildlife Management*, *68*, 493–502.

Larivière, S., Jolicoeur, H., & Crête, M. (2000). Status and conservation of the gray wolf (*Canis lupus*) in wildlife reserves of Québec. *Biological Conservation*, *94*, 143–151.

Loveridge, A. J., Valeix, M., Elliot, N. B., & Macdonald, D. W. (2017). The landscape of anthropogenic mortality: How African lions respond to spatial variation in risk. *Journal of Applied Ecology*, *54*, 815–825.

Martinez Cano, I., Taboada, F. G., Naves, J., Fernández-Gil, A., & Wiegand, T. (2016). Decline and recovery of a large carnivore: Environmental change and long-term trends in an endangered brown bear population. *Proceedings of the Royal Society B: Biological Sciences*, *283*, 20161832.

McLoughlin, P. D., Dunford, J. S., & Boutin, S. (2005). Relating predation mortality to broad-scale habitat selection. *Journal of Animal Ecology*, *74*, 701–707.

Morales-González, A., Fernández-Gil, A., Quevedo, M., & Revilla, E. (2022). Patterns and determinants of dispersal in grey wolves (*Canis lupus*). *Biological Reviews*, *97*, 466–480.

Murray, D. L. (2006). On improving telemetry-based survival estimation. *The Journal of Wildlife Management*, *70*, 1530–1543.

Newby, J. R., Newby, J. R., Mills, L. S., Ruth, T. K., Pletscher, D. H., Mitchell, M. S., Quigley, H. B., Murphy, K. M., & DeSimone, R. (2013). Human-caused mortality influences spatial population dynamics: Pumas in landscapes with varying mortality risks. *Biological Conservation*, *159*, 230–239.

Novaro, A. J., Funes, M. C., & Walker, R. S. (2005). An empirical test of source–sink dynamics induced by hunting. *Journal of Applied Ecology*, *42*, 910–920.

Palumbo, M. D., Petrie, S. A., Schummer, M. L., Rubin, B. D., & Benson, J. F. (2022). Influence of resource selection on nonbreeding season mortality of mallards. *The Journal of Wildlife Management*, *86*, e22292.

Patterson, B. R., & Murray, D. L. (2008). Flawed population viability analysis can result in misleading population assessment: A case study for wolves in Algonquin park, Canada. *Biological Conservation*, *141*, 669–680.

Penjor, U., Astaras, C., Cushman, S. A., Kaszta, Ż., & Macdonald, D. W. (2022). Contrasting effects of human settlement on the interaction among sympatric apex carnivores. *Proceedings of the Royal Society B: Biological Sciences*, *289*, 20212681.

Person, D. K., & Russell, A. L. (2008). Correlates of mortality in an exploited wolf population. *The Journal of Wildlife Management*, *72*, 1540–1549.

Pritchard, J. K., Stephens, M., & Donnelly, P. (2000). Inference of population structure using multilocus genotype data. *Genetics*, *155*, 945–959.

Robinson, H. S., Goodrich, J. M., Miquelle, D. G., Miller, C. S., & Seryodkin, I. V. (2015). Mortality of Amur tigers: The more things change, the more they stay the same. *Integrative Zoology*, *10*, 344–353.

Rutledge, L. Y., Desy, G., Fryxell, J. M., Middel, K., White, B. N., & Patterson, B. R. (2017). Patchy distribution and low effective population size raise concern for an at-risk top predator. *Diversity and Distributions*, *23*, 79–89.

Rutledge, L. Y., Garroway, C. J., Loveless, K. M., & Patterson, B. R. (2010). Genetic differentiation of eastern wolves in Algonquin Park despite bridging gene flow between coyotes and grey wolves. *Heredity*, *105*, 520–531.

Seehausen, O. (2004). Hybridization and adaptive radiation. *Trends in Ecology & Evolution*, *19*, 198–207.

Smith, D. W., Smith, D. W., Bangs, E. E., Oakleaf, J. K., Mack, C., Fontaine, J., Boyd, D., Jimenez, M., Pletscher, D. H., Niemeyer, C. C., Meier, T. J., Stahler, D. R., Holyan, J., Asher, V. J., & Murray, D. L. (2010). Survival of colonizing wolves in the northern Rocky Mountains of the United States, 1982–2004. *The Journal of Wildlife Management*, *74*, 620–634.

Suutarinen, J., & Kojola, I. (2018). One way or another: Predictors of wolf poaching in a legally harvested wolf population. *Animal Conservation*, *21*, 414–422.

Therneau, T. M., & Grambsch, P. M. (2000). *Modeling survival data: Extending the cox model*. Springer Science & Business Media.

Thurfjell, H., Ciuti, S., & Boyce, M. S. (2014). Applications of step-selection functions in ecology and conservation. *Movement Ecology*, *2*, 1–12.

Wayne, R. K., & Shaffer, H. B. (2016). Hybridization and endangered species protection in the molecular era. *Molecular Ecology*, *25*, 2680–2689.

Woodroffe, R., & Ginsberg, J. R. (1998). Edge effects and the extinction of populations inside protected areas. *Science*, *280*, 2126–2128.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Supporting methods.

Table S1. Number of animals tracked from each canid group in each model set used to investigate factors influencing mortality risk in central Ontario, 2002–2020.

Table S2. Model fit for strongly supported Cox proportional hazard models and null models used to investigate mortality risk for canids in central Ontario with all radiocollared resident and non-resident animals included.

Table S3. Model fit for strongly supported Cox proportional hazard models and null models used to investigate mortality risk for canids in central Ontario with only radiocollared residents included.

Table S4. Model fit for strongly supported Cox proportional hazard models and null models of mortality risk relative to proximity to and selection of secondary roads for GPS collared canids in central Ontario, 2002–2020.

Table S5. Parameter estimates for 8 plausible competing models (ΔAICc < 2) for Cox proportional hazards model used to investigate mortality risk for all radiocollared canids across the recovery area inside and outside of Algonquin Provincial Park (model set 1), Ontario, Canada, 2002–2020.

Table S6. Parameter estimates for plausible competing models (ΔAICc < 2) for Cox proportional hazards model used to investigate mortality risk for all radiocollared canids inside (Model Set 2; 3 competing models) and outside (Model Set 3; 3 competing models) Algonquin Provincial Park, Ontario, Canada, 2002–2020.

Table S7. Parameter estimates for 4 plausible competing models (ΔAICc < 2) for Cox proportional hazards model used to investigate mortality risk for resident canids (non-residents excluded) inside and outside of Algonquin Provincial Park (model set 4), Ontario, Canada, 2002–2020.

Table S8. Parameter estimates for 10 plausible competing models (ΔAICc < 2) for Cox proportional hazards model used to investigate mortality risk for GPS-collared canids across the recovery area inside and outside of Algonquin Provincial Park (model set 5), Ontario, Canada, 2002–2020.

Table S9. Parameter estimates for 9 plausible competing models (ΔAICc < 2) for Cox proportional hazards model used to investigate mortality risk for GPS-collared canids outside of Algonquin Provincial Park (model set 6), Ontario, Canada, 2002–2020.

How to cite this article: Benson, J. F., Mahoney, P. J., Wheeldon, T. J., Thompson, C. A., Ward, M. E., McLaren, A. A. D., Desy, G. E., Fryxell, J. M., & Patterson, B. R. (2024). Humans drive spatial variation in mortality risk for a threatened wolf population in a *Canis* hybrid zone. *Journal of Applied Ecology*, *00*, 1–13. https://doi.org/10.1111/1365-2664.14589