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A protected area influences genotype-specific survival and the structure of a *Canis* hybrid zone

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Abstract. It is widely recognized that protected areas can strongly influence ecological systems and that hybridization is an important conservation issue. However, previous studies have not explicitly considered the influence of protected areas on hybridization dynamics. Eastern wolves are a species of special concern and their distribution is largely restricted to a protected population in Algonquin Provincial Park (APP), Ontario, Canada, where they are the numerically dominant canid. We studied intrinsic and extrinsic factors influencing survival and cause-specific mortality of hybrid and parental canids in the three-species hybrid zone between eastern wolves, eastern coyotes, and gray wolves in and adjacent to APP. Mortality risk for eastern wolves in areas adjacent to APP was significantly higher than for other sympatric *Canis* types outside of APP, and for eastern wolves and other canids within APP. Outside of APP, the annual mortality rate of all canids by harvest (24%) was higher than for other causes of death (4–7%). Furthermore, eastern wolves (hazard ratio = 3.5) and nonresidents (transients and dispersing animals, hazard ratio = 2.7) were more likely to die from harvest relative to other *Canis* types and residents, respectively. Thus, eastern wolves dispersing from APP were especially vulnerable to harvest mortality. For residents, eastern wolf survival was more negatively influenced by increased road density than for other *Canis* types, further highlighting the sensitivity of eastern wolves to human disturbance. A cycle of dispersal from APP followed by high rates of mortality and hybridization appears to maintain eastern wolves at low density adjacent to APP, limiting the potential for expansion beyond the protected area. However, high survival and numerical dominance of eastern wolves within APP suggest that protected areas can allow rare hybridizing species to persist even if their demographic performance is compromised and barriers to hybridization are largely absent in the adjacent matrix.

Key words: Algonquin Provincial Park, Ontario, Canada; Canis latrans; Canis lupus; Canis lycaon; competing risks; conservation reserves; eastern coyote; eastern wolf; gray wolf; harvest; hybridization; survival.

INTRODUCTION

The evolutionary and practical implications of interbreeding between species are strongly influenced by the relative fitness of parental and hybrid genotypes within a hybrid zone (Allendorf et al. 2001, Burke and Arnold 2001). An important consideration when studying hybrid zones is to determine whether demographic performance of individuals is driven primarily by endogenous (intrinsic) or exogenous (extrinsic) factors (Barton and Hewitt 1985, Ross and Harrison 2002). Hybrids may exhibit increased fitness due to heterosis or decreased fitness due to genetic mismatches between parental types (Burke and Arnold 2001). Alternatively,

fitness in hybrid zones is often influenced more strongly by environmental conditions that vary over time (Grant and Grant 1992) or space (Moore 1977). Identifying environmental conditions influencing genotype-specific survival and reproduction improves our understanding of hybrid zone structure and can provide critical information for the conservation of rare hybridizing species.

Protected areas have become crucial to the persistence of species that are sensitive to environmental perturbation and human disturbance (Diamond 1975, Soulé and Simberloff 1986). Additionally, studies comparing ecological systems in and adjacent to protected areas facilitate understanding the effects of human disturbance on a range of processes, including population dynamics (e.g., Knight and Eberhardt 1985), animal behavior (e.g., Schtickzelle and Baguette 2003), and community structure (e.g., Shears and Babcock 2002). Hybridization is an important and enigmatic issue impacting conservation, with potentially positive and negative outcomes for the persistence of species (Allen-

dorf et al. 2001, Seehausen 2004). Rates of hybridization are often increased in disturbed areas (Anderson 1948, Lamb and Avise 1986), and hybrids sometimes thrive in habitats that are marginal for parental species (Moore 1977), so it follows that hybridization should be more prevalent outside of protected areas. However, despite recognition of the important practical and theoretical implications of hybridization, and the potentially strong influence of protected areas on the structure and function of ecological systems, we are unaware of studies explicitly considering the role of protected areas in influencing hybridization.

The diverse hybrid zone between eastern wolves (*Canis lycaon*), eastern coyotes (*C. latrans*), and gray wolves (*C. lupus*) in and around Algonquin Provincial Park (APP), Ontario, Canada, allowed us to investigate the influence of a protected area on interspecific hybridization dynamics. Eastern wolves are a "species of special concern" in Ontario under the provincial Species at Risk Act (COSSARO 2004 [Committee on the Status of Species at Risk in Ontario], *available online*).[5] They are also listed as a "species of special concern" by the federal Species at Risk Act (COSEWIC 2001 [Committee on the Status of Endangered Wildlife in Canada], *available online*).[6] Their current distribution appears to be largely restricted to a genetically distinct population within APP, where they are the numerically dominant canid (Rutledge et al. 2010, Benson et al. 2012). Eastern wolves are rarer in areas immediately adjacent to APP, where the hybrid zone comprises a mosaic of eastern wolves, coyotes, gray wolves, and hybrids (Benson et al. 2012). Wolf and coyote ancestry in resident animals was negatively and positively associated, respectively, with road densities outside of APP (Benson et al. 2012). This suggests that wolves are more sensitive to human disturbance than other canids in the APP region, consistent with the widespread elimination of wolves and increase in coyotes across North America in the 20th century that was concurrent with intense human persecution and habitat alteration (Fritts et al. 2003). However, the extent to which spatially varying fitness among *Canis* types influences the genetic structure of the hybrid zone remains unclear.

Accordingly, we modeled and estimated survival and cause-specific mortality of radio-collared wolves, coyotes, and hybrids by combining telemetry, genetic, and environmental data from areas inside and adjacent to a large protected area (APP). Based on the limited and patchy distribution of eastern wolves outside of APP, and their negative association with areas with greater access for trapping and hunting (Benson et al. 2012), we hypothesized that (1) eastern wolves outside of APP survive poorly compared with sympatric *Canis* types adjacent to APP and eastern wolves within APP; (2)
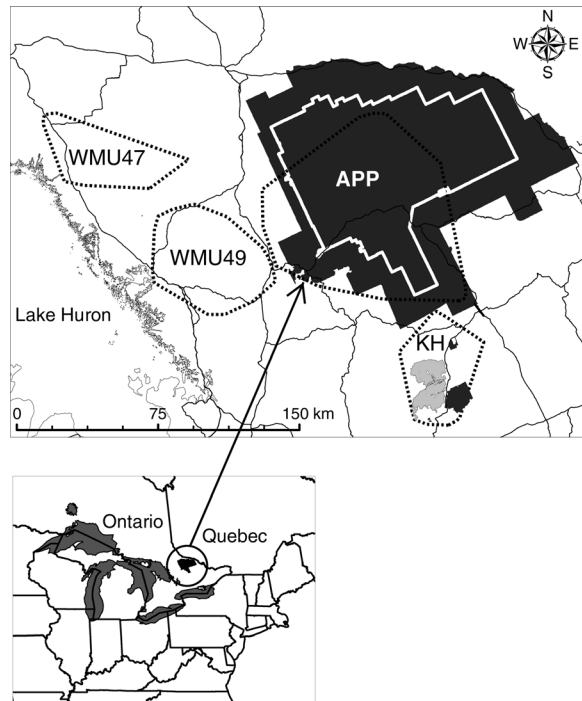
FIG. 1. The four study units (APP, Algonquin Provincial Park; WMU47 and WMU49, Wildlife Management Units 47 and 49; KH, Kawartha Highlands) in central Ontario, Canada, denoted by minimum convex polygons (dotted outlines) created using telemetry data from study animals (*Canis* spp.). Dark gray shading represents areas where wolves and coyotes were protected from harvest, whereas light gray shading indicates that trapping (but no hunting) was allowed. The white outline shows the APP boundary, and black lines represent major roads.

eastern wolves survive poorly relative to other *Canis* types in areas of higher road densities; and (3) eastern wolves are more susceptible to harvest mortality than other *Canis* types outside of APP. The federal conservation status for eastern wolves in Canada is currently (as of 2013) being reviewed and our results inform this process by clarifying whether patchily distributed eastern wolves in unprotected landscapes adjacent to APP can contribute positively to the viability of this genetically distinct wolf population. More broadly, our study elucidates demographic mechanisms by which a large protected area can influence the structure of hybrid zones and dynamics between hybridizing species.

METHODS

Study area

We studied wolves and coyotes from October 2004 to May 2011 in four study units: western Algonquin Provincial Park and the surrounding harvest ban area (APP, 2006–2011, 7780 km²); Wildlife Management Unit 49 (WMU49, 2006–2011; 2720 km²); Kawartha Highlands (KH, 2009–2010, 1810 km²); and Wildlife Management Unit 47 (WMU47, 2004–2007, 1800 km²); see Fig. 1. In Algonquin Park and the surrounding

harvest ban area (park plus ban area = 15 623 km², wolf and coyote harvest was illegal (Fig. 1). Wolf and coyote harvest by trapping and hunting was allowed, on a seasonal or year-round basis, in the three study units adjacent to APP, except in several smaller areas within KH (Fig. 1). However, all study animals that we monitored outside of APP were at risk of harvest as their movements and home ranges extended into unprotected areas. Additional information on the study area can be found elsewhere (Benson et al. 2012, 2013, Benson and Patterson 2013).

Field methods

We captured 147 canids using padded foothold traps or nets fired from helicopters. We estimated age classes of captured animals, using tooth wear (Gipson et al. 2000) and staining, as pups (0–1 year), yearlings (1–2 years), or adults (>2 years old). We deployed mortality-sensitive Global Positioning System (GPS) or Very High Frequency (VHF) radio collars on captured animals (see collar details in Appendix A). We targeted locations within our study units for trapping to capture animals in areas not covered by our active telemetry collars. In the central Ontario hybrid zone, all canid packs are spatially segregated regardless of genetic ancestry (Benson and Patterson 2013). Thus, when we successfully captured and collared resident animals in a given area (1–4 per pack), we relocated our trapping efforts to new areas. With this strategy, we captured individuals from a high proportion of the resident canid packs across our study units, as evidenced by the relatively contiguous arrangement of territories estimated from GPS telemetry data (Appendix B). Although our sample was relatively small from a statistical perspective, it is representative and should allow for biologically meaningful inference. Additionally, we captured nonresident (dispersing or transient animals) opportunistically. All capture and handling of animals was approved by Trent University and Ontario Ministry of Natural Resources Animal Care Committees. We monitored survival and movements of radio-collared animals at least once per week by fixed-wing aircraft. We investigated mortalities and retrieved carcasses promptly (generally within 24 hours of detection). We assigned cause of death using field evidence and/or necropsies by experienced veterinarians and pathologists (Canadian Cooperative Wildlife Heath Center, Guelph, Ontario). We captured most pups during den visits, which were only conducted in APP and WMU49, where canids were mostly eastern wolves and coyotes or hybrids, respectively (Benson et al. 2013). This meant that our sample of pups was genetically stratified between protected and unprotected portions of the study area and was not conducive to testing our current hypotheses regarding survival in relation to genetic ancestry and harvest protection. Thus, we excluded pups from our analyses and focused on adult survival, the most important demographic parameter influencing population growth of eastern wolves (Pat-

terson and Murray 2008). However, all nine radio-collared pups that became yearlings were entered into our models when they reached 1 year of age. We used data from 139 adult and yearling canids.

Ancestry, age, sex, residency, and harvest protection

We used capture, telemetry, and environmental data to create a number of discrete and continuous independent variables (Table 1) for use in regression-based survival and competing risk models. All study animals were eastern wolves, coyotes, coyote × eastern wolf hybrids, or admixed gray wolves, based on genetic analysis of blood samples from captured animals described in detail in Benson et al. (2012). The admixed gray wolf class included gray wolves, gray wolf × eastern wolf hybrids, gray wolf × coyote hybrids, and hybrids admixed between all three *Canis* types, which we combined into a single ancestry category due to small sample sizes. We dummy-coded the ancestry variables with 1 for their assigned genotype and 0 for all other genotypes. We included all four dummy-coded ancestry variables in global models and considered models retaining 0–3 of these variables, such that at least one group was always withheld as the reference category in our regression models (Table 1). This strategy meant that the reference category could change depending on the relative survival of each ancestry group, allowing us to objectively compare survival among groups and explicitly test our hypotheses regarding eastern wolf survival in relation to harvest and human disturbance.

We created dichotomous age (yearlings coded 0, adults coded 1) and sex (females coded 0, males coded 1) variables (Table 1). We created a resident variable by classifying all animals as residents (1) or nonresidents (0). Residents were associated with social groups (packs) and restricted movements to well-defined home ranges, whereas nonresidents were solitary and exhibited transient or dispersing behavior. We created an APP variable by classifying all radio-collared animals that entirely, or primarily, restricted movements to APP and the surrounding harvest ban area as APP (coded 1) and all radio-collared animals outside of APP as non-APP (coded 0; see additional details in Appendix A). Twelve animals dispersed in or out of APP during the study and we reclassified their APP and non-APP variables accordingly. Sample sizes for all categorical variables are provided in Appendix C.

Landscape variables

Moose (*Alces alces*) and deer (*Odocoileus virginianus*) are important prey for canids in and adjacent to APP (Forbes and Theberge 1996). We estimated moose density (number/km²) within home ranges of resident canids, using aerial survey data collected by the Ontario Ministry of Natural Resources. We used a Geographic Information System (GIS) to estimate the proportion of each home range comprising deer wintering habitat as an index of winter deer availability. These variables

TABLE 1. Variables included in analyses with overall data, all data separated by study unit in and adjacent to Algonquin Provincial Park (APP and non-APP), and data from residents only for models of mortality risk of radio-collared adult and yearling wolves, coyotes, and hybrids, 2004–2010.

		Variables included, by model set		
Variables and interaction	Reference group	Overall	APP and non-APP	Residents
Discrete variables				
Residency status	nonresidents	yes	yes	no
APP	non-APP	yes	no	yes
Male	female	yes	yes	yes
Adult	yearling	yes	yes	yes
2010	2004–2009	yes	yes	no
Eastern wolf	varied†	yes	yes	no
Eastern wolf × coyote	varied†	yes	yes	yes
Coyote	varied†	yes	yes	yes
Admixed gray wolf	varied†	yes	yes	yes
Continuous variables				
Moose density	NA	no	no	yes
Deer availability	NA	no	no	yes
2° road density‡	NA	no	no	yes
Interaction				
2° road density × eastern wolf	other genotypes§	no	no	yes

Note: We considered models with all possible combinations of four or fewer variables for both model sets; NA means not applicable.

† The reference group changed depending on which ancestry variables were retained in a given model.

‡ Density of secondary roads.

§ Coyotes, eastern wolf × coyotes, admixed gray wolves.

allowed us to test the hypotheses that moose density and/or deer availability influenced survival of resident canids. We estimated road densities (km/km^2) for each wolf and coyote range by developing a GIS layer for secondary roads to test the hypothesis that the density of these roads across home ranges increased mortality risk for canids. Secondary roads were mostly paved roads that were classified as arterial, collector, or local roads. Secondary roads can influence wolf and coyote survival directly through collisions with vehicles or indirectly by allowing access for harvest and/or through fragmentation (Thiel 1985, Fuller et al. 2003). Additional details regarding prey and road variables are in Appendix A.

Survival models

We modeled survival and investigated factors influencing mortality risk using the Anderson-Gill (AG) extension to Cox proportional hazards (Cox PH) regression modeling (Therneau and Grambsch 2000). We tested the proportional hazards assumption of Cox PH using the formal test recommended by Therneau and Grambsch (2000) and found no significant violations of proportionality in any of the predictor variables included in our survival models (all $P > 0.05$). We used a 365-day (recurrent) time scale to model the baseline hazard (Fieberg and DelGiudice 2009), standardized to a biological year beginning on 1 May (approximate mean birthdate for canids in our study area) and ending on 30 April. Newly captured animals were entered into the models the day following capture and, if still alive, were right-censored on 30 April and entered into the models again on 1 May the following year. We right-censored animals whose radio collars dropped off or failed, or if they dispersed outside of the study area on the last day that we recorded an active signal. We assumed that censoring was independent of fate, and this assumption appeared to be justified (Appendix A). To accommodate state changes for the resident and APP variables, we censored animals on the day prior to detecting the state change and entered them into the model again with their new covariates on the day of detection. All other time-varying covariates (i.e., age class, landscape variables associated with annual home ranges) varied on an annual basis. Preliminary modeling indicated that survival was similar across years of the study, except for 2010, during which we observed higher mortality for radio-collared animals (in terms of raw number of deaths) compared to previous years. We included a dichotomous temporal variable that separated data from 2010 (coded 1) vs. data from earlier years of the study (coded 0) to test and account for this potential temporal variation.

We conducted survival modeling in a hierarchical manner, which allowed us to effectively test our hypotheses. First, we conducted an overall analysis with data from all radio-collared resident and nonresident animals ($n = 139$) to test the hypothesis that mortality risk was greater in areas adjacent to APP compared with the protected area. Next, we modeled non-APP (hereafter non-APP analysis) and APP (hereafter APP analysis) separately to isolate potentially different factors influencing mortality risk within the two areas.

This approach eliminated the confounding issue of different harvest regulations and their potentially strong influence on survival. Conducting only a single overall analysis would have necessitated multiple interactions between APP and variables of interest, which would have greatly increased the chance of over-fitting models. Finally, we conducted an analysis restricted to resident animals in packs for which we had sufficient GPS telemetry data to estimate home ranges and associated prey availability and road density ($n = 87$). We could not include the environmental variables in the overall, non-APP, and APP analyses because we did not have suitable telemetry data to reliably estimate environmental conditions associated with space use of nonresidents. In the global model set for residents, we included an interaction between eastern wolf and secondary road density to test the hypothesis that eastern wolf survival was more negatively influenced by human disturbance than other *Canis* types (Table 1).

For all global model sets, we considered models with all possible combinations of 0–4 variables relevant to our hypotheses (Table 1). We did not consider individual models with more than four variables to avoid over-fitting models. We ranked models using Akaike's information criteria corrected for small samples (AIC_c; Burnham and Anderson 2002), with the number of mortalities as the sample size in our calculation of AIC_c (Therneau and Grambsch 2000). Using number of mortalities as the sample size (rather than number of animals or number of records) was conservative and further emphasized parsimony in our model selection process. We considered models with $\Delta AIC_c < 2$ to have strong empirical support (Burnham and Anderson 2002). We assessed significance of variables retained in supported models with robust z tests, hazard ratios (hazard; exponentiated β coefficients), and 95% confidence intervals for hazard ratios (shown in brackets after each hazard ratio; Therneau and Grambsch 2000). For categorical variables, the hazard ratio provides an estimate of the ratio of the instantaneous risk of mortality relative to the reference group. For continuous variables, we report the hazard ratios corresponding to a 0.1 unit change in the covariate. We selected increments of 0.1 to provide hazard ratios that were easily interpreted biologically, because differences of this magnitude in the estimates of prey availability and road density were common among individuals in our data set. We estimated robust ("sandwich") standard errors for parameter estimates based on data clustered by individual (for the overall analysis) or pack (for resident analysis; Therneau and Grambsch 2000). To assess the relative importance of individual variables based on the model selection results, we summed Akaike model weights across all models retaining a given variable, following Burnham and Anderson (2002). We calculated these variable weights for all model sets for which we identified factors that influenced survival during model selection. Finally, we

also derived annual survival rates by harvest protection (APP and non-APP) and genetic ancestry categories using the Kaplan-Meier product limit estimator generalized for staggered entry. These survival rates were equivalent to null Cox PH models with data separated into categories (Therneau and Grambsch 2000). We provide these estimates as intuitive measures of annual survival, but restrict inferences to our models of instantaneous mortality risk with strong empirical support, which are more powerful and appropriate for assessing the influence of multiple covariates on survival (Therneau and Grambsch 2000).

Cause-specific mortality

To model the relative importance of different mortality agents affecting wolves and coyotes, we estimated cause-specific mortality rates using the non-parametric cumulative incidence function estimator (CIF; Heisey and Patterson 2006). We attributed mortality of radio-collared adults and yearlings to (1) vehicular collisions, (2) harvest trapping or shooting, (3) natural causes, or (4) unknown causes. Natural causes of death included mange, starvation, being killed by other canids or prey, and unknown natural causes (necropsy failed to determine cause of death, but harvest and vehicular collision were ruled out). Next, we combined all non-harvest mortalities into a single cause to identify classes of animals outside of APP that were more or less likely to die of harvest; we used Cox PH models (at $P < 0.05$), following methods described by Lunn and McNeil (1995) and Heisey and Patterson (2006). Specifically, we (1) created multiple records for each individual (one set for each cause of death), with an associated stratum variable indicating the specific cause; (2) fit models that included this stratum identifier in the model statement to allow fitting of separate hazard functions for harvest and non-harvest mortality; and (3) included interactions between covariates of interest and the cause of death/stratum identifier to allow the effect of covariates to differ for harvest and non-harvest mortality. We conducted all survival and cause-specific mortality analyses using the "survival," "MASS," and "gtools" packages in R version 2.15.1 (R Development Core Team 2011).

RESULTS

Overall, non-APP, and APP survival

We documented 58 deaths of radio-collared canids across the four study units during 2004–2010. The top model predicting adult and yearling mortality risk retained APP, resident, eastern wolf, and male variables (Table 2). Based on the top model, animals in APP survived better than animals outside of APP ($z = -4.4$, $P < 0.001$, hazard ratio = 0.18, 95% CI [0.09–0.39]). Additional results from the overall analysis are in Appendix D. The top model with non-APP data ($n = 49$ deaths) retained the resident and eastern wolf variables (Table 2). Based on the top model, residents

TABLE 2. Candidate models of mortality risk of radio-collared adult and yearling wolves, coyotes, and hybrids in and adjacent to Algonquin Provincial Park, 2004–2010, from model sets with all data (Overall), all data outside APP (non-APP), and residents in and out of APP (residents).

Model set	k	AIC_c	ΔAIC_c
Overall model			
Resident + APP† + eastern wolf + male	4	557.16	0
Resident + APP + eastern wolf	3	557.65	0.49
Resident + APP + eastern wolf + 2010‡	4	558.09	0.93
Null model	0	579.70	21.54
Non-APP			
Resident + eastern wolf	2	428.74	0
Resident + eastern wolf + male	3	429.59	0.84
Resident + eastern wolf + adult	3	429.89	1.14
Resident	1	430.39	1.64
Resident + eastern wolf + hybrid§	3	430.39	1.65
Resident + eastern wolf + 2010	3	430.45	1.71
Resident + eastern wolf + coyote	3	430.67	1.93
Resident + eastern wolf + male + adult	4	430.71	1.96
Null model	0	441.58	12.83
Residents			
2° road density + deer¶ + 2010 + eastern wolf × 2° road density	4	211.41	0
Null model	0	227.45	16.05

Note: We show the number of variables retained (k), AIC for small samples (AIC_c), and AIC_c differences (ΔAIC_c), for all models with strong empirical support ($\Delta AIC_c < 2$), as well as the null model.

† Coded 1 for animals in APP, 0 for animals outside.
‡ Coded 1 for data from 2010, 0 for data from 2004–2009.
§ Eastern wolf × coyote hybrid.
¶ Index of deer availability within home ranges of resident canids.

survived better than nonresidents ($z = -4.2$, $P < 0.001$, hazard = 0.34, [0.21–0.56]), whereas eastern wolves survived worse than other *Canis* types ($z = 3.1$, $P = 0.002$, hazard = 2.12, [1.32–3.38]). No other variables included in the non-APP analysis significantly influenced the survival of adult and yearling canids (Appendix E). Parameter estimates, confidence intervals, and significance tests were very consistent for individual variables across supported models (Appendix E). Variable weights also identified residency status and eastern wolf ancestry as the most influential factors in survival outside of APP (Table 3).

For APP, the null model was strongly supported ($\Delta AIC_c = 0.96$). Thus, there was little evidence that any of the variables considered influenced the survival of adults and yearlings in APP. Annual survival rate for all canids in APP was 0.852 ± 0.05 (mean ± SE; $n = 58$ [39 eastern wolves, 8 eastern wolf × coyote, 8 admixed gray wolves, 3 coyotes]). Outside of APP, annual survival rates were 0.662 ± 0.07 for coyotes ($n = 35$), 0.551 ± 0.09 for eastern wolf × coyote hybrids ($n = 22$), 0.625 ± 0.10 for admixed gray wolves ($n = 20$), and 0.388 ± 0.12 for eastern wolves ($n = 15$).

Resident survival

The top model for mortality risk of radio-collared adult and yearling residents ($n = 25$ deaths) retained the main effects of 2010, secondary roads, and deer availability, as well as the interaction between eastern wolf and secondary roads (Table 2). Residents survived

poorly in 2010 compared with other years ($z = 3.4$, $P < 0.001$, hazard ratio = 4.9, 95% CI [1.95–12.55]). Secondary road density within home ranges negatively influenced survival ($z = 5.0$, $P < 0.001$, hazard ratio = 1.22, [1.13–1.32]), whereas deer availability within home ranges positively influenced survival of residents ($z = -3.4$, $P < 0.001$, hazard = 0.34, [0.19–0.63]). The significant interaction between eastern wolf ancestry and secondary roads ($z = 4.8$, $P < 0.001$) indicated that

TABLE 3. Variable weights for all predictor variables included in the overall analysis outside of APP and resident survival analyses calculated by summing the Akaike model weights across all models retaining a given variable (Burnham and Anderson 2002).

Variable	Outside APP	Residents
Resident	0.97	NA
Eastern wolf	0.56	0.10
Male	0.34	NA
Adult	0.29	NA
Coyote	0.28	0.08
2010	0.25	0.97
Admixed gray wolf	0.22	0.05
Eastern wolf × coyote hybrid	0.22	0.05
Deer availability	NA	0.96
All 2° road density variables†	NA	0.94
2° road density	NA	0.81
Eastern wolf × 2° road density	NA	0.62
All eastern wolf variables†	NA	0.70
APP	NA	0.10
Moose density	NA	0.06

† Included as a main effect or interaction.

resident eastern wolves had lower survival at increasing secondary road density than all other genotypes combined. To investigate the relationships between eastern wolf mortality risk at increased secondary road density and that of each of the other three ancestry groups individually, we reversed the reference group for this interaction (i.e., from all other genotypes to eastern wolves). Resident coyotes ($z = -5.0$, $P < 0.001$, hazard = 0.57, [0.46–0.71]), coyote × eastern wolf hybrids ($z = -3.9$, $P < 0.001$, hazard = 0.62, [0.48–0.79]), and admixed gray wolves ($z = -2.4$, $P = 0.017$, hazard = 0.57, [0.35–0.90]) each survived better than resident eastern wolves as road density increased (Fig. 2). Given the relatively modest sample size, we repeated the analysis while sequentially removing data from each resident eastern wolf that died during the study to ensure that it was not unduly influenced by any single mortality events (Appendix F). Variable weights also indicated that temporal effects (2010), road density, deer availability, and the eastern wolf × secondary road interaction had the greatest influence on survival of residents.

Cause-specific mortality

Across the study area, based on the nonparametric cumulative incidence function estimator, CIF, the mortality rate due to harvest (CIF = 15.8% ± 2.7%, mean ± SE; $n = 29$, 95% CI [11.3–20.2%]) was greater than the rate due to natural deaths (CIF = 6.6% ± 1.9%; $n = 12$, 95% CI [3.6–9.7%]), vehicular collisions (4.9% ± 1.5%; $n = 9$, 95% CI [2.0–7.5%]), or unknown causes (4.8% ± 1.7%; $n = 8$, 95% CI [1.6–6.7%]). Outside of APP, the mortality rate due to harvest (CIF = 24.0% ± 3.9%; $n = 29$, 95% CI [17.6–30.5%]) was also greater than for all other causes (Appendix G). No harvest mortality was documented in APP (Appendix G). Outside of APP, eastern wolves ($z = 3.0$, $P = 0.003$, hazard = 3.45, 95% CI [1.52–7.84]) were more likely to be killed by harvest than all other *Canis* types, whereas residents ($z = -2.6$, $P = 0.008$, hazard ratio = 0.37, [0.18–0.78]) were less likely to die of harvest than nonresidents.

DISCUSSION

Adult survival is the most important demographic parameter influencing population growth of many large carnivores (e.g., Carroll and Miquelle 2006), including eastern wolves (Patterson and Murray 2008). We demonstrated that adult and yearling survival of eastern wolves in harvested areas was poor relative to (1) sympatric *Canis* types in areas adjacent to APP, and (2) eastern wolves and other canids within APP. In APP, annual survival was high ($\hat{s} = 0.85$) for all canids and mortality risk did not differ significantly in relation to genetic ancestry or any other factors that we investigated. Conversely, mortality risk was strongly influenced by residency status and eastern wolf ancestry outside of APP, where annual survival of eastern wolves was low ($\hat{s} = 0.39$) and they were more likely than other *Canis* types to be trapped or shot. Eastern wolves are the dominant

canid within APP, but are rare in adjacent areas (Benson et al. 2012) and outside of central Ontario (Rutledge et al. 2010). Our results indicate that genotype-specific *Canis* survival is environmentally mediated by variable harvest regulations and road densities, and that this is an important demographic mechanism underlying the spatial genetic structure of the hybrid zone.

Survival in APP was not significantly higher for eastern wolves, which raises the question of how they have maintained their numerical dominance within the park. Despite some hybridization with gray wolves and coyotes (Rutledge et al. 2010, 2011), eastern wolves have apparently been the dominant canid within APP since at least the beginning of the 20th century (reviewed by Kyle et al. 2006). All canids are territorial with each other within the central Ontario hybrid zone, reducing opportunities for entire packs of coyotes, gray wolves, and hybrids to establish in APP where the landscape is saturated with occupied canid territories (Benson and Patterson 2013). Canids usually disperse individually (Mech and Boitani 2003), such that solitary gray wolves, coyotes, and hybrids dispersing into APP probably join existing packs occasionally. However, most reproduction within APP involves eastern wolf pairs (Rutledge et al. 2010, Benson et al. 2012) and eastern wolf pups produced within the park also join existing packs (B. Patterson and J. Benson, *unpublished data*). This means that immigration of gray wolves, coyotes, and hybrids is probably balanced by dispersal of eastern wolves within APP. Thus, the combination of historical eastern wolf abundance within the park, strong territoriality, assortative mating, and high survival in APP probably explains the continued numerical dominance of eastern wolves within the park, even without surviving better than other *Canis* types. Nonetheless, given the conservation status of eastern wolves and their scarcity outside of APP, it would be prudent to continue to monitor the genetic structure of APP canids to determine whether eastern wolves remain numerically abundant within APP in the future.

In contrast to the apparent stability of the APP population (Patterson and Murray 2008), our findings indicate that the unprotected areas adjacent to APP probably represent a population sink for eastern wolves. Fuller et al. (2003) estimated that wolf populations should stabilize (with no population growth or decline) with an annual survival rate of 0.66, which is considerably higher than the survival of eastern wolves that we documented. Thus, poor survival of eastern wolves is likely to limit population growth outside of APP and also influences hybridization dynamics by keeping population density low. The lower density of eastern wolves outside of APP (Rutledge et al. 2010, Benson et al. 2012) probably exacerbates hybridization because of limited conspecific mating opportunities (Stephens and Sutherland 1999, Adams et al. 2003). Indeed, Rutledge et al. (2010) suggested that assortative mating was responsible for the lower levels of coyote and gray wolf
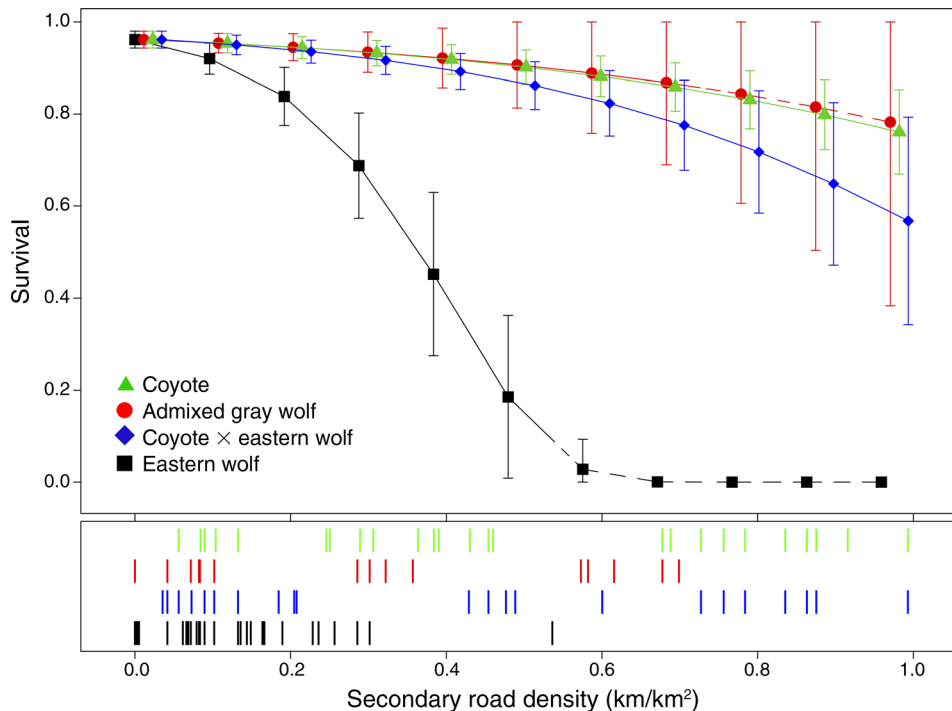
FIG. 2. Genotype-specific survival rates in relation to increasing secondary road density predicted by the Cox proportional hazard survival model for resident radio-collared *Canis* spp. in and adjacent to Algonquin Provincial Park, 2004–2010. Survival rates (mean ± robust SE) were predicted at a range of secondary road densities between 0 and 1.0. Road densities within the home ranges of each individual are indicated below the *x*-axis with colors corresponding to those used to show survival trends for each *Canis* type. Dashed trend lines indicate survival rates predicted above the range of road densities where animals of a given ancestry group were monitored.

introgression in the APP population, where >70% of breeding unions were between eastern wolves. Furthermore, high levels of human-caused mortality during intensive wolf culls temporarily lowered eastern wolf density in APP during the 1960s, and appears to have facilitated increased coyote introgression during that period (Rutledge et al. 2011). We documented definitive (*n* = 5, i.e., confirmed by genetic analysis of pups; Benson et al. 2012) or apparent (*n* = 2; telemetry data only) breeding unions outside of APP involving eastern wolves. Four of these unions were eastern wolves paired with hybrids (*n* = 3) or coyotes (*n* = 1), supporting the contention that assortative mating by eastern wolves is less common at lower density outside of APP. Whereas many wolf populations can withstand significant harvest mortality because of their high reproductive potential (Fuller et al. 2003), much of the eastern wolf reproduction outside APP involves hybridization and does not contribute to eastern wolf population growth.

Populations subjected to high harvest mortality may be sustained by sufficient immigration from nearby reserves (Pulliam 1988, Lariviere et al. 2000), which probably explains the persistence of eastern wolves in patches outside of APP. Because both residency status and eastern wolf ancestry were important predictors of survival and harvest mortality outside of the protected area, these nonresident eastern wolves were at especially

high risk of harvest outside of APP. Indeed, four of five radio-collared eastern wolves that dispersed from APP into adjacent unprotected areas during the study (but remained within the study area) were harvested before establishing residency less than one year after leaving APP (175 ± 47 days, mean ± SE). The fifth dispersing eastern wolf died of unknown causes 153 days after leaving APP. Clearly, some eastern wolves were able to establish residency, which reduced their risk of mortality, but their survival was still poor relative to other *Canis* types in these areas. Our results with respect to residency status were consistent with many previous studies of wolf and coyote survival indicating that residents survive better than nonresidents in harvested populations (e.g., Berger and Gese 2007, Smith et al. 2010), but that residency status does not affect survival in protected areas (e.g., Fuller et al. 1989).

Lower survival and higher harvest mortality of eastern wolves relative to other genotypes may suggest that most eastern wolves in adjacent, unprotected landscapes originated from APP, and are therefore naïve regarding mortality risk from humans and roads. In protected areas, wolves may be attracted to roads to facilitate rapid movement across rugged terrain and increase predation efficiency (James and Stuart-Smith 2000, Whittington et al. 2005). In harvested areas, trapping and shooting mortality of canids is often

associated with roads (Person and Russell 2008). Canids raised in harvested areas may adopt behavioral mechanisms to mitigate harvest risk, such as avoidance of roads during daytime when human activity is highest (Hebblewhite and Merrill 2008). These behavioral mechanisms may be absent or poorly developed in animals originating from APP, where wolves are accustomed to exploiting the beneficial qualities of roads without increased risk of mortality. Thus, roads could represent an ecological trap (sensu Gates and Gysel 1978) or an attractive sink (sensu Delibes et al. 2001) for eastern wolves dispersing into harvested landscapes from protected areas.

Previous research has identified two main mechanisms leading to source–sink population dynamics: constrained dispersal (Pulliam 1988, Dias 1996, Diffendorfer 1998) and maladaptive habitat selection (Remeš 2000, Delibes et al. 2001). Generally these two mechanisms have been considered as separate, alternative explanations for source–sink dynamics, where individuals either move into sinks because of density-dependent or density-independent constraints on dispersal (e.g., Dias 1996, Diffendorfer 1998), or because they incorrectly assess the mortality risk or reproductive potential of these habitats (Remeš 2000, Delibes et al. 2001). Our results suggest that both dispersal and poor habitat decisions may operate in a hierarchical manner, at different scales, to create source–sink dynamics in systems structured around protected areas. For instance, at the landscape level, some animals were constrained to disperse out of the source (APP), probably due to territoriality (Benson and Patterson 2013) and/or to density-dependent forces operating on the stable wolf population within the protected area (Patterson and Murray 2008). Once outside of the protected area, individuals dispersing through the matrix may make maladaptive habitat choices at finer scales, such as establishing home ranges in areas of high road density. Given the hierarchical nature of animal habitat selection (Johnson 1980), it makes sense that processes governing movement from source to sink habitats would also be hierarchical. This is especially true when mortality risk itself is hierarchical, for example, when landscapes differ in relative risk (protected vs. unprotected) and specific habitat features within these landscapes further increase risk (e.g., roads).

Two main theoretical models explain the maintenance of stable hybrid zones. The tension zone model predicts that a stable genetic cline is maintained by a balance between dispersal and endogenous selection against hybrids (Barton and Hewitt 1985). Alternatively, environmentally mediated models predict stable hybrid zones where hybrid and parental genotypes are favored by different environmental conditions, rather than because they are intrinsically superior or inferior (Moore 1977, Rand and Harrison 1989). The structure of the central Ontario *Canis* hybrid zone appears to be maintained by regular dispersal of eastern wolves from

APP into the matrix, consistent with a tension zone. However, in direct contrast to the tension zone model, relative fitness of hybrid and parental types and the structure of the *Canis* hybrid zone were influenced strongly by environmental heterogeneity rather than endogenous selection. Higher mortality of eastern wolves in harvested landscapes and regular dispersal from APP probably contribute to their patchy distribution, similar to mosaic hybrid zones of other species influenced by extinction–recolonization dynamics (Bridle et al. 2002). The *Canis* hybrid zone is structured by spatially variable harvest regulations that appear to have simultaneously supported the persistence of a genetically distinct population within APP (Rutledge et al. 2010) and maintained eastern wolves at low density adjacent to the protected area through a cycle of dispersal, high mortality, and hybridization. We suggest that protected areas can influence hybrid zone structure and stability through a combination of mechanisms that are both consistent with and contradictory to predictions of classical hybrid zone models.

Our results, in combination with those of Benson et al. (2012), demonstrate that protected areas can exert a powerful influence on hybridization dynamics between species and suggest that rare hybridizing taxa are able to maintain genetic distinctiveness within protected areas, even when reproductive barriers are few, and hybrids and other parental types are more abundant, outside the reserve. Thus, efforts to maintain or restore naturally regulated systems by protecting rare, hybridizing species from exploitation can help to address the challenge of conserving hybridizing species. Although large protected areas similar to APP may be difficult to establish in many human-altered landscapes, our results highlight the importance of existing parks and reserves with respect to their potential to influence the structure of hybrid zones involving rare species. Additionally, many hybridizing species are of taxa (e.g., birds, fish, amphibians) with modest space requirements compared to wolves, which may facilitate mitigation of undesirable consequences of hybridization through the influence of protected areas considerably smaller than APP.

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SUPPLEMENTAL MATERIAL

Appendix A

Supporting methods (*Ecological Archives* E095-022-A1).

Appendix B

Sampling of resident animals (*Ecological Archives* E095-022-A2).

Appendix C

Sample sizes for categorical variables (*Ecological Archives* E095-022-A3).

Appendix D

Additional overall survival results (*Ecological Archives* E095-022-A4).

Appendix E

Additional non-APP survival results (*Ecological Archives* E095-022-A5).

Appendix F

Secondary roads × eastern wolf: supporting analysis (*Ecological Archives* E095-022-A6).

Appendix G

Additional cause-specific mortality results (*Ecological Archives* E095-022-A7).