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Resource selection at homesites by wolves and eastern coyotes in a *Canis* hybrid zone

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Abstract. We modeled resource selection by wolves (*Canis* spp.), eastern coyotes (*C. latrans*), and admixed canids during the pup-rearing season at den and rendezvous sites (collectively, homesites) within a largely unprotected landscape proposed as the recovery zone for federally and provincially threatened eastern wolves (*C. lycaon*) in Ontario, Canada. Overall, canids selected wetlands, while avoiding secondary roads and open-structure rock-grass habitat patches. Packs with greater wolf ancestry selected wetlands and tertiary roads more strongly, while avoiding mixed conifer-hardwood forests. Contrary to our prediction, canids with greater coyote ancestry did not establish homesites closer to roads, which likely mitigated their risk of human-caused mortality during pup-rearing. Packs exhibited increased selection of wetlands within territories as a function of increasing availability of wetlands. Packs with abundant access to wetlands may prioritize this habitat type to exploit beavers, a valuable prey species during pup-rearing. Packs with higher pup survival selected hardwood forests and avoided conifer forests more than packs with lower pup survival. This is consistent with our understanding of habitat relations of the main prey species for canids in central Ontario and suggests that selecting prey-rich habitat types at homesites increases fitness. A proposed goal of eastern wolf recovery is numerical and geographical expansion outside of the population core in Algonquin Provincial Park. Thus, our results provide valuable information for conservation by quantifying resource selection of wolves, coyotes, and hybrids during pup-rearing and identifying links between fitness and homesite selection.

Key words: eastern coyote; eastern wolf; homesites; Ontario; pup survival; resource selection.

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INTRODUCTION

Resource selection by animals involves interactions between local environmental conditions, such as the nature and availability of resources, and intrinsic characteristics of the animals (Bolnick and Doebeli 2003, Sacks et al. 2004). Investigating resource selection during critical periods of the annual cycle of a given species is

especially important for identifying the functional consequences of wildlife-habitat relationships (McLoughlin et al. 2006, Roever et al. 2014). Additionally, studying variation in species-specific resource selection strategies for closely related taxa can improve understanding of key processes such as niche partitioning (Morris 2003) and help to refine management approaches for similar species of different conservation

status (Kaczenky et al. 2008). Individual-level resource selection patterns are also important to consider, especially if the goal is to understand different behavioral strategies influencing fitness (Leclerc et al. 2016). Finally, linking resource selection directly to estimates of survival and reproduction facilitates linking individual behavioral decisions to demographic processes that drive population dynamics (Morris 2003).

For wolves (*Canis* spp.) and coyotes (*Canis latrans*), the pup-rearing season (spring to fall) is a critical period of the annual cycle because pup survival strongly impacts the growth of populations (Fuller et al. 2003). In spring or early summer, canids give birth in natal dens, after which the pups spend most of the next 5–6 months at homesites (den or rendezvous sites, Mech and Boitani 2003). Specifically, for approximately six weeks, pups are at one or more den sites, after which the pack occupies a succession of rendezvous sites where pups are reared until fall when they begin to move with the rest of the pack (Mech and Boitani 2003, Benson et al. 2015a). Pup mortality can be high during late summer and fall in some populations, from natural (e.g., starvation, disease, strife) or human-related causes (e.g., persecution, vehicle collisions; Fuller et al. 2003, Benson et al. 2013). Thus, elucidating patterns of resource selection at homesites is critical for understanding links between environmental conditions, pup survival, and canid population dynamics.

Although genotypic and phenotypic similarities can result in similar patterns of resource use and niche overlap between wolves and coyotes (e.g., Ballard et al. 1999, McVey et al. 2013), they appear to exhibit different roles within ecological communities (e.g., Atwood and Gese 2010, Benson et al. 2017). However, coyotes have expanded their geographical range and ascended to the role of top predator in many portions of eastern North America as a result of widespread extirpation of wolves and anthropogenic landscape alteration, creating confusion regarding their ecological roles (Gompper 2002, Kays et al. 2008). In Ontario, Canada, where eastern coyotes and wolves are sympatric and territorial with one another (Benson and Patterson 2013), wolves appear to occupy different niches with respect to predation on ungulates (Benson et al. 2017). Investigating aspects of resource selection

beyond predation by sympatric canids would help achieve a more comprehensive understanding of niche overlap between wolves and eastern coyotes. For instance, coyotes tend to be more tolerant of open habitat types and human disturbance. Indeed, several studies have suggested that forests, the dominant vegetative cover type in eastern North America, represent poor habitat for eastern coyotes (Crête et al. 2001, Boisjoly et al. 2010, but see Kays et al. 2008). Given the importance of pup survival to canid population growth, and the superior ability of coyotes to persist in human-impacted landscapes, investigating resource selection at pup-rearing sites in systems where wolves and coyotes are harvested by humans would be informative to better understand mechanisms underlying the relative persistence of wolves and coyotes in harvested landscapes.

Patterns of resource selection by canids may be strongly influenced by local environmental characteristics (e.g., resource availability), leading to considerable variation among individuals and packs occupying heterogeneous landscapes (Benson et al. 2015b). For instance, resource selection of both natural and anthropogenic resources can vary as a function of resource availability, resulting in individual or pack-level patterns referred to as functional responses in resource selection (Hebblewhite and Merrill 2008, Holbrook et al. 2019). Canids likely balance risk of human-caused mortality with attempting to maximize foraging efficiency when selecting resources, highlighting the importance of investigating selection in a multivariate context that considers resources associated with both risks and rewards, and how behavioral responses may vary between packs (Hebblewhite and Merrill 2008, Houle et al. 2010).

The unique, three-species *Canis* hybrid zone between eastern wolves (*Canis lycaon*), eastern coyotes (*Canis latrans*), and Great Lakes type gray wolves (*Canis lupus*) in Ontario, Canada is an excellent system for investigating intrinsic and extrinsic factors influencing homesite selection by canids. Eastern wolves are designated as threatened federally in Canada and provincially in Ontario, and their distribution is mainly restricted to the protected area of Algonquin Provincial Park (APP) and adjacent areas where canids are legally harvested (Rutledge et al. 2010,

Benson et al. 2012). Eastern wolves are the numerically dominant canid within APP, but are rare and patchily distributed adjacent to APP (Benson et al. 2012, Rutledge et al. 2017) where they are sympatric with eastern coyotes, Great Lakes wolves, and admixed canids with whom they are territorial (Benson and Patterson 2013). Recent research in APP showed different resource selection patterns by wolves at den and rendezvous sites, and that these patterns appeared to influence pup survival within this large protected area (Benson et al. 2015a). However, homesite selection by wolves and coyotes has not been studied in the more fragmented landscape adjacent to APP that is characterized by greater human presence. The landscape adjacent to APP is conducive to investigating intrinsic and extrinsic influences on resource selection because it is occupied by a more diverse assemblage of parental and admixed canids that are subjected to shooting and trapping mortality (Benson et al. 2014). Thus, studying homesite selection of canids adjacent to APP will inform conservation efforts for eastern wolves in Ontario where a proposed goal of recovery is to facilitate numerical and geographical expansion outside of APP (Beacon Environmental Limited and Wildlife 2000 Consulting 2018).

Accordingly, we investigated resource selection at den and rendezvous sites by canids across the heterogeneous, unprotected landscape of central Ontario adjacent to APP. We tested several hypotheses and predictions regarding resource selection with respect to variation in intrinsic and environmental factors, as well as the influence of homesite selection on pup survival. First, we hypothesized that canids would select dens and rendezvous sites differently (H1), as different resources may be required during different periods of pup growth and development (Benson et al. 2015a). Second, we hypothesized that wolves and eastern coyotes occupy different niches such that variation in the proportion of wolf and eastern coyote ancestry in resident packs would result in different patterns of homesite selection (H2). More specifically, as coyotes tend to be more tolerant of human disturbance and thrive in open, fragmented landscapes (Richer et al. 2002, Boisjoly et al. 2010, Benson et al. 2012), we predicted that packs with greater coyote ancestry would select homesites closer to

roads and non-forested habitat types. Third, we hypothesized that canids would exhibit pack-level variation in resource selection at homesites by responding to differences in the availability of important resources across the study area (H3). Here, we predicted that packs would exhibit functional responses in resource selection by exhibiting variation in selection as a function of the availability of resources associated with humans and seasonally important prey. Fourth, given the presumed links between homesite selection, fitness, and population dynamics, we hypothesized that resource selection patterns would influence mortality risk of pups (H4). Specifically, we predicted that pups would survive better in packs that (1) avoided roads to minimize mortality risk, and (2) selected landscape attributes associated with important prey. Practically, our results will inform conservation efforts for eastern wolves within the proposed recovery zone. More broadly, our work helps to disentangle ecological relationships between hybridizing canids and increases understanding of variation in resource selection relative to human disturbance and natural habitat features.

MATERIALS AND METHODS

Study area

We studied canids in four areas within the *Canis* hybrid zone adjacent to Algonquin Provincial Park (APP) in central Ontario between 2005 and 2016. These areas included Wildlife Management Unit 47 (WMU47; 2005), Wildlife Management Unit 49 (WMU49; 2008–2011), the Kawartha Highlands Provincial Park and surrounding areas (KH; 2009–2010), and the Queen Elizabeth II Wildlands Provincial Park and surrounding areas (QE; 2015–2016; Fig. 1). These areas were a combination of private and public lands that were primarily used for logging, hunting, and seasonal or year-round residences. Eastern coyotes were the most abundant *Canis* type among adults within the packs we studied (52%), followed by wolf (eastern or Great Lakes wolves) × eastern coyote hybrids (31%), and wolves (eastern wolves, Great Lakes wolves, and eastern wolf × Great Lakes wolf hybrids; 17%). Wolf and coyote harvest by trapping and/or hunting was allowed throughout the study area on a seasonal or year-round basis, except in the

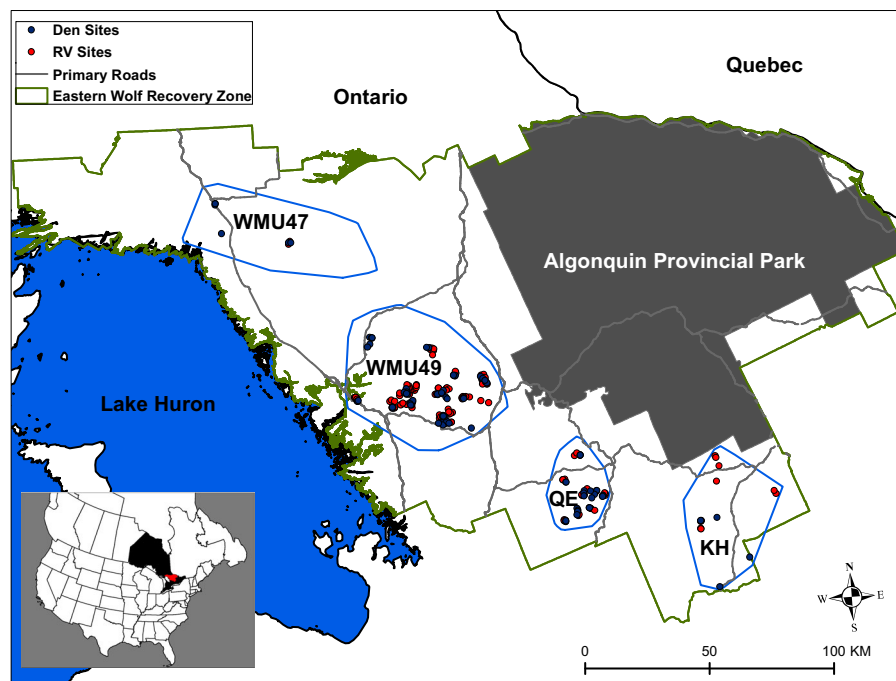


Fig. 1. Study area in central Ontario including the 4 areas (Wildlife Management Units 47 (WMU47) and 49 (WMU49), Queen Elizabeth II Wildlands (QE), and the Kawartha Highlands (KH)) within which we studied wolves and coyotes. Also shown are major roads, the eastern wolf recovery zone, and Algonquin Provincial Park (APP).

last several months of our study in portions of KH and QE after 15 June 2016 due to regulations implemented for eastern wolf recovery efforts. The major natural habitat types in our study area were hardwood forests, conifer forests, mixed hardwood-conifer forests, wetlands, lakes, and open areas with rocks and grassy meadows. Elevations ranged from 175 to 510 m. The main prey for canids were white-tailed deer (*Odocoileus virginianus*), moose (*Alces alces*), and beavers (*Castor canadensis*; Benson et al. 2017). Additional details about the study area are provided in Appendix S1.

Field methods and data

We captured wolves, coyotes, and hybrids using foothold traps, modified neck-snares, and nets fired from helicopters to deploy Global Positioning System (GPS) and Very High Frequency (VHF) radio-collars (Lotek Wireless, Newmarket, Ontario, Canada or Telonics, Mesa, Arizona, USA). We captured and handled animals in accordance with protocols approved by the Trent

University (08039, 24219) and Ontario Ministry of Natural Resources and Forestry (5–75 to 11–75 and 14–75 to 16–75) Animal Care Committees. During spring, we used GPS and/or VHF telemetry to determine denning status and locate dens for all focal packs. When radio-collared canids restricted movements (breeding females) or continually returned to specific areas, we suspected they were visiting a den site. Most (71%) of our den and rendezvous site data came from WMU49 where our most intensive field study was conducted. In WMU49, once a potential den was located, we visited the location on the ground to capture 3- to 5-week-old pups and implant them with internal VHF radio-transmitters (details in Benson et al. 2013). We used GPS (adults) and aerial VHF radiotracking (pups) throughout spring, summer, and early fall to locate subsequent dens and rendezvous sites. Canids moved dens frequently, with or without disturbance from research activities, such that we often located multiple dens within the same year for focal packs, as reported elsewhere

(Argue et al. 2008, Benson et al. 2015a). In WMU49, we considered locations where pups were located repeatedly >6 weeks following parturition until 31 October to be rendezvous sites. To obtain coordinates for rendezvous sites, we matched VHF locations of pups at rendezvous sites to the centroid of clusters of GPS data from collared adults in each pack.

We did not visit dens or track pups in WMU47, KH, and QE (29% of data), and instead used the clustering algorithm Animal Site Fidelity (rASF; Mahoney and Young 2017) implemented in R (version 3.4.1) along with visual inspection of GPS data to identify dens (April–June) and rendezvous (June–August) sites. We used spatial buffers of 50–75 m including ≥ 5 locations over ≥ 7 consecutive days to identify clusters representing possible den and rendezvous sites (modified from Mahoney and Young 2017). We then visually inspected each cluster, as well as all available sequential locations for each focal pack from 1 April to 31 August to determine which clusters of locations represented den and rendezvous sites. Additional details about homesite identification are provided in Appendix S1.

Ancestry analysis

We collected blood samples from all captured animals for genetic analysis. We amplified 12 autosomal microsatellite loci for each sample using markers and laboratory methods described by Benson et al. (2012). We determined family relationships of canids from results of previous pedigree analyses (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. The Structure analysis allows for estimation of admixture proportions which are estimates of the proportion of an individual's genome derived from a given genetic population. We ran the admixture model of Structure, assuming correlated allele frequencies for $K = 3$ for 10^6 iterations following a burn-in period of 250,000 as in Benson et al. (2012). We assumed $K = 3$ for the analysis given strong support for 3 genetically distinct *Canis* types (corresponding to putative eastern wolves, eastern coyotes, and Great Lakes wolves) in the hybrid zone within and adjacent to APP (e.g., Rutledge

et al. 2010, Benson et al. 2012, Heppenheimer et al. 2018). We estimated the proportion of overall wolf ancestry for each individual by combining the admixture proportions for eastern wolves and Great Lakes wolves (Appendix S1). Most wolf ancestry in the Ontario hybrid zone derives from eastern wolves, whereas a considerably smaller proportion derives from Great Lakes wolves (Rutledge et al. 2010, Benson et al. 2012). For most (72%) packs, we estimated pack-level ancestry by either averaging admixture proportions from the breeding pair or using ancestry of pups born in the pack. We excluded genotypes of offspring when both breeders were genotyped, whereas we excluded single parents when offspring were used. For the remaining packs (28%) we used mean ancestry from 1 or more adults to estimate pack-level ancestry. See additional details of ancestry analyses in Appendix S1 and Appendix S1: Fig. S1.

Resource use and availability

We investigated resource selection with an approach similar to Johnson's (1980) 3rd order of selection by comparing locations used by canids at homesites to those available within seasonal home ranges. Specifically, we estimated 95% fixed kernel home ranges with the plug-in estimator to determine bandwidth (Sheather and Jones 1991), using all GPS telemetry data from a single individual in the pack collected during the pup-rearing season between 1 April and 30 November. Canids are strongly territorial and home ranges are stable in the hybrid zone (Benson and Patterson 2013). Thus, we used all GPS data collected across the pup-rearing season to estimate home ranges. However, as we were not able to monitor all packs continuously from April to November (due to collar failure or death of collared animals), some (47%) of our home ranges (and therefore measures of availability) corresponded to shorter periods of the pup-rearing season that were identical to the periods within which we documented homesites. Regardless, we estimated all home ranges with a minimum of 30 d monitoring. Additional details of home range estimation are available in Appendix S1.

For used locations, we identified 30-m pixels (30 × 30 m) on the landscape that contained den or rendezvous sites. For availability, we

systematically sampled 30-m pixels separated by 150 m throughout each seasonal home range resulting in 44 pixels/km² to estimate resources available to each canid pack (Benson 2013). We developed a GIS layer for 6 broad habitat classes (hardwood forest, conifer forest, mixed forest, wetlands, rock/grass, and water; Appendix S1: Table S1) with raw Ontario Forest Resource Inventory (OMNR 2008, *unpublished data*) data which we converted into habitat classes using Ontario's Landscape Tool 3.0 (Benson et al. 2015a). We followed the recommendations of Maxie et al. (2010) for combining forested habitat classes to improve classification success based on their field validation analyses conducted within the study area. We developed separate roads layers for secondary and tertiary roads using the 2010 Ontario Roads Network (ORN). Secondary roads were small and medium-sized paved roads classified as arterial, local/street, or collector roads, whereas tertiary roads were dirt roads and trails with light, slower-moving traffic by vehicles and hikers (Appendix S1: Table S1). Larger (primary) paved roads such as major highways were rare and not found in most canid home ranges precluding meaningful inference regarding 3rd order resource selection. We calculated distances to habitat types and secondary/tertiary roads from the centroid of all 30-m pixels used by (homesites) and available to (systematic locations) canids (additional details of the datasets included in our models are provided in Appendix S1). We also estimated slope and elevation from digital elevation models (DEM) in ArcGIS 10.1. DEM data were estimated at 10-m resolution, but we averaged these values across 30 m used and available pixels for our analyses (Appendix S1: Table S1). None of our variables were highly correlated (all $r < 0.45$), so we included all variables described above. Additionally, we rescaled values for all continuous variables by subtracting their mean and dividing by 2 standard deviations (Gelman 2008).

Resource selection models

We modeled resource selection at homesites with generalized linear mixed models (GLMMs) implemented in the R (version 3.4.1) package lme4 with a binary (0 = available, 1 = used) response variable. We included random intercepts for pack and year in each model, with year

nested in pack. Including random intercepts for pack mitigated effects of unbalanced homesite data across packs (range 1–34 locations) and the lack of independence between used locations from the same packs (Gillies et al. 2006). The random intercept of year accounted for lack of independence between sites used within a given year by the same pack and paired the year-specific used and available data appropriately within our models. Thus, in each resource selection model we paired homesite locations (use) with locations distributed across pack and year-specific seasonal home range (availability).

We created a number of models to test our hypotheses, predictions, and questions regarding resource selection at homesites. First, at the population level, we hypothesized that canids selected resources differently at den and rendezvous sites (H1; Appendix S1: Table S2). Thus, we used all data (dens = 103, rendezvous sites = 148) from all packs ($n = 29$) to build a global model that included all resource variables, a den variable (0 = rendezvous sites, 1 = dens), and interactions between the den variable and each resource variable to investigate possible differences. Second, we tested the hypothesis that population-level resource selection would vary relative to wolf-coyote ancestry in canid packs by including interactions between each resource variable and the continuous variable of pack-level wolf ancestry (H2; Appendix S1: Table S2). Specifically, we tested the predictions that packs with greater wolf ancestry would establish homesites farther from roads and closer to forested habitat types.

Third, we tested the hypothesis that resource selection at homesites varied among packs relative to variation in available resources (H3; Appendix S1: Table S2). We studied canids across a heterogeneous landscape that differed with respect to human presence, road densities, and proportion of natural habitat types (see *Materials and Methods: Study area*). Thus, we included random slopes in our models to estimate pack-level selection of resources associated with humans and critical spring-summer resources (water and prey) to investigate possible differences in resource selection at homesites relative to differences in the availability within home ranges (functional responses in resource selection). Canids in our study area exhibit

strong behavioral responses to roads, which represent significant mortality risk from hunting and trapping (Benson et al. 2012, 2014, 2015b). Previous work in the region has demonstrated the importance of beavers as a spring-fall food resource and its influence on pup survival (Benson et al. 2013). Beavers are associated with water, wetlands, and areas of lower elevation in central Ontario (Donkor and Fryxell 1999, Benson et al. 2013). Thus, we investigated pack-level responses to roads (secondary and tertiary), water, wetlands, and elevation by including random slopes for these variables in our resource selection models (Hebblewhite and Merrill 2008). We predicted that canids would avoid roads more strongly when they were more common to avoid humans, and would select water, wetlands, and low elevations more strongly when they were scarce to ensure access to beavers. To investigate functional responses in the selection of these resources at homesites, we extracted pack-level coefficients and included them as response variables in generalized additive models (GAMs; Wood 2006, Benson et al. 2015b). We created a separate GAM for each variable of interest and included the mean distance (roads, water, wetlands) or value (elevation) of the resource of interest across the home range of each pack as the predictor variable. These means represented distance-based or classification-based availability of the resource to the pack in question. We fit 5 separate GAMs in the R package *mgcv* version 1.8-22 (Wood 2006). We specified predictor variables as non-parametric smooth functions (splines) in the GAMs to allow for the possibility of non-linear relationships.

Fourth, we tested the hypothesis that resource selection at homesites influenced mortality risk of pups (H4; Appendix S1: Table S2) by including an interaction between resource variables and fate of litters for the subset of pack-years ($n = 16$ litters from 12 packs, all in WMU49, 2008–2010) in which we monitored pup survival via telemetry (survival data from Benson et al. 2013). We created a binary fate variable contrasting high (coded 1; 75–100% of the litter survived, $n = 10$) and low (coded 0; 0–50% of the litter survived, $n = 6$) pup survival. In most of these litters (10 of 16), all pups survived or all pups died such that our fate variable effectively captured packs with good or poor pup survival in a given

year. We also ran two additional models, with data from high and low pup survival in separate models, to allow for simpler interpretation of selection coefficients without interactions. The use and available data were the same for pack-year combinations included in the models for each hypothesis test, although the pup survival model only included a subset of these data. Additional details about the datasets used to test each hypothesis are available in Appendix S1.

Within each model set, we compared models of varying complexity, that is, with and without interactions (H1, H2, H4) or random slopes (H3), using Akaike's information criteria (AIC; Burnham and Anderson 2002) to evaluate whether there was empirical support for considering the more complex models. We also compared these models to a null model with no variables to evaluate whether the variables included in models with the strongest support represented substantial information gain. We calculated the difference (Δ) in AIC (lower values indicate better fit) between the models within each model set. If model fit was clearly worse ($\Delta\text{AIC} \geq 10$) with or without interactions or with or without random slopes, we considered the coefficients from the superior model to evaluate our hypotheses. In cases where simpler and more complex models were both plausible competing models ($\Delta\text{AIC} < 10$; Bolker et al. 2009), we considered coefficients from both models. We use the terms selection and avoidance, respectively, throughout to indicate (1) that used locations (homesites) were significantly closer to or farther from distance-based resource variables (habitat types, roads) than were available locations, or (2) that values of classification-based resource variables (elevation, slope) were significantly greater or lesser at used locations relative to available locations. Specifically, we inferred selection or avoidance of resource variables when 95% confidence intervals of fixed-effect beta coefficients did not overlap 0.

RESULTS

Homesite locations

We identified a total of 103 dens and 148 rendezvous sites from 29 packs. We located dens in conifer forests ($n = 13$), mixed forests ($n = 11$), hardwood forests ($n = 47$), rock/grass ($n = 20$),

wetlands ($n = 7$), water ($n = 4$), and in a gravel pit ($n = 1$).

Resource selection at homesites

There was mixed support for whether resource selection varied at den and rendezvous sites (H1). The best model did not retain interactions between the den variable and each resource variable; however, the model with interactions was a plausible competing model (Table 1). In the strongest model with all homesite data and no interactions, canids strongly avoided secondary roads, selected wetlands, and avoided rock/grass (Table 2). However, the model considering interactions indicated that canids selected steeper slopes at dens than at rendezvous sites (Appendix S2: Table S1). Given that model fit was better for the simpler model and that selection only differed between den and rendezvous sites for a single resource, we pooled homesites for the remainder of our analyses.

Ancestry influenced resource selection at homesites as the model with interactions between resource variables and proportion of wolf ancestry in packs was strongly supported (H2; Table 1). Selection of tertiary roads and

Table 2. Estimated coefficients (β) and lower and upper 95% confidence limits (LCL and UCL, respectively) for the mixed-effect resource selection models at canid homesites (den and rendezvous sites pooled), in central Ontario, Canada.

Parameter	β	95% LCL	95% UCL	Mean	SE
Intercept	-6.78	-7.23	-6.35
2° Roads	0.89	0.51	1.27	1862.86	98.62
3° Roads	0.20	-0.16	0.56	2019.07	104.68
Hardwood	0.10	-0.35	0.53	494.30	61.20
Conifer	0.13	-0.15	0.41	590.38	42.18
Mixed	0.14	-0.14	0.40	613.26	36.84
Wetland	-0.31	-0.60	-0.04	225.43	14.74
Water	0.13	-0.15	0.40	307.43	15.86
Rock/Grass	0.36	0.05	0.65	541.78	34.13
Elevation	-0.07	-0.61	0.48	306.03	2.44
Slope	-0.09	-0.37	0.17	4.20	0.27
Den	-0.47	-0.73	-0.20

Notes: Means and standard errors (SE) of values at locations used as homesites are also shown. Significant fixed effects are shown in bold. All resource variables were distance-based except for slope and elevation. ... = not applicable.

wetlands, and avoidance of mixed forests, increased with greater wolf ancestry (Table 3). The main effects for secondary and tertiary roads

Table 1. Comparison of model fit between models with and without interactions, and each respective null model, used to test our hypothesis about canid homesite selection (H1–H4).

Models	AIC	Δ AIC	Conclusion
Den vs. Rendezvous sites (H1)			Mixed support for interactions
No interactions + den	3948.3	0	
Interactions (Den \times each variable)	3954.5	6.2	
Null model	3979.2	30.9	
Wolf vs. Coyote ancestry (H2)			Interactions supported
Interactions (Wolf \times each variable)	3636.0	0	
No interactions	3648.7	12.7	
Null model	3671.6	35.6	
Pack-level (H3)			Pack-level variation supported
Selected random Slopes† + variables	3577.3	0	
No Random Slopes	3648.7	71.4	
Null model	3671.6	94.3	
Pup survival (H4)			Interactions supported
Interactions (Fate \times each variable)	2211.2	0	
No interactions	2223.9	12.7	
Null model	2292.6	81.4	

Note: Shown are Akaike's information criteria (AIC), differences between AIC (Δ AIC), and the conclusion whether there was support for the interactions.

† 2° Roads, 3° Roads, Wetlands, Water, Elevation.

Table 3. Estimated coefficients (β) and lower (LCL) and upper (UCL) 95% confidence limits from mixed-effects models for resource selection at canid homesites considering potential interactions with wolf ancestry in central Ontario, Canada.

Parameter	β	95% LCL	95% UCL
Intercept	-5.67	-6.19	-5.17
2° Roads	0.79	0.16	1.44
Wolf	-2.14	-5.21	-1.16
3° Roads	0.80	0.15	1.44
Hardwood	-0.18	-0.93	0.59
Conifer	0.17	-0.50	0.43
Mixed	-0.35	-0.81	0.09
Wetland	0.01	-0.40	0.40
Water	0.19	-0.22	0.58
Rock/Grass	0.41	-0.16	0.96
Elevation	0.24	-0.55	1.07
Slope	0.21	-0.23	0.62
Wolf × 2° Roads	0.26	-0.81	1.32
Wolf × 3° Roads	-1.45	-2.72	-0.20
Wolf × Hardwood	-0.05	-1.11	1.02
Wolf × Conifer	0.37	-0.46	1.20
Wolf × Mixed	1.16	0.41	2.02
Wolf × Wetlands	-1.11	-2.16	-0.11
Wolf × Water	-0.41	-1.39	0.55
Wolf × Rock/Grass	-0.12	-1.17	0.92
Wolf × Elevation	-0.68	-2.31	0.87
Wolf × Slope	-0.75	-1.69	0.15

Notes: Significantly selected or avoided resources and significant ancestry interactions are shown in bold. Wolf is proportion of ancestry attributed to eastern or Great Lakes wolves. All resource variables were distance-based except for slope and elevation.

from this model also indicated that highly assigned coyote packs (e.g., if wolf ancestry = 0) were predicted to strongly avoid secondary and tertiary roads (Table 3).

Functional response modeling

Model fit improved when considering pack-level variation in resource selection by including random slopes for landscape features associated with humans and critical spring-summer resources (H3; Table 1). Packs exhibited a positive, non-linear functional response in resource selection of wetlands, as they selected wetlands more when the mean distance to wetlands across their home range was lower (indicating higher availability; $P = 0.006$, $\text{edf} = 1.37$, % Deviance explained = 32.6, $n = 29$; Fig. 2). However, despite pack-level variation in selection of other resources, there were no detectable functional

responses in resource selection for secondary roads ($P = 0.533$), tertiary roads ($P = 0.527$), water ($P = 0.388$), or elevation ($P = 0.382$).

Resource selection in relation to pup mortality

There was strong support for considering differences in resource selection at homesites between packs with higher and lower pup survival (H4; Table 1). Packs with higher pup survival avoided secondary roads, conifer forests, and rock/grass, but selected hardwood forests (Table 4, Appendix S3: Table S1). Packs with lower pup survival avoided both secondary and tertiary roads, but selected conifer forests (Table 4, Appendix S3: Table S1).

DISCUSSION

Our study contributes to a greater understanding of canid homesite selection by evaluating resource selection at pup-rearing sites of sympatric wolves and eastern coyotes. We found that canids generally selected resources consistently at den and rendezvous sites, except that they selected steeper slopes at dens (H1). Previous work indicated that eastern wolves in APP also selected steeper slopes at dens relative to rendezvous sites (Benson et al. 2015a). Wolves in APP also selected wetlands and water more and avoided secondary roads more at dens than at rendezvous sites (Benson et al. 2015a). In our current study adjacent to the largely unprotected landscape outside of APP, resource selection by canids appeared to be most strongly influenced by human presence. Indeed, we found that canids established homesites further from secondary roads and open areas with reduced vegetative cover. These results are consistent with previous studies of canid homesite selection in areas where canids are harvested (e.g., Kaartinen et al. 2010, Iliopoulos et al. 2014, Sazatornil et al. 2016). The selection of wetlands at homesites in our current study, as well as in APP (Benson et al. 2015a), reflects the importance of this habitat type during pup-rearing season. Beavers are commonly associated with wetlands and water sources (Donkor and Fryxell 1999) and are an important seasonal source of food for canids in central Ontario (Benson et al. 2013), as well as across North America and Europe (Latham et al. 2013, Newsome et al. 2016, Gable et al. 2018).

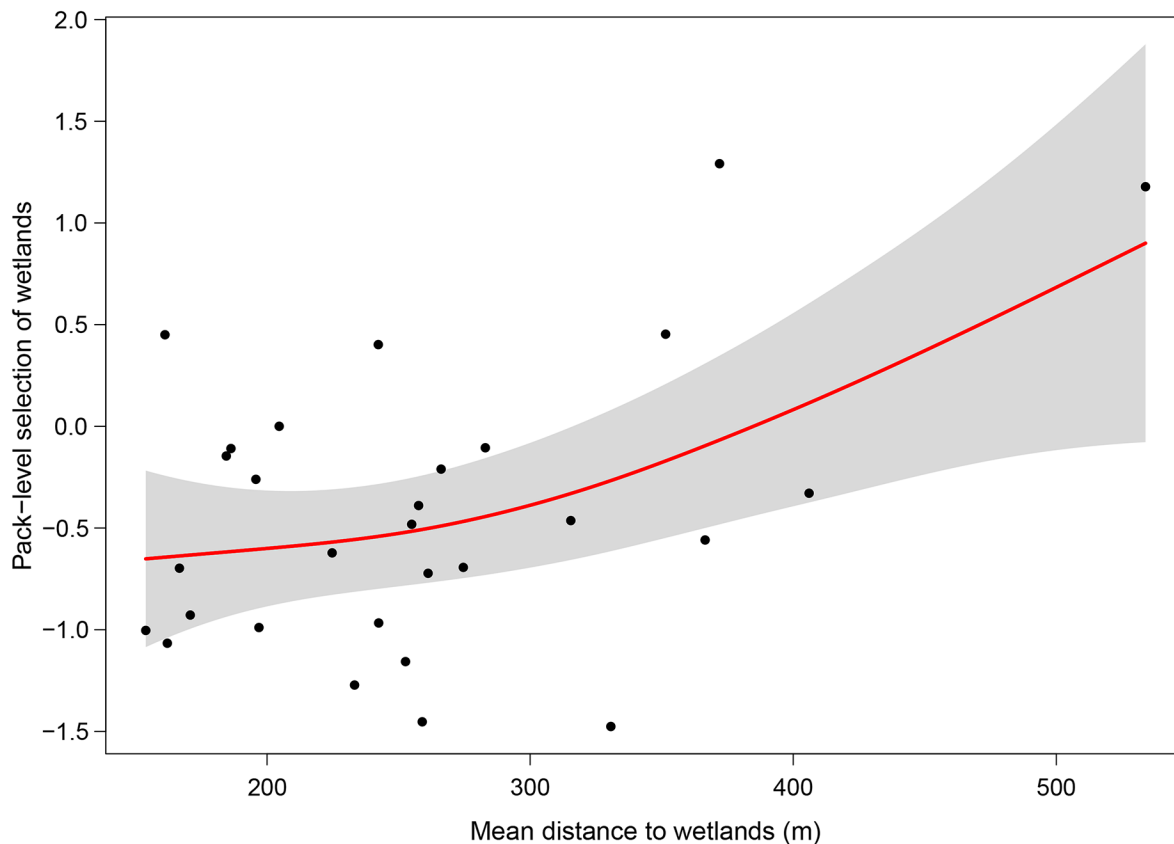


Fig. 2. Selection of wetlands by canids at homesites as a function of distance-based availability of wetlands within territories as predicted by a generalized additive model. Dots represent the data used to build the model.

Ancestry strongly influenced resource selection at homesites (H2) as packs with greater wolf ancestry exhibited greater selection for tertiary roads and wetlands, similar to eastern wolves in APP (Benson et al. 2015*b*). The use of roads by wolves can be advantageous by improving traveling efficiency and potentially increasing hunting success (e.g., Dickie et al. 2017, James and Stuart-Smith 2000). Therefore, establishing homesites closer to tertiary roads might be especially beneficial to wolves for navigating to and from homesites during the pup-rearing period when energetic demands are high, given their larger home ranges compared coyotes. However, roads in our study area are associated with greater mortality risk because they provide access to hunters and trappers (Benson et al. 2014), suggesting that it may be adaptive to select homesites farther from roads. The majority of eastern wolves in Ontario are located in APP

(Rutledge et al. 2010, Benson et al. 2012), such that many of the wolves inhabiting adjacent areas are likely to have dispersed from APP. Thus, the greater selection of roads by packs with wolf ancestry outside the park could be related to prior experience with roads in the protected area of APP where roads do not carry the same mortality risk (Benson et al. 2015*a*).

Packs with greater wolf ancestry also selected wetlands more strongly. A previous study of sympatric wolves and coyotes in Montana documented that beavers comprised a greater proportion of the diet of wolves relative to coyotes (Arjo et al. 2002). Previous work has established that beavers are important prey for wolves in the Algonquin region (Voigt et al. 1976, Benson et al. 2013), and recent evidence from stable isotope analysis indicates that beavers are consumed more by animals with greater wolf ancestry in the central Ontario hybrid zone (Benson et al.,

Table 4. Estimated coefficients (β) and lower (LCL) and upper (UCL) 95% confidence limits from two mixed-effect models for canid resource selection at homesites considering potential influence of resource selection on pup survival in central Ontario, Canada.

Parameter	High pup survival			Low pup survival		
	β	95% LCL	95% UCL	β	95% LCL	95% UCL
Intercept	-6.12	-7.02	-5.22	-5.62	-7.27	-3.98
2° Roads	3.21	2.24	4.22	1.55	0.06	2.99
3° Roads	0.57	-0.21	1.35	0.80	0.12	1.53
Hardwood	-1.84	-3.44	-0.40	-2.56	-8.42	1.95
Conifer	0.88	0.44	1.33	-1.51	-2.43	-0.69
Mixed	-0.18	-0.65	0.28	-0.23	-0.73	0.23
Wetland	0.26	-0.19	0.69	-0.03	-0.49	0.40
Water	-0.05	-0.52	0.39	0.46	-0.06	0.96
Rock/ Grass	0.77	0.18	1.34	0.50	-0.12	1.12
Elevation	0.59	-0.66	1.84	0.49	-0.76	1.90
Slope	-0.01	-0.54	0.48	-0.03	-0.53	0.41

Notes: Shown are results from model for packs with high pup survival (>75%) and low pup survival (<50%). Significantly selected and avoided resources are shown in bold. All resource variables were distance-based except for slope and elevation.

unpublished data). Thus, the greater selection of wetlands at homesites by packs with greater wolf ancestry may reflect the greater importance of beavers to the diet of wolves during the pup-rearing season.

Coyotes usually exhibit considerable flexibility in habitat selection, including the selection of open and urban areas (Arjo and Pletscher 2004, Hinton et al. 2015, Mitchell et al. 2015). Additionally, previous research in central Ontario showed that canids with greater coyote ancestry established their territories in areas with higher road density at the landscape level, suggesting a greater tolerance of human disturbance relative to wolves (Benson et al. 2012). Therefore, although coyotes may tolerate higher levels of human presence at the landscape level in the region, our current results suggest they mitigate risks at finer scales during important activities like pup-rearing by avoiding roads, which may help to reduce mortality risk in these human-occupied areas. Ungulates exhibit trade-offs in resource selection between broad and fine scales to reduce predation risk and maximize fitness (Hebblewhite and Merrill 2008), and our results

suggest coyotes in Ontario may adopt similar scale-dependent strategies to mitigate risk of human-caused mortality. Interestingly, coyotes in western North America appear to adopt a similar strategy to mitigate risk from larger predators (wolves) as they select home ranges within those of wolves, but exhibit adaptive resource selection patterns within their home ranges to mitigate predation risk (Atwood and Gese 2010). Mitigation of mortality risk during pup-rearing in risky landscapes could be an important behavioral mechanism underlying the ability of coyotes to persist in human-dominated areas and may have aided in their successful range expansion across eastern North America in the 20th century.

In general, there was considerable pack-level variation in homesite selection. However, this pack-level variation only manifested in a clear functional response in resource selection for wetlands, offering partial support for our hypothesis (H3). Contrary to our prediction, the selection of wetlands was strongest in home ranges where they were most common and weakened in home ranges with fewer wetlands in a consistent but non-linear fashion. As the importance of wetlands is likely at least partially due to the presence of beavers in these habitat types, this functional response may suggest that packs in territories with abundant wetlands exploit beavers as a central component of their diet. Conversely, packs with few wetlands in their territories may have to subsist largely on ungulate prey (deer and moose) during pup-rearing, such that selection of wetlands becomes less important.

Previous research has shown that environmental factors and behavior patterns affect pup survival (e.g., Harrington et al. 1983, Benson et al. 2013, 2015a). We found that different patterns of resource selection at homesites were associated with higher and lower pup survival (H4) with a subset of our data for which we had pup survival estimates from known-fate analyses. While all packs clearly avoided secondary roads, those with higher pup survival exhibited an effect size for avoidance that was more than twice that of packs with lower pup survival, although variation was high (Table 4). Additionally, packs with higher pup survival selected hardwood forests more and conifer forests less than packs with lower pup survival. Hardwood forests in central

Ontario are probably associated with greater prey availability in terms of both ungulates and beavers relative to conifer forests (Fryxell and Doucet 1993, Fryxell 2001, McLoughlin et al. 2011). It should be noted that we had a relatively small sample for the pup survival analysis (16 litters from 12 packs) which precluded meaningful investigation of genotype-specific patterns of resource selection relative to pup survival. Nonetheless, known-fate pup survival data from pups of wolves and coyotes are extremely rare so our results are valuable for beginning to elucidate relationships between resource selection at homesites and a key component of fitness for wolves and coyotes.

Studies have suggested that coyotes are filling the ecological role of wolves in eastern North America, primarily through their predation on white-tailed deer (Ballard et al. 1999). However, recent findings suggest that wolves and coyotes occupying the same landscape, but free from interspecific competition within home ranges, exhibited different predation patterns and likely play different ecological roles (e.g., Benson et al. 2017). Our current results increase understanding of ecological differences between wolves and eastern coyotes by showing that packs with varying degrees of *Canis* ancestry select different resources during pup-rearing season, further suggesting that eastern coyotes are not occupying the niche of wolves in eastern North America. These different niches with respect to pup-rearing may have implications for the greater ability of coyotes to persist in human-dominated landscapes relative to wolves. Specifically, the scale- and context-dependent responses of eastern coyotes to human presence (i.e., selection at broad scales, avoidance at homesites) could contribute to their persistence in human-dominated landscapes where persecution is high by balancing the risk and rewards associated with humans. Clearly, more research is needed to fully elucidate the niches of eastern coyotes and wolves and to better understand their variable demographic responses to human disturbance and persecution.

The proposed goal of eastern wolf recovery in Ontario is to expand the existing population numerically and geographically to areas in central Ontario adjacent to the population core in APP (Beacon Environmental Limited and Wildlife

2000 Consulting 2018). Our results suggest that areas with abundant wetlands and fewer secondary roads are suitable habitat for parturition and pup-rearing of canids throughout the spring and summer. Packs with greater wolf ancestry selected wetlands more strongly than other canids, further highlighting the apparent value of this landscape feature, and the valuable prey they support for eastern wolves. Areas with greater proportions of hardwood forests and wetlands were also strongly associated with greater pup survival suggesting that prioritizing these prey-rich habitat types in areas with lower densities of secondary roads may provide canids with homesites offering the greatest fitness benefits (prey) while minimizing risk of human-caused mortality. Indeed, previous work has shown that pup mortality results from a relatively balanced combination of starvation and human causes in the unprotected landscape outside of APP (Benson et al. 2013). Our work also shows that animals with varying degrees of wolf and coyote ancestry select homesites differently indicating that their strategies for raising pups vary. Thus, future research linking pup survival to homesite selection patterns for eastern wolves specifically would provide important additional information to inform recovery efforts. However, such data will remain difficult to obtain as mated pairs of eastern wolves are rare outside of APP where hybridization is prevalent (Benson et al. 2012, Rutledge et al. 2017).

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