Spatiotemporal variation in selection of roads influences mortality risk for canids in an unprotected landscape

John F. Benson, Peter J. Mahoney and Brent R. Patterson

Ecologists are increasingly documenting individual variation in resource selection across populations in response to temporal or spatial environmental context. These behavioral patterns are assumed to be adaptive although previous studies have not linked them directly to survival and reproductive data to verify the assumed relationship between behavior and fitness. Recent work documented that higher density of secondary roads within home ranges of free-ranging canids (wolves, coyotes and hybrids) increased mortality risk in the hybrid zone adjacent to Algonquin Park in Ontario, Canada. Here, we examine individual behavioral responses of canids to spatially varying levels of human-disturbance and determine whether these responses to secondary roads resulted in differential mortality risk for canids across the hybrid zone. Specifically, we investigated resource selection within home ranges with GPS telemetry to determine whether canids selected roads more at night than during the day to minimize dangerous encounters with humans. Next, we modeled individual variation in spatial and temporal responses to secondary roads to evaluate the relative importance of intrinsic (Canis ancestry) and extrinsic (resource availability) influences on their behavior. Behavioral responses to roads were not well explained by variation in Canis ancestry. Instead, canids avoided roads more during day than at night as a non-linear function of increased road availability. Furthermore, canids that survived exhibited a stronger relationship between day–night selection of roads and road availability than canids that died suggesting an adaptive nature of this behavior. By modifying their selection of roads between day and night, canids appear to be able to exploit the beneficial attributes of roads while mitigating human-caused mortality risk. However, not all canids responded adaptively highlighting the importance of explicitly linking patterns of resource selection to components of fitness to accurately model and interpret individual variation in resource selection behavior of animals.

An individual’s selection of resources is a manifestation of complex interactions between resource traits, resource availability, and the individual’s phenotype (Bolnick et al. 2003). Individual variation in resource selection within animal populations can reflect important fitness tradeoffs associated with specific resources (Creel and Christianson 2008). Ecologists often study behavioral responses to provide insight into these tradeoffs because quantifying fitness directly is difficult and time-consuming (Beyer et al. 2013). Using behavior to infer fitness consequences assumes that animals are behaving adaptively such that their responses accurately reflect the costs and benefits of selecting or avoiding a given resource.

However, animals can be attracted to the benefits associated with certain resources while failing to perceive the risks (Delibes et al. 2001). Such maladaptive resource selection behavior may be especially prevalent in human-altered habitats because the causes of mortality or reduced reproduction are often different from those experienced during their evolutionary histories (Delibes et al. 2001). Although poorly understood, individual variation in response to risk within populations influences both individual fitness and how populations respond to environmental change (Wilson 1998, Sih et al. 2004). Thus, to better understand the responses of animals to human disturbance, ecologists should link behavioral patterns directly with measures of survival or reproduction to ensure the relationship between behavior and fitness is accurately characterized.

Selection of a given resource by individuals in a population may vary as a function of its availability, referred to as a functional response in resource selection (Mysterud and Ims 1998). Hebblewhite and Merrill (2008) showed that a functional response by wolves Canis lupus to human activity interacted with time of day such that individuals in areas of high human activity moved closer to human activity at night but avoided these areas during the day. Cougars Puma concolor in Alberta exhibited functional responses to a number of environmental variables, but not to roads or buildings; however, they modified their behavior temporally by avoiding roads and buildings more during day than at night (Knopff et al. 2014). Godvik et al. (2009) demonstrated a population-level functional response by red deer Cervus
elaphus to pasture habitat which varied in strength across seasons. These studies suggest that animals may vary resource selection patterns in response to both spatial (resource availability) and temporal (daily or seasonal) variation in environmental context. However, despite this recognition, no previous studies have explicitly modeled how individual-level differences in temporal selection behavior might vary as a function of resource availability across a population. This could provide valuable insight if the degree of temporal modification in resource selection behavior influences fitness at certain levels of an important resource, rather than degree of selection per se. Furthermore, previous studies documenting variation in selection behavior relative to resource availability have assumed these patterns were adaptive, but have not linked the observed behavior to survival or reproduction (Hebblewhite and Merrill 2008, Godvik et al. 2009, Houle et al. 2010, Beyer et al. 2013).

Wolves Canis spp. and coyotes Canis latrans have been persecuted across their ranges such that interactions with humans represent significant mortality risk (Musiani and Paquet 2004). However, both species can also exploit beneficial qualities of human presence in a variety of ways such as capitalizing on human food sources and using roads as travel routes (Fedriani et al. 2001, Whittington et al. 2005). Thus, the relationship between wolves and roads can be thought of in a similar context as tradeoffs faced by prey species between mortality risk and foraging efficiency (Lima and Dill 1990, Creel and Christianson 2008). One way that canids appear to balance the tradeoff between costs and benefits of human presence is by modifying their use of roads between day and night to minimize direct encounters with humans (Theuerkauf et al. 2003, Hebblewhite and Merrill 2008). The three-species hybrid zone between road gray wolves C. lupus, eastern wolves C. lycaon and eastern coyotes C. latrans adjacent to Algonquin Park in Ontario, Canada provides an opportunity to study intrinsic and extrinsic factors influencing individual variation in response to human disturbance. Human-caused mortality from trapping, shooting and vehicular collisions accounted for 75% of mortality in the hybrid zone adjacent to APP (Benson et al. 2014). Furthermore, secondary road (paved roads smaller than highways) densities within the home ranges of resident wolves, coyotes and hybrids varied considerably across the hybrid zone and negatively influenced survival (Benson et al. 2014). The considerable phenotypic and landscape heterogeneity across this hybrid zone facilitated our investigation into sources of individual variation in response to human disturbance.

We developed day–night and season-specific resource selection models for canids using GPS telemetry data collected from 2004–2011 in the Ontario Canis hybrid zone to address several questions and hypotheses. First, we investigated whether canids selected secondary roads more at night than during the day. Second, we quantified the degree to which individuals modified their selection of secondary roads between night and day and modeled these individual-level differences as a function of availability. This allowed us to test the hypothesis (H1) that individual variation in the difference in selection of roads between night and day would vary across the population as a function of the availability of roads. We predicted that individuals at higher road density would select roads more at night to exploit the benefits, whereas they would avoid them during day to minimize encounters with humans and associated mortality risks. We also hypothesized (H2) that surviving individuals would exhibit a stronger relationship between day–night behavioral modification and road availability than individuals that died to evaluate the adaptive nature of this behavior. Our results provide insight into behavioral mechanisms by which wolves and coyotes respond to both spatial and temporal heterogeneity in mortality risk in human-dominated landscapes and advance understanding of the mechanistic link between individual variation in resource selection and fitness within animal populations.

Material and methods

Study system

We studied canids in central Ontario immediately west (Wildlife Management Unit [WMU] 49), northwest (WMU 47), and south (Kawartha Highlands) of the large protected area of Algonquin Provincial Park (APP). The study area (110 000 km²) was a combination of private and public lands that were primarily used for logging, hunting and seasonal or year-round residences. White-tailed deer Odocoileus virginianus, moose Alces alces and beaver Castor canadensis were likely the main prey for canids (Forbes and Theberge 1996, Benson and Patterson 2013a). Eastern wolves are listed as a ‘species of special concern’ in Canada and their known distribution is largely restricted to APP and the surrounding areas where they are sympatric with eastern coyotes, admixed gray wolves and wolf × coyote hybrids (Benson et al. 2012). Habitat alteration, human-caused mortality and hybridization appear to be important threats to their persistence (COSEWIC 2001, Benson et al. 2014). Wolf and coyote harvest by trapping and hunting was allowed, on a seasonal or year-round basis throughout most of the study area except in several relatively small (2–375 km²) protected areas in the Kawartha Highlands. Importantly, all animals we studied were at risk of legal harvest, even those using portions of the protected areas, as their movements and home ranges overlapped with unprotected areas (Benson et al. 2014). Our study area has been described extensively, and depicted visually, elsewhere (Benson et al. 2012, 2014, Benson and Patterson 2013b).

Telemetry data

We captured canids using padded foothold traps or with nets fired from helicopters during 2004–2010. Specifically, we captured eastern coyotes (hereafter coyotes, n = 15), coyote × wolf hybrids (n = 12, either coyote × eastern wolf hybrids [n = 9] or coyote × gray wolf hybrids [n = 3]), and wolves (n = 9, either eastern wolves [n = 5] or eastern wolf × gray wolf hybrids [n = 4]). These ancestry classifications are based on the population genetic analyses of Benson et al. (2012). We deployed mortality sensitive GPS-collars on captured animals (intentionally targeting resident adults) and also drew blood for DNA analysis. We used 64 524 GPS locations from 36 canids in 33 packs for our analyses. Some
GPS collars were programmed with variable fix schedules both within and across collars, so we subsampled data when necessary such that data used in our models were collected at regular intervals (1–6 h) within datasets for each individual. We conducted repeated aerial and ground tracking surveys to count animals and tracks to determine if GPS-collared animals were resident animals traveling with a pack. Only adult or yearling, resident, pack animals for which we obtained > 1 month of continuous telemetry data within a given season were included in the analyses, whereas we excluded data from all solitary, transient or dispersing animals. The mean GPS telemetry monitoring period per animal was 281 days (range 31–708). We estimated 95% fixed kernel seasonal home ranges with the plug-in estimator to determine bandwidth (Sheather and Jones 1991) for all study animals during winter (1 Dec–31 Mar) and summer (1 Apr–30 Nov). The winter season corresponded approximately to the period of ice on lakes and continuous snow cover. We classified all telemetry locations as either day (08:00–19:59) or night (20:00–07:59) based on our experiences encountering humans on roads during different times of day throughout the study area during field activities. Fix success of GPS collars deployed on canids was 91%. A concurrent study in APP using GPS collars found mean location error for all fixes to be 12.5 m and no evidence of habitat-induced GPS bias (Maxie 2009). Thus, we assumed that our results and inferences were not strongly affected by location error or missed telemetry fixes. Additional details on field methods and telemetry data are in Supplementary material Appendix 1–2.

**Resource selection modeling**

We investigated resource selection at Johnson’s (1980) 3rd order of selection by comparing locations used by radio-collared animals to those available within their seasonal home ranges. We identified 30 m pixels (30 × 30m) on the landscape used by canids with GPS telemetry data. We systematically subsampled 30 m pixels throughout each seasonal home range (resulting in a mean of 37 pixels km$^{-2}$) to estimate availability of resources for each canid using GIS methods described by Benson (2013). We measured the distance between used and available locations to three road types (primary, secondary, tertiary) and six habitat classes (hardwood forest, conifer forest, mixed forest, wetlands, water, and rock/grass; see additional details on resource variables in Supplementary material Appendix 1). Primary roads were paved roads with relatively high traffic volume classified as freeways or expressways or highways. Secondary roads were generally paved and were classified as arterial, local/street, or collector roads. Tertiary roads were unpaved roads and trails that received light traffic, mostly from recreational vehicles and hikers, classified as resource/recreation roads or trails. Distance-based variables are effective for assessing selection and/or avoidance of habitat classes (Conner et al. 2003). Additionally, using continuous, distance-based variables for habitat classes, rather than categorical variables, eliminated the need to base inference on subjectively chosen reference categories in resource selection models. Topographical features can strongly influence canid resource selection patterns (Whittington et al. 2005), so we also estimated slope and elevation at used and available locations from digital elevation models (DEM) in ArcGIS10 (Supplementary material Appendix 1).

We developed seasonal resource selection function (RSF) models for canids with Bayesian generalized linear mixed models (GLMMs) implemented in the R package ‘MCMCglmm’ ver. 2.17 (Hadfield 2010) with a binary (0 = available, 1 = used) response variable (see additional details on model specification and diagnostics in Supplementary material Appendix 1). Bayesian mixed-effect regression models are naturally suited for understanding hierarchical processes such as resource selection (Wikle 2003, Bakian et al. 2012) and Markov chain Monte Carlo (MCMC) sampling yields robust parameter estimates and credible intervals which alleviate concerns regarding model-based standard errors derived from traditional (frequentist) mixed effect RSF models (Fieberg et al. 2010, van Beest et al. 2010). We included random intercepts for individual and pack in each model, with individuals nested in packs. Including random intercepts for individuals mitigated effects of the unbalanced telemetry datasets among animals and the potential lack of independence between sequential telemetry locations due to spatial autocorrelation (Gillies et al. 2006). The random intercept for pack accounted for the social nature of wolves and coyotes and the potential lack of independence in resource use within packs (Hebblewhite and Merrill 2008). packs consisted of multiple (2–10) animals of either a single *Canis* type, or multiple *Canis* types within the same pack. All packs were territorial with, and spatially segregated from, neighboring packs regardless of the genetic ancestry of pack members (Benson and Patterson 2013b). Thus, there should have been minimal influence on resource selection behavior within home ranges due to interactions among *Canis* types from different packs. We included data from all GPS collared canids in our RSF models regardless of their genetic ancestry, but accounted for potential differences in resource selection among *Canis* types when assessing individual-level responses to specific resource variables of interest.

The full model for each seasonal day–night combination included main effects for all fixed predictor variables (Supplementary material Appendix 3). The resulting coefficients for fixed main effects represented population-level (marginal) responses. We also developed a random slope-intercept model for each seasonal day–night combination that was identical to the full model except that instead of including secondary roads as a fixed effect, we allowed it to interact with the random term for individual. Thus, different intercepts and slopes were fit for each canid to model individual variation in selection of secondary roads. This allowed us to derive individual-level (conditional) coefficients for the selection of secondary roads by each canid. We compared the fit of five models (four marginal and one conditional) of varying complexity using deviance information criteria (DIC), a Bayesian analogue to Akaike’s information criteria (Spiegelhalter et al. 2002). We assessed selection or avoidance of resource variables using 95% highest posterior density (HPD) credible intervals derived from MCMC simulation to identify fixed-effect beta coefficients that differed significantly from 0 (i.e. when 95% HPD interval did not overlap 0). The terms ‘selection’ and ‘preference’ have sometimes been used synonymously or inconsistently in the resource selection literature (Beyer et al. 2010, Lele et al. 2013). To
avoid confusion, we use the terms selection and avoidance throughout to indicate that a resource variable was used significantly more or less, respectively, relative to its availability throughout an individual’s home range in either a distance or classification-based context.

Modeling individual variation in selection of roads

First, we modeled the individual-level conditional coefficients for selection of secondary roads as a function of availability during day and night (separately), similar to studies investigating functional responses (Hebblewhite and Merrill 2008). Next, for each individual, we subtracted the conditional coefficient for selection of secondary roads at night from the corresponding coefficient for selection during the day for both winter and summer models. These calculations yielded differences in selection of secondary roads between day and night for each canid in both seasons. Positive values indicated secondary roads were selected more during the night, negative values indicated that secondary roads were selected more during the day, and values close to zero indicated little difference between day and night selection of roads. These temporal differences in selection provided standardized measures of individual-level behavioral modifications between night and day that we then modeled in relation to road availability across the population.

We used generalized additive models (GAMs) implemented in the R package ‘mgcv’ (ver. 1.7-19) to investigate variation in the responses of canids to human disturbance by modeling differences in selection of secondary roads between night and day as a function of their availability. GAMs were appropriate because they allowed us to detect linear or non-linear changes in selection behavior as a function of availability. We did not include a random effect of pack because coefficients used to calculate the response variable of the GAMs were derived from GLMMs that had already accounted for potential correlations within pack and because we only included >1 animal in 3 of 33 packs. For each GAM, we included individual differences between day and night coefficients as the response variable and potential intrinsic or extrinsic influences as predictor variables. We included a smooth (non-parametric) term for the mean distance to secondary roads in each individual’s home range (range = 320–3354 m) to represent the (distance-based) availability of roads. We also considered a non-parametric term for the proportion of coyote ancestry for each individual (range = 0.01–0.98; inverse was proportion of wolf ancestry; values derived from genetic structure analyses of Benson et al. 2012) to investigate whether day–night selection of roads varied as a function of Canis ancestry. We considered three models with only main effects: availability, ancestry and availability and ancestry together.

Next, we considered a model set with interactions between predictors. We tested the hypothesis that spatiotemporal variation in response to secondary roads influenced mortality risk (H2) by creating a dichotomous fate variable which separated individuals based on whether they survived (n = 20) or died (n = 15) during the study. Specifically, we considered an interaction between the non-parametric term for availability of secondary roads and the parametric fate variable to determine whether animals that survived and died exhibited differences in their response to secondary roads. Canids could be legally harvested during fall and winter so we assumed that, if spatial and temporal variation in response to roads influenced mortality, the difference between animals that survived and died would be stronger in winter than summer. Indeed, most (82%) of the mortality of radiocollared canids in our study area occurred from October to April, so we tested H2 using the coefficients derived from winter models. However, we also present the results from the summer model to determine if the pattern was generally consistent across seasons. We investigated this interaction using the ‘by’ command in ‘mgcv’ which estimates a separate smooth function of the continuous variable (availability) for each level of the factor variable (fate; Wood 2006). We also included fate as a parametric main effect to account for the fact that smooth terms are subjected to a centering constraint that is not required in the presence of a smooth × factor interaction (Wood 2006). We considered models with lower generalized cross validation scores (GCV) to be superior (Wood and Augustin 2002).

Field methodology for monitoring survival and evaluating cause of death was described in detail by Benson et al. (2014). Thirteen of 15 canid mortality events were known (n = 12) or suspected (n = 1) to be due to human causes. We also included the two natural deaths in our analyses because we were interested in both positive and negative effects of roads. However, we also modeled spatiotemporal responses to roads without the two natural mortality events to verify that the results were not strongly influenced by considering mortality from both human and natural sources (additional details on mortality data and their treatment in our analyses are in Supplementary material Appendix 1–2).

Results

Resource selection models

The best marginal resource selection model included all habitat classes, slope, elevation and the three road variables (Table 1). Canids exhibited stronger selection for secondary roads at night than during the day (Table 2). Population-level resource selection coefficients for each variable are provided in Table 2. Inclusion of random slopes to account for the fact that smooth terms are subjected to a centering constraint that is not required in the presence of a smooth × factor interaction (Wood 2006). We considered models with lower generalized cross validation scores (GCV) to be superior (Wood and Augustin 2002).

Individual variation in selection of roads

No functional response was detected when we modeled individual-level selection of secondary roads as a function of their availability during day (winter: EDF = 1, F = 0.8, p = 0.376; summer: EDF = 1.4, F = 0.2, p = 0.757) or night (winter: EDF = 1.1, F = 2.2, p = 0.140, summer: EDF = 1, F = 2.7, p = 0.142) separately. However, availability of secondary roads was a significant, non-linear predictor of differences in selection of secondary roads between day and night in winter (EDF = 1.9, F = 5.1, p = 0.010, n = 30; Fig. 1a) and summer (EDF = 2.0, F = 3.6, p = 0.031, n = 54; Fig. 1b) supporting our first hypothesis (H1). GLMs fit with the same data and parameters as the GAMs showed
similar overall trends for winter and summer, but model fit was better for GAMs suggesting our use of non-linear models was justified (Supplementary material Appendix 4).

During winter, model fit improved with the inclusion of the availability × fate interaction indicating there were differences in the behavioral response of canids that survived and died (Table 3). The two models with the availability × fate interaction (with and without the effect of ancestry) were the best overall models explaining differences between day–night selection of secondary roads during winter and summer (Table 3). These two models differed only slightly in terms of GCV scores and also yielded consistent parameter estimates for the different responses of animals that survived and died (Table 3, 4). In winter, day–night differences in secondary road selection varied significantly as a non-linear function of availability for animals that survived, but not for animals that died supporting our second hypothesis (H2; Table 4, Fig. 2, Supplementary material Appendix 5a). In summer, day–night differences in secondary road selection varied significantly as a non-linear function of availability for canids that survived in both top models (Table 4). For canids that died, day–night differences in secondary road selection during summer varied significantly as a non-linear function of availability in the model retaining ancestry, and marginally significantly in the model without ancestry (Table 4). In both summer models, the relationship between day–night differences in road selection and availability was weaker for canids that died relative to those that survived (Table 4, Supplementary material Appendix 5b). During summer, the main effect of fate indicated that canids that survived changed their selection for secondary roads more from day to night than canids that died (Table 4). Results of models with only human-caused mortality were consistent with models including all mortality events (Supplementary material Appendix 6).

Discussion

Canids in the Ontario hybrid zone did not exhibit a classical functional response in resource selection because selection of roads did not vary significantly as a function of road availability during day or night. Instead, the degree of behavioral modification by individuals between day and night increased at higher road densities. More specifically, canids in the Ontario hybrid zone avoided secondary roads more strongly during the day than at night as a non-linear function of increasing road availability. Several recent studies investigating resource selection at varying levels of resource availability across populations have acknowledged their inability to link resource selection with mortality or other fitness measures, but noted the value of doing so (Hebblewhite

Table 1. Model selection results for seasonal, night and day resource selection function models in central Ontario, Canada, 2004–2011. Shown are deviance information criteria values (DIC) and difference between DIC of a given model the strongest supported model (ΔDIC) for each model considered.

<table>
<thead>
<tr>
<th>Model</th>
<th>Winter Day</th>
<th>Winter Night</th>
<th>Summer Day</th>
<th>Summer Night</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>DIC</td>
<td>ΔDIC</td>
<td>DIC</td>
<td>ΔDIC</td>
</tr>
<tr>
<td>Random slope†</td>
<td>84035</td>
<td>0</td>
<td>85068</td>
<td>0</td>
</tr>
<tr>
<td>Habitat and roads</td>
<td>84952</td>
<td>917</td>
<td>85934</td>
<td>866</td>
</tr>
<tr>
<td>Habitat‡</td>
<td>85074</td>
<td>1039</td>
<td>85969</td>
<td>901</td>
</tr>
<tr>
<td>Roads§</td>
<td>85733</td>
<td>1698</td>
<td>86685</td>
<td>1617</td>
</tr>
<tr>
<td>Null model</td>
<td>85904</td>
<td>1869</td>
<td>86707</td>
<td>1639</td>
</tr>
</tbody>
</table>

† random slope for use of secondary roads by each individual included in best marginal model (i.e. ancestry, habitat and roads).
‡ habitat variables: slope, elevation, distance to each habitat class.
§ road variables: distance to primary, secondary, tertiary roads.

Table 2. Summary of mixed-effect Bayesian resource selection models separated by season and by night and day for radiocollared canids in central Ontario, 2004–2011. Shown are β coefficients with lower and upper 95% highest posterior density (HPD) credible intervals. Significant effects shown in bold. For slope and elevation, positive β indicates selection. All other variables are distance-based such that positive β indicates avoidance.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Winter-day β</th>
<th>95% HPD</th>
<th>Winter-night β</th>
<th>95% HPD</th>
<th>Summer-day β</th>
<th>95% HPD</th>
<th>Summer-night β</th>
<th>95% HPD</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>-2.57</td>
<td>(-3.11, -2.02)</td>
<td>-2.55</td>
<td>(-3.09, -2.03)</td>
<td>-2.51</td>
<td>(-2.90, -2.10)</td>
<td>-2.50</td>
<td>(-2.91, -2.11)</td>
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<tr>
<td>Water</td>
<td>-0.04</td>
<td>(-0.08, 0.00)</td>
<td>-0.24</td>
<td>(-0.28, -0.19)</td>
<td>-0.08</td>
<td>(-0.12, -0.04)</td>
<td>-0.19</td>
<td>(-0.23, -0.15)</td>
</tr>
<tr>
<td>Conifer</td>
<td>-0.06</td>
<td>(-0.10, -0.01)</td>
<td>0.01</td>
<td>(-0.03, 0.05)</td>
<td>-0.05</td>
<td>(-0.10, -0.00)</td>
<td>-0.06</td>
<td>(-0.10, -0.01)</td>
</tr>
<tr>
<td>Wetlands</td>
<td>-0.62</td>
<td>(-0.67, -0.57)</td>
<td>-0.33</td>
<td>(-0.37, -0.28)</td>
<td>-0.42</td>
<td>(-0.47, -0.38)</td>
<td>-0.30</td>
<td>(-0.35, -0.26)</td>
</tr>
<tr>
<td>Rock/grass</td>
<td>-0.01</td>
<td>(-0.06, 0.03)</td>
<td>-0.20</td>
<td>(-0.25, -0.16)</td>
<td>-0.13</td>
<td>(-0.18, -0.09)</td>
<td>-0.27</td>
<td>(-0.32, -0.23)</td>
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<tr>
<td>Hardwood</td>
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<td>(-0.15, -0.01)</td>
<td>-0.03</td>
<td>(-0.11, 0.05)</td>
<td>-0.29</td>
<td>(-0.37, -0.21)</td>
<td>-0.25</td>
<td>(-0.34, -0.18)</td>
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<tr>
<td>Mixed</td>
<td>-0.01</td>
<td>(-0.06, 0.04)</td>
<td>-0.08</td>
<td>(-0.12, -0.03)</td>
<td>-0.01</td>
<td>(-0.05, 0.04)</td>
<td>0.06</td>
<td>(0.01, 0.11)</td>
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<tr>
<td>Slope</td>
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<td>(0.13, 0.21)</td>
<td>0.18</td>
<td>(0.14, 0.22)</td>
<td>-0.28</td>
<td>(-0.32, -0.24)</td>
<td>-0.16</td>
<td>(-0.24, -0.14)</td>
</tr>
<tr>
<td>Elevation</td>
<td>-0.58</td>
<td>(-0.68, -0.47)</td>
<td>-0.86</td>
<td>(-0.97, -0.75)</td>
<td>-0.87</td>
<td>(-0.98, -0.74)</td>
<td>-1.00</td>
<td>(-1.13, -0.86)</td>
</tr>
<tr>
<td>Primary roads</td>
<td>0.20</td>
<td>(0.10, 0.28)</td>
<td>0.23</td>
<td>(0.14, 0.32)</td>
<td>0.27</td>
<td>(0.19, 0.35)</td>
<td>0.34</td>
<td>(0.26, 0.42)</td>
</tr>
<tr>
<td>Secondary roads</td>
<td>0.30</td>
<td>(0.24, 0.37)</td>
<td>-0.04</td>
<td>(-0.11, 0.02)</td>
<td>0.52</td>
<td>(0.46, 0.58)</td>
<td>0.21</td>
<td>(0.15, 0.28)</td>
</tr>
<tr>
<td>Tertiary roads</td>
<td>0.13</td>
<td>(0.08, 0.18)</td>
<td>0.12</td>
<td>(0.07, 0.16)</td>
<td>0.37</td>
<td>(0.32, 0.42)</td>
<td>0.32</td>
<td>(0.27, 0.37)</td>
</tr>
</tbody>
</table>
Figure 1. Relationship derived from a generalized additive model (GAM) between the difference in day–night selection of secondary roads by individual canids and the mean distance to secondary roads across their home ranges during (a) winter and (b) summer in Ontario, Canada. Note that the Y-axis is centered on 0 by the GAM. Gray shading shows the 95% confidence region and vertical bars on the x-axis show distance-based measures of availability.

Table 3. Generalized cross-validation (GCV) scores (lower indicates better fit) and percent (%) deviance explained for generalized additive models used to investigate the relationship between differences in selection of secondary roads between day and night by individual canids and 1) the mean distance to secondary roads within home ranges (availability), 2) % of their ancestry derived from coyotes (ancestry), and 3) interactions between availability of secondary roads and whether they survived or died during the study (fate).

<table>
<thead>
<tr>
<th>Model</th>
<th>Winter GCV</th>
<th>Winter % Deviance</th>
<th>Summer GCV</th>
<th>Summer % Deviance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Availability × fate + fate + Ancestry</td>
<td>0.87</td>
<td>59.2</td>
<td>0.34</td>
<td>63.8</td>
</tr>
<tr>
<td>Availability × fate + fate</td>
<td>0.88</td>
<td>53.4</td>
<td>0.32</td>
<td>62.9</td>
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<tr>
<td>Availability</td>
<td>0.92</td>
<td>33.6</td>
<td>0.40</td>
<td>25.6</td>
</tr>
<tr>
<td>Availability + ancestry</td>
<td>0.93</td>
<td>37.1</td>
<td>0.41</td>
<td>27.2</td>
</tr>
<tr>
<td>Ancestry</td>
<td>1.01</td>
<td>21.6</td>
<td>0.43</td>
<td>14.9</td>
</tr>
</tbody>
</table>

Table 4. Results for top two generalized additive models explaining individual differences in day–night selection for secondary roads by canids in central Ontario, 2004–2011. Availability = mean distance to secondary roads throughout home ranges, Ancestry = % coyote ancestry derived from genetic structure analysis, Fate = whether canids survived or died during the monitoring period.

<table>
<thead>
<tr>
<th>Model 1: Availability × Fate + Fate Non-parametric terms</th>
<th>EDF</th>
<th>F</th>
<th>p</th>
<th>n</th>
<th>EDF</th>
<th>F</th>
<th>p</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>Availability (survived)</td>
<td>3.5</td>
<td>4.8</td>
<td>0.005</td>
<td>18</td>
<td>2.2</td>
<td>5.9</td>
<td>0.005</td>
<td>20</td>
</tr>
<tr>
<td>Availability (died)</td>
<td>1.2</td>
<td>2.0</td>
<td>0.163</td>
<td>12</td>
<td>5.6</td>
<td>2.6</td>
<td>0.042</td>
<td>14</td>
</tr>
<tr>
<td>Parametric term</td>
<td>β</td>
<td>t</td>
<td>p</td>
<td>n</td>
<td>β</td>
<td>t</td>
<td>p</td>
<td>n</td>
</tr>
<tr>
<td>Fate</td>
<td>0.59</td>
<td>1.8</td>
<td>0.091</td>
<td>30</td>
<td>0.56</td>
<td>2.1</td>
<td>0.042</td>
<td>34</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Model 2: Availability × Fate + Fate + Ancestry Non-parametric terms</th>
<th>EDF</th>
<th>F</th>
<th>p</th>
<th>n</th>
<th>EDF</th>
<th>F</th>
<th>p</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>Availability (survived)</td>
<td>3.6</td>
<td>3.9</td>
<td>0.014</td>
<td>18</td>
<td>2.1</td>
<td>3.9</td>
<td>0.027</td>
<td>20</td>
</tr>
<tr>
<td>Availability (died)</td>
<td>1.0</td>
<td>0.9</td>
<td>0.356</td>
<td>12</td>
<td>5.5</td>
<td>3.8</td>
<td>0.081</td>
<td>14</td>
</tr>
<tr>
<td>Ancestry</td>
<td>1.5</td>
<td>1.2</td>
<td>0.311</td>
<td>30</td>
<td>1.</td>
<td>0.6</td>
<td>0.326</td>
<td>34</td>
</tr>
<tr>
<td>Parametric term</td>
<td>β</td>
<td>t</td>
<td>p</td>
<td>n</td>
<td>β</td>
<td>t</td>
<td>p</td>
<td>n</td>
</tr>
<tr>
<td>Fate</td>
<td>0.44</td>
<td>1.3</td>
<td>0.208</td>
<td>30</td>
<td>0.53</td>
<td>2.1</td>
<td>0.048</td>
<td>34</td>
</tr>
</tbody>
</table>

and Merrill 2008, Godvik et al. 2009, Beyer et al. 2013). We did not quantify lifetime reproductive success and recognize the limitations in our fate variable as a fitness proxy. Nonetheless, survival is a critical component of fitness and strongly influences population growth in animal populations (Oli and Dobson 2003) including canids in the Algonquin region (Patterson and Murray 2008). Hebblewhite and Merrill (2008) quantified a functional response in selection for areas of higher human activity by wolves that varied in relation to availability and between night and day. We build on their work by showing that different behavioral strategies around roads in time and space led to different mortality risks.

A limitation of our study was the relatively small sample sizes of individual animals (n = 36) and mortality events (n = 15). Nonetheless, we note that our sample size in terms of number of animals, packs and telemetry locations was considerably larger than previous studies investigating resource selection by canids with GPS telemetry, including those documenting functional responses with non-linear models (McLoughlin et al. 2004, Hebblewhite and Merrill 2008, Houle et al. 2010, Lesmerises et al. 2012). Furthermore, our sample allowed us to link mortality risk with behavioral patterns of canids to derive novel, biologically plausible results regarding phenomena speculated upon by previous researchers (Hebblewhite and Merrill 2008).
Resource selection by canids is influenced by the need to acquire sufficient food resources (Mech and Boitani 2003), travel efficiently (Whittington et al. 2005), and temporally or spatially avoid areas of increased mortality risk from humans (Hebblewhite and Merril 2008). We interpret the strong selection of wetlands and water by canids as reflections of the association of beavers with these habitats (Donkor and Fryxell 1999) and the importance of beavers as a food resource for canids in central Ontario (Forbes and Theberge 1996). Furthermore, beaver density is higher in areas with lower stream gradients (Beier and Barrett 1987) and was negatively associated with elevation in nearby APP (Benson et al. 2013). Thus, predation on beavers may at least partially explain the strong negative association with areas of steeper slopes and higher elevations during summer, when beavers become a more important resource for canids in central Ontario (Forbes and Theberge 1996). Conversely, canids selected steeper slopes during winter when slopes may increase vulnerability of ungulate prey and allow for more successful predation on deer and moose (Muntz and Patterson 2004, Benson and Patterson 2013a).

While selecting or avoiding natural landscape features, such as slopes and wetlands, may provide fitness benefits with minimal costs, anthropogenic features likely have conflicting effects on fitness of canids. Wolves, coyotes and other canids benefit from roads through access to human food sources (Fedriani et al. 2001, Newsome et al. 2013), greater traveling efficiency (Whittington et al. 2005) and perhaps increased predation rates (James and Stuart-Smith 2000). Indeed, we documented canids feeding on garbage at landfills, carcass piles from hunters and highly concentrated deer that were supplemental feeding in close proximity to human residences (Benson and Patterson unpubl.). These potential benefits could positively influence either survival or reproduction. However, human-caused deaths from harvest and vehicular collisions accounted for 75% of all mortality of canids in our study area and secondary road density negatively influenced survival (Benson et al. 2014). The individual-level differences in selection of roads from day to night were greatest at higher road densities showing that these responses to temporal changes in environmental context varied across the population as a function of the spatial environmental context. This pattern was most evident during winter when the tradeoff in terms of fitness costs (higher risk of mortality) and benefits (e.g. ease of travel, large concentrations of deer) associated with roads was likely most pronounced.

Individual variation in response to human disturbance can be a powerful selective force in human-altered landscapes (Bolnick et al. 2003). Natural selection should favor individuals that adjust their resource selection to maximize fitness in the face of processes that influence mortality (McLoughlin et al. 2008). A genetic-basis for behavioral traits such as shyness and boldness has been suggested for a variety of animals, and expression of these traits may be context-specific (Wilson 1998, Réale et al. 2000). Natural selection can act directly on specific behavioral traits, or indirectly on behavioral plasticity which allows animals to adjust behavioral states to appropriately match environmental context (West-Eberhard 1989, Thompson 1991). Our results show that individuals that exhibited greater variation between day and night in their selection of roads at higher road densities were more likely to survive. Thus, this greater individual-level behavioral flexibility to temporal changes in environmental context allowed canids to mitigate mortality risk.

Human-caused mortality of canids in central Ontario is relatively recent in evolutionary time, but nonetheless represents a strong selective pressure. Furthermore, high rates of genetic variation and novel allele combinations present in hybrid zones may facilitate elevated rates of natural selection and rapid adaptation to environmental change (Grant and Grant 1992, Rieseberg et al. 2003). Colonizing populations that engage in interspecific hybridization may exhibit especially rapid adaptation as they invade new environments (Seehausen 2004). Indeed, it has been suggested...
that hybridization between coyotes and wolves could have facilitated their successful, rapid colonization of southeastern Canada during the 20th century (Kyle et al. 2006, Kays et al. 2010). Previous discussion of rapid evolutionary change associated with Canis hybridization has primarily focused on potential morphological adaptations to effectively hunt large ungulate prey (Kyle et al. 2006, Kays et al. 2010). Our results suggest that behavioral traits are also under selective pressure from human disturbance in the contemporary Canis hybrid zone adjacent to APP and demonstrate behavioral and demographic mechanisms by which evolutionary change could be occurring.

The behavioral response to roads was probably also influenced by ontogenetic processes resulting from variation in prior experience with human-caused mortality risk by individual canids. Wolves and coyotes are social animals that learn skills crucial for their survival while traveling with their natal packs (Packard 2003). Thus, canids raised in areas of high road density and human-caused mortality risk probably adopt risk-averse behavior learned from their parents and should be more adept at balancing the tradeoffs associated with roads. Conversely, animals raised in areas without substantial human-caused mortality risk may be attracted to resources associated with roads (e.g. remains of hunted animals) without perceiving the risks (e.g. hunters) consistent with an attractive sink (sensu Delibes et al. 2001). For instance, wolves from protected areas tend to be less fearful of humans and individuals that are less cautious are more likely to be killed by hunting and trapping (McNay 2002). Reserves are designed to maximize species density by providing large areas of protected, homogenous habitat, but also may serve to minimize intrapopulation variation necessary to respond to environmental change (Bolnick et al. 2003).

In addition to the absence of human-caused mortality risk during their behavioral development, canid populations in protected areas may also lack variation in behavioral traits and experience relatively weak selective pressure for behavioral plasticity. Thus, despite strong natural selection for behavior that mitigates mortality risk in unprotected areas of central Ontario, canids exhibiting maladaptive resource selection behavior may continue to disperse into the hybrid zone from areas such as APP where this selective pressure is reduced or absent.

The increased mortality risk for canids associated with secondary roads in the hybrid zone adjacent to APP has conservation implications for eastern wolves. Resident and dispersing eastern wolves were at higher risk of human-caused mortality and survived poorly at higher road densities relative to other canids (Benson et al. 2014). Adult survival is the most important demographic parameter influencing population growth of eastern wolves in APP (Patterson and Murray 2008) and high rates of hybridization outside of APP may limit the degree to which reproduction can compensate for their poor survival in unprotected landscapes (Benson et al. 2014). If eastern wolves dispersing from the protected area lack adaptive behavioral traits necessary to mitigate human-caused mortality risk, this could explain their poor survival and have negative implications for population expansion outside of APP for this species of special concern.

Our results highlight the importance of adaptive behavioral responses by persecuted species to habitat features representing fitness tradeoffs in human-dominated landscapes. Whereas most studies documenting functional responses in resource selection have implicitly assumed that all individuals respond appropriately to changes in availability, our results suggest that spatial and temporal variation in behavior that influences survival or reproduction within populations must be considered to effectively model individual variation in resource selection. Model fit improved substantially with the inclusion of the availability × fate interaction revealing a strong spatiotemporal response to roads by canids that survived, and a non-significant or weaker response by those that died. Considering variation in adaptive behavior is especially important in human-altered landscapes because cues used by animals to perceive costs and benefits associated with specific resources can deteriorate (Remes 2000). If we had not considered the fate of individuals in our models, we would have underestimated the importance of the behavioral response across the population and inferred a considerably weaker relationship between secondary road availability and canid behavior. Thus, resource selection studies that fail to link behavioral patterns presumed to influence fitness directly with survival or reproductive success could result in erroneous or imprecise inferences regarding the response of animals to human disturbance.

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References


Supplementary material (available online as Appendix oik.01883 at <www.oikosjournal.org/readers/appendix>). Appendix 1–6.