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Ungulate predation and ecological roles of wolves and coyotes in eastern North America

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Abstract. Understanding the ecological roles of species that influence ecosystem processes is a central goal of ecology and conservation biology. Eastern coyotes (*Canis latrans*) have ascended to the role of apex predator across much of eastern North America since the extirpation of wolves (*Canis* spp.) and there has been considerable confusion regarding their ability to prey on ungulates and their ecological niche relative to wolves. Eastern wolves (*C. lycaon*) are thought to have been the historical top predator in eastern deciduous forests and have previously been characterized as deer specialists that are inefficient predators of moose because of their smaller size relative to gray wolves (*C. lupus*). We investigated intrinsic and extrinsic influences on per capita kill rates of white-tailed deer (*Odocoileus virginianus*) and moose (*Alces alces*) during winter by sympatric packs of eastern coyotes, eastern wolves, and admixed canids in Ontario, Canada to clarify the predatory ability and ecological roles of the different canid top predators of eastern North America. Eastern coyote ancestry within packs negatively influenced per capita total ungulate (deer and moose combined) and moose kill rates. Furthermore, canids in packs dominated by eastern coyote ancestry consumed significantly less ungulate biomass and more anthropogenic food than packs dominated by wolf ancestry. Similar to gray wolves in previous studies, eastern wolves preyed on deer where they were available. However, in areas where deer were scarce, eastern wolves killed moose at rates similar to those previously documented for gray wolves at comparable moose densities across North America. Eastern coyotes are effective deer predators, but their dietary flexibility and low kill rates on moose suggest they have not replaced the ecological role of wolves in eastern North America.

Key words: *Canis latrans*; *Canis lupus*; *Canis lycaon*; deer; eastern coyote; eastern wolf; functional response; kill rate; moose; predator–prey.

INTRODUCTION

Understanding interactions between species, and the influence of individual species on ecosystem dynamics, have been central pursuits in ecology (Paine 1969, Holt 1977, Estes et al. 2011). Species are not equal with respect to their influence on community dynamics, meaning that losing certain species can have disproportionate effects on the structure and function of ecosystems (Walker 1992, Lawton 1994, Tilman et al. 1997). However, conservation efforts directed at endangered species are often undertaken without consideration of their roles within ecological communities (Soulé et al. 2003, Tylianakis et al. 2010). In part, this may be because environmental legislation such as the United States Endangered Species Act was enacted prior to the development of conservation biology as a formal scientific discipline (Soulé

et al. 2005). More practically, understanding roles that individual species play within ecosystems is extremely complex (Mills et al. 1993), such that many species could go extinct before sufficient understanding is attained. Nonetheless, elucidating ecological functions performed by individual species increases understanding of community dynamics, and will help identify species whose protection or restoration would contribute to maintaining important ecosystem processes (Wallach et al. 2010, Ritchie et al. 2012).

Loss of apex predators can have broad implications for population dynamics of prey species, abundance and distribution of smaller predators, and community structure (Crooks and Soulé 1999, Ritchie and Johnson 2009, Estes et al. 2011, Ripple et al. 2014). When top predators are extirpated, the role they play in the ecosystem may also be lost because smaller predators are unlikely to exert similar predation pressure on large prey species (Messier et al. 1986, Gompert 2002, Boisjolly et al. 2010). Thus, the absence of large carnivores can greatly reduce predation on large herbivores and potentially destabilize both plant and animal communities (McCullough et al. 1997, Côté et al. 2004, Ripple et al. 2014). Medium-sized predators may increase in the absence of large carnivores

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(Crooks and Soulé 1999) and can negatively impact ungulate populations if their generalist strategy allows them to switch among several prey species (Patterson and Messier 2000, Prugh 2005) or if they prey more heavily on neonates (Berger et al. 2008). Alternatively, large and medium-sized predators could be ecologically redundant (*sensu* Walker 1992) if both are capable of performing similar ecological roles with respect to predation on ungulates (e.g., Ballard et al. 1999). Empirical evaluation of predation by large and medium-bodied carnivores under similar environmental conditions is required for a rigorous understanding of the ecological consequences of losing top predators from an ecosystem.

Ritchie et al. (2012) argued that conservation biology has emphasized studying taxonomy and origins of predators at the expense of understanding their ecological function. Indeed, significant research attention and debate during the last 15 years has focused on taxonomy and evolutionary history of canids in eastern North America (e.g., Wilson et al. 2000, Kyle et al. 2006, vonHoldt et al. 2011, 2016, Rutledge et al. 2012, 2015, Monzon et al. 2014), whereas studies evaluating predation patterns of wolves and coyotes in northeastern North America have been conspicuously absent. Indeed, the evolutionary origins of eastern wolves (*Canis lycaon*) remain controversial as some research suggests they are a unique species (e.g., Rutledge et al. 2012, 2015), whereas other work suggests they are the result of hybridization between gray wolves (*C. lupus*) and coyotes (*C. latrans*; e.g., vonHoldt et al. 2011, 2016). Regardless, in 2015, the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) recommended that eastern wolves be recognized as a unique species (*C. lycaon*) rather than a subspecies of gray wolf (*C. lupus lycaon*) and elevated their federal conservation status to “Threatened” in Canada due to low population numbers and their restricted distribution (COSEWIC 2015). Eastern wolves may have once occupied most of the deciduous forests of eastern North America (e.g., Wilson et al. 2000), but currently the majority of remaining eastern wolves inhabit areas in and adjacent to Algonquin Provincial Park (APP) in central Ontario (Rutledge et al. 2010a, Benson et al. 2012, COSEWIC 2015). Earlier studies in APP found that eastern wolves preyed mainly on white-tailed deer and rarely killed moose (Pimlott et al. 1969, Forbes and Theberge 1992, 1996); however, moose have replaced deer as the most abundant ungulate in APP since the 1960s (Quinn 2004). Thus, reevaluating eastern wolf predation patterns relative to their contemporary prey base will provide an improved understanding of their ecological role on the modern landscape and inform conservation efforts.

Eastern coyotes have become apex predators across most of eastern North America in the absence of wolves and there is considerable interest and confusion regarding their ecological role (Crête et al. 2001, Gompper 2002, Prugh et al. 2009). Eastern coyotes are effective predators of fawns and adult white-tailed deer (*Odocoileus*

virginianus) in some systems (e.g., Messier et al. 1986, Whitlaw et al. 1998, Patterson and Messier 2000, Kilgo et al. 2012) and have been documented occasionally killing adult moose (*Alces alces*; Benson and Patterson 2013a). Their greater size and predation on deer relative to western coyotes have led some researchers to suggest that eastern coyotes have replaced the ecological role of wolves (Mathews and Porter 1992, Ballard et al. 1999); whereas others have argued that coyotes cannot completely fill the niche of wolves due to their inability to effectively kill larger ungulates (Crête et al. 2001, Gompper 2002, Kays et al. 2008, Prugh et al. 2009). If eastern wolves prey mainly on deer and rarely kill moose (Pimlott et al. 1969, Forbes and Theberge 1992, 1996), even where moose are abundant, this would tend to support the hypothesis that eastern wolves and eastern coyotes play similar ecological roles. However, erroneously concluding that eastern coyotes have replaced the ecological role once performed by wolves could detract from wolf restoration efforts and the conservation of naturally functioning ecosystems (Crête et al. 2001). Thus, studies of predation patterns of eastern wolves and eastern coyotes are needed to critically evaluate the ecological functions performed by canids in eastern North America.

The contemporary hybrid zone between eastern coyotes, eastern wolves, and admixed gray wolves (hereafter Great Lakes-boreal wolves, *sensu* Rutledge et al. [2015]) in central Ontario, Canada (Benson et al. 2012) presents a unique opportunity to study ungulate predation by sympatric eastern coyotes, eastern wolves, and admixed canids that form packs representing a continuum of *Canis* ancestry. Unlike wolves and coyotes in western North America, all canid packs within the Ontario hybrid zone are territorial with each other regardless of the ancestry of individual pack members (i.e., home ranges of sympatric wolf and coyote packs are spatially segregated; Benson and Patterson 2013b). Thus, although competition may occur at the landscape level, eastern coyotes and wolves generally have exclusive access to prey within their territories without interference or exploitation competition from neighboring packs in central Ontario.

We combined GPS telemetry, field investigations, DNA analysis, and environmental data to quantify predation on deer and moose by canids of varying *Canis* ancestry in and adjacent to APP in central Ontario to address several questions. First, we estimated per capita ungulate kill rates by wolves, eastern coyotes, and hybrids preying on deer and moose during winter and investigated the relative influences of intrinsic, social, and environmental factors. We hypothesized that coyote ancestry within packs would negatively influence kill rates on ungulates, because the larger body size of wolves in central Ontario (Benson et al. 2012) should require them to rely on large prey more than coyotes. Second, we directly compared ungulate kill rates between packs dominated by eastern wolf and eastern coyote ancestry,

which represent estimates of predation pressure on ungulates by the functional social units in wolf and eastern coyote populations. Third, we estimated ungulate biomass consumed at kills by packs dominated by wolf and coyote ancestry. We hypothesized that canids in packs dominated by wolves would consume more ungulate biomass than canids in packs dominated by coyotes, suggesting different ecological roles with respect to ungulate predation. Finally, we compared per capita moose kill rates by eastern wolves inhabiting areas where deer were scarce and moose were the main ungulate prey to the classic functional response of gray wolves preying on moose across North America (Messier 1994). We hypothesized that eastern wolves would prey mainly on moose in areas where deer were scarce, given the reliance of wolves on ungulate prey (e.g., Fuller et al. 2003). However, we also hypothesized that the kill rates of eastern wolves would be lower than those previously documented for the larger gray wolf. The ecological basis for all our hypotheses were that larger predators should prey more heavily on ungulates, and especially larger ungulates, due to their greater (1) energetic requirements (Carbone et al. 1999, Sinclair et al. 2003) and (2) predatory ability (Stanley 1973, Gittleman 1985, MacNulty et al. 2009) relative to medium-sized predators. We tested our hypotheses in a multivariate context, given previous theoretical and empirical work establishing that predator group size (Creel 1997, Vucetich et al. 2004) and environmental factors, such as prey availability (Holling 1959, Messier 1994) and snow depth (Post et al. 1999, Patterson and Messier 2000) should also influence kill rates. We provide novel insight into predator-prey relationships of wolves and coyotes of varying *Canis* ancestry in eastern North America and clarify confusion regarding their ecological roles. Our results have practical implications for conservation of eastern wolves in Canada, wolf recovery in the northeastern United States, and management of coyotes and ungulates in landscapes where eastern coyotes are now the top predator.

METHODS

Study area

We studied ungulate predation by canids in Algonquin Provincial Park (APP) and in Wildlife Management Unit 49 (WMU49; Fig. 1) in central Ontario. Eastern wolves were the dominant, resident canids in APP (estimated 63%) where they are sympatric with smaller numbers of eastern wolf \times Great Lakes-boreal wolf hybrids and wolf (eastern and Great Lakes-boreal) \times eastern coyote hybrids with whom they sometimes form packs (Benson et al. 2012). Eastern coyotes (estimated 64%) and eastern coyote \times wolf (eastern and Great Lakes-boreal) hybrids (29%) were the dominant, resident canids in WMU49, whereas wolves were much rarer (7%; Benson et al. 2012). APP and WMU49 are both characterized by hardwood, conifer, and mixed forests interspersed with wetlands, lakes, and rocky

meadows. Elevations range from 180–580 m in APP and 79–549 m in WMU49. APP is mostly contiguous natural habitat with only a single paved road extending through the southern portion, whereas road densities and other anthropogenic landscape features are more common in WMU49 (Benson et al. 2012, Benson and Patterson 2013b). Canids are fully protected from harvest within APP and a buffer area surrounding the park (Fig. 1), whereas they can be legally shot and trapped in WMU49 during winter. Timber harvesting occurs in both areas but is more restricted in APP where clearcutting is prohibited and selective harvesting is the main method of extracting timber. Forestry practices have resulted in mature forest conditions throughout most of APP (Quinn 2004), whereas early successional habitat is more common in WMU49. White-tailed deer and moose occur in both APP and WMU49, although their densities vary spatially (Benson et al. 2012). However, deer are scarce in APP during winter and congregate in deer yards (areas where conifer trees provide shelter from deep snow and cold wind) outside of the park (Cook et al. 1999). Beavers (*Castor canadensis*) are an important summer food item for canids in central Ontario (Forbes and Theberge 1996, Benson et al. 2013) and occur throughout WMU49 and APP. Although density of beavers has not been estimated for our study area, they likely exist at higher densities in WMU49 due to greater availability of early successional habitat. Black bear (*Ursus americanus*) densities were estimated at 37 bears/100 km² (95% CI 21–66) and 32 bears/100 km² (95% CI 15–57) for WMU49 (2006) and APP (2006–2008), respectively (Ontario Ministry of Natural Resources and Forestry [OMNRF], unpublished data).

Field data

We captured wolves (*C. lycaon* and *C. lycaon* \times *C. lupus*), eastern coyotes, and coyote-wolf hybrids (*C. latrans* \times *C. lycaon* or *C. latrans* \times *C. lycaon* \times *C. lupus*) using padded foothold traps, modified neck snares, and helicopter net-gunning during 2005–2010 in APP and WMU49 to deploy Global Positioning System (GPS) or Very High Frequency (VHF) radio-collars and collect DNA samples (blood). All capture and handling were done in accordance with protocols approved by Trent University and the OMNRF Animal Care Committees under permit numbers 08039 and 5-75 to 10-75, respectively.

We visited clusters of GPS telemetry locations obtained from wolves, coyotes, and hybrids during the late fall, winter, and early spring (1 November–20 April) of 2005–2006 and 2006–2007 in APP, and in the winter (1 December–31 March) of 2009–2010 in WMU49 to investigate ungulate predation and scavenging. We truncated our data from APP such that all data used in our analyses came from winter (1 December–31 March) for consistency. We programmed collars to collect a fix every 90 minutes and mean acquisition success for collars from all packs was 87% (SE = 0.02, n = 23). We investigated

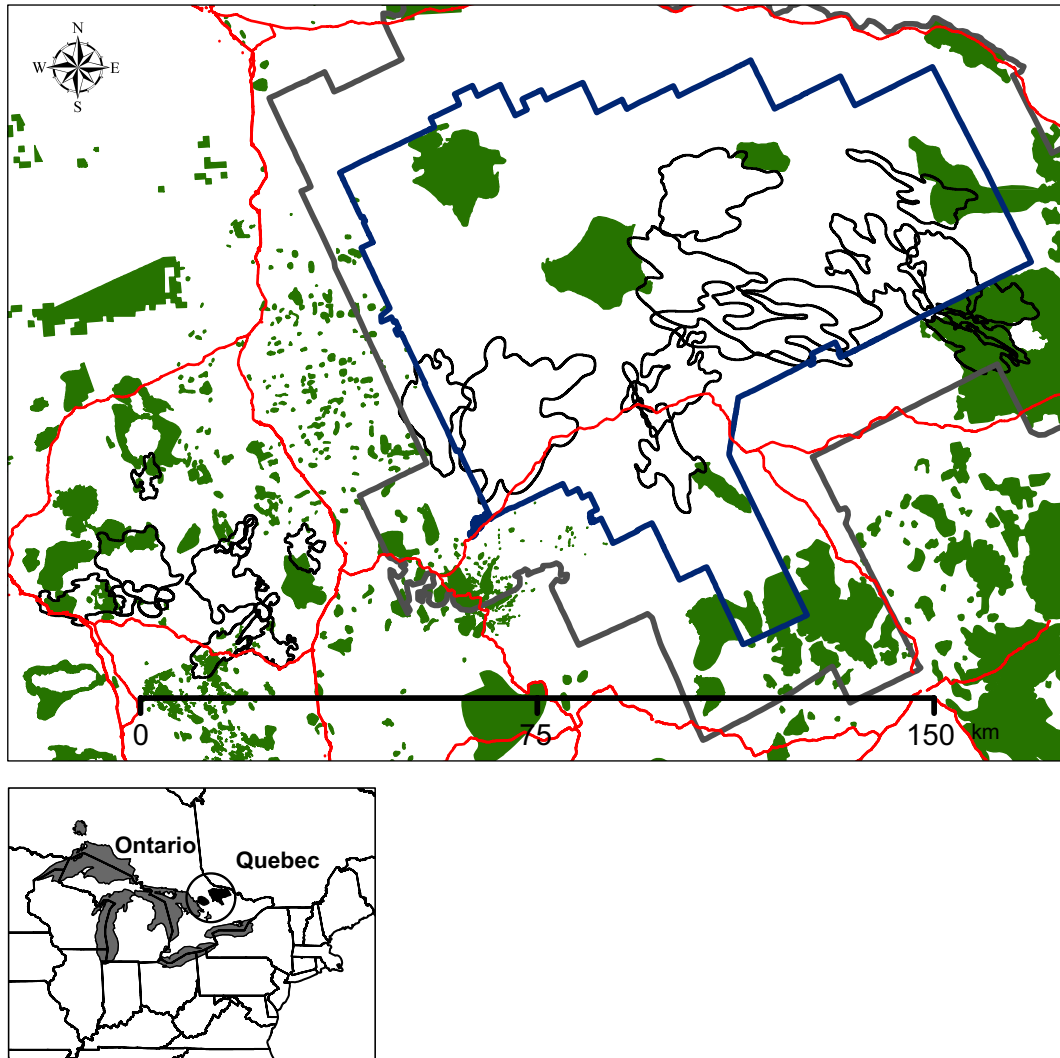


FIG. 1. Map of study area showing Algonquin Provincial Park, Ontario, Canada (APP, blue boundary) and Wildlife Management Unit 49 (WMU49). Canid home ranges are shown with black polygons, harvest ban area around APP is shown with gray border, deer wintering areas are in green, and major roads are in red.

most (94%) clusters of GPS telemetry data representing locations where focal packs spent ≥ 3 hours within a ≤ 200 m radius throughout the winter. We suspect canids often spent < 3 hours consuming smaller prey (e.g., beavers or snowshoe hare [*Lepus americanus*]) and may not have remained at these kill sites long enough to be detected by our sampling protocol. Thus, we assumed that we found most ungulates (deer or moose) killed by focal packs, but acknowledge that our data were not sufficient to estimate kill rates of smaller species.

We searched ≥ 100 m radius around each location in each cluster until we found evidence of predation or determined that the cluster was not associated with a carcass. When we found prey remains, we investigated the site to evaluate if the remains were killed or scavenged (i.e., discovered and consumed post-mortem) by the study animals. We interpreted the following as evidence

of predation: (1) broken vegetation (cleanly broken off) indicating struggle between predator and prey, (2) blood sprayed on vegetation, rocks, and/or snow, (3) clumps of prey hair embedded in bark of trees, (4) disarticulation of the skeleton or removal and shredding of the rumen (both indicating it was not frozen when the study animals arrived), and (5) awkward body position or location of prey species following previous studies of wolf or coyote predation (e.g., Mech 1970, Buskirk and Gipson 1978, Messier and Crête 1985, Benson and Patterson 2013a). Carcasses that were not killed by the focal pack appeared to have died of natural causes or were killed by packs of canids in adjacent territories (determined by examining telemetry data from all radiocollared packs). Where possible, we collected jawbones of deer or moose at kill sites to estimate the age of prey via cementum annuli analysis (Matson's Lab, Milltown, Montana, USA). Although we

collected jawbones at the majority of moose kills, we found few jawbones of deer as canids often carried deer skulls away from the kill sites.

Estimation of kill rates

We estimated kill rates in multiple ways to address different questions while accounting for differences in sizes of social groups, prey, and areas used by canids. First, we summed the number of deer and moose that were killed by each pack during each winter and divided these totals by the number of days the pack was monitored to estimate the kill rates by pack (kills/d). Second, we divided per pack kill rates by the number of canids in the pack to estimate per capita kill rates (kills·d⁻¹·canid⁻¹). Third, we estimated the proportion of biomass (kg) available to each pack from deer and moose carcasses killed by canids based on published masses of moose and deer from central Ontario (Kolenosky 1972, Quinn and Aho 1989; see additional details in Appendix S1). We divided estimates of biomass available from kills by the number of days the pack was monitored and the number of animals in each pack to estimate mass consumed daily per animal at kills and scavenged carcasses (kg biomass·d⁻¹·canid⁻¹). Finally, we divided the per pack kill rates by the home range size for each pack to estimate kill rates per pack per unit area (kills·d⁻¹·km⁻²).

We estimated the home range for each pack during the period we monitored their predation using GPS telemetry and 95% fixed kernels with the plug-in bandwidth estimator (Sheather and Jones 1991). Individuals in some packs in APP (5 of 13) and WMU49 (1 of 10) left their spring-summer-fall territories during portions of the winter to visit areas of highly concentrated deer in deer yards. Additionally, two packs in WMU49 expanded their spring-summer-fall ranges to include areas where deer were more abundant. Canids in APP and WMU49 are highly territorial and generally maintain exclusive home ranges (Benson and Patterson 2013b). This territoriality appears to be relaxed during winter forays to deer yards such that canids from different packs are no longer strictly spatially segregated (Cook et al. 1999). Thus, we estimated home ranges for packs that left their territories during winter in two ways. First, we estimated a home range using all locations, including those from periods when canids were visiting the deer yards, to estimate the entire areas used by the pack during the monitoring period. We used these first home ranges to estimate the availability of prey and snow depth (explained in *Intrinsic and extrinsic variables potentially influencing kill rates*) for each pack across the entire areas they used during the monitoring period. Second, we estimated a home range in which we excluded the locations obtained during extra-territorial forays. We used these second home ranges for estimates of kill rates per unit area to capture the areas that each pack occupied on the landscape in a territorial manner.

Kill rates can vary across seasons and within winter due to shifting prey availability, vulnerability, and snow conditions (Loveless 2010, Metz et al. 2012). Thus,

because we monitored some packs for less than the entire 121 day winter (mean = 81 days, range = 28–121 days, $n = 23$), we investigated whether there were significant differences in deer or moose kill rates between early winter (December and January) and late winter (February and March) using *t*-tests assuming unequal variances. We also quantified scavenging of ungulate carcasses to determine if scavenging negatively influenced kill rates and because previous research suggested wolves in APP obtained substantial meat from scavenging (Forbes and Theberge 1992).

Intrinsic and extrinsic variables potentially influencing kill rates

To estimate genetic ancestry (hereafter ancestry) of canids we collected blood samples from all captured animals. We drew blood from the cephalic vein and deposited it on FTA cards (Whatman, GE Healthcare Ltd, Buckinghamshire, UK) that were stored at room temperature until lab processing. We amplified 12 autosomal microsatellite loci for each sample (cxd225, cxd2, cxd377, cxd250, cxd204, cxd172, cxd109, cxd253, cxd442, cxd410, cxd147) using laboratory methods described in detail by Rutledge et al. (2010a) and Benson et al. (2012). We determined family relationships of captured wolves and coyotes of all ages using a combination of field data (telemetry monitoring and den visits; Benson et al. 2013, 2015) and results of previous pedigree analyses (Rutledge et al. 2010b, Benson et al. 2012). For most (19 of 23) packs, we included genotypes of both members of the breeding pair and excluded offspring and siblings of breeding animals. Most packs were composed only of a breeding pair and their offspring, but we also included adults unrelated to the breeding pair if they were present ($n = 2$). In one of the three packs from which we were missing a breeding animal, we included the genotype of a pup to provide representation of the missing parental genotype. Our pedigree was unresolved for one pack, but we included genotypes from three unrelated adults (one female and two males) in the pack that we suspect included the breeding female, breeding male, and an unrelated male.

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 proportion (Q), which is an estimate 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 and inferring the parameter alpha, for $K = 3$ for 10⁶ iterations following a burn-in period of 250000 as in Benson et al. (2012). We assumed $K = 3$ for the analysis given strong support for three genetically distinct *Canis* types (corresponding to putative eastern wolves, eastern coyotes, and Great Lakes-boreal wolves) in the hybrid zone surrounding APP (e.g., Rutledge et al. 2010a, Benson et al. 2012). We used genotypes from the same

161 canids included in the Structure analysis of Benson et al. (2012) combined with genotypes from 25 additional canids for our analysis. Specifically, our sample included animals from the focal packs whose predation we studied ($n = 46$), as well as other resident canids from APP and adjacent areas ($n = 100$), and highly assigned Great Lakes-boreal wolves from northeast Ontario ($n = 40$; out-group used by Benson et al. 2012). Thus, we used a balanced and representative sample (total $n = 186$) containing relatively equal numbers of the three *Canis* types found in our study area (eastern wolves [$n = 48$], eastern coyotes [$n = 47$], and Great Lakes-boreal wolves [$n = 43$]), as well as canids representing admixture between these three types ($n = 48$) to estimate the proportion of each focal animal's genome that was derived from eastern wolves, eastern coyotes, and Great Lakes-boreal wolves. We classified individual canids with $Q \geq 0.80$ for a single *Canis* type (eastern coyote, eastern wolf, or Great Lakes-boreal wolf) as highly assigned to that genetic population, whereas other canids were classified as admixed (Rutledge et al. 2010a, Benson et al. 2012). We averaged Q scores for each *Canis* type across individuals within each pack to generate mean admixture proportions for each pack.

We estimated moose density across our study area, and mean moose density within home ranges of canids, using aerial survey data collected by the OMNRF during 2003–2010. The data were collected by helicopter transects during January–March following a standardized protocol with the goal of seeing every moose in 25-km² plots by scanning visually and investigating all fresh tracks. Plots were selected for survey during a given year using a stratified random design. We combined data across years and performed a kriging analysis using the Geostatistical Analyst Wizard in ArcGIS 10 to estimate moose density (additional details provided by Benson et al. 2012, 2013). We used a Geographic Information System (GIS) layer of deer wintering areas, compiled and digitized by OMNRF, and intersected these with canid home ranges to estimate the proportion of each home range comprising deer wintering habitat as an index of winter deer availability. We used these estimates of moose density and deer wintering habitat to test the hypothesis that prey availability would positively influence kill rates. We hypothesized that deer availability would influence kill rates more strongly than moose density given that wolves prey preferentially on deer even when larger ungulates are available (Van Ballenberghe et al. 1975, Fritts and Mech 1981, Potvin et al. 1988). Furthermore, we hypothesized that the relationship between deer availability and per capita kill rate might be nonlinear given theoretical and empirical support for Type 2 and Type 3 functional responses of predators in general (Holling 1959), and wolves in particular (Messier 1994).

We estimated the number of animals in each pack during all winters of the study by counting tracks and/or animals. These counts were made during cluster investigations, or from fixed-wing aircraft or helicopter at low elevation (≥ 500 feet above ground). We conducted these

aerial monitoring surveys one to three times per week for the duration of the study. We hypothesized that pack size would positively influence kill rates on moose and negatively influence kill rates on deer because killing moose generally facilitates larger packs given the surplus of meat available (Mech and Boitani 2003, Vucetich et al. 2004).

We used snow depth values from the North American Regional Reanalysis (NARR) from the National Centers for Environmental Prediction, which provides daily estimates of snow depth at locations separated horizontally by approximately 32 km across North America (Mesinger et al. 2006). We used NARR data from one to four locations within or ≤ 15 km from the nearest boundary of each pack's home range to estimate snow depth for each pack. We averaged snow depth values across each day of the period that we monitored ungulate predation for each pack. We hypothesized that snow depth would positively influence kill rates, consistent with previous findings indicating that wolf and coyote predation success and kill rates on ungulates are increased by deep snow (e.g., Peterson and Allen 1974, Nelson and Mech 1986, Patterson and Messier 2000).

Per capita kill rate modeling

We used per capita kill rates as the response variable in all models investigating intrinsic and extrinsic influences on variation in kill rates to account for variation in pack size (e.g., Messier 1994, Vucetich et al. 2002). We modeled variation in total ungulate kill rates (deer and moose combined) using kg biomass·d⁻¹·canid⁻¹ to adopt a common currency for the different sized ungulates (Mech and Peterson 2003). We also modeled variation in per capita deer and moose kill rates separately, using kills·d⁻¹·canid⁻¹. We modeled the influence of intrinsic and extrinsic variables on these ungulate, deer, and moose per capita kill rates using multiple linear regression. We used an information theoretic approach, implemented in the R package MuMIn v.1.15.1, to select a subset of strongly supported models ($\Delta AIC_c < 2$; Burnham and Anderson 2002). We included all possible combinations of our five predictor variables (pack size, moose density, proportion of deer wintering habitat, snow depth, and proportion of eastern coyote ancestry), but we restricted inference to individual models with ≤ 2 predictor variables to avoid overfitting models given our relatively small sample size ($n = 23$ packs). We considered whether these strongly supported models met the assumptions of linear regression using a combination of statistical tests for normality, heteroscedasticity, and linearity implemented in the R package gvlma. We also visually inspected plots of studentized residuals and relationships between response and predictor variables for departures from normality and linearity. When we detected departures from linearity, we used semi-parametric generalized additive models (GAMs), which do not assume linearity (Wood 2006). GAMs can identify nonlinear relationships when predictor variables are specified as “smooth” terms

using thin-plate regression splines (Wood 2006). As noted above, we specifically hypothesized that models retaining the influence of prey availability might violate linearity assumptions given that predators often exhibit nonlinear functional responses to increased prey density (Holling 1959, Messier 1994). We report percentage of deviance explained for GAMs, and estimated degrees of freedom (edf; a measure of nonlinearity where increasing values >1 indicate greater nonlinearity; Wood 2006), F statistics, and P values for variables within these models. For linear regression models, we report beta coefficients (β), standard errors of these β , t statistics, and P values for variables in strongly supported models. We considered independent variables to have significantly and marginally significantly influenced response variables when $P < 0.05$ and $0.10 \geq P \geq 0.05$, respectively.

We did not include proportion of eastern wolf ancestry because it was highly negatively correlated ($r = -0.94$) with (and redundant to) proportion of eastern coyote ancestry given that the ancestry of most animals in our study was primarily derived from eastern wolves or eastern coyotes (Appendix S2). We also did not include Great Lakes-boreal wolf ancestry because it made up a relatively small proportion of the ancestry of most packs as only five packs had $q > 0.07$ for this ancestry type (Appendix S2). Thus, our ancestry variable reflected the degree to which the ancestry of packs was attributed to eastern coyotes rather than to wolves (eastern and Great Lake-boreal), with the majority of wolf ancestry derived from eastern wolves. Pack size was negatively correlated with eastern coyote ancestry ($r = -0.63$) and positively correlated with eastern wolf ancestry ($r = 0.60$). Other variables in our models were not strongly correlated (all $r < 0.34$). We addressed potential multicollinearity in two ways. First, we estimated variance inflation factors (VIFs), which can help identify problematic levels of collinearity in regression models. Common thresholds for acceptable VIFs are <10 or <4 (e.g., O'Brien 2007). Variance inflation factors for all variables in our models were <2 . Second, given their correlation, we did not make inference on predictor variables within individual models retaining both coyote ancestry and pack size to avoid misleading coefficient values and conclusions. We assumed that if one or both of these correlated variables were influential they would also appear in other strongly supported models, either alone or with other variables with which they were not strongly correlated. Statistical issues aside, we acknowledge that it was difficult to completely separate the influences of pack size and genetic ancestry in our models given that packs dominated by wolf ancestry were generally larger.

Kill rate comparisons between wolf and coyote packs

We used per pack kill rates and per area kill rates for our direct comparisons between packs dominated by wolf and eastern coyote ancestry to provide estimates that are relevant to managers working in areas

dominated by either wolves or eastern coyotes. Per pack kill rates provide estimates of the kill rates by the functional social units in wolf and eastern coyote populations. Additionally, considering kill rates relative to size of each packs' home range size provided insight on predation pressure that packs of different canids exert on ungulates on a per unit area basis. Eastern coyotes used smaller home ranges and, thus, their kill rates could have a greater influence on ungulate populations than wolf packs exhibiting similar, or even higher, kill rates over a much larger area.

We considered packs to be dominated by wolf ancestry if they comprised either (1) all highly assigned wolves ($n = 9$, i.e., combined Q scores for eastern and Great Lakes-boreal wolf >0.80 for all individuals) or (2) at least 1 highly assigned wolf, no highly assigned eastern coyotes, and ≥ 0.85 mean wolf ancestry ($n = 1$). We considered packs to be dominated by eastern coyote ancestry that comprised either (1) all highly assigned eastern coyotes ($Q \geq 0.80$ for all individuals, $n = 5$) or (2) at least one highly assigned eastern coyote, no highly assigned wolves, and ≥ 0.62 mean eastern coyote ancestry ($n = 4$). We used t tests assuming unequal variances to directly compare kill rates per pack and by pack per unit area between packs dominated by wolf and coyote ancestry. The four remaining packs were a more balanced combination of wolf and coyote ancestry and were excluded from these comparisons.

Biomass available from prey

We then estimated the amount of total ungulate, deer, and moose biomass obtained from kills per day (1) per canid and (2) per kg of canid within packs dominated by wolves and eastern coyotes using t tests assuming unequal variances. We estimated the kg biomass/kg canid for each pack using genotype-specific body mass estimates because eastern coyotes and hybrids were generally smaller than wolves in the hybrid zone (Benson et al. 2012). For each pack, we used mean body mass values for adults of each canid type to estimate the weight of the breeding pair. We used yearling weights (smaller than adults) for other pack members because most packs in our study area comprised a breeding pair and their offspring, rather than a breeding pair and unrelated adults (Rutledge et al. 2010b, Benson et al. 2012). If eastern coyotes play a similar ecological role as wolves with respect to ungulate predation, we would expect that they would be consuming similar amounts of ungulate, deer, and moose biomass from kills. Following Loveless (2010), we estimated biomass lost to scavenging by ravens (*Corvus corvax*) using a rate that varied by pack size based on data and calculations from Kaczensky et al. (2005) and modified to account for the pack sizes in our study. Finally, we report the proportion of moose and deer of each sex and age category killed by packs dominated by wolf ancestry, eastern coyote ancestry, or of mixed ancestry (Appendix S3).

Comparison to gray wolf–moose functional response

We calculated mean per capita moose kill rate and moose density across the territories of wolf packs in western APP and compared them to the functional response of gray wolves responding to different moose densities across North America summarized by Messier (1994). Messier (1994) estimated the functional response of gray wolves with data from studies where moose were the main ungulate prey (>75% ungulate biomass) and wolves fed mainly on moose. We similarly limited our data for this comparison to packs in western APP that did not visit deer yards and remained on their territories during winter where moose were the main ungulate prey and deer were scarce ($n = 6$). Mean body mass of male and female eastern wolves were 28 and 25 kg, respectively (Benson et al. 2012), putting them above the body mass threshold at which carnivores are predicted to require large prey (Carbone et al. 1999). We hypothesized that eastern wolves in western APP would prey mainly on moose, but at kill rates less than those of gray wolves at similar moose density, given that we expected their energy requirements and predatory ability would be slightly lower due to their smaller body mass (MacNulty et al. 2009).

RESULTS

Ungulate predation and dietary patterns

Overall, 22 of the 23 focal packs killed ungulates during the monitoring period. The proportion of ungulate biomass obtained from kills by these packs comprising deer and moose was 0.64 (range 0–1, SE = 0.08) and 0.36 (range 0–1, SE = 0.08; Appendix S4), respectively. Packs dominated by wolf ancestry ($n = 10$) obtained 0.46 and 0.54 of the ungulate biomass they consumed from deer and moose kills, respectively (0.39 and 0.61, prior to adjusting for losses to ravens). Nine focal packs were dominated by eastern coyote ancestry and eight of these killed ungulates during the monitoring period. These eight packs obtained 0.89 and 0.11 of ungulate biomass from deer and moose kills, respectively (0.84 and 0.16 prior to adjusting for ravens). Packs of mixed eastern coyote and wolf ancestry ($n = 4$) obtained 0.90 and 0.10 of their total ungulate biomass from deer and moose kills, respectively (0.87 and 0.13 prior to adjusting for ravens). Only two packs consumed substantial amounts of anthropogenic food and both of these packs contained only highly assigned ($Q > 0.80$) eastern coyotes. Specifically, we found no ungulates killed by a pack of six eastern coyotes, which appeared to feed primarily on a carcass pile created by humans. A different pack of three eastern coyotes occupied a small home range centered on a municipal landfill, fed extensively on garbage, and also killed three deer. There were no differences between early and late winter in terms of per capita kill rates (Appendix S5). Scavenging was relatively uncommon and kill rates

did not appear to be strongly influenced by scavenging (Appendix S6).

Kill rate modeling

We identified two models with strong empirical support explaining variation in per capita total ungulate kill rates (Table 1). Both models met linearity assumptions. In these models, only proportion of eastern coyote ancestry negatively influenced ungulate kill rates ($\beta = -2.27$, SE = 0.72, $P = 0.005$; Fig. 2). We identified three models with strong empirical support for per capita deer kill rates (Table 1). However, there appeared to be a violation of the linearity assumption for the model retaining only deer availability. Thus, we drew inference on two linear models and 1 GAM to evaluate per capita deer kill rates. Deer habitat positively and nonlinearly influenced per capita deer kill rate (edf = 1.8, $F = 3.7$, $P = 0.039$; Fig. 3a). Pack size negatively influenced per capita deer kill rates ($\beta = -0.004$, SE = 0.002, $P = 0.055$; Fig. 3b). The GAM retaining deer availability as the sole predictor explained 30.9% of the deviance in per capita deer kill rate.

We identified three models with strong empirical support explaining variation in per capita moose kill rates (Table 1). However, two of the three models did not meet linearity assumptions. Thus, we drew inference on one linear model and two GAMs. Specifically, we modeled the influence of deer availability and pack size on per capita moose kill rates with a GAM that explained 75.8% of the deviance. We also modeled the influence of deer availability and eastern coyote ancestry with a GAM that explained 73.6% of the deviance. Pack size positively influenced per capita moose kill rates ($\beta = 0.001$, SE < 0.001, $P = 0.007$; Fig. 4a). In a separate model, coyote ancestry negatively influenced per capita moose kill rates ($\beta = -0.007$, SE = 0.002, $P = 0.006$; Fig. 4b). Deer availability negatively, nonlinearly influenced per capita moose kill rate (edf = 3.1, $F = 7.7$, $P = 0.001$;

TABLE 1. Strongly supported linear models explaining per capita ungulate (deer and moose), deer, and moose kill rates in central Ontario, 2005–2010.

Model	AIC _c	ΔAIC _c	R ²
Ungulate kill rate (kg·canid ⁻¹ ·d ⁻¹)			
Coyote ancestry	79.98	0.00	0.29
Coyote ancestry + Snow depth	81.62	1.64	0.30
Deer kill rate (deer·canid ⁻¹ ·d ⁻¹)			
Pack size + Deer	-108.81	0.00	0.26
Pack size	-108.03	0.79	0.17
Deer	-107.43	1.38	0.15
Moose kill rate (moose·canid ⁻¹ ·d ⁻¹)			
Pack size + Deer	-170.17	0.00	0.40
Coyote ancestry + Deer	-170.13	0.04	0.40
Pack size	-169.20	0.97	0.32

Notes: Variables included were coyote ancestry (Coyote), proportion of deer wintering habitat (Deer), moose density, pack size (number of canids), and snow depth. Shown are Akaike's Information Criterion for small samples (AIC_c), differences in AIC_c (ΔAIC_c), and adjusted R².

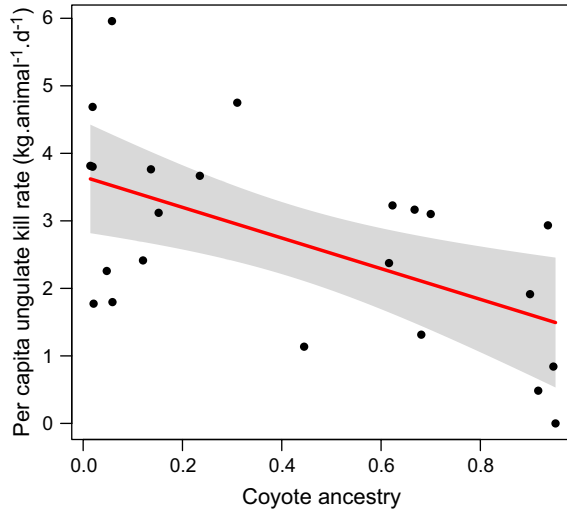


FIG. 2. Relationship between per capita ungulate kill rate ($\text{kg. animal}^{-1} \cdot \text{d}^{-1}$) and proportion of eastern coyote ancestry in canid packs. Red line is trend line from linear regression model, gray shading is 95% confidence interval, and black dots are partial residuals.

Fig. 4c). Results for variables retained in all strongly supported models are provided in Appendix S7.

Kill rates by packs dominated by wolf and coyote ancestry

Packs dominated by wolf ancestry (mean = 0.12 deer/d, $n = 10$) had marginally higher deer kill rates than packs dominated by coyote ancestry (mean = 0.06 deer/d, $n = 9$) when kill rates were estimated by pack ($t = -1.99$, $P = 0.068$). Packs dominated by wolf ancestry (mean = 0.062 moose/d, $n = 10$) had higher moose kill rates than packs dominated by eastern coyote ancestry (mean = 0.006 moose/d, $n = 9$; $t = -2.66$, $P = 0.024$). Deer kill rates per unit area ($\text{deer} \cdot \text{d}^{-1} \cdot \text{km}^{-2}$) were not significantly different for packs dominated by eastern coyote ancestry ($0.0018 \text{ deer} \cdot \text{d}^{-1} \cdot \text{km}^{-2}$, $n = 9$) and packs dominated by wolf ancestry ($0.0006 \text{ deer} \cdot \text{d}^{-1} \cdot \text{km}^{-2}$, $n = 10$; $t = 1.71$, $P = 0.118$). Moose kill rates per unit were higher for packs dominated by wolf ancestry ($0.00022 \text{ moose} \cdot \text{d}^{-1} \cdot \text{km}^{-2}$, $n = 10$) than for packs dominated by eastern coyote ancestry ($0.00006 \text{ moose} \cdot \text{d}^{-1} \cdot \text{km}^{-2}$, $n = 9$; $t = -2.43$, $P = 0.027$).

Biomass consumption of packs dominated by wolf and coyote ancestry

Estimates of total ungulate biomass obtained daily from kills were greater per canid ($t_{17} = -2.4$, $P = 0.027$) and marginally greater per mass of canid ($t_{16} = -1.90$, $P = 0.076$) in packs dominated by wolf ancestry. Deer biomass obtained daily from kills per canid ($t_{13} = 0.93$, $P = 0.368$) or per mass of canid ($t_{13} = 1.25$, $P = 0.234$) did

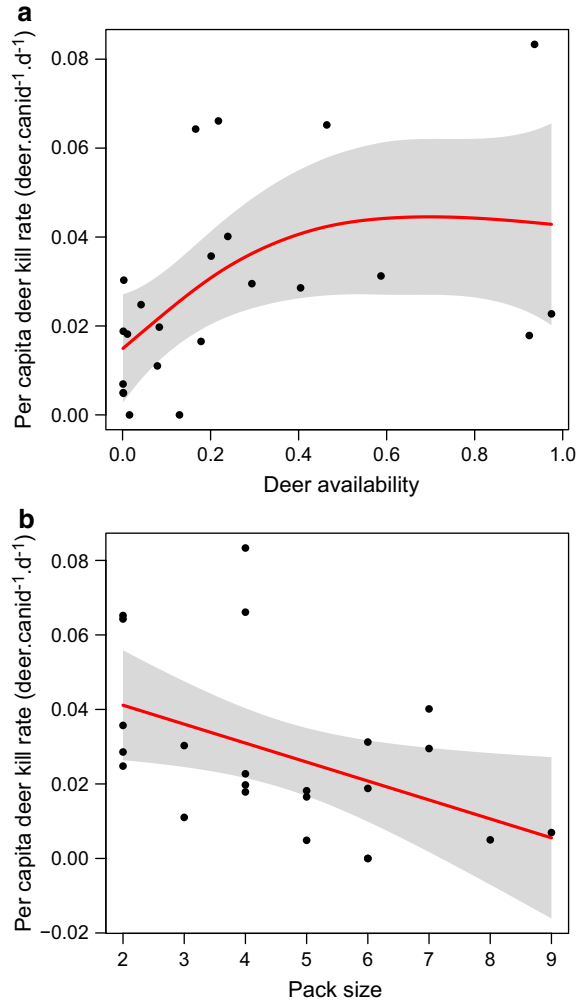


FIG. 3. Relationships between per capita deer kill rate (no. deer.canid⁻¹.d⁻¹) and (a) index of deer availability and (b) pack size (number of canids). Red lines are predicted trends from generalized additive (a) or linear (b) regression models, gray shading is 95% confidence interval, and black dots are partial residuals.

not differ in packs dominated by wolf and eastern coyote ancestry. Moose biomass obtained daily from kills was greater per canid ($t_{14} = -2.89$, $P = 0.012$) and per mass of canid ($t_{15} = -2.70$, $P = 0.017$) in packs dominated by wolf ancestry compared with packs dominated by eastern coyote ancestry. Mean biomass estimates for packs dominated by wolf and coyote ancestry are reported in Appendix S8.

Eastern wolf moose predation relative to the gray wolf functional response

The relationship between per capita moose kill rate and moose density for eastern wolf packs in western APP was consistent with rates predicted by the functional

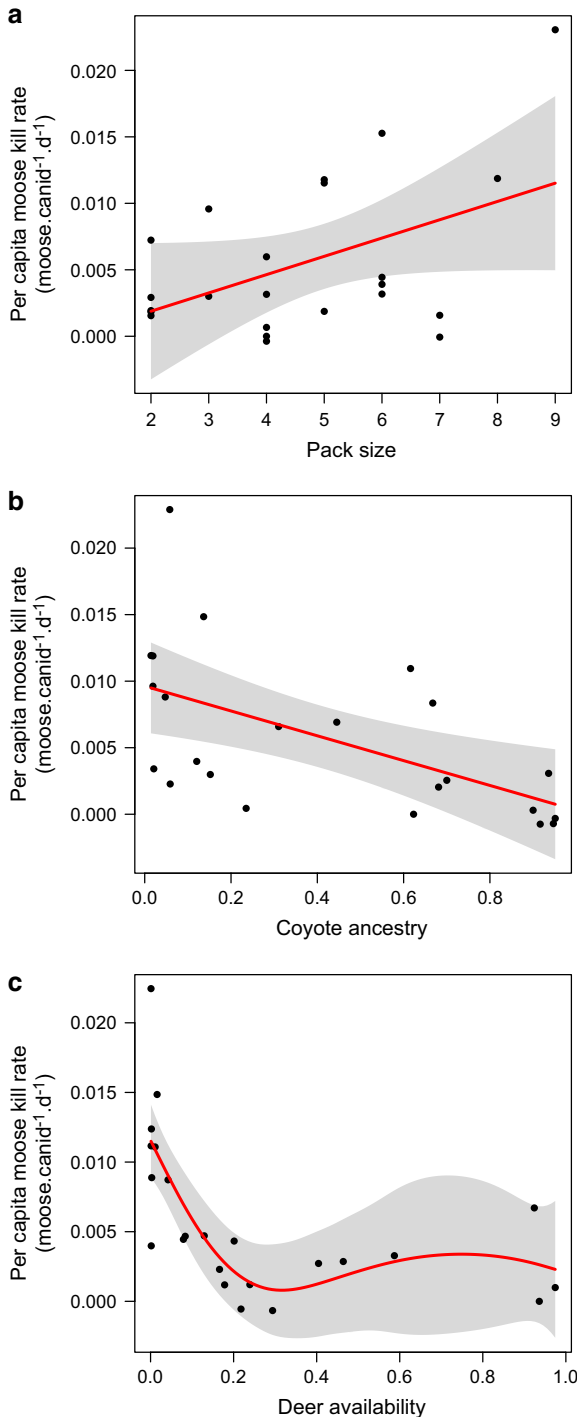


FIG. 4. Relationships between per capita moose kill rate ($\text{moose} \cdot \text{canid}^{-1} \cdot \text{d}^{-1}$) and (a) pack size (number of canids), (b) proportion of eastern coyote ancestry in canid packs, and (c) an index of deer availability. Red lines are predicted trends from linear (a, b) and generalized additive (c) regression models, gray shading is 95% confidence interval, and black dots are partial residuals.

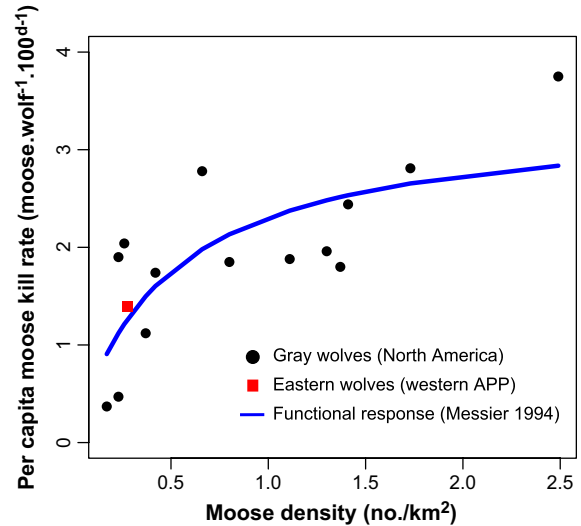


FIG. 5. Per capita moose kill rates ($\text{moose} \cdot \text{wolf}^{-1} \cdot 100 \text{d}^{-1}$) of gray wolves at different moose densities across North America (black circles), the functional response fit by Messier (1994) with a hyperbolic, Michaelis-Menten equation (blue line), and the per capita moose kill rate of eastern wolves in western APP (red square, $n = 6$ packs).

response documented for gray wolves and moose across North America (Messier 1994, Fig. 5). Although eastern wolves in areas where moose were the most abundant ungulate (western APP) preyed primarily on moose, contrary to our hypothesis, these wolves did not exhibit kill rates lower than those predicted by the functional response for gray wolves across North America (Fig. 5).

DISCUSSION

Traditionally, studies of predator kill rates focused attention on the influence of prey density (e.g., Holling 1959, Messier 1994); however, our results reinforce more recent recognition that predation is a complex process that can be influenced by a variety of intrinsic, social, and environmental factors (e.g., Jędrzejewski et al. 2002, Sand et al. 2012). Eastern coyotes, wolf \times coyote hybrids, and wolves all preyed on deer and moose in central Ontario, but eastern coyote ancestry was an important predictor of lower per capita kill rates with respect to total ungulate biomass and numbers of moose killed. Packs dominated by wolf ancestry had deer kill rates that were twice that of packs dominated by coyote ancestry. However, pack size and home range size are potentially confounding variables for investigating kill rates by social predators such as canids, as coyote-dominated packs comprised fewer animals and occupied considerably smaller territories than wolf-dominated packs. When estimated per unit area, mean deer kill rates were actually higher for packs dominated by eastern coyote

ancestry, although variation was high and they did not differ statistically from those of packs dominated by wolf ancestry. Additionally, we note that many of the wolf packs in our study would presumably have killed more deer if they were not also preying on moose. Nonetheless, our results suggest that estimating kill rates per unit area is an important consideration for understanding the impact of predator kill rates on prey populations, especially when comparing predation by individuals, populations, or species that have very different home range sizes.

The nonlinear relationship between deer availability and per capita deer kill rate resembled a type-2 functional response (Holling 1959, Messier 1994; Fig. 3a), as kill rate appeared to be density-dependent at low and moderate deer availability, and plateaued when canid territories comprised ≥ 0.5 wintering habitat. Per capita moose kill rates were not influenced by moose density, but were nonlinearly, negatively influenced by availability of deer. Thus, canids in central Ontario generally preyed on deer when they were available, whereas packs (especially those with wolves) without access to abundant deer exhibited higher kill rates on moose. These results are consistent with previous research showing that wolves prey more heavily on deer in systems with both deer and moose (e.g., Van Ballenberghe et al. 1975, Fritts and Mech 1981, Potvin et al. 1988). Our results are also consistent with the prediction that predators should target larger, more dangerous prey only when easier prey are scarce (MacNulty et al. 2011). Due to the size and aggressiveness of larger prey such as moose, predators are likely at greater risk of injury when preying on moose relative to deer, a consideration that likely influences prey selection in multi-prey systems (Mukherjee and Heithaus 2013). Canids preying on larger prey generally exhibit larger group sizes (Mech and Boitani 2003), consistent with our documentation of strong positive and negative influences of pack size on per capita moose and deer kill rates, respectively. Canids preying on moose should accrue inclusive fitness benefits by maintaining larger packs through delayed dispersal of offspring if packs are family-based (Rodman 1981, Vucetich et al. 2004), as they were in our study (Rutledge et al. 2010b, Benson et al. 2012). However, catastrophic fitness costs of debilitating injury or death from dangerous prey may be sufficient to outweigh benefits of wolves (Barber-Meyer et al. 2016) and other large carnivores preying on larger ungulates (e.g., leopards [*Panthera pardus*], Hayward et al. 2006). Indeed, we documented a breeding eastern wolf being killed by a moose in APP in an apparent failed predation attempt during our study (Benson et al. 2014).

Previous work indicated that eastern wolves in APP preyed mainly on deer and very rarely killed moose (Pimlott et al. 1969, Forbes and Theberge 1992, 1996). Forbes and Theberge (1992, 1996) concluded that eastern wolves consumed moose mainly through scavenging and that their smaller size relative to gray wolves made them inefficient predators of moose. We also found that eastern wolves preyed mainly on deer when they were available,

but that they exhibited relatively high kill rates on moose in western APP where deer were scarce. During the work of Pimlott et al. (1969) in the 1950s and 1960s, deer were at higher density and moose were relatively scarce compared to our study period (Quinn 2004; APP, OMNRF, *unpublished data*). Thus, wolves in APP appear to have shifted their predation patterns over the last 50 years to respond to temporal changes in ungulate densities. However, deer and moose densities in APP were likely relatively similar during our study and that of Forbes and Theberge (1992, 1996, Quinn 2004; OMNRF, *unpublished data*). The apparent discrepancy in our findings may be explained by the fact that Forbes and Theberge (1992, 1996) mainly studied radiocollared wolves in the eastern portion of APP (see territory map in Theberge 1998), where wolves left the park during winter to prey on deer in deeryards (Forbes and Theberge 1996). We tracked wolves in both eastern and western APP, and found that most wolves in western APP remained on territory during winter and preyed mainly on moose.

Interestingly, mean per capita kill rates on moose relative to moose density within the territories of eastern wolves in western APP corresponded very closely to the mean kill rate predicted by the functional response of gray wolves across North America (Messier 1994; Fig. 5). Thus, eastern wolves do appear to be able to kill moose effectively during winter in areas where deer are scarce. However, we found no evidence of a functional response to moose by canids within our study area as moose density was not a significant predictor of moose kill rates. Moose are not hunted in western APP, which resulted in an older age structure than in hunted populations where harvest occurs (Murray et al. 2012). Indeed, wolves in western APP killed more old (≥ 11 years) moose relative to their availability in the population (Loveless 2010). Thus, eastern wolves in western APP may have been able to exhibit kill rates similar to those of larger gray wolves at similar moose densities, in part because there may have been more moose vulnerable to wolf predation due to poorer condition in this unhunted population. The highest reported kill rates of moose by gray wolves across North America come from the high density, protected moose population in Isle Royale National Park (Peterson and Page 1988, Messier 1994). Protected prey populations are often characterized by both high density and older age structure, making the influences of prey density and age-based vulnerability difficult to separate. Although eastern wolves in western APP exhibited relatively high kill rates on moose during winter, summer predation on moose could be more difficult for these smaller wolves in the absence of nutritionally stressed moose and favorable snow conditions. Future studies of summer predation habits of eastern wolves will be needed to test this hypothesis. This is especially important because eastern wolf population growth and the potential for expansion into areas outside of APP may be reduced by poor pup survival associated with shortages of important summer foods such as beavers in areas where moose are the main prey (Benson et al. 2013, 2015).

Our results were consistent with predictions from energetic models that carnivores >21.5 kg require large prey, whereas carnivores <21.5 kg are more likely to feed on smaller prey and be omnivorous (Carbone et al. 1999). Mean body masses in central Ontario (with sexes pooled as in Carbone et al. [1999]) were 19.9 kg, 22.0 kg, and 26.6 kg for eastern coyotes, eastern coyote \times eastern wolf hybrids, and eastern wolves, respectively (Benson et al. 2012). Wolves were more likely than eastern coyotes and wolf \times coyote hybrids to switch to moose in areas where deer are scarce, such as in western APP during winter. The only pack dominated by coyote ancestry that relied heavily on moose was a pack in WMU49 with a breeding male eastern coyote, a breeding female wolf \times coyote hybrid, and their pups. This pack had the lowest proportion (<0.01) of deer wintering habitat in their home range of any pack monitored in WMU49, highlighting the strong influence of deer availability on predation patterns of both deer and moose throughout the hybrid zone.

Wolf restoration in the northeastern United States

Reintroducing wolves to the northeastern United States has been evaluated by ecologists and management agencies (Harrison and Chapin 1998, Mladenoff and Sickley 1998, U.S. Fish and Wildlife Service 2000, 2003, Kays et al. 2008). Areas where human persecution is low and ungulate prey are abundant would be most favorable for wolf restoration in the northeastern United States, as they were when wolves recolonized the Midwest (Mladenoff et al. 1999). However, recolonization or reintroduction of eastern wolves in the northeast would be greatly complicated by their propensity to hybridize with coyotes. Forests, the dominant cover type in the northeastern United States, have been characterized as relatively poor habitat for eastern coyotes (Crête et al. 2001, Richer et al. 2002). However, coyotes in New York were abundant in relatively young, disturbed forests with open canopies, but less abundant in large tracts of mature forest (Kays et al. 2008). Kays et al. (2008) suggested the availability of small prey, deer, and fruit in disturbed forests likely increases suitability for coyotes, whereas wolves would be favored in mature forests occupied by moose, such as those in Adirondack Park, New York. Our work supports these contentions as eastern coyotes appear to thrive in the more disturbed forests of WMU49 by exploiting deer and anthropogenic food sources, whereas they were rare in the mature forests of APP. Indeed, eastern coyotes in WMU49 maintained interspecific territories in a landscape that was also occupied by wolves (Benson and Patterson 2013b), survived better than eastern wolves as subadults and adults (Benson et al. 2014), and successfully produced and raised pups (first year pup survival = 0.74; Benson et al. 2013).

Large, remote tracts of mature forest inhabited primarily by moose rather than deer are rare in the northeastern United States, which will make eastern wolf establishment difficult in the presence of abundant coyote

populations. If wolves were reintroduced to the northeastern United States, we agree with Wheeldon and Patterson (2012) that reintroducing Great Lakes-boreal wolves, rather than eastern wolves may be advantageous given that hybridization between sympatric Great Lakes-boreal wolves and coyotes appears to be minimal in areas where they overlap (Wheeldon et al. 2010, Wheeldon and Patterson 2012). Great Lakes-boreal wolves are aggressive with and behaviorally dominant to coyotes (Mech 2011), whereas eastern wolves appear to treat coyotes similar to conspecifics in territorial interactions, at least at the home range level (Benson and Patterson 2013b). Great Lakes-boreal wolves have successfully recolonized areas in Minnesota, Wisconsin, and Michigan that were characterized by younger forests, habitat fragmentation, and abundant coyotes suggesting they could also persist in the northeast (Mladenoff et al. 1999).

Have coyotes replaced the ecological role of wolves?

Although eastern coyotes and wolves both prey on deer and moose in central Ontario, there are important differences in the ecological roles played by wolves and coyotes with respect to predation on ungulates. Canids in packs dominated by wolf ancestry killed almost twice as much ungulate biomass per day as canids in packs dominated by eastern coyote ancestry. Eastern coyotes supplemented predation on ungulates with anthropogenic food, and presumably with smaller prey as well. The greater dietary flexibility of coyotes relative to wolves makes their predation on ungulates less predictable and could decouple the numerical response of coyotes and their ungulate prey. Indeed, Patterson et al. (1998) showed that eastern coyotes in Nova Scotia continued to feed largely on deer when deer densities were low, even in the presence of alternative prey. We predict that eastern coyotes are more likely than wolves to have destabilizing effects on prey populations through apparent competition (Holt 1977, Prugh 2005) and due to subsidization by anthropogenic resources (Holt 1984, Rodewald et al. 2011). As generalist top predators, eastern coyotes may be more likely to drive prey species to low levels than wolves because coyotes could remain at high density and remain efficient predators even when prey species become scarce, as suggested by Patterson and Messier (2000) and Prugh et al. (2009). Conversely, wolves are obligate predators of large prey and their numerical responses to ungulate density are well documented (e.g., Messier 1994, Fuller et al. 2003). More generally, our results suggest that body mass and associated energetic requirements are important in influencing the ecological role of predators within ecosystems. Thus, as large predators become increasingly absent from ecosystems globally (Ripple et al. 2014), we should not assume that medium-sized predators will fill their roles with respect to predation on large herbivores without empirical evidence. Smaller predators that can subsist on smaller prey and omnivorous diets will likely be less predictable predators of large prey, meaning that important

ecological functions may be lost from communities when large carnivores are extirpated.

Cope's rule predicts a tendency in animal groups to evolve towards larger size, with one of the perceived advantages being greater ability to capture prey (Stanley 1973, Kingsolver and Pfennig 2004). Within canid populations and hybrid zones, selection may favor larger individuals given the greater net predation success of larger wolves (MacNulty et al. 2009). Thus, eastern coyotes and wolf-coyote hybrids could be under selection for greater size and predatory ability to exploit abundant white-tailed deer in eastern North America, as suggested previously (e.g., Larivière and Crête 1993, Kays et al. 2010). We cannot rule out that eastern coyotes will increase in size and become more consistent predators of deer and larger ungulates. However, the success and ubiquity of coyotes across North America may be partially related to their dietary flexibility and ability to persist in human-dominated landscapes (Gese and Bekoff 2004), both of which may be enhanced by smaller size (Bateman and Fleming 2012). Thus, selective pressure on canids to facilitate predation on ungulates may be balanced by selection for maintaining a size at which they can also effectively exploit smaller prey, vegetation, and anthropogenic food. This would be consistent with the highly plastic predation and feeding habits of eastern coyotes across space and time (e.g., Patterson et al. 1998, Dumond et al. 2001).

CONCLUSIONS

Our research provides empirical support for the contention made by previous authors that eastern coyotes have not completely replaced the ecological role of wolves because they are unlikely to prey as effectively or consistently on large ungulates (e.g., Crête et al. 2001, Gompper 2002, Kays et al. 2008, Prugh et al. 2009). Instead, the generalist foraging habits of eastern coyotes suggest that they play a less predictable, and potentially destabilizing, ecological role than wolves with respect to their effect on prey populations and community structure. Similar to other wolves that are sympatric with white-tailed deer, eastern wolves appear to prey mainly on deer when they are available, but are also capable of relying on larger ungulates when deer are scarce. Coyotes will likely continue to be ubiquitous across eastern North America for the foreseeable future. However, the ascension of eastern coyotes to apex predator on contemporary landscapes, and their superficial similarity to wolves, should not detract from efforts to facilitate the restoration of wolves in eastern North America. Conservation of naturally functioning ecosystems requires maintaining stable interactions between species, such as predator-prey dynamics and relationships among predators (Ritchie et al. 2012, Ripple et al. 2014). Thus, we suggest that understanding and conserving ecological roles of species that influence community structure, and may promote ecosystem resilience, should be increasingly important goals of

endangered species management in the face of widespread global environmental degradation.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/eap.1499/full>

DATA AVAILABILITY

Data associated with this paper have been deposited in a Dryad digital repository <https://doi.org/10.5061/dryad.3jd1g>