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Moose (*Alces alces*) predation by eastern coyotes (*Canis latrans*) and eastern coyote × eastern wolf (*Canis latrans* × *Canis lycaon*) hybrids

J.F. Benson and B.R. Patterson

Abstract: It has been widely assumed that coyotes (*Canis latrans* Say, 1823) are incapable of killing adult moose (*Alces alces* (L., 1758)) and previous studies of coyote predation support this assumption. However, eastern coyotes and eastern coyote × eastern wolf (*Canis lycaon* Schreber, 1775) are larger than western coyotes and appear to rely on larger prey in some areas. We used a combination of GPS telemetry, genetic analysis, and field investigation to test the hypothesis that eastern coyotes and coyote × wolf hybrids are capable of preying on adult moose in central Ontario. Our hypothesis was supported, as we documented four definitive cases of eastern coyotes and (or) eastern coyote × eastern wolf hybrids killing moose ≥1.5 years old. Predation by coyotes and coyote × wolf hybrids probably does not represent a threat to moose population viability in central Ontario, but our results suggest that researchers and managers in other areas with declining moose populations that are sympatric with eastern coyotes and (or) coyote × wolf hybrids should consider coyote predation as a potential source of mortality.

Key words: *Alces alces*, *Canis latrans*, eastern coyotes, hybridization, moose, predation.

Résumé : Il est largement tenu pour acquis que les coyotes (*Canis latrans* Say, 1823) sont incapables de tuer des orignaux (*Alces alces* (L., 1758)) adultes, et des études passées sur la prédation par le coyote appuient ce postulat. Cela dit, le coyote de l'Est et les hybrides coyote de l'Est × loup de l'Est (*Canis lycaon* Schreber, 1775) sont plus imposants que le coyote de l'Ouest et semblent dépendre de proies plus grandes dans certaines régions. Nous avons utilisé une combinaison de télémétrie GPS, d'analyse génétique et de levés de terrain pour tester l'hypothèse voulant que les coyotes de l'Est et les hybrides coyote × loup soient capables de tuer des orignaux adultes dans le centre de l'Ontario. Notre hypothèse est appuyée par quatre cas documentés d'orignaux de plus de 1,5 an tués par des coyotes de l'Est et (ou) des hybrides coyote de l'Est × loup de l'Est. Si la prédation par les coyotes et les hybrides coyote × loup ne présente probablement pas une menace pour la viabilité des populations d'orignaux dans le centre de l'Ontario, nos résultats suggèrent que les chercheurs et aménagistes œuvrant dans d'autres régions caractérisées par une baisse des populations d'orignaux sympatriques avec des coyotes de l'Est et (ou) des hybrides coyote × loup devraient tenir compte de la prédation par les coyotes comme source potentielle de mortalité. [Traduit par la Rédaction]

Mots-clés : *Alces alces*, *Canis latrans*, coyotes de l'Est, hybridation, orignal, prédation.

Introduction

Coyotes (*Canis latrans* Say, 1823) are generalist predators that exhibit substantial variability in behavior and diet across their extensive geographic range (Clark 1972; Bekoff 1978; Parker 1986). In much of their historic range, coyotes prey mainly on smaller animals such as rodents and rabbits, supplemented with carrion from larger animals, vegetation, and human food (e.g., Hamilton 1974; Bowyer et al. 1983; Fedriani et al. 2001). However, coyotes can also prey effectively on adult deer (species of the genus *Odocoileus* Rafinesque, 1832), as well as neonates of larger ungulates such as caribou (*Rangifer tarandus* (L., 1758)) or elk (*Cervus elaphus* L., 1758; Messier et al. 1986; Paquet 1992; Gese and Grothe 1995; Lingle 2002; Patterson and Messier 2003). There are also reports of coyotes attacking and killing adult ungulates of species larger than deer, such as elk (Paquet 1992; Gese and Grothe 1995), and killing adult ungulates appears to be especially prevalent among eastern coyotes (Gompper 2002).

There is evidence from scat analyses that eastern coyotes eat moose (*Alces alces* (L., 1758)) in some areas; however, this has previously been assumed to be the result of coyotes feeding on moose carrion or perhaps occasionally preying on calves (Major and

Sherburne 1987; Litvaitis and Harrison 1989; Samson and Crête 1997; Dumond and Villard 2001; Richer et al. 2002; Boisjoly et al. 2010). Coyotes have long been considered ineffective moose predators (Wolfe 1974) and Kays et al. (2008) asserted that eastern coyotes never kill large prey such as moose. A recent study in Quebec found that moose was the dominant food item in eastern coyote scats and attributed this mostly to coyotes feeding on carcasses rather than attacking and killing moose, noting that moose calves are vulnerable to eastern coyote predation only up to 6 months of age (Boisjoly et al. 2010). However, hybridization with eastern wolves (*Canis lycaon* Schreber, 1775) during their colonization of northeastern North America has apparently contributed to larger body size of eastern coyotes relative to western coyotes (Larivière and Crête 1993; Way 2007), and resulted in craniodental characteristics that should allow them to be more effective predators of ungulates (Kays et al. 2010). Little is known about the predatory behavior or ecological role of coyote × wolf hybrids, but researchers have speculated that these hybrids in central Ontario would have difficulty preying on moose (e.g., Kyle et al. 2006). We are unaware of previous documentation of eastern coyotes or coyote × wolf hybrids preying on moose >6 months of age.

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Accordingly, we combined genetic analysis, global positioning system (GPS) telemetry data, and field study of resident packs of eastern coyotes and (or) eastern coyote \times eastern wolf (*Canis latrans* \times *Canis lycaon*) hybrids to test the hypothesis that these canids occasionally preyed on adult moose. We conducted this study in an area of relatively high moose density in central Ontario (Murray et al. 2012), where contemporary hybridization between eastern coyotes and eastern wolves is common (Benson et al. 2012). Our results will advance understanding of mammalian predator–prey relationships in areas of northeastern North America where eastern coyotes and (or) coyote \times wolf hybrids are sympatric with moose. Specifically, our findings provide new insight relevant to recent discussions regarding the ecological role of eastern coyotes and their potential to fill the niche left vacant by the extirpation of wolves from much of northeastern North America (e.g., Kays et al. 2008; Prugh et al. 2009).

Materials and methods

We captured eastern coyotes, wolves, and eastern coyote \times wolf hybrids using padded foothold traps and helicopter net-gunning during 2006–2010 in Wildlife Management Unit (WMU) 49 to deploy GPS radio collars and collect DNA samples (blood) as part of a study of wolf–coyote ecology and hybridization dynamics in the central Ontario (Benson et al. 2012). Capture and handling of study animals was approved by Trent University and Ontario Ministry of Natural Resources (OMNR) Animal Care committees under permit Nos. 08039 and 6-75 to 10-75, respectively. WMU49 is a combination of forested (hardwood, conifer, and mixed) and unforested (wetlands and rocky areas) habitat interspersed by numerous lakes and fragmented by roads, towns, and residences. Moose, deer, and beavers (*Castor canadensis* Kuhl, 1820) occur in WMU49 and are the main prey for wolves in Algonquin Provincial Park approximately 50 km to the east (Forbes and Theberge 1996); however, food habits of eastern coyotes and coyote \times wolf hybrids in WMU49 have not been studied. Moose hunting and canid (wolf and coyote) trapping and hunting are legal in WMU49 on a seasonal basis. Additional details on the study area are available elsewhere (Benson et al. 2012, 2013; Patterson et al. 2013). Intensive capture and telemetry monitoring demonstrated that eastern coyotes (64%) and eastern coyote \times wolf hybrids (29%) were the dominant, resident canids in WMU49, whereas wolves were much rarer (7%; Benson et al. 2012). The genetic ancestry of all study animals in our current study was determined by microsatellite genotyping and detailed population genetic analyses described in Benson et al. (2012).

The moose kills we report were all visited during the same winter (9 Feb. – 9 April) that the kills occurred (mean = 48 days between kill and visit; range = 19–74 days). During winter of 2008–2009, our GPS collars collected a fix every 15 min, 90 min, or 5 h on different days within each month and we visited clusters of locations where animals spent ≥ 3 h (for 15 and 90 min fix intervals) and ≥ 10 h (for 5 h fix intervals) within a 200 m radius. Based on our experiences during 2008–2009, we determined that GPS fix intervals of ≤ 90 min were desirable for locating kills effectively. Thus, during 2009–2010, we programmed GPS collars to collect a fix every 90 min for the entire winter and visited clusters of locations indicating the animals had spent ≥ 3 h within a 200 m radius. We searched at least a 100 m radius around each GPS location in each of these clusters until we found evidence of predation or determined that the cluster was not associated with a kill.

When we found prey remains, we investigated the site to determine if the remains were killed or scavenged (i.e., discovered and consumed after death) by the study animals. Following previous studies of wolf or coyote predation (e.g., Mech 1970; Buskirk and Gipson 1978; Messier and Cr  te 1985), we interpreted the following as evidence of predation: (i) broken vegetation (cleanly broken off), indicating struggle between predator and prey (distinguished

from vegetation that had been chewed); (ii) blood sprayed on vegetation, rocks, and (or) snow; (iii) clumps of prey hair embedded in bark of trees (distinguished from smaller numbers of hairs stuck, but not embedded); (iv) disarticulation of the skeleton (i.e., legs ripped off), indicating it was not frozen into the snow when the study animals arrived; (v) removal and shredding of the rumen (indicating it was not frozen when the study animals arrived); and (vi) awkward body position or location of prey species (rather than resting position or location of an animal dying of natural causes). If the above criteria were observed, we considered moose to have been killed by canids, rather than being discovered and scavenged after death.

Where possible, we collected jawbones of moose at kill sites to estimate the age or age category. We considered any jawbone with six cheek teeth fully erupted to be from a moose ≥ 1.5 years old (Peterson et al. 1983; Jensen 2001). In two cases, we subsequently obtained an age estimate via cementum annuli analysis (Matson's Lab, Milltown, Montana, USA), whereas in two cases, we simply estimated the moose to be ≥ 1.5 years old. We also examined the marrow from the femurs of moose killed by canids (Cheatum 1949). Marrow that was red, yellow, gelatinous, or wet was considered evidence of malnourishment. We recognize marrow that did not show noticeable characteristics of malnourishment (i.e., marrow that was white and solid) can still be characteristic of animals in marginal or even poor condition (Mech and Delgiudice 1985), so we used this inspection only to provide evidence of severe malnourishment at the time of death.

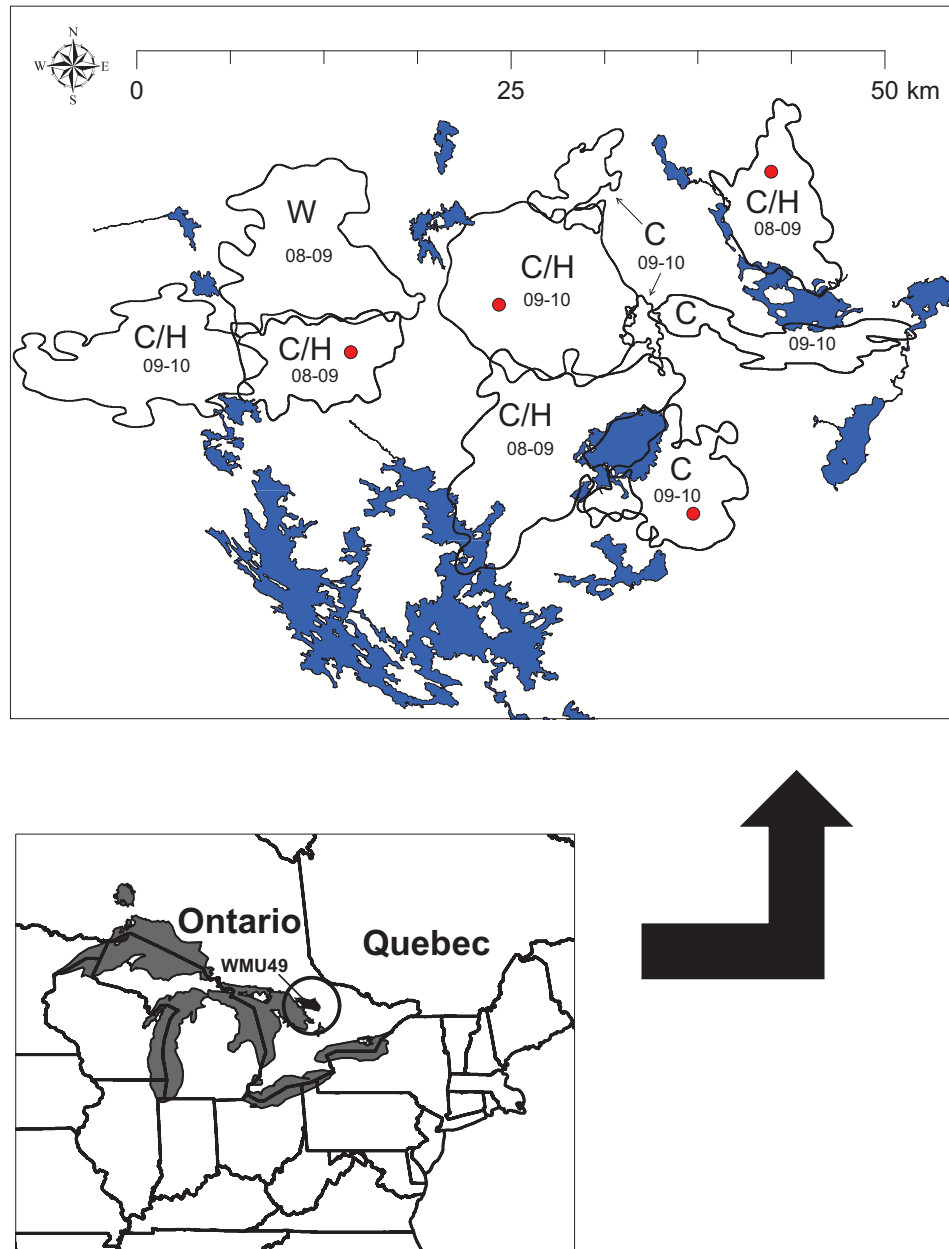
We monitored a high proportion of the resident, territorial canid packs in WMU49 (Fig. 1; Benson and Patterson 2013). Thus, we also examined GPS telemetry data to determine whether any other collared wolf, coyote, and hybrid packs were detected at the kill site prior to the arrival of the focal pack to ensure that we correctly identified the pack responsible for the initial kill. In three of the four kills reported here, we had ≥ 1 neighboring pack collared. If field evidence at the kill site was conclusive and no other packs (of any ancestry) were detected at the kill, we considered the moose to have been killed by the focal pack. We determined number of days that the radio-collared study animals attended kills to further evaluate whether these packs were consuming the majority of the moose or scavenging remains of a kill made by another pack. We estimated the numbers of animals in each pack during both winters of the study by counting tracks in the snow while doing cluster investigations and by direct observation of tracks and (or) animals in radio-collared packs from fixed-wing aircraft or helicopter while circling or hovering at low elevation (≥ 500 feet above ground). We conducted these aerial monitoring surveys 1–3 times per week for the duration of the study.

Results

We studied predation by 10 packs of eastern coyotes and (or) eastern coyote \times eastern wolf hybrids during the two winters of the study ($n = 4$ in 2008–2009; $n = 10$ in 2009–2010; three packs were studied in both winters) based on location data from 11 GPS-collared coyotes and hybrids. During 2008–2009, we visited 209 location clusters (mean = 52 clusters per pack; range = 46–90) during 356 monitoring days (mean = 89 days per pack; range = 55–121). During 2009–2010, we visited 602 clusters (mean = 67 clusters per pack; range = 17–143) over 765 monitoring days (mean = 77 days per pack; range 28–212). We visited 59%–87% (mean = 78%) and 90%–99% (mean = 94%) of all clusters that met our criteria (see Materials and methods) from our focal packs during winters of 2008–2009 and 2009–2010, respectively.

We documented four cases where four different packs of two to five eastern coyotes and (or) eastern coyote \times eastern wolf hybrids killed adult moose (≥ 1.5 years old; Table 1). We also documented five other cases where moose appeared to have been killed by

Fig. 1. The 95% fixed kernel territories of canids in Wildlife Management Unit (WMU) 49, Ontario, Canada. Red circles indicate locations of moose (*Alces alces*) kills within territories of focal packs and blue areas are major lakes. Ancestry of each pack is indicated for wolves (W), eastern coyotes (*Canis latrans*; C), or eastern coyote × eastern wolf hybrids (H). We estimated territories with telemetry data from 2008 to 2009 (08–09) or from 2009 to 2010 (09–10).



eastern coyotes and (or) coyote × wolf hybrids (rather than scavenged), but we only report the details of the four cases where evidence was definitive. For all four of the packs that definitively killed moose, the genetic ancestry of both breeding animals in the pack was known. For three of the four packs, we confirmed that the breeding pair was intact throughout the winters we studied their predation using a combination of telemetry and noninvasive DNA identification at kill sites. For the fourth pack, we genotyped the male breeder 1 year after the predation event of interest (Table 1). We recovered mandibles of the four moose and estimated their ages to be ≥ 1.5 years ($n = 2$), 20 months (i.e., a yearling in its second winter, $n = 1$, Skeleton pack kill), and 20.5 years old ($n = 1$, Axe pack kill; Table 1). We recovered and examined marrow of two femurs from these moose and found no evidence of severe malnourishment, as both had marrow that was white and either

solid ($n = 1$, Axe pack kill) or spongy ($n = 1$, Skeleton pack kill; Table 1).

Discussion

We demonstrate that eastern coyotes and eastern coyote × eastern wolf hybrids preyed on adult moose in central Ontario. To our knowledge, these are the first scientific reports of coyotes and (or) coyote × wolf hybrids killing moose >6 months of age. Mean masses of eastern coyotes in our study area (females = 18 kg, males = 22 kg; Benson et al. 2012) were among the largest reported across their range (reviewed in Way 2007) and coyote × eastern wolf hybrids in our study area were larger (female = 20 kg, males = 24 kg). Nonetheless, mean masses of both eastern coyotes and eastern coyote × eastern wolf hybrids in central Ontario were

Table 1. Moose (*Alces alces*) predation involving eastern coyotes (*Canis latrans*) and eastern coyote × eastern wolf (*Canis latrans* × *Canis lycaon*) hybrids in Wildlife Management Unit 49 in central Ontario during winters of 2008–2009 and 2009–2010.

Pack name	Genotype (sex)	Date of kill	Pack size	No. genotyped ^a	Moose		Days on kill
					Age	Sex	
Ripple	Coyote (F), hybrid (M)	Jan. 2009	5	5 ^b	>1.5 years	Female	14
Axe	Coyote (M), hybrid (F)	Jan. 2010	5	5 ^b	20.5 years	Female	8 ^c
Turtle	Coyote (F), hybrid (M)	Feb. 2009	4	2 ^c	>1.5 years	Unknown	12
Skeleton	Coyote (M and F)	Dec. 2009	2	2 ^d	20 months	Female	18

Note: We show the name of each pack, the genotype class and sex of known animals in each pack, the month and year of the kill, the number of animals in the pack, number of animals genotyped in the pack, the estimated age and sex of the moose, and the number of days the focal pack attended the kill site based on telemetry data.

^aNumber of animals in the pack for which we obtained genotype from DNA analysis.

^bAll pack members were genotyped and confirmed to be with pack during winter of kill.

^cBreeding pair genotyped and with pack during winter of kill; unknown pack members presumed to be offspring.

^dBreeding female genotyped and documented at kill; male was genotyped the following winter.

^eAnimal captured near kill site after predation event occurred, so total number of days spent on kill is unknown.

significantly smaller than those of sympatric eastern wolves (female = 25 kg, male = 28 kg) and qualitatively smaller than gray wolves (*Canis lupus* L., 1758) and admixed gray wolves (Benson et al. 2012).

Although our hypothesis was supported by strong field evidence, we also considered whether it was possible that the moose were actually killed by wolves and that coyotes and coyote × wolf hybrids had scavenged the moose. We rejected this alternative explanation based on considerable additional evidence. First, resident wolves were relatively rare in WMU49 and represented only an estimated 7% of the resident *Canis* in this area during 2006–2010 (Benson et al. 2012). Second, wolves, coyotes, and hybrids in central Ontario (including WMU49) are territorial with each other such that coyotes and hybrids do not establish home ranges within those of wolves, but rather establish exclusive territories and exhibit minimal overlap with neighboring packs (Benson and Patterson 2013). Third, we had a high proportion of the local resident *Canis* packs radio-collared in our study area (Fig. 1). Finally, the kills we documented in the current study were made within relatively interior portions of the territories of the focal packs, well beyond the area of normal overlap between adjacent packs (Fig. 1) (Benson and Patterson 2013). Thus, we had strong evidence from multiple data sources supporting the contention that these moose were killed by the focal packs of eastern coyotes and eastern coyote × eastern wolf hybrids.

Our small sample size precluded formal analysis of landscape characteristics associated with moose kills; however, we suggest that at least five factors may have contributed to the ability of these coyotes and hybrids to kill moose. First, snow conditions probably facilitated canid predation similar to findings in previous studies (Paquet 1992; Gese and Grothe 1995; Patterson and Messier 2000). For example, eastern coyotes (Skeleton pack; Table 1) killed a moose during a period when a firm layer of crust on top of deep snow likely impeded moose travel and facilitated hunting success of coyotes (J.F. Benson, personal observation). Second, the moose killed by the Skeleton pack was killed on a steep (approximately 40°–45°) slope such that the coyotes could have used this to their advantage by attacking the moose where it had poor footing and (or) by slowing it down while climbing the hill in deep snow. Muntz and Patterson (2004) similarly reported eastern coyotes using a steep slope to facilitate the killing of an adult male white-tailed deer (*Odocoileus virginianus* (Zimmermann, 1780)) in Nova Scotia. Third, we noted that two of four moose killed by coyotes and hybrids (Ripple and Turtle packs; Table 1) were in relatively dense conifer stands such that it appeared the moose were able to fit between the trees, but probably would not have been able to maneuver effectively. Moose generally attempt to fight off predators by facing them and using hooves and (or)

antlers (Peterson 1977; Mech and Peterson 2003), so these dense trees may have limited their ability to swing around and face coyotes that generally attack the hind quarters (Gese and Grothe 1995). Fourth, age may have influenced the predation, as one of the predated moose was 20.5 years old (Axe pack kill; Table 1). This cow was within the upper range of ages reported for wild moose (Peterson et al. 2010) and was older than any captured moose aged by cementum annuli during a recent study in WMU49 and Algonquin Provincial Park (range 1–14, $n = 80$; Murray et al. 2012). Older-age moose are generally more susceptible to canid predation (Peterson 1977) and often develop osteoarthritis, which can further increase their vulnerability to predation (Peterson et al. 2010). Although the two moose whose ages were estimated by cementum annuli were young (20 month) or old (20.5 years) moose, it is worth noting that at least one of the moose appeared to be a prime-age moose between 4.5–8.5 years of age (Ripple pack kill; Table 1) based on our visual inspection of tooth wear. Finally, coyotes and coyote × wolf hybrids may be more likely to prey on moose in areas where other ungulates (i.e., deer) or other food sources are scarce. Indeed, packs of coyotes and (or) hybrids that killed moose in WMU49 occupied territories with lower proportions of deer wintering habitat (a proxy for deer availability) than packs that were not documented killing moose (supplementary material).¹

Recent studies found that the moose population in WMU49 and Algonquin Provincial Park was increasing and that canid predation was apparently not a major cause of adult (Murray et al. 2012) or calf (Patterson et al. 2013) mortality. Thus, it seems unlikely that predation by coyotes and hybrids is cause for conservation concern in central Ontario. Nonetheless, these smaller canids were more capable of killing large ungulates than previously believed. Given our results, it may be prudent for managers of declining populations of moose (e.g., Minnesota; Lenarz et al. 2010) and threatened or endangered caribou populations (e.g., Canada; Boisjoly et al. 2010) to investigate whether coyote predation occurs and determine if it significantly adds to other sources of mortality. Alternatively, the situation in Ontario could be relatively unique because ongoing hybridization between coyotes and wolves (Benson et al. 2012) coincides with a local moose population at relatively high density (Murray et al. 2012). We encourage other studies of eastern coyotes and (or) coyote × wolf hybrids to investigate and quantify predation on ungulates to clarify effects on community structure that have resulted from replacing wolves with these smaller canids across much of northeastern North America.

¹Supplementary material is available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjz-2013-0160>.

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References

- Bekoff, M. 1978. Coyotes: biology, behavior, and management. Academic Press, New York.
- Benson, J.F., and Patterson, B.R. 2013. Inter-specific territoriality in a *Canis* hybrid zone: spatial segregation between wolves, coyotes, and hybrids. *Oecologia*. [Online ahead of print.] doi:10.1007/s00442-013-2730-8. PMID:23864253.
- Benson, J.F., Patterson, B.R., and Wheelodon, T.J. 2012. Spatial genetic and morphologic structure of wolves and coyotes in relation to environmental heterogeneity in a *Canis* hybrid zone. *Mol. Ecol.* 21: 5934–5954. doi:10.1111/mec.12045. PMID:23173981.
- Benson, J.F., Mills, K.J., Loveless, K.M., and Patterson, B.R. 2013. Genetic and environmental influences on pup mortality risk for wolves and coyotes within a *Canis* hybrid zone. *Biol. Conserv.* 166: 133–141. doi:10.1016/j.biocon.2013.06.018.
- Boisjoly, D., Ouellet, J.-P., and Courtois, R. 2010. Coyote habitat selection and management implications for the Gaspésie Caribou. *J. Wildl. Manage.* 74: 3–11. doi:10.2193/2008-149.
- Bowyer, R.T., McKenna, S.A., and Shea, M.E. 1983. Seasonal changes in coyote food habits as determined by fecal analysis. *Am. Midl. Nat.* 109: 266–273. doi:10.2307/2425406.
- Buskirk, S.W., and Gipson, P.S. 1978. Characteristics of wolf attacks on moose in Mount McKinley National Park, Alaska. *Arctic*, 31: 499–502.
- Cheatum, E.L. 1949. Bone marrow as an index of malnutrition in deer. *N.Y. State Conserv.* 3: 19–22.
- Clark, F.W. 1972. Influence of jackrabbit density on coyote population change. *J. Wildl. Manage.* 36: 343–356. doi:10.2307/3799064.
- Dumond, M., and Villard, M.A. 2001. Does coyote diet vary seasonally between a protected and an unprotected forest landscape? *Ecoscience*, 8: 301–310.
- Fedriani, J.M., Fuller, T.K., and Sauvajot, R.M. 2001. Does availability of anthropogenic food enhance densities of omnivorous mammals? An example with coyotes in southern California. *Ecography*, 24: 325–331. doi:10.1034/j.1600-0587.2001.240310.x.
- Forbes, G.J., and Theberge, J.B. 1996. Response by wolves to prey variation in central Ontario. *Can. J. Zool.* 74(8): 1511–1520. doi:10.1139/z96-165.
- Gese, E.M., and Grothe, S. 1995. Analysis of coyote predation on deer and elk during winter in Yellowstone National Park, Wyoming. *Am. Midl. Nat.* 133: 36–43. doi:10.2307/2426345.
- Gompper, M.E. 2002. Top carnivores in the suburbs? Ecological and conservation issues raised by the colonization of north-eastern North America by coyotes. *Bioscience*, 52: 185–190.
- Hamilton, W.J. 1974. Food habits of the coyote in the Adirondacks. *N.Y. Fish Game J.* 21: 177–181.
- Jensen, B. 2001. Aging moose. *North Dakota Outdoors*, 64: 17–20.
- Kays, R., Curtis, A., and Kirchman, J.J. 2010. Rapid adaptive evolution of north-eastern coyotes via hybridization with wolves. *Biol. Lett.* 6: 89–93. doi:10.1098/rsbl.2009.0575. PMID:19776058.
- Kays, R.W., Gompper, M.E., and Ray, J.C. 2008. Landscape ecology of eastern coyotes based on large-scale estimates of abundance. *Ecol. Appl.* 18: 1014–1027. doi:10.1890/07-0298.1. PMID:18536259.
- Kyle, C.J., Johnson, A.R., Patterson, B.R., Wilson, P.J., Shami, K., Grewal, S.K., and White, B.N. 2006. Genetic nature of eastern wolves: past, present and future. *Conserv. Genet.* 7: 273–287. doi:10.1007/s10592-006-9130-0.
- Larivière, S., and Crête, M. 1993. The size of eastern coyotes (*Canis latrans*): a comment. *J. Mammal.* 74: 1072–1074. doi:10.2307/1382446.
- Lenarz, M.S., Fieberg, J., Schrage, M.W., and Edwards, A.J. 2010. Living on the edge: viability of moose in northeastern Minnesota. *J. Wildl. Manage.* 74: 1013–1023. doi:10.2193/2009-493.
- Lingle, S. 2002. Coyote predation and habitat segregation of white-tailed deer and mule deer. *Ecology*, 83: 2037–2048. doi:10.1890/0012-9658(2002)083[2037:CPAHSO]2.0.CO;2.
- Litvaitis, J.A., and Harrison, D.J. 1989. Bobcat–coyote niche relationships during a period of coyote population increase. *Can. J. Zool.* 67(5): 1180–1188. doi:10.1139/z89-170.
- Major, J.T., and Sherburne, J.A. 1987. Interspecific relationships of coyotes, bobcats, and red foxes in western Maine. *J. Wildl. Manage.* 51: 606–616. doi:10.2307/3801278.
- Mech, L.D. 1970. The wolf: the ecology and behavior of an endangered species. The Natural History Press, Garden City, N.Y.
- Mech, L.D., and Delgiudice, G.D. 1985. Limitations of the marrow-fat technique as an indicator of body condition. *Wildl. Soc. Bull.* 13: 204–206.
- Mech, L.D., and Peterson, R.O. 2003. Wolf–prey relations. In *Wolves: behavior, ecology, and conservation*. Edited by L.D. Mech and L. Boitani. University of Chicago Press, Chicago, Ill. pp. 131–160.
- Messier, F., and Crête, M. 1985. Moose–wolf dynamics and the natural regulation of moose populations. *Oecologia*, 65: 503–512. doi:10.1007/BF00379664.
- Messier, F., Barrette, C., and Huot, J. 1986. Coyote predation on a white-tailed deer population in southern Quebec. *Can. J. Zool.* 64(5): 1134–1136. doi:10.1139/z86-170.
- Muntz, E.M., and Patterson, B.R. 2004. Evidence for the use of vocalization to coordinate the killing of a white-tailed deer, *Odocoileus virginianus*, by coyotes, *Canis latrans*. *Can. Field-Nat.* 118: 278–280.
- Murray, D.L., Hussey, K.F., Finnegan, L.A., Lowe, S.J., Price, G.N., Benson, J., Loveless, K.M., Middel, K.R., Mills, K., Potter, D., Silver, A., Fortin, M.-J., Patterson, B.R., and Wilson, P.J. 2012. Assessment of the status and viability of a population of moose (*Alces alces*) at its southern range limit in Ontario. *Can. J. Zool.* 90(3): 422–434. doi:10.1139/z2012-002.
- Paquet, P.C. 1992. Prey use strategies of sympatric wolves and coyotes in Riding Mountain National Park, Manitoba. *J. Mammal.* 73: 337–343. doi:10.2307/1382067.
- Parker, G.R. 1986. The seasonal diet of coyotes, *Canis latrans*, in northern New Brunswick. *Can. Field-Nat.* 100: 74–77.
- Patterson, B.R., and Messier, F. 2000. Factors influencing killing rates of white-tailed deer by coyotes in eastern Canada. *J. Wildl. Manage.* 64: 721–732. doi:10.2307/3802742.
- Patterson, B.R., and Messier, F. 2003. Age and condition of deer killed by coyotes in Nova Scotia. *Can. J. Zool.* 81(11): 1894–1898. doi:10.1139/z03-189.
- Patterson, B.R., Benson, J.F., Middel, K.R., Mills, K.J., Silver, A., and Obbard, M.E. 2013. Moose calf mortality in central Ontario, Canada. *J. Wildl. Manage.* 77: 832–841. doi:10.1002/jwmg.516.
- Peterson, R.O. 1977. Wolf ecology and prey relationships on Isle Royale. U.S. Natl. Park Serv. Sci. Monogr. Ser. No. 11. U.S. National Park Service, Washington, D.C.
- Peterson, R.O., Schwartz, C.C., and Ballard, W.B. 1983. Eruption patterns of selected teeth in three North American moose populations. *J. Wildl. Manage.* 47: 884–888. doi:10.2307/3808633.
- Peterson, R.O., Vucetich, J.A., Fenton, G., Drummer, T.D., and Larsen, C.S. 2010. Ecology of arthritis. *Ecol. Lett.* 13: 1124–1128. doi:10.1111/j.1461-0248.2010.01504.x. PMID:20618843.
- Prugh, L.R., Stoner, C.J., Epps, C.W., Bean, W.T., Ripple, W.J., Laliberte, A.S., and Brashares, J.S. 2009. The rise of the mesopredator. *Bioscience*, 59: 779–791. doi:10.1525/bio.2009.59.9.9.
- Richer, M.-C., Crête, M., Ouellet, J.-P., Rivest, L.-P., and Huot, J. 2002. The low performance of forest versus rural coyotes in northeastern North America: inequality between presence and availability of prey. *Ecoscience*, 9: 44–54.
- Samson, C., and Crête, M. 1997. Summer food habits and population density of coyotes, *Canis latrans*, in boreal forests of southeastern Quebec. *Can. Field-Nat.* 111: 227–233.
- Way, J.G. 2007. A comparison of body mass of *Canis latrans* (coyotes) between eastern and western North America. *Northeast. Nat.* 14: 111–124. doi:10.1656/1092-6194(2007)14[111:ACOBMO]2.0.CO;2.
- Wolfe, M.L. 1974. An overview of moose coactions with other animals. In *Alces: moose ecology*. Edited by J. Bedard. Les Presses de l'Université Laval, Quebec. pp. 437–456.