

## Coyotes, Red Foxes, and the Prevalence of Lyme Disease

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**Abstract** - Lyme disease is the most prevalent vector-borne disease in north temperate areas worldwide, with the majority of cases reported in the northeastern United States. The transmission cycle involves ticks, deer, small mammalian hosts such as mice, and numerous other species. Levi et al. (2012) suggested that *Canis latrans* (Coyote) abundance and *Vulpes vulpes* (Red Fox) scarcity are strong predictors of Lyme disease cases in eastern North America, with *Odocoileus virginianus* (White-tailed Deer) abundance being less important. This suggestion was based on correlations of disease dynamics with human harvests of canids, as it has been suggested that Red Foxes occur at a lower abundance because of Coyote predation. Because Red Foxes are more effective predators of small mammals, the authors of that work contend that the lower Red Fox abundance results in an increase in the incidence of Lyme disease. This paper re-examines the evidence used by Levi et al. (2012) to reach their conclusions. We address the following points: 1) Levi et al. did not provide data on rodent populations or Lyme disease incidence; 2) Coyotes eat rodents, so a Coyote-induced reduction of Red Fox populations might not result in increased rodent populations; 3) Coyote harvests are poor indicators of Coyote abundance; 4) both Red Fox numbers and rodent numbers fluctuate dramatically due to factors such as disease and weather; 5) some of the data used by Levi et al. (2012) were from regions with western Coyotes, while other data were from areas with hybrid eastern Coyotes, thus confounding the situation; and 6) Levi et al. did not consider important alternative hypotheses, such as habitat fragmentation and climate change. Additionally, the historical dynamics of the Lyme disease system are unknown given that *Canis lupus lycaon* (= *Canis lycaon*) (Eastern Wolf) and *Urocyon cinereoargenteus* (Gray Foxes) originally lived in most of the northeast, while Red Foxes and Coyotes were historically absent from most of the area. We suggest proceeding with caution before concluding that the presence of Coyotes (or the reduction of Red Foxes) is the primary cause of increased incidence of Lyme disease cases in the eastern United States.

### Introduction

Lyme disease prevalence involves multi-species interactions including ticks and a variety of mammalian hosts. The disease has caused many human ailments in North America, as well as in Europe and Asia (Bacon et al. 2008). The majority of cases have been reported in the northeastern region of the United States (Bacon et al. 2008). It is the most prevalent vector-borne disease in North America, with both the annual incidence and geographic range still increasing (Bacon et al. 2008, Barbour and Fish 1993). Ecological changes, resulting in the century-long population increase of *Odocoileus virginianus* Zimmermann (White-tailed Deer) in the northeastern and midwestern United States, are largely responsible for the recent emergence of Lyme disease as a public health problem in the past 30 years

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(Barbour and Fish 1993, Ostfeld 2011). Additionally, a growing body of evidence implicates small-mammal abundance as a key determinant of infected nymph-tick density—the primary measure of entomological risk for Lyme disease (Levi et al. 2012, Ostfeld et al. 2006).

Levi et al. (2012) analyzed correlations of numbers of canids killed by humans and found that *Canis latrans* Say (Coyote) abundance and *Vulpes vulpes* L. (Red Fox) scarcity were the strongest predictors of Lyme disease cases in eastern North America. They concluded that a change in predator numbers, mainly the arrival and increase of Coyotes and the subsequent decrease in Red Foxes, in eastern North America have caused a recent spike in the number of Lyme disease cases. Further, the authors concluded that White-tailed Deer abundance did not correlate with the number of Lyme cases but, rather, the scarcity of Red Foxes caused a likely increase in small mammals, such as *Peromyscus* spp. (mice) and *Sorex* spp. (shrews), and this subsequently increased the incidence of Lyme cases.

Coyotes eat a variety of foods including fruits, berries, insects, small mammals, ungulates, phocids, and livestock (see Andelt 1985, Gese et al. 1996a, Harrison and Harrison 1984, Parker 1995, Patterson and Messier 2000, Sacks et al. 1999, Way 2008, Way and Horton 2004). They prey mostly on medium- to large-sized animals in northeastern North America (see Parker 1995 for a review), but small rodents are an important component of their diet, especially where ungulate prey or their carcasses are not readily available (Crabtree and Sheldon 1999a,b; Crabtree and Varley 1995, Gese et al. 1996b). In this paper, we re-examine the data used by Levi et al. (2012) and suggest that there have been a variety of major ecological changes in eastern North America in the past  $\approx 30$  years (since Lyme disease became an epidemic), and Coyote presence and Red Fox scarcity represent one element of the fabric of the complex multi-species Lyme disease system.

### Available Data on Mouse Populations and Lyme Disease Incidence

Levi et al. (2012) developed a complex host-vector disease model, and reported theoretical Lyme disease cases based on calculated infected tick numbers from the model. Yet, there are no empirical data from organizations like the Centers for Disease Control and Prevention ([www.cdc.gov](http://www.cdc.gov)) to support (or refute) the number of Lyme cases predicted by their model output. Additionally, the authors did not report on any direct field data collected on either tick or small-mammal abundance (see their methods section: pp. 10,946–10,947), yet the tenet of their paper relied on increased mouse abundance with a concomitant increase in tick abundance due to reduced Red Fox numbers.

Lyme disease is a recently described (within  $\approx 30$  years) disease (Bacon et al. 2008, Barbour and Fish 1993). There is a likelihood that, in addition to the other factors discussed in this paper, we are simply witnessing exponential growth and reporting of cases of this new disease, from its infancy to its current epidemic as a public health threat as it spreads in range, and increases in frequency. This exponential growth as depicted on the graphs of Levi et al. (2012: e.g., Figs. 5, S1) could have occurred regardless of Red Fox or Coyote abundance.

### Coyote Predation on Small Mammals

While the food habits of Coyotes are quite variable, small rodents are a main part of their diet in many regions, especially during snow-free months where ungulate prey or carcasses are not readily available (Crabtree and Sheldon 1999a, b; Crabtree and Varley 1995, Gese et al. 1996a, Hidalgo-Mihart et al. 2001, Morey et al. 2007, Parker 1995). For example, Coyotes in Yellowstone National Park consumed 76.2 % of the estimated yearly available microtine biomass, which constituted 32.4 % of their overall diet (Crabtree and Varley 1995, Crabtree and Sheldon 1999a). At the same time (during pre-*Canis lupus* L. [Gray Wolf] conditions in the park, i.e., when Coyotes lived at saturated densities before Gray Wolves inhabited the area), Coyotes were the number one predator on *Cervus elaphus* L. (Elk), doing so not by specialization, but through comparable abundance relative to other carnivores (mainly *Puma concolor* L. [Mountain Lions], *Ursus arctos* L. [Brown Bear], and *U. americana* Pallas [American Black Bear]; Crabtree and Varley 1995, Crabtree and Sheldon 1999a, b). This was a high-density, saturated population of Coyotes that was not exploited by people. Therefore, Coyotes maximized their predation capability on prey species including small rodents, lagomorphs, and ungulates, removing three-quarters of the microtine population every year (Crabtree and Sheldon 1999b).

Counter to Levi et al.'s (2012) claims that Coyote presence caused an increase in small-mammal abundance, a described benefit of the restoration of Gray Wolves to Yellowstone was to lower Coyote numbers so more rodent prey were available to a variety of other meso-predators such as Red Foxes (Johnson and Crabtree 1999). Thus, it is possible that low Coyote numbers may result in higher rodent numbers. Conversely, high Coyote numbers (i.e., in a saturated population like Yellowstone) may allow Coyotes to maximize their use of rodents resulting in lower rodent numbers. If this were the case, then Coyotes would effectively replace Red Foxes as predators of small mammals in the eastern US, and influence the Lyme disease system in a way comparable to Red Foxes, contrary to Levi et al.'s (2012) claim that a reduction in Red Foxes may be increasing Lyme disease incidence.

### Coyote Harvests are Poor Indicators of and May Lower Coyote Populations

Levi et al. (2012) relied on Coyote, Red Fox, and White-tailed Deer harvests (in MN, WI, PA, VA) from the past 30 years to infer the relative abundance of each species. The strongest relationship they found was that reduced numbers of harvested Red Foxes correlated indirectly with increased cases of Lyme disease. However, reliance on harvest data as a proxy for abundance is a problematic component of Levi et al.'s (2012) methodology. While the precept of Levi et al.'s (2012) paper was that harvests are a good metric for assessing canid abundance (Levi et al. 2012), we are not aware of any data suggesting that this is true, and we recommend that this assumption be re-examined. In fact, harvest records in general are inherently biased as estimates of abundance and they do not provide reliable monitoring data (O'Connell et al. 2006, Ray 2000). For instance, *Lynx lynx* L. (Canada Lynx) population sizes fluctuate greatly over an approximately decadal cycle, tracking the

abundance of *Lepus americanus* Erxleben (Snowshoe Hare) with a one- to two-year lag (Poole 2003, Slough and Mowat 1996). Removal of Canada Lynx by trapping is a major cause of mortality in some populations in Canada, but it may be compensatory to natural mortality during the decline phase of some populations (Poole 2003). However, coupled with human-caused and natural mortality factors, declining pelt values have caused overall Canada Lynx trapping-harvests to decrease, making it difficult to decipher the status of regional Canada Lynx population sizes using harvest numbers as an index of abundance (Slough and Mowat 1996).

Research indicates that canids are highly intelligent, social, and family-oriented animals that raise their young cooperatively (e.g., Smith et al. 2009, Way and Timm 2008). Coyotes, like wolves, are territorial and live in social groups that guard their home range from other packs (Mech and Boitani 2003; Patterson and Messier 2000; Way et al. 2002, 2009). Populations are self-limiting in undisturbed populations, and territories often are arranged in a non-overlapping, honey-comb-like fashion (Crabtree and Sheldon 1999a, Crabtree and Varley 1995, Mech and Boitani 2003, Way et al. 2002). Killing canids often creates openings in territories for new individuals to colonize (Way et al. 2009). Research on *Canis lupus dingo* Meyer (Dingo; Wallach et al. 2009) and Coyotes (Way et al. 2009) has shown that the effect of lethal management on abundance was neither consistent nor predictable as control actions severely fractured social groups. Wallach et al. (2009) recommended that management decisions involving social predators consider social stability to ensure the species' conservation and ecological functioning. Levi et al. (2012) noted that Coyotes, especially in the Northeast, live at much lower densities than Red Foxes (e.g., Way et al. 2002). Thus, intense human hunting of *Canis* species may influence population dynamics and prevent the animals from performing their full ecological roles, such as top-down predation on prey systems (Wallach et al. 2009), which would likely influence the Lyme disease system.

Predicting what type of biological effect the killing of Coyotes has on White-tailed Deer and rodent populations is logistically problematic as there would be no way to control for the many variables (e.g., Coyote and Red Foxes, prey abundance, location, environmental conditions) under study. But it is difficult to imagine that the documented hyper-harvests of 25,000–50,000 Coyotes per state per year (Levi et al. 2012:10,944, figure 3) would not affect their density, and hence, their ability to prey on the very rodent species that they are claimed to increase. Therefore, we disagree with Levi et al.'s (2012:10,942) statement that “somewhat paradoxically, the expansion of Coyotes likely decreased predation rates on small mammals by suppressing more-efficient predators (foxes)”. They did not collect any field data to verify this, and rely only on correlations to make their claim. Clearly empirical data needs to be collected in eastern North America to better understand the relationship between Coyotes, Red Foxes, and Lyme disease.

### **Fox and Rodent Numbers Fluctuate Independently of Coyote Populations**

With or without Coyotes being present in the east, Red Fox populations are historically cyclical, with diseases such as mange (caused by the mite *Sarcoptes scabiei* De

Geer), that infects Red Foxes and can spread throughout the population, reducing Red Fox number and density (Baker et al. 2000, Lindström et al. 1994, Trainer and Hale 1969). Other diseases such as canine distemper virus, canine parvovirus, and rabies have an important impact on Red Foxes where present, and likely influence Red Fox abundance, with or without Coyotes present (Almberg et al. 2009). These diseases pre-date the arrival of Coyotes in the eastern US and, if Red Fox abundance is negatively correlated with prevalence of Lyme disease, their influence should have affected the incidence of Lyme disease, with more Lyme cases theoretically being present when Red Foxes were temporarily reduced in abundance and rodent numbers were cyclically higher.

### **Study Sites not in Eastern Coyote Range and Historical Lyme Disease Dynamics**

Levi et al. (2012) obtained their data from states in described western Coyote range (MN, WI), or in states that are at the overlapping edge of the ranges of eastern and western Coyotes (e.g., PA, VA, NY; Bozarth et al. 2011, Kays et al. 2010). Thus, the authors' discussion of the hybrid nature of the Coyote in northeastern North America (mainly New England and eastern NY and eastern PA; Bozarth et al. 2011, Kays et al. 2010, Way et al. 2010) and their associated larger size and greater reliance on White-tailed Deer is accurate, but a fairly moot point for their study. In other words, the authors use data from states with western Coyotes (e.g., WI, MN), and these animals often feed on small mammals (Crabtree and Sheldon 1999a,b; Morey et al. 2007). The exception to this would be Levi et al.'s (2012: Fig. 4a) data from New York, which is in eastern Coyote range (Kays et al. 2010). Thus, Coyotes probably should not be treated as a single group acting the same throughout their entire range, especially in eastern North America. Future research should examine the role of both western and eastern Coyotes and the relation that they have to the Lyme disease system.

The eastern Coyote is a hybrid between the western Coyote and the nearly extirpated (outside of the Algonquin Park, Ontario region) *Canis lupus lycaon* (= *Canis lycaon*) Schreber (Eastern Wolf). It is closely related to the original Eastern Wolf that likely lived in most of eastern North America until the 1800s (Chambers et al. 2012, Rutledge et al. 2012, Way 2013, Way et al. 2010). Due to human exploitation, it is unknown what ecological role this smaller, deer-eating Eastern Wolf historically had, and how it could have influenced the Lyme disease system, but evidence suggests that Red Foxes historically did not occur south of the boreal forest (roughly around the border of VT and NH with MA; Aubrey et al. 2009, Kamler and Ballard 2002). Instead, *Urocyon cinereoargenteus* Schreber (Gray Fox) occurred in the hardwood deciduous forests of most of the eastern US. Gray Foxes are omnivorous, and although they prey on small vertebrates like rodents and other small mammals, fruit and invertebrates also form a substantial part of their diet (Fritzell and Haroldson 1982). Thus, it is unknown what influence these original canid inhabitants of eastern North America had on the Lyme disease system, but it is noteworthy that the species Levi et al. (2012) identify as the main biological control agent of

mice (i.e., Red Foxes) likely did not historically inhabit many of the areas discussed in their paper. Rather, a European strain of Red Fox, introduced to more southern (Northeast, mid-Atlantic), agricultural areas of the United States by early Europeans, is the animal that now lives in much of eastern North America south of the boreal forest (Kamler and Ballard 2002).

### **Alternative Hypotheses: Habitat Fragmentation and Climate Change**

Unrelated to Coyotes and foxes are other, more regional, factors that potentially influence the Lyme disease system including habitat fragmentation and climate change. For brevity, we discuss each topic briefly here with hope that these ideas stimulate further research.

#### **Habitat fragmentation**

Concurrent with the increase of Coyotes and Lyme disease cases, habitat fragmentation is ongoing in eastern North America. Fragmentation produces ideal *Peromyscus leucopus* Rafinesque (White-footed Mouse) habitat, and increases their populations (Bender et al. 1998). Similarly, *P. maniculatus* Wagner (Deer Mice) are significantly more abundant at edges of farm woodlots than in interiors (Bayne and Hobson 1998). Incidentally, one potential consequence of reduced species diversity and high mouse density in small fragments is a potential increase in human exposure to Lyme disease. A dramatic increase in the density of infected tick nymphs, and therefore in Lyme disease risk, was found with decreasing forest patch size, suggesting that by influencing the community composition of vertebrate hosts for disease-bearing vectors, habitat fragmentation can influence human health (Allan et al. 2003). Forests are connected over large regions, but fragmentation is so pervasive that edge effects potentially influence ecological processes on most forested lands (Ritters et al. 2002). Levi et al. (2012) do not discuss nor account for the important role of habitat fragmentation and increased mouse abundance on the recent spike in Lyme cases. It is possible that even with a higher density of Red Foxes (or Coyotes), mice might exist in sufficient abundance in the fragmented eastern US to elevate the number of Lyme disease cases.

#### **Climate change**

Climate change is pervasive and affects everything from tree distribution and tree migration (Iverson and Prasad 1998) to pathogen development and survival rates, disease transmission, and host susceptibility (Harvell et al. 2002). The past 10–30 years have produced record warmth (NOAA 2012), and future analyses should correlate climate change dynamics and warming trends with Lyme disease outbreaks. It is possible that warmer winters are allowing more ticks to survive year-round, a phenomenon that could serve as a positive feedback mechanism for additional Lyme disease cases being reported in the past 30 years. Although speculative, this possibility is worth further examination and warrants future research on the subject to see if the effects of climate change are robust on tick populations (e.g., Harvell et al. 2002).

As suggested by Harvell et al. (2002), vector-borne human pathogens such as malaria, African trypanosomiasis, Lyme disease, tick-borne encephalitis, yellow fever, plague, and dengue fever have increased in incidence or geographic range in recent decades. The hypothesis that climate warming has caused latitudinal shifts of vectors and diseases is supported by laboratory and field studies showing that 1) arthropod vectors and parasites die or fail to develop below threshold temperatures; 2) rates of vector reproduction, population growth, and biting increase (up to a limit) with increasing temperature; and 3) parasite development rates and period of infectivity increase with temperature (Patz et al. 1998).

## Conclusion

### Proceed with caution when discussing predator manipulation

While Levi et al. (2012) hypothesize that the eastern Coyote has displaced the Red Fox throughout much of the eastern US, causing an increase in Lyme disease cases, it important to realize that the Eastern Coyote now occupies the former range of the Eastern Wolf and to some extent has replaced the Eastern Wolf's ecological function (Rutledge et al. 2012, Way 2013). Yet, Levi et al. (2012:10,945–10,946) conclude their paper with a discussion of predator manipulation in which they state that "Detailed studies and experimental manipulation of predators could help elucidate whether controlling Lyme disease might be best accomplished by a combination of predator manipulation and severe reductions in deer densities necessary to reduce tick abundance." However, there are many variables influencing Lyme disease, and we have discussed some of them here. The manipulation experiment suggested by Levi et al. (2012) also ignores the myriad of ecological benefits of Coyote presence, such as promoting higher species diversity (e.g., songbirds and rodents) by decreasing the abundance of smaller meso-predators (Prugh et al. 2009) such as Red Foxes, *Mephitis mephitis* Schreber (Striped Skunk), and *Felis catus* L. (Domestic Cat) by direct killing, altering their behavior, or potentially inducing people to keep their pets (in the case of Domestic Cats) inside (Crooks and Soule 1999, Henke and Bryant 1999). Urban Coyotes may also help reduce overabundant *Branta canadensis* L. (Canada Geese) populations in some metropolitan areas (Gehrt et al. 2010). And the presence of Coyotes may even benefit preferred game (i.e., human hunted) species such as waterfowl (Sovada et al. 1995) and *Centrocercus urophasianus* Bonaparte (Sage Grouse; Mezguida et al. 2006). Because of these documented ecological benefits of Coyotes, we suggest areas of study where predator numbers (mainly Coyotes) are not manipulated through hunter harvest to determine if saturated populations of Coyotes reduce rodent populations (Crabtree and Varley 1995) enough to lower the incidence of Lyme disease in an area. Even if Levi et al. (2012) are correct in their assessment that increased Coyote populations increase Lyme disease incidence, their impacts should be viewed in a broader ecosystem services context.

In conclusion, Levi et al. (2012) provide interesting results from a study of correlational statistics. However, there are additional and important variables to consider when determining whether Coyotes are likely contributing to an increase

in Lyme disease cases because of reduced Red Fox abundance. The reduction of Coyotes through human hunting may reduce their ability to prey on and potentially control mouse numbers. Furthermore, other factors potentially influencing the Lyme system, such as disease, habitat fragmentation, and climate change, may also influence the number of Lyme cases reported. We suggest proceeding with caution when concluding that Coyotes are the most robust mechanism causing an increase in Lyme disease cases in the eastern United States.

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### Literature Cited

- Allan, B.F., F. Keesing, and R.S. Ostfeld. 2003. Effect of forest fragmentation on Lyme disease risk. *Conservation Biology* 17(1):267–272.
- Almberg, E.S., L.D. Mech, D.W. Smith, J.W. Sheldon, and R.L. Crabtree. 2009. A serological survey of infectious disease in Yellowstone National Park's canid community. *PLoS ONE* 4(9): e7042. doi:10.1371/journal.pone.0007042.
- Andelt, W.F. 1985. Behavioral ecology of Coyotes in south Texas. *Wildlife Monographs* 49:1–45.
- Aubrey, K.B., M.J. Statham, B.N. Sacks, J.D. Perrine, and S.M. Wisely. 2009. Phylogeography of North American Red Fox: Vicariance in Pleistocene forest refugia. *Molecular Ecology* 18:2668–2686.
- Bacon, R.M., K.J. Kugeler, and P.S. Mead. 2008. Surveillance for Lyme disease—United States, 1992–2006. *Morbidity and Mortality Weekly Report (Centers for Disease Control, Atlanta)*. 57(SS-10):1–12.
- Baker, P.J., S.M. Funk, S. Harris, and P.C.L. White. 2000. Flexible spatial organization of urban Foxes, *Vulpes vulpes*, before and during an outbreak of sarcoptic mange. *Animal Behaviour* 59(1):127–146.
- Barbour, A.G., and D. Fish. 1993. The biological and social phenomenon of Lyme disease. *Science* 260:1610–1616.
- Bayne, E.M., and K.A. Hobson. 1998. The effects of habitat fragmentation by forestry and agriculture on the abundance of small mammals in the southern boreal mixedwood forest. *Canadian Journal of Zoology* 76:62–69.
- Bender, D.J., T.A. Contreras, and L. Fahrig. 1998. Habitat loss and population decline: A meta-analysis of the patch size effect. *Ecology* 79:517–533.
- Bozarth, C.A., F. Hailer, L.L. Rockwood, C.W. Edwards, and J.E. Maldonado. 2011. Coyote colonization of northern Virginia and admixture with Great Lakes wolves. *Journal of Mammalogy* 92(5):1070–1080.
- Chambers, S.M., S.R. Fain, B. Fazio, and M. Amaral. 2012. An account of the taxonomy of North American wolves from morphological and genetic analyses. *North American Fauna* 77:1–67. doi:10.3996/nafa.77.0001.
- Crabtree, R.L., and J.D. Varley. 1995. The ecological and sociodemographic role of the Coyote on Yellowstone's Northern Range. Pp. 63–84, *In* A.P. Curlee, A.M. Gillesburg, and D. Casey (Eds.). *Proceedings of the 3<sup>rd</sup> biennial science conference on the Greater Yellowstone Ecosystem, Greater Yellowstone's Predators*. Yellowstone National Park and Northern Rockies Conservation Cooperative, Mammoth, WY.



- Crabtree, R.L., and J.W. Sheldon. 1999a. The ecological role of Coyotes on Yellowstone's Northern Range. *Yellowstone Science* 7:15–24.
- Crabtree, R.L., and J.W. Sheldon. 1999b. Coyotes and canid coexistence in Yellowstone. Pp. 127–163, *In* T.W. Clark, A.P. Curlee, S.C. Minta, and P.M. Kareiva (Eds.). *Carnivores in Ecosystems: The Yellowstone Experience*. Yale University Press, New Haven, CT.
- Crooks, K.R., and M.E. Soule. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. *Nature* 400:563–566.
- Fritzell, E. K., and K. J. Haroldson. 1982. *Urocyon cinereoargenteus*. *Mammalian Species* 189:1–8.
- Gehrt, S.D., S.P.D. Riley, and B.L. Cypher (Eds.). 2010. *Urban carnivores: Ecology, Conflict, and Conservation*. Johns Hopkins University Press, Baltimore, MD.
- Gese, E.M., R.L. Ruff, and R.L. Crabtree. 1996a. Foraging ecology of Coyotes (*Canis latrans*): The influence of extrinsic factors and a dominance hierarchy. *Canadian Journal of Zoology* 74:769–783.
- Gese, E.M., R.L. Ruff, and R.L. Crabtree. 1996b. Intrinsic and extrinsic factors influencing Coyote predation of small mammals in Yellowstone National Park. *Canadian Journal of Zoology* 74:784–797.
- Harrison, D.J., and J.A. Harrison. 1984. Foods of adult Maine Coyotes and their known-age pups. *Journal of Wildlife Management* 48:922–926.
- Harvell, C.D., C.E. Mitchell, J.R. Ward, S. Altizer, A.P. Dobson, R.S. Ostfeld, and M.D. Samuel. 2002. Climate warming and disease risks for terrestrial and marine biota. *Science* 296(5576):2158–2162.
- Henke, S.E., and F.C. Bryant. 1999. Effects of Coyote removal on the faunal community in western Texas. *Journal of Wildlife Management* 63:1066–1081.
- Hidalgo-Mihart, M.G., L. Cantu-Salazar, C.A. Lopez-Gonzalez, E. Martinez-Meyer, and A. Gonzalez-Romero. 2001. Coyote (*Canis latrans*) food habits in a tropical deciduous forest of western Mexico. *American Midland Naturalist* 146:210–216.
- Iverson, L.R., and A.M. Prasad. 1998. Predicting abundance of 80 tree species following climate change in the eastern United States. *Ecological Monographs* 68:465–485.
- Johnson, K.A., and R.L. Crabtree. 1999. Small prey of carnivores in the Greater Yellowstone Ecosystem. Pp. 239–263, *In* T.W. Clark, A.P. Curlee, S.C. Minta, and P.M. Kareiva (Eds.). *Carnivores in Ecosystems: the Yellowstone Experience*. Yale University Press, New Haven, CT.
- Kamler, J.F., and W.B. Ballard. 2002. A review of native and non-native Red Foxes in North America. *Wildlife Society Bulletin* 30(2):370–379.
- Kays, R., A. Curtis, and J.J. Kirchman. 2010. Rapid evolution of northeastern Coyotes via hybridization with wolves. *Biology Letters* 6:89–93.
- Levi, T., A.M. Kilpatrick, M. Mangel, and C.C. Wilmers. 2012. Deer, predators, and the emergence of Lyme disease. *Proceedings of the National Academy of Science* 109(27):10942–10947.
- Lindström, E.R., H. Andrén, P. Angelstam, G. Cederlund, B. Hörnfeldt, L. Jäderberg, P.-A. Lemnell, B. Martinsson, K. Sköld, and J.E. Swenson. 1994. Disease reveals the predator: Sarcoptic mange, Red Fox predation, and prey populations. *Ecology* 75(4):1042–1049.
- Mech, L.D., and L. Boitani (Eds.). 2003. *Wolves: Behavior, Ecology, and Conservation*. University of Chicago Press, Chicago, IL.
- Mezguida, E.T., S.J. Slater, and C.W. Benkman. 2006. Sage-grouse and indirect interactions: Potential implications of Coyote control on Sage-grouse populations. *The Condor* 108:747–759.

- Morey, P.S., E.M. Gese, and S. Gehrt. 2007. Spatial and temporal variation in the diet of Coyotes in the Chicago metropolitan area. *American Midland Naturalist* 158:147–161.
- National Oceanic and Atmospheric Administration (NOAA). 2012. US records warmest March; more than 15,000 warm temperature records broken. Available online at <http://www.ncdc.noaa.gov/sotc/summary-info/national/2012/3>. Accessed 5 September 2012.
- O’Connell, A.F., Jr., N.W. Talancy, L.L. Bailey, J.R. Sauer, R. Cook, and A.T. Gilbert. 2006. Estimating site occupancy and detection probability parameters for meso- and large mammals in a coastal ecosystem. *Journal of Wildlife Management* 70(6):1625–1633.
- Ostfeld, R.S. 2011. *Lyme Disease: The Ecology of a Complex System*. Oxford University Press, New York, NY.
- Ostfeld, R.S., C.D. Canham, K. Oggenfuss, R.J. Winchcombe, and F. Keesing. 2006. Climate, deer, rodents, and acorns as determinants of variation in Lyme-disease risk. *PLoS Biol* 4:e145.
- Parker, G.R. 1995. *Eastern Coyote: The Story of Its Success*. Nimbus Publishing, Halifax, NS, Canada.
- Patterson, B.R., and F. Messier. 2000. Factors influencing killing rates of White-tailed Deer by Coyotes in eastern Canada. *Journal of Wildlife Management* 64:721–732.
- Patz, J.A, K. Strzepek, S. Lele, M. Hedden, S. Greene, B. Noden, S.I. Hay, L. Kalkstein, and J.C. Beier. 1998. Predicting key malaria transmission factors, biting and entomological inoculation rates, using modelled soil moisture in Kenya. *Tropical Medicine and International Health* 3:818–827.
- Poole, K.G. 2003. A review of the Canada Lynx, *Lynx canadensis*, in Canada. *Canadian Field-Naturalist* 117(3): 360–376.
- Prugh, L.R., C.J. Stoner, C.W. Epps, W.T. Bean, W.J. Ripple, A.S. Laliberte, and J.S. Brashares. 2009. The rise of the mesopredator. *BioScience* 59:779–791.
- Ray, J.C. 2000. Mesocarnivores of northeastern North America: Status and conservation issues. *Wildlife Conservation Society Working Papers No. 15*, Bronx, NY.
- Ritters, K.H., J.D. Wickham, R.V. O’Neill, K.B. Jones, E.R. Smith, J.W. Coulston, T.G. Wade, and J.H. Smith. 2002. Fragmentation of continental United States forests. *Ecosystems* 5(8):815–822.
- Rutledge, L.Y., P.J. Wilson, C.F.C. Klütsch, B.R. Patterson, and B.N. White. 2012. Conservation genomics in perspective: A holistic approach to understanding *Canis* evolution in North America. *Biological Conservation* 155:186–192.
- Sacks, B.N., M.M. Jaeger, J.C.C. Neale, and D.R. McCullough. 1999. Territoriality and breeding status of Coyotes relative to sheep predation. *Journal of Wildlife Management* 63:593–605.
- Slough, B.G., and G. Mowat. 1996. Lynx population dynamics in an untrapped refugium. *Journal of Wildlife Management* 60: 946–961.
- Smith, D.W., D.R. Stahler, E. Albers, R. McIntyre, M. Metz, K. Cassidy, J. Irving, R. Raymond, H. Zaranek, C. Anton, and N. Bowersock. 2010. *Yellowstone Wolf Project: Annual Report, 2009*. National Park Service, Yellowstone Center for Resources, Yellowstone National Park, Wyoming, YCR-2010-06.
- Sovada, M.A., A.B. Sargeant, and J.W. Grier. 1995. Differential effects of Coyotes and Red Foxes on duck nest-success. *Journal of Wildlife Management* 59:1–9.
- Trainer, D.O., and J.B. Hale. 1969. Sarcoptic mange in Red Foxes and Coyotes of Wisconsin. *Bulletin of Wildlife Disease Association* 5:387–391.
- Wallach, A.D., E.G. Ritchie, J. Read, and A.J. O’Neill. 2009. More than mere numbers: The impact of lethal control on the social stability of a top-order predator. *PLoS ONE* 4(9):e6861:1–8.

- Way, J.G. 2008. Eastern Coyotes, *Canis latrans*, observed feeding on Periodical Cicadas, *Magicicada septendecim*. Canadian Field-Naturalist 122(3):271–272.
- Way, J.G. 2013. Taxonomic Implications of body mass differences found in northeastern Coyotes (coywolves, *Canis latrans x lycaon*), western Coyotes, and Eastern Wolves. Canadian Field-Naturalist 127(1):1–16.
- Way, J.G., and J. Horton. 2004. Coyote kills Harp Seal. Canid News 7.1:1–4. Available online at [http://www.canids.org/canidnews/7/Coyote\\_kills\\_harp\\_seal.pdf](http://www.canids.org/canidnews/7/Coyote_kills_harp_seal.pdf).
- Way, J.G., and B.C. Timm. 2008. Nomadic behavior of an old and formerly territorial eastern Coyote, *Canis latrans*. Canadian Field-Naturalist 122(4):316–322.
- Way, J.G., I.M. Ortega, and P.J. Auger. 2002. Eastern Coyote home range, territoriality and sociality on urbanized Cape Cod, Massachusetts. Northeast Wildlife 57:1–18.
- Way, J.G., B.C. Timm, and E.G. Strauss. 2009. Coywolf (*Canis latrans x lycaon*) pack-density doubles following the death of a resident territorial male. Canadian Field Naturalist 123(3):199–205.
- Way, J.G., L. Rutledge, T. Wheeldon, and B.N. White. 2010. Genetic characterization of eastern “Coyotes” in eastern Massachusetts. Northeastern Naturalist 17:189–204.