



Letter to the Editor

White-Tailed Deer and Coyote Colonization: A Response to Kilgo et al. (2019)

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We appreciate the comments by Kilgo et al. (2019) on our recent paper and welcome the opportunity to expand the discussion of the effects of coyotes (*Canis latrans*) on white-tailed deer (*Odocoileus virginianus*) in eastern North America. This exchange allows us to reaffirm and elaborate on our finding that coyotes have not had large-scale effects on white-tailed deer population growth in eastern North America.

A scientific evaluation of how any predator affects prey numbers is typically a complex challenge that requires a variety of approaches at a variety of scales. The evaluation becomes especially challenging for populations that interact across a complex and variable landscape because the dynamics of individual populations affect each other through immigration and emigration. Thus, for vagile wildlife species with a broad distribution, studies of single populations cannot fully answer how the predator affects the prey species across the larger connected landscape. Of course, intensive and detailed site- and time-specific studies on local predator-prey dynamics are critically important, and necessary to a mechanistic understanding of processes of predation. By themselves, however, a collection of such local studies over short time periods cannot determine how predator-prey dynamics play out over large spatial and temporal scales.

Coyotes and white-tailed deer in the eastern United States are an example of a spatially complex predator-prey system. Following the extinction of wolves (*Canis lupus*) and cougars (*Puma concolor*) in the region, coyotes colonized all eastern states over the last half-century (Hody and Kays 2018). Coyotes now occupy all land cover types in the region, where they overlap, and prey on, white-tailed deer. In Bragina et al. (2019), we noted site-specific field studies conducted (Vreeland et al. 2004, Kilgo et al. 2012,

Chitwood et al. 2015) on coyotes and deer in various parts of this system and agree that several of these studies show local effects of coyotes on white-tailed deer vital rates or numbers (Vreeland et al. 2004, Howze et al. 2009, Chitwood et al. 2015); however, the results of these studies have not always been consistent, demonstrating the predator-prey dynamic is variable over space or time. For example, Kilgo et al. (2016:747) concluded that “predation by coyotes on adult females was not important,” Kilgo et al. (2014:1261) stated that “despite an initial increase, the overall effect of coyote removal on neonate [deer] survival was modest,” and Gulsby et al. (2017) reported that coyote predation on fawns depended on habitat fragmentation. In short, the full collection of field studies reveal coyote-deer interactions in certain places at certain times, but they were not designed to answer the question addressed in Bragina et al. (2019): How have coyotes affected deer population growth from 1981 to 2014 across multiple states in the eastern United States?

In answering this question, nothing in Bragina et al. (2019) dismissed the valuable time- and place-specific field studies of coyotes and white-tailed deer to which Kilgo et al. (2019) referred. It is apparent the concerns of Kilgo et al. (2019) arise from an incomplete appreciation of the different strengths, scope of inference, and types of questions that can be addressed with local and time-specific field studies, versus broader space and time studies such as ours.

Faced with the overarching question of whether coyotes have affected white-tailed deer population dynamics over 531,312 km² and more than 3 decades, we would ideally use rigorously collected population estimates of both species from across the entire region. These estimates exist in vanishingly few cases. Therefore, with full awareness and appreciation of the promise and pitfalls of indices relative to rigorous estimates of abundance (Pollock et al. 2002, Mills et al. 2005, Johnson 2008), we used the only data available over time and space from 6 state agencies: indices of trends in white-tailed

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deer and coyote relative abundance. These indices are most reliable when seeking strong signals across large data sets (e.g., broad-scale disease outbreaks) and are appropriate for detecting the large (1–2 orders of magnitude) changes in prey populations seen in other natural experiments where new predators are added or reintroduced to a system (Levi et al. 2012, Ripple et al. 2014). In this analysis, we documented no negative association between relative numbers of coyotes and white-tailed deer across 6 states over more than 3 decades, supporting our conclusion that coyotes have not had large effects on white-tailed deer numbers across time and space in the eastern United States.

In addition to reaffirming our conclusions, we address specific concerns of Kilgo et al. (2019). Kilgo et al. (2019) suggested that harvest records should be adjusted for amount of harvest effort, which, in turn, could depend on changes in hunting regulations. We initially attempted to account for harvest effort using 3 states for which we could obtain metrics of effort, and detected no change in results. We decided there was little value in a correction because of incomplete records at the wildlife management agencies, and the multiple components and nuances of defining effort (e.g., regulations on baiting, weapon type, land access, hunter efficiency). Nevertheless, we noted that deer harvest regulation changes expanded hunter opportunity in 5 of 6 states over the time period we examined. Because agencies typically increase hunter effort in response to an increase (not decrease) in the hunted species, expanded hunting opportunities adds further qualitative support that agencies were not adjusting white-tailed deer harvest as might be expected if coyotes were causing a collapse of the deer population.

Kilgo et al. (2019:1637) expressed concerns that our analytic framework did not account for spatial variability in coyote population growth, and that we assumed “that coyotes would affect deer linearly through time.” We never made this assumption. In Bragina et al. (2019:920), we used log-transformed deer population growth rate (λ): $\ln(\lambda_{\text{deer}}) = \beta_0 + \beta_1 \text{coyote}_{ij} + \beta_2 \text{snow cover}_{ij} + \beta_3 \text{human population}_{ij} + \text{other covariates}$. This formula makes no assumptions that coyotes in any particular area have the same inherent growth rate or density-dependent function (e.g., from territoriality or food). Our approach asks, across the full spectrum of sites and time, whether time since coyote arrival predicts deer population trends.

Kilgo et al. (2019:1637) claimed that “Bragina et al. (2019) acknowledged that their study area spanned a range of climatic, elevational, and land cover ranges among states but apparently assumed coyote population growth among the 6 states was similar.” Their assertion is incorrect; our statistical models incorporated county-specific climate and land cover covariates to account for variance of coyote population expansion in the context of spatial differences in snow cover, human population density, precipitation, land cover, canopy openness and net primary productivity.

Kilgo et al. (2019) expressed concern that eastern coyotes may have negatively affected white-tailed deer harvest outside of the times we analyzed. Their hypothesis cannot be supported or rejected for a given data set. Moreover, our

paper did not discuss coyote effect on deer before the time period which our study spanned (i.e., before 2004 in SC).

Kilgo et al. (2019) stated that we did not acknowledge regional variability in coyote predation rate. This point is incorrect because the linear mixed model framework used in our analysis accounted for regional variability using a random effect for state. Of course, some of the 384 counties had deer $\lambda < 1$, but the average deer λ across 384 counties in 6 states was >1 in the presence of coyotes (e.g., Bragina et al. 2019:figure 1).

In various parts of their critique, Kilgo et al. (2019) assembled lists of individual field studies in the southeastern United States that documented high predation rates by coyotes, but these do not counter the implication of our results. First principles of population ecology distinguish between changes in individual vital rates and changes in population numbers. Predation rates can be massive without affecting population growth, depending on a host of factors, including compensation of mortality (via survival, reproduction, or immigration), reproductive values of individuals killed, and relative importance of specific vital rates to population growth (Morris and Doak 2002, Mills 2013). Local mortalities due to predation do not equal range-wide predator control of prey numbers.

Kilgo et al. (2019) ended their critique with a focus on implications of our paper for conservation and wildlife management. Their arguments are perplexing and seemingly self-contradictory. For example, in a single sentence Kilgo et al. (2019:1639) agrees verbatim with our main conclusion but then closes with a separate point as if it counters the first: “Thus, although it is true that coyotes, strictly speaking, ‘are not controlling deer populations’ the important point for wildlife managers to consider is that coyotes nevertheless have influenced significant changes in harvest planning and hunter opportunity.” The implication is that coyote importance to wildlife management at local scales somehow diminishes our result that deer are not being controlled at the large spatial scale. Rather, we believe that these ideas are not in opposition to each other: no evidence connects coyote colonization to range-wide white-tailed deer collapse in the eastern United States, and coyotes have had and do have local effects on deer and other prey and so absolutely should continue to be considered when planning harvest and other conservation management activities.

Thus, we believe that Kilgo et al. (2019) have created a redundant and unnecessary dichotomy between our results (that over the full scope of space and time since coyotes colonized the eastern United States, no white-tailed deer collapse has occurred) and their concern (that coyotes can locally affect white-tailed deer in the eastern United States). We believe these are entirely compatible views. Although we detected no signal of range-wide deer collapse influenced by coyotes, we remain fully aware that predators, such as coyotes, are capable of affecting numbers of their prey in fundamental ways that can, for example, affect trophic cascades (Crooks and Soule 1999, Levi and Wilmsers 2012) or influence local population declines (Witczuk et al. 2013, Chitwood et al. 2015).

We hope this exchange has been constructive and can lead to future discussion around the relationships between coyotes and white-tailed deer in the eastern United States. We suggest future research emphasize the factors influencing local- and regional-scale variation in coyote-deer dynamics, whether related to land cover, coyote densities, deer densities, coyote harvest, or some combination. Moreover, we recommend wildlife managers monitor white-tailed deer and coyote populations locally and appropriately adjust harvest regulations in the presence of predation by coyotes and other species.

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