



Letter to the Editor

Coyotes and White-Tailed Deer Populations in the East: A Comment on Bragina et al. (2019)

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Nearly 10 years ago, Kilgo et al. (2010) published a commentary that raised the question, “Can coyotes affect deer populations in southeastern North America?” Since then, numerous field studies have shed light on, if not unequivocally answered, that question. Those studies, which have spanned the region in question, have been virtually unanimous in concluding that coyotes (*Canis latrans*) can indeed influence deer population dynamics through heavy predation pressure on neonate deer. These were all field studies, conducted at a particular location and at a particular time. In contrast, Bragina et al. (2019) assembled an 87-year dataset from eastern states as widespread as New York and Florida, USA, to assess the question of whether coyotes can affect white-tailed deer (*Odocoileus virginianus*) populations at large spatial scales in the East. From those data, they concluded that “coyotes are not controlling deer populations at a large spatial scale in eastern North America” (Bragina et al. 2019:916). We commend Bragina et al. (2019) for examining the question at a large scale. However, a combination of problems inherent in their approach and in their data led to erroneous conclusions and overly simplistic inferences. We are concerned that assertions by Bragina et al. (2019) may perpetuate misconceptions among deer managers and the public about the nature of the deer-coyote dynamic in the region and may therefore be potentially harmful to the resource. Here we detail our primary concerns with Bragina et al. (2019).

Use of Deer Harvest Data to Index Deer Population Size

Bragina et al. (2019) used deer harvest data as a proxy for relative abundance, an approach they acknowledged had limitations in tracking true abundance, but they justify the approach by citing Cattadori et al. (2003) and Imperio et al. (2010). Although Cattadori et al. (2003) validated the use of harvest data as an indirect measure of abundance, the authors indicated the applicability of their results were

limited to red grouse (*Lagopus lagopus scotica*) in the United Kingdom, a species and study system much different from white-tailed deer in the eastern United States. In contrast, Imperio et al. (2010) focused on 5 ungulate species in Italy, making their findings more relevant to Bragina et al. (2019). Imperio et al. (2010), however, suggested that the use of bag records not corrected for hunting effort and without any previous validation, conditions not met by Bragina et al. (2019), could produce misleading estimates of abundance. Rosenberry and Woolf (1991) similarly reported that white-tailed deer harvest data adjusted for hunter effort had a more linear relationship with population size than did the overall harvest.

Without adjustments for hunter effort throughout the study period, several sources of potential bias could decrease the reliability of deer harvest data as an index of deer abundance. One source of bias, which Bragina et al. (2019) acknowledged, is the changes in deer management regulations by state wildlife agencies during the study period. Bragina et al. (2019:table 1) provided a summary of the most important deer management regulation changes for the 6 states used in their analysis. In 5 of those states, Bragina et al. (2019) reported regulation changes that expanded hunter opportunity (FL was the only state that did not increase opportunity during the study), which positively affects hunter harvest (Van Deelen et al. 2010). Conversely, 3 states also decreased opportunity for male harvest during the study period, 2 via antler size restrictions (NY, FL) and 1 via bag limit or season restrictions (NJ). We contend that the objective of all of these regulation changes was to alter harvest rates which, if successful, confounded the relationship between harvest data and population size.

The use of data from South Carolina is particularly concerning, especially given its timeframe, and offers a useful case study on how deer harvest can be confounded by regulation changes. Specifically, Bragina et al. (2019:table 1) reported that in 2004, the first year in their dataset, South Carolina began reducing the number of days on which deer of either sex could be harvested. These reductions continued periodically through 2014 and were implemented in response to a decline in the deer population, which the reductions

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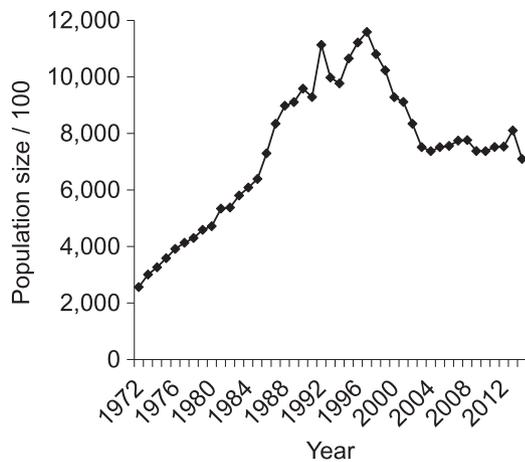


Figure 1. Estimated statewide deer population size in South Carolina, USA, 1972–2014 (Ruth and Cantrell 2018).

apparently slowed or halted (Fig. 1). Clearly, from 2004–2014, South Carolina’s deer harvest, which steadily declined because of reduced hunter opportunity (Ruth and Cantrell 2018), did not reflect the deer population trend, which had stabilized because of reduced harvest. Furthermore, South Carolina’s deer harvest estimates were derived from an annual hunter survey, which the state’s Deer Project Coordinator indicated is robust at the state level but sufficiently imprecise at the county level (as Bragina et al. [2019] used it) as to render its use highly questionable at that level (C. R. Ruth, South Carolina Department of Natural Resources, personal communication). Thus, our main contentions with their approach of using harvest data as an index of deer abundance are that use of unadjusted deer harvest numbers as a proxy for abundance is not supported by the literature and there are a number of factors (mainly changes in harvest regulations during the study period) that would bias deer harvest over time, even if this metric were a suitable proxy for abundance.

Use of Time Since Coyote Arrival to Index Coyote Abundance

Another limitation of this study is the use of time since coyote arrival to evaluate the effect of coyotes on deer populations. Although we applaud the attempt of Bragina et al. (2019) to depict coyote colonization through space and time, we think the use of time since arrival as a predictor variable for understanding potential effects of coyotes on deer populations relies on faulty assumptions. For example, the assumption that coyotes would affect deer linearly through time does not seem reasonable given coyote population growth, and by extension their potential to affect prey, likely varies spatially. Studies have demonstrated abundance of eastern coyotes varies with landscape composition and configuration (Kays et al. 2008, Cherry et al. 2017). Therefore, variation in local and regional landscape conditions likely would result in a mosaic of population growth rates and time to population stabilization. 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 and linear. Additionally, coyote abundance can be regulated by food availability and social factors associated with territoriality (Gese et al. 1989, Knowlton et al. 1999). Thus, coyotes do not have infinite growth potential. The test of a linear effect of time since coyote arrival on deer populations assumes that any negative influence of coyotes on deer populations continues linearly through time. These assumptions seem unrealistic, and it seems more likely that if coyotes negatively influenced deer populations, the effects eventually stabilized as coyotes became saturated across the landscape and their populations reached carrying capacity. Furthermore, as demonstrated by Bragina et al. (2019:figure 2), if one assumes harvest reflects abundance, as the authors did with regard to deer harvest, coyote population growth is nonlinear and, in fact, appears to be exponential in numerous states. These issues are likely compounded by the mismatch in scale of the timing of coyote colonization and deer harvest records, as the authors reported changes in deer abundance from 1981–2014 in states colonized by coyotes during the 1910s–1970s.

Incongruity Between Time Periods of Analysis and Timing of Coyote Influence

The deer harvest data Bragina et al. (2019) used from Florida, Ohio, and South Carolina spanned time periods after the establishment of coyotes, allowing for the possibility that effects of coyotes on deer populations had already occurred. For example, the time period Bragina et al. (2019) used for South Carolina was 2004–2016. As described by Kilgo et al. (2010), South Carolina’s deer population peaked in the mid-1990s after a period of increase following the restocking programs of the 1950s and 1960s. From 1997 through 2004, coincident with the establishment and increase of coyotes in the state, but just prior to the period examined by Bragina et al. (2019), the deer population declined by about 35%. Extending Kilgo et al. (2010:figure 1) to 2014 (the limit of the Bragina et al. [2019] data; Fig. 1) demonstrates that the statewide deer population in fact remained relatively stable during the period Bragina et al. (2019) used; the potential effect of coyotes on the population (i.e., the negative relationship that their models failed to detect) had already occurred, prior to the timeframe covered by their data. Similarly, by their own estimation, the data used by Bragina et al. (2019) for Florida (2005–2016) covers a period 15–25 years after coyote arrival and their data for Ohio covers a period 11–51 years after coyote arrival. Therefore, as with South Carolina, their data may simply have been for the wrong time period. Failure to detect a relationship between coyotes and deer does not necessarily mean that one does not exist, only that it was not evident in the data they used.

Regional Differences in Predation Rate

Any effect of coyotes on deer likely varies spatially, independent of time since coyote arrival, because habitat

selection of eastern coyotes is nonrandom (Hinton et al. 2015, Stevenson et al. 2018), and diets can vary substantially, even at small spatial scales (Etheredge et al. 2015, Ward et al. 2018). Additionally, landscape composition and configuration can influence coyote abundance (Cherry et al. 2017) and their effects on fawn survival (Gulsby et al. 2017, Gingery et al. 2018). This variation and resultant regional trends complicate analysis of coyote effects on deer at the scale of eastern North America. For example, predation pressure appears generally greater in the South than in the Midwest and Northeast (Fig. 2). Among studies assessing cause-specific mortality on neonatal deer, the coyote-specific predation rate (percentage of all neonates in the sample that were depredated by coyotes) averaged 16% among 9 studies in the Midwest and Northeast and 44% among 10 studies in the South (Fig. 2). Speculation on mechanisms influencing this regional pattern are beyond the scope of this commentary. But the very existence of this pattern, combined with regional differences in timing of coyote arrival (i.e., earlier in the North than the South), requires careful interpretation of results when data are pooled across regions. For example, Bragina et al. (2019) report population change (λ) ≥ 1 for all 7 time periods analyzed. Visual inspection of their figure 3 (λ values were not provided) suggests that mean values for λ were quite high for periods during the 1980s and 1990s, when deer populations range-wide were growing

rapidly, but these values tended to be lower for later periods, especially the last period (2011–2014; Bragina et al. 2019:figure 3). For early periods in figure 3, counties that had been occupied <30 years were in northern states where predation tends to be low, whereas in later periods, those counties were in southern states where predation tends to be greater. As expected then, λ values during early periods in counties <30 years since arrival were >1.0 , but for later periods, in counties <30 years since arrival, λ tended to be <1.0 . Bragina et al. (2019) seem to have disregarded as unimportant what appear to be roughly half or more of the 384 counties in their dataset with λ values <1.0 since 2005.

Interpretation of Negative Results

Given that their conclusion is based on the lack of detecting an effect, we are concerned that Bragina et al. (2019) did not qualify the strength of the conclusion, other than acknowledging that coyotes may affect deer populations in isolated local situations. We think it is prudent to exercise caution when interpreting negative results, given that the failure to detect a signal could result from flaws or limitations in experimental design or procedures. Negative results can stem from lack of statistical power, inadequate or mismatched spatial or temporal scales of the investigation relative to the scale of the process under study, failure to



Figure 2. Coyote-specific predation rates (% of neonates in sample that were depredated by coyotes) among studies conducted in the core range of white-tailed deer on areas where coyotes and bobcats (*Lynx rufus*) were the primary predators (i.e., black bears [*Ursus americanus*], wolves [*Canis lupus*], and cougars [*Puma concolor*] were not present; Cook et al. 1971, Carroll and Brown 1977, Garner et al. 1976, Bartush and Lewis 1981, Huegel et al. 1985, Nelson and Woolf 1987, Long et al. 1998, Brinkman et al. 2004, Burroughs et al. 2006, Rohm et al. 2007, Saalfeld and Ditchkoff 2007, Hiller et al. 2008, Piccolo et al. 2010, Grovenburg et al. 2011, Kilgo et al. 2012, Jackson and Ditchkoff 2013, Chitwood et al. 2015b, Nelson et al. 2015, Watine and Giuliano 2016).

select the correct variables or to characterize them adequately, or inappropriate model assumptions (e.g., linear model when process of interest is non-linear). Obviously, establishing a study at the scale at which one thinks the process occurs and reporting negative results is valid. Nonetheless, we suggest the limitations of the approach should be considered thoroughly before drawing strong inference from the lack of detection of a signal. The fact that none of the models fit in this study had significant predictive power (as evidenced by the fact that the null model was universally the most supported model) should further induce caution. Considering the issues described here associated with the deer population response variable and the time since coyote arrival predictor variable, it is not surprising they were not related.

Potential Harm to the Resource

Perhaps our greatest concern lies with the implications of asserting that “coyotes are not controlling deer populations at a large spatial scale in eastern North America” (Bragina et al. 2019:916). We do not dispute that statement *per se* because it has been recognized that hunter harvest, not predation, is the single most important factor controlling (or capable of controlling) white-tailed deer populations. However, such statements represent a considerable oversimplification of a complex predator-prey dynamic and minimize the important role that coyotes have come to play in the population dynamics of white-tailed deer in eastern North America during recent decades. Every published study of cause-specific fawn mortality conducted in southeastern North America since coyotes have been present, not including those where coyotes were controlled, has demonstrated very high predation rates by coyotes, leading to recruitment rates much lower than before coyotes arrived (Saalfeld and Ditchkoff 2007, Kilgo et al. 2012, Jackson and Ditchkoff 2013, Chitwood et al. 2015b, Nelson et al. 2015, Watine and Giuliano 2016). Yet Bragina et al. (2019:922) dismiss (or fail to cite) this body of literature as representing only “localized negative effects,” which they propose are somehow overcome through spatial compensation, an explanation we consider implausible given the size of the study areas considered and the dispersal capabilities of white-tailed deer. With recruitment as low as these studies have shown, heavy harvest of adult female deer (which prior to the arrival of coyotes was often inadequate to control the population) is in many situations no longer sustainable. Reduced harvest of adult female deer is necessary to mitigate effects of increased fawn predation by coyotes (Robinson et al. 2014), and reductions in adult female harvest may be inadequate to offset population declines in some situations (Chitwood et al. 2015a). If harvest is not reduced in such areas, populations decline, and indeed several states have implemented state-wide regulations restricting antlerless harvest in response to declining recruitment rates (e.g., AL, GA, SC). Population reduction may be beneficial where deer are overabundant but not necessarily where they occur at low density. Thus, although it is true that coyotes, strictly speaking, “are not controlling

deer populations” (Bragina 2019:916), the important point for wildlife managers to consider is that coyotes nevertheless have influenced significant changes in harvest planning and hunter opportunity. Because Bragina et al. (2019) did not qualify or expound on their conclusions about the effects of coyotes on deer, readers are left to assume that because the authors did not detect a relationship between them, coyotes need not be considered in deer management at all.

Conclusion

The number of uncertainties associated with the data and the scope of the problems with the analysis employed by Bragina et al. (2019:916) were of such magnitude as to render unwarranted their sweeping conclusion “that coyotes are not controlling deer populations at a large spatial scale in eastern North America.” Furthermore, we contend that, although the scale of their question might be interesting from a basic science standpoint, it should not be used to inform deer management policy, which should be implemented at a statewide, or smaller, scale. More concerning, however, was the manner in which Bragina et al. (2019) oversimplify the complexity of this important wildlife management issue, boiling it down to a binary question of whether or not coyotes directly control deer, when in fact the issue is far more nuanced than that, with hunter harvest continuing to play a central role. As recent researchers have demonstrated, after the arrival of coyotes, many Southeastern deer populations have not been able to sustain harvest at levels previously insufficient to control those populations (Kilgo et al. 2012, Robinson et al. 2014, Chitwood et al. 2015a). Declines in these populations are thus not attributable solely to coyotes but to the combination of coyote predation and high harvest rates. In contrast, northern populations seem less affected, presumably because of lower predation and antlerless harvest rates. Still, coyote predation represents an important influence on deer populations that should not be dismissed but instead be clearly understood and accounted for in harvest management because it plays a key role in the dynamics of these populations.

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