





A broader approach to understanding urbanization effects on freshwater turtles: Reply to Lambert and Steen 2019

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We thank Lambert and Steen (2019) for the attention they have given to our paper (Bowne et al. 2018) and welcome productive discussions of how human activities affect turtle populations. Scientists who study the conservation biology of turtles do so from a commitment to scientific integrity and preservation of these species. We share the sentiment of Lambert and Steen that those prioritizing management initiatives should not base their decisions on any single paper. With this in mind, we do not agree with all Lambert and Steen's criticisms.

Lambert and Steen's article impact statement says "recent research has not provided sufficient evidence to suggest roads and urbanization are not threats to turtle populations." This implies that we claim roads and urbanization are not threats to turtle populations. We make no such claim. We simply report a positive relationship between proportion of adult female painted turtles (*Chrysemys picta*) and urbanization. Our finding is unexpected but not isolated (Buchanan 2017). This positive relationship could be a threat if the unknown

mechanism contributing to the relationship (e.g., excess deaths of males and altered thermal nesting environment) leads to population declines. We recognize our findings are not applicable to every study system but argue that a blanket generalization about roads and urbanization causing a decrease in the proportion of adult females is not supported by the published literature (e.g., Dorland et al. 2014; Buchanan 2017; Carstairs et al. 2018; Vanek & Glowacki 2019). It is also important to acknowledge that road mortality can increase extinction probability of turtle populations even if mortality is equal between the sexes (Howell & Seigel 2019).

Lambert and Steen used a method different from ours to reanalyze our data in an attempt to detect the expected negative relationship between proportion of adult females and urbanization or roads. Their reanalysis yielded no significant relationship. Thus, they should have concluded that our study contributes to the growing number of studies that do not find a negative relationship between proportion of adult females and urbanization or roads.

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The results of their reanalysis, therefore, do support a reevaluation of the relationship between turtles and urbanization. Instead, they say our “. . . evidence is insufficient to warrant reevaluation of the growing consensus that roads and urbanization are critical threats to North American freshwater turtles.” Given their reanalysis and the clearly mixed literature on the relationship between sex ratio and urbanization (e.g., Roe et al. 2011; Mali et al. 2013; Dorland et al. 2014; Hamer et al. 2016; Buchanan 2017), they provide evidence for the very reevaluation that they reject. We agree with Lambert and Steen that roads and urbanization can be and in many cases are threats to freshwater turtles, but we argue that male-biased sex ratio is not a universal result of anthropogenic activity.

Lambert and Steen do not acknowledge the possibility that multiple mechanisms underlie the effects of roads and urbanization on sex ratio. They assume deviation from parity in adult sex ratio results from differential mortality and thus that adult females have greater mortality than adult males because of nesting migrations. In other words, they assume the primary sex ratio is equal. Both of these assumptions may be incorrect. Carstairs et al. (2018) found no difference in male and female turtle admission rates to a wildlife clinic due to vehicular collisions for 3 of 4 species. Moreover, thermal modification of nesting habitat is a known driver of primary sex ratio in painted turtles (Janzen 1994). Adult sex ratios can emerge from multiple mechanisms that affect the production or viability of males and females at multiple life stages. For example, by following a population over time in an agricultural landscape, Freedberg and Bowne (2006) found a female-biased juvenile sex ratio and parity at maturity. They attributed the biased sex ratio among juveniles to warm nesting sites causing an overproduction of females. Greater mortality for adult females than males would return the sex ratio to parity. If Freedberg and Bowne (2006) had analyzed only adult sex ratio, the population would have appeared to lack female-biased mortality, when in fact, it was likely present. In our article, we stressed that more data were needed to test the hypothesis that the thermal environment of urban sites affects sex ratio, but the thermal hypothesis is not mutually exclusive of road effects on adult mortality (Francis et al. 2019). Although Lambert and Steen (2019) reject the thermal hypothesis for our study, changes in the thermal environment can potentially affect juvenile recruitment and adult sex ratios. Having a better understanding of how thermal environmental change due to urbanization, climate change, or both affects turtle populations is especially important given recent findings that temperature fluctuations increase production of female turtles (Valenzuela et al. 2019).

Lambert and Steen criticized our commonly used method (e.g., Marchand & Litvaitis 2004; Steen et al. 2012) to characterize urbanization. Specifically, they dis-

agree with our collapsing 4 National Land Cover Dataset classes of development into 1 category. In their reanalysis, they kept the 4 classes separate. On a practical level, keeping 4 separate development classes for relatively few ponds means the variation within each class can be low. Indeed, Lambert and Steen found the range of high intensity development surrounding our ponds was 0–8%. Fitting models for each class of development is questionable given that a low range of variation limits explanatory power (e.g., r^2 [Bland & Altman 2011]). We disagree with their assertion that only impervious surfaces immediately adjacent to nesting sites can influence incubation temperature. Soil warming beneath herbaceous vegetation occurs up to 5 km from the city center, where cover by impervious surface is often greatest (Edmondson et al. 2016). A study in the greater Baltimore, Maryland (U.S.A.), area showed urban turf-grass sites are over 4 °C higher in July than rural turf-grass sites (Savva et al. 2010). This 4 °C increase is the temperature change predicted to eliminate production of male painted turtles (Janzen 1994). Thus, adjacent land use can affect the thermal properties of nests even in developed open spaces.

Lambert and Steen used questionable techniques to analyze spatial structure in our data. They likely overfit their regression models by fitting a model with 10 states to a data set of $n = 19$ ponds. Because political entities vary in shape and size, they are not ideal to model geography. They do not report exact p values for the effects of their development metrics on sex ratio; instead, they report that all $p > 0.05$ at the 250-m scale and $p > 0.09$ at the 1000-m scale. Using a hard cutoff of 0.05 for the significance value, given the low sample size in our study, potentially confuses statistical and biological significance. They detected a similar spatial nonindependence that we alluded to in our conclusion, namely, a clustering of male-biased sex ratios in Massachusetts, although we would not characterize $r = 0.3$ and a 95% CI overlapping 0 as “strong spatial structure” (quoted from their Supporting Information). Unfortunately, most studies on this topic are likely subject to spatial nonindependence because each examines a few ponds within a small region. We agree with Lambert and Steen’s suggestion to replicate urban and road gradients across large spatial scales. Having coupled urban-rural study systems in a variety of geographic locations would greatly improve our collective ability to discern the processes causing observed patterns.

Lambert and Steen suggest we should have analyzed both relative and absolute sex ratios. For the latter, they mean we should have statistically analyzed deviation from parity. We disagree because we had inadequate population estimates on which to estimate absolute sex ratio. A limitation of our and much published work on this topic is the lack of data with which to estimate capture probabilities and population sizes. We acknowledged this in our article as well as the possibility that our trapping

method may be male biased. We also note that relative sex ratio is the standard most used in the literature on turtle sex ratio (e.g., Marchand & Litvaitis 2004; Steen & Gibbs 2004). We support any effort to improve our collective understanding of the relationship between turtle populations and urbanization by generating better population estimates, but that is different from treating relative population ratios as absolute population ratios.

Lambert and Steen demonstrate the need for a reevaluation of the relationship between urbanization metrics and freshwater turtle populations. Roads and urbanization clearly can be threats to turtles, but the literature provides ample evidence that this relationship is not as simple and general as to always result in a male-biased sex ratio. Although we have 6 specific areas of disagreement with Lambert and Steen on technical aspects of analysis and interpretation, we agree with them that improvements in study design, population estimation, and analysis will provide better insight into the factors affecting freshwater turtles. This better scientific understanding will promote better conservation outcomes.

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