ORIGINAL RESEARCH

Ecology and Evolution

WILEY

# Biogeography and predictors of wildlife killed on roads at peninsular Florida State Parks

David G. Jenkins[1] [iD] | Leo Ohyama[2] | Federico López-Borghesi[1] | Jacob D. Hart[1] |
Juan D. Bogotá-Gregory[1] | Rhett M. Rautsaw[3] | Vanessa Correa Roldán[1,4] |
Kevin Guilfoyle[1] | Anik Jarvis[1] | Jennifer Loch[1] | Kathryn Mercier[5,6] | Olivia Myers[7] |
Rachel Shaw[1] | Daniel Volk[8] | Alice M. Bard[9]

[1]Department of Biology, University of Central Florida, Orlando, FL, USA

[2]Department of Entomology and Nematology, University of Florida, Gainesville, FL, USA

[3]Department of Biological Sciences, Clemson University, Clemson, SC, USA

[4]Department of Ichthyology, Museum of Natural History, Universidad Nacional Mayor de San Marcos, Lima, Perú

[5]Department of Biology, City College of New York, New York, NY, USA

[6]PhD Program in Biology, The Graduate Center of the City University of New York, New York, NY, USA

[7]Hillsborough County Utilities, Tampa, FL, USA

[8]Cleveland Metroparks, Parma, OH, USA

[9]Florida Department of Environmental Protection, Florida Park Service, Apopka, FL, USA

**Correspondence**
David G. Jenkins, Department of Biology, University of Central Florida, Orlando, FL, 32816-2368, USA.
Email: david.jenkins@ucf.edu

## Abstract

Wildlife-vehicle collisions (WVCs) are a major source of wildlife mortality and should affect regional wildlife diversity and abundance, yet most WVC studies are locally scaled. Here, we evaluated biogeographic diversity (i.e., species richness, effective diversity) and abundance of WVCs at state parks across the Florida peninsula to answer two questions aimed to help inform wildlife conservation efforts: which parks have greatest WVC diversity, and why? We processed and compiled 9,254 WVC survey records collected by Florida State Parks personnel at 42 parks during a decade (2005–2015). Data for birds (138 species), mammals (35 species), reptiles (64 species), and all taxa combined were analyzed for patterns among parks (for the first question) and for biogeographic, climatic, ecoregion, and anthropogenic predictors of those patterns (for the second). Predictors represented nonexclusive alternative a priori hypotheses and were evaluated by model comparison. Parks differed widely in WVC diversity and abundance; we identify "hot spot" parks where management may most effectively reduce WVCs. Biogeographic and anthropogenic hypotheses were supported, but climatic and ecoregion hypotheses were not. Models for overall diversity fit data better ($R^2$s > 0.50) than did models for specific taxa (e.g., birds). Larger parks closer to Florida's highly populated Atlantic Coast and with greater park attendance and perhaps faster speeds on adjacent roads have more WVC diversity and numbers. Of these predictors, attendance and speed limits are manageable. Traffic management in and near-identified "hot spot" parks in Florida can most effectively reduce WVC effects on wildlife populations and diversity amidst a growing human population.

**KEYWORDS**
abundance, bird, diversity, mammal, regional, reptile, roadkill, species richness, wildlife, wildlife-vehicle collisions

# 1 | INTRODUCTION

Wildlife populations are indirectly and directly affected by humans, and those effects may also affect wildlife diversity. Indirect anthropogenic effects include changes to environmental resources (i.e., foods and habitat quality) or other species (e.g., predators) that may impact wildlife populations (e.g., Bennett, 2017; Coffin, 2007). Direct effects include mortality or altered breeding success (e.g., Bar-Massada et al., 2014; Muhly et al., 2011; Shackelford et al., 2018). Among the various effects on wildlife, mortality exerts a strong effect on populations and potentially on assemblage diversity. Human-induced wildlife mortality occurs purposefully by harvest (i.e., hunting and trapping) and accidentally, such as by wildlife-vehicle collisions (WVCs) on roads (e.g., Seiler, 2004). For wildlife species that are not purposely harvested, WVCs are likely a main driver of recorded mortality (Forman & Alexander, 1998; Laurance et al., 2009). As a result, WVC-induced mortality is a global research theme (e.g., Fahrig & Rytwinski, 2009; Forman & Alexander, 1998; Forman et al., 2003; van der Ree et al., 2015).

Despite extensive attention to WVCs, two deficits are apparent and addressed here. First, most WVC studies evaluate populations for one or several species (e.g., large mammals) but more rarely evaluate assemblage diversity or abundance. For example, an extensive review summarized effects of roads on animal abundance and found only 34 of 191 effects (18%) described species richness, diversity, or abundance for >1 species (Fahrig & Rytwinski, 2009). Viewed another way, 23 of the 79 reviewed papers (29%) included a diversity measure; 71% did not.

Secondly, with relatively few exceptions (e.g., Canal et al., 2019; González-Suárez et al., 2018; Grilo et al., 2009, 2020; Morelli et al., 2020; Visintin et al., 2017), most WVC studies are conducted on local spatial scales (e.g., a road segment or circuit) for brief study intervals (e.g., several years). The scarcity of large-scale WVC studies echoes a broader pattern in ecology (Ricklefs, 2008) because it is universally difficult to amass accurate data on the ground over large areas for multiple years. That difficulty is being reduced with technology and citizen science projects that evaluate data quality (Chyn et al., 2019; Hampton et al., 2013; Tiedeman et al., 2019; Waetjen & Shilling, 2017). Local-scale studies may best address local questions (e.g., placement of obstacles or passageways) but do not translate well to regional scales (Bard et al., 2002; Olson et al., 2014; Shilling & Waetjen, 2015). A better understanding of regional WVC patterns will help to understand the generality of WVC impacts and develop systematic management strategies beyond local interventions.

Here, we evaluated WVC diversity and abundance at a regional scale for birds, mammals, reptiles, and all taxa combined to address two questions relevant to wildlife conservation at biogeographic scales. Data were collected by Florida State Park personnel (including professional wildlife biologists) over a decade along the full Florida peninsula (Figure 1). We evaluated those data for evidence supporting alternative hypotheses on biogeographic and anthropogenic mechanisms that may cause patterns in WVC diversity and abundance. Results may help guide wildlife conservation on the
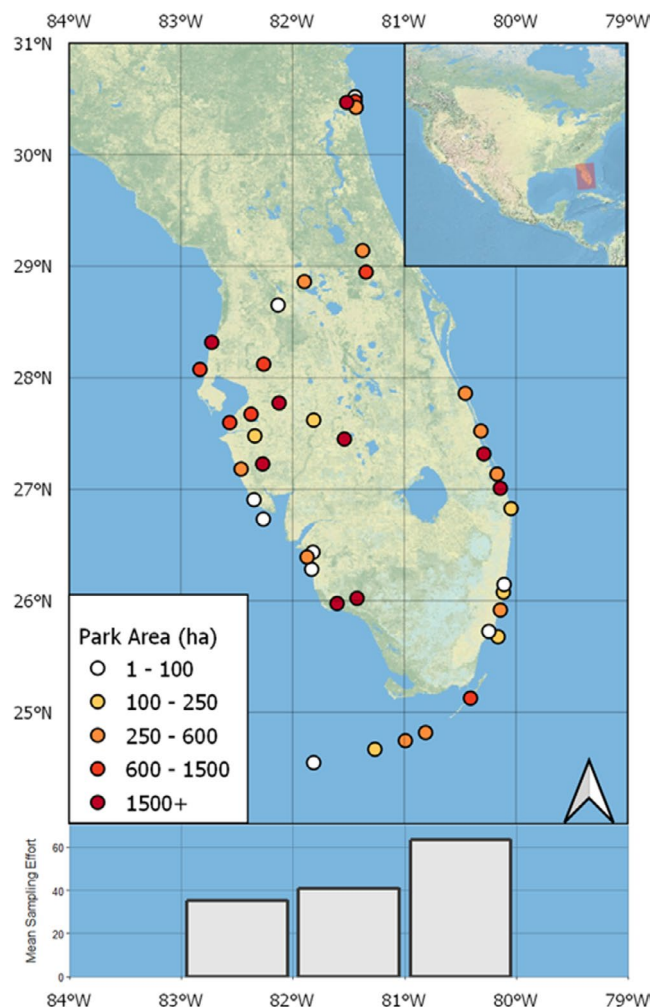


**FIGURE 1** Peninsular Florida, on the North American continent (see inset). Forty-two Florida State Parks included in this study (circles) were distributed across the peninsula. Park area, sampling effort, and longitude were important in analytical results and depicted here: Circle colors correspond to park area (see legend), and sampling effort (months per year; see histogram) is ordered by longitude

Florida peninsula; a goal all the more pressing as human population has tripled there since 1970 (https://worldpopulationreview.com/states/florida-population).

We first asked "which parks have the most WVC diversity and abundance?" with the goal to understand biogeographic pattern in WVCs and identify Florida State Parks that may most benefit from management to reduce WVCs. We expected WVC diversity and abundance would differ among State Parks due to species–area effects (Rosenzweig, 1995) and location (e.g., peninsula effect (Jenkins & Rinne, 2008)), and especially due to anthropogenic factors (e.g., human population density, and traffic, etc.) given that WVC data reflect traffic.

We expected the choice of diversity metric would influence our answer to this first question. We used species richness (SR), effective diversity (D), and total abundance per taxon (N). Species richness (SR) should be a relatively coarse detector of WVC effects within a

park because it simply tallies species observed, regardless of abundance per species. On the other hand, SR may be more stable than abundance-based measures given varied sampling among parks through the years. For example, WVC surveys efficiently estimate SR of living wildlife, compared to more intensive sampling (Canova & Balestrieri, 2019; González-Gallina et al., 2015).

In contrast to diversity metrics, total abundance ($N$) of WVCs may be relatively insensitive to species-based effects, depending on relative densities, but quite relevant to management of wildlife abundance in general and WVC mitigation. A combination approach is to estimate effective diversity ($D$), which is based on the sum of numerical proportions per species (Jost, 2006). We expected $D$ to be potentially useful, but that management decisions would be most readily based on species richness and abundance.

The second question addressed was "what best explains WVC differences among parks?". This analysis compared and then combined models based on alternate hypotheses (Table 1) for biogeographic, climatic, ecoregion, and anthropogenic effects on estimated WVC diversity and abundance. If WVC patterns are best fit by biogeography, climate, or ecoregions, then park managers have limited options to reduce WVCs. However, anthropogenic effects (e.g., traffic) are directly manageable, so that evidence for effects on WVCs will support management actions to reduce wildlife mortality.

In general, we expected WVC patterns to be related to both biogeographic and anthropogenic factors, with a stronger effect due to humans simply because WVCs reflect direct impacts of human vehicular traffic on wildlife populations. If so, this outcome would reflect an anthropogenic basis for WVC diversity and abundance, meaning an opportunity for wildlife management also exists. Alternatively, regional diversity patterns are affected by natural factors, including species–area and species–energy effects (Storch et al., 2005) and potentially a peninsula effect (Jenkins & Rinne, 2008). Given that WVC diversity reflects wildlife diversity (Canova & Balestrieri, 2019; González-Gallina et al., 2015), natural factors may still relate to WVC diversity and abundance amidst the ever-growing urban sprawl in Florida. We also expected different outcomes among analyses for birds, mammals, reptiles, and overall. Because birds are more mobile in three dimensions and may have larger ranges (especially migratory birds) than most mammals and reptiles, we expected WVC patterns for birds to be less clearly modeled than for mammals and reptiles. We also expected climatic variables to be more relevant for poikilothermic reptiles than for mammals.

Data here were similar to citizen science datasets (e.g., eBird. org) that are collected by many others and then processed for consistency and errors. In such studies, a fundamental trade-off exists between uncertainty because data were collected by others and the advantage that many more data can be collected. Accordingly, we were careful in analyses and inferences to avoid undue precision. Also, one may expect that WVC data here could be compared with park wildlife inventories, but such inventories do not exist at matching spatial and temporal extent (42 parks during a decade) to match the WVC data. Thus, inferences here focus on potential management to reduce WVCs but are not extrapolated or compared with living wildlife diversity in parks.

## 2 | METHODS

### 2.1 | Data acquisition and processing

Florida State Park personnel collected WVC data as part of a statewide program, where data forms included date, general location (not GPS coordinates), species, and number of individuals for organisms killed on roads. Organisms were further identified as being on roads inside parks or on through roads (i.e., roads adjacent to or passing through parks). This study used park data on peninsular Florida (Figure 1) during a decade, where 42 state parks encompassed a variety of Florida's ecosystems from barrier islands and the Everglades to pine flatwoods, sandhills, and urban areas. Climate ranged from subtropical in South Florida to warm temperate in North Florida.

Parks varied in how data were collected (staff or volunteers, temporal frequency and extent, roads) but all surveys were conducted while driving (i.e., none were conducted by walking road margins). Taxonomic identifications were recorded by park personnel to species (and often subspecies). Florida State Park Districts representing the Florida peninsula (Figure 1) provided original paper records and/ or spreadsheets. Subspecies identifications were simplified here to the species level. Taxa included birds, mammals, and reptiles; amphibians were sometimes recorded but excluded from analyses here because amphibian counts in driving surveys are artificially low (Beebee, 2013) and WVC detectability is known to be a function of animal body size and sampling intervals (Santos et al., 2016). Because of detectability limits, we expect that WVC estimates reported here underestimate actual rates. We entered those data into a common spreadsheet and iteratively cleaned data to assure consistency (e.g., taxonomy and road names).

We analyzed the years 2005–2015 because data for >20 parks each year were consistently available starting in 2005, whereas fewer parks reported data prior to 2005 (one park began in 1989). With this strategy, we could include 42 of the 51 parks with WVC data. Some parks exerted more sampling effort than others, with their results reported monthly (i.e., lowest common data frequency was one month). We used the number of months that a park collected samples during the 10 years as an index of effort, to represent their persistence in this long-term effort. The effect of sampling effort on diversity and abundance was modeled as two alternative analytical hypotheses: a linear increase in observations with sampling effort; or a quadratic increase with sampling effort, such as when rare species are detected only with more effort. For interpretations here, the sampling effort covariate accounted for data-collecting differences among parks that are apart from other biological differences (biogeography, area, etc.), leaving signals of those fundamental effects better revealed.

Monthly data per park were computed per taxon and overall, using two diversity measures: (a) monthly species richness

**TABLE 1** Predictors of wildlife roadkill diversity (species richness, effective diversity) and abundance, organized by theme, and with the a priori hypotheses for their potential effect. Predictors per theme were evaluated by model selection, and then most plausible models for each set were in turn compared in model selection. See Methods for details

| Predictors | Hypothesis ("the predictor causes differences in WVC diversity &/or abundance because...") |
|---|---|
| **Sampling effort (calculated from data)** | |
| Months of roadkill sampling by a park | more WVCs are found if one looks more often |
| Months + months² | either WVC observations saturate with effort or rare species are only observed after extensive searching |
| **Biogeography[a]** | |
| Park latitude (centroid) | a peninsula effect may occur, related to distance from the mainland |
| Park longitude (centroid); called easting for greater East Coast values | human population is often most dense on the East coast and natural lands are more common inland |
| Area (ha) | a species–area effect occurs, especially if parks are habitat islands amidst human land use |
| **Climate[b]** | |
| Grand mean of monthly mean temperatures (°C), 2005–2015 | a thermal gradient on the N-S-oriented peninsula may drive patterns |
| Grand mean of monthly mean temperature range (maximum – minimum), 2005–2015 | variation in thermal conditions on the N-S-oriented peninsula may drive patterns |
| Minimum freezing degree days, 2005–2015 | cold temperatures limit organismal ranges |
| Maximum heating degree days, 2005–2015 | hot temperatures limit organismal ranges |
| Grand mean of monthly mean relative humidity (%), 2005–2015 | humidity affects heat tolerance limits for multiple animals and may better reflect moisture effects |
| Grand mean of monthly mean precipitation (mm), 2005–2015 | rainfall affects habitat conditions and resource availability and may better reflect moisture effects |
| Ecoregions (Level IV)[c] | major vegetation zones denote distinctive habitats that may affect animal distributions |
| **Human effects** | |
| Traffic on through roads (mean FLDOT[d] annual average daily traffic estimates, 2005–2015) | WVCs reflect wildilfe interactions with traffic; more traffic may contribute to more WVCs |
| Number of lanes on through roads[e] | wider roads are bigger barriers and often have more traffic |
| Posted speed limits on through roads (in- parks are constant 15 mph posted)[e] | faster vehicles are less likely to avoid WVCs |
| Length of through-park road (km)[a] | more road corresponds to more opportunities for WVCs |
| Length of in-park road (km)[a] | more road corresponds to more opportunities for WVCs |
| Road density (in-park road length/park area; km/ha)[a] | standardized roads per unit area better represent WVC probabilities than other road measures |
| Monthly park attendance[a] | in-park traffic may be at least as important as traffic on through roads |
| Presence of attractive water features (access to beaches, estuaries, rivers or lakes)[a] | these features attract more traffic, including boat trailers (more wheels, longer stopping time, less maneuverable) |
| County human population and housing density[f] | human population causes traffic *and* habitat changes that increase animal exposure to traffic |

[a]From https://floridadep.gov/parks/park-mapping-databases; Districts 2–5.
[b]Wang et al. (2016).
[c]https://www.epa.gov/eco-research/ecoregion-download-files-state-region-4#pane-08
[d]Florida Department of Transportation:https://www.fdot.gov/statistics/trafficdata
[e]Google Maps, street view.
[f]US Census data:http://edr.state.fl.us/Content/population-demographics/2010-census/data/countyshare.xls

(SR) and (b) monthly effective diversity (i.e., $D = e^{(H')}$, where $H'$ is Shannon diversity, or $-\Sigma p_i \ln(p_i)$ and $p_i$ is the proportional abundance of a species per park in that month (Jost, 2006)). Our third measure was monthly total abundance ($N$) of a taxon (e.g., birds).

Animals with uncertain identification (e.g., unidentifiable bird) were excluded from analyses of species richness or effective diversity but were included in total abundance analyses. The three measures for each of the four taxon sets resulted in twelve sets

of analyses for each question. See Appendix S1 for R code (R Core Team, 2018).

## 2.2 | Question 1: Which parks have more WVC diversity and abundance?

Differences among parks were evaluated for each of twelve data sets representing combinations of the three response variables (SR, *D*, and *N*) per each of four taxa (birds, mammals, reptiles, and overall). Data were analyzed by mixed-effect models to address temporal autocorrelation, where a response variable (e.g., bird SR) was simply modeled as a function of park name and sampling effort. To be consistent with different sampling regimes among parks, two separate terms (i.e., 1|Month + 1|Year) were used to represent the crossed random intercept effects. Preliminary modeling using months nested in years for the random effect obtained singular fits, a symptom of an overly complex random effect term given the heterogeneity of temporal patterns among parks.

Spatial autocorrelation among parks was also evaluated by plotting residuals of the above models as a function of longitude and latitude, and by plotting spatial correlations as a function of distance, based on Matern correlations using the spaMM package in R (Rousset & Ferdy, 2014). However, virtually no spatial autocorrelation was observed for diversity and abundance of taxa and so results below were not adjusted for that effect.

The models used either Gaussian or negative binomial distributions, where lmer in the lme4 package of R was used for *D* and glmer.nb in MASS was used for count data (SR or *N*; Bates et al., 2015, R Core Team, 2018). Models were compared with weights ($w_i$) for the corrected Akaike information criterion (AICc; Burnham & Anderson, 2002), using bbmle in R (Bolker et al., 2017). An AIC $w_i$ value represents the probability that a model is most plausible among those in the compared set and is thus the main criterion to identify the most plausible model (Burnham & Anderson, 2002). We also evaluated δAICc values, where δAICc < 2 indicates a second model is about as plausible. Where that was the case, different model predictors were more closely scrutinized between models (Arnold, 2010). We also calculated trigamma pseudo-$R^2$ values for the most plausible model (using MuMIn; Bartoń, 2018).

We compared parks for WVC diversity and abundance by their fixed effect estimates (i.e., the first alphabetical park (Alafia River State Park) estimate + Park × estimate) and their 95% confidence intervals (hereafter CIs). As a reminder, park estimates for each variable (e.g., bird SR) thus accounted for sampling effort and temporal autocorrelation. Park estimates were compared with the overall mean (e.g., grand mean of all bird SR park means), and parks that exceeded the overall mean (according to the 95% CI) were identified as having a high value. Parks were also ranked for SR and *N* of all species, birds, mammals, and reptiles. We expected management decisions to be more easily justified using SR and *N* than by the more abstract *D*, so we did not rank parks by *D*. For brevity, we graphed only ranked parks for overall SR and *N*, and present all results in Appendices S2 and S3.

## 2.3 | Question 2: What best explains WVC differences among parks?

For this answer, we compared alternative regression models for the mean park values described above (i.e., park coefficients from Question 1 models). In other words, we evaluated the patterns observed above rather than raw data again (e.g., bird SR) so that our analytical structure matched our two questions rather than a new question (e.g., what *else* predicts diversity?). Computed models used suites of predictors representing biogeography, climate, ecoregions, and human effects (Table 1). Predictor variables were fixed for a park (e.g., area) or averaged among several values (e.g., annual average daily traffic counts) and did not represent repeated measures. Thus, single predictors per year and park were used, so that models for our second question were generalized linear models and yielded effect sizes for variation among parks.

Analyses for this question were conducted in two stages. First, linear models for separate and combined variables *within* a hypothetical suite (e.g., biogeography) were compared by AICc $w_i$. Next, terms of the most plausible model for a suite were retained (if $w_i$ of the most plausible model exceeded that for a null model) for use in a combination model, because predictor suites were not mutually exclusive. Strongly collinear terms (as measured by variable inflation factors >3) in models at either stage were handled by omitting a term that was conceptually least related to the response variable. All predictors in models were scaled (as *Z* scores) and thus directly comparable for effect size.

Finally, a most parsimonious version of the combination model per response variable (e.g., bird SR ~ *biogeography* + human effects) was obtained, with the goal that results would help clear communication to park management. We simplified by iteratively omitting variables with the least scaled effect size until AICc was minimized. This process was based on overall model AICc values (not predictor *p* values). A minimum AICc occurred because removal of confounding or uninformative variables more efficiently represented variance, whereas removal of contributing terms had the reverse effect. This step yielded the most parsimonious models to "explain" WVC patterns among parks. Models were also compared at this step by δAICc values, where a value >2 for the next model indicates substantial difference in plausibility, and where δAICc < 2, model details were scrutinized to ensure interpretations were based on informative predictors (Arnold, 2010).

## 3 | RESULTS

### 3.1 | Data breadth

We compiled 9,254 WVC records for the 42 state parks during 2005–2015 (see *Data Accessibility*). Those data resulted in 1,955 monthly values for parks and represented 237 species. Bird data included 615 records, representing 138 bird species in 33 parks. Mammal data included 1,592 records, representing 35 mammal species in 35 parks.

Reptile data included 1,005 records, representing 64 reptile species in 42 parks.

Parks spanned about 6° of latitude (24.5° N to 30.5° N), ranged from 4 to 32,325 ha in area, were in landscapes ranging from rural to intensively urban and represented a variety of natural habitats, ranging from upland forests to islands. See Appendix S2 for statistical output summarized below.

## 3.2 | Question 1: Which parks have more WVC diversity and abundance?

Statistical models using sampling effort as a fixed effect and time and space as random effects were rather predictive for overall SR and N but less so for other data (Table 2). Using effort as a predictor achieved the majority of signal, given the ratio of marginal to conditional pseudo-$R^2$ values. We concluded that statistical models were a reasonable basis to understand overall WVC diversity and abundance patterns, as well as predictors for those patterns. Models were a weaker basis for inferences on select data (e.g., bird $D$—explained below). We note that comparisons among parks using these models account for variation in sampling effort and years.

Species richness (SR) of all taxa was most plausibly modeled as a function of park and a quadratic effect of sampling effort ($w_i = 0.86$, next $\delta$AICc = 3.6), where SR increased with squared effort. The mixed-effects model represented data patterns well ($R^2_m = 0.48$, $R^2_c = 0.51$), and parks varied significantly in overall SR (Table 2). Eight parks had overall SR clearly greater than the overall mean (Figure 2a); in descending order, they were Big Talbot Island, Jonathan Dickinson, John Pennekamp/Key Largo Hammocks, Myakka River, Blue Spring, Collier-Seminole, Sebastian Inlet, and Fakahatchee Strand Preserve. Abundance (N) was similarly modeled with a quadratic effect of sampling effort ($w_i = 0.98$, next $\delta$AICc = 7.8) and again represented data well ($R^2_m = 0.52$, $R^2_c = 0.54$) with significant differences among parks. Ten parks had WVC abundance clearly greater than the overall mean, the same eight parks as for SR plus Dr. Von D. Mizell-Eula Johnson and Curry Hammock. Five parks were consistently ranked as in the top 5 for both overall SR and N: Big Talbot Island, Jonathan Dickinson, John Pennekamp/Key Largo Hammocks, Myakka River, and Blue Spring (Table 3). Overall effective diversity (D) was clearly modeled most plausibly by a simpler linear effort model (i.e., no effort$^2$ term; $w_i = 0.99$, next $\delta$AICc = 9.2). However, that model was less explanatory than SR or N models; $R^2_m = 0.32$ and $R^2_c = 0.33$ (Table 2).

As expected, bird diversity in WVC data was modeled less effectively than other taxa; we generally discounted bird models in interpretations. The model for SR with a quadratic effect of effort was again most plausible ($w_i = 0.88$, next $\delta$AICc = 3.9), but effort now had a hump-shaped effect (i.e., intermediate effort yielded most species). More importantly, relatively few parks differed from the overall mean (Table 2) and the SR model was relatively weak ($R^2_m = 0.22$ and $R^2_c = 0.26$; Table 2). Bird abundance (N) was a little more clearly modeled (Table 2), with the most plausible model showing exponential increase in N with sampling. Only two parks clearly had more

bird SR (Blue Spring) and N (John Pennekamp/Key Largo Hammocks) than overall mean values (see Appendix S3). Effective diversity (D) of birds was least clearly modeled (Table 2) with relatively low fit to the data ($R^2_m = 0.13$ and $R^2_c = 0.14$; Table 2).

Models for mammal SR and N were clearly plausible and predictive; mammal D was less clearly modeled. Mammal SR increased with greater sampling effort (again as an exponential increase), and strong differences were clearly observed among parks (Table 2). The most plausible mixed-effects model was clearly so ($w_i = 0.86$, next $\delta$AICc = 3.6) and represented variation fairly well ($R^2_m = 0.37$ and $R^2_c = 0.40$; Table 1). The same eight parks as listed above for high overall SR had mammal SR clearly greater than the overall mean. Mammal N was similarly affected by sampling effort, and strong differences were again clearly observed among parks (Table 2). The mixed-effects model with a quadratic effect of sampling effort was again clearly most plausible ($w_i = 0.97$, next $\delta$AICc = 7.1) and represented variation well ($R^2_m = 0.44$ and $R^2_c = 0.47$; Table 2). Nine parks had mammal N clearly greater than the overall average: John Pennekamp/Key Largo Hammocks, Big & Little Talbot Islands, Jonathan Dickinson, Myakka River, Blue Spring, Fakahatchee Strand Preserve, Curry Hammock, John D. MacArthur Beach, and Sebastian Inlet (see Appendix S3 for details). Unlike relatively clear and strong signals for SR and N, the most plausible mammal D model included a nonsignificant and linear effect of effort that was barely more plausible than a quadratic effect ($w_i = 0.38$, next $\delta$AICc = 0.1). That model was also relatively weak in explaining variation with mammal D ($R^2_m = 0.10$ and $R^2_c = 0.10$; Table 2); we discount it below in interpretations.

Models for reptile WVCs reflect similar strengths and behavior as those for mammals. Reptile SR increased similarly as a function of sampling effort and strong differences were again apparent among parks ($w_i = 0.98$, next $\delta$AICc = 7.6; Table 2). Variation among parks was again represented fairly well by the mixed-effects model ($R^2_m = 0.36$, $R^2_c = 0.39$; Table 2). Similar outcomes were observed for the reptile N model (Table 2). Despite fairly strong model fits, only two parks had effect sizes greater than the overall average for both SR and N, Jonathan Dickinson and Blue Spring (see Appendix S3). Though the reptile D model was clearly plausible ($w_i = 0.72$, next $\delta$AICc = 2.6), effort terms were not significant in the model and it represented relatively low variance ($R^2_m = 0.13$, $R^2_c = 0.14$; Table 2).

To directly answer our first question, the top five parks for WVC are listed in Table 3, based on overall species richness or abundance, which were the best-supported models evaluated for this question. Other parks mentioned above for specific taxa may also be justifiably considered for specific WVC mitigation efforts (e.g., Fakahatchee Strand Preserve for mammal SR), but the top five parks (Table 3) were consistently ranked highly among up to 42 parks. We concluded that WVC mitigation efforts are justifiable in those five parks.

## 3.3 | Question 2: What best explains WVC differences among parks?

As a reminder, response variables here were park coefficients from models obtained in answer to the Question 1. Predictor variables

**TABLE 2** Summary of most plausible regression results for relative differences among Florida State Parks in wildlife-vehicle collision species richness (SR), effective diversity (D), and abundance (N) of all taxa, birds, mammals, and reptiles

| | All taxa | | | Birds | | | Mammals | | | Reptiles | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | SR | N | D | SR | N | D | SR | N | D | SR | N | D |
| **Random effects** | | | | | | | | | | | | |
| Month | 0.11 | 0.10 | 0.09 | 0.11 | 0.18 | <0.01 | 0.07 | 0.04 | <0.01 | 0.16 | 0.20 | <0.01 |
| Year | 0.11 | 0.12 | 0.06 | 0.16 | 0.18 | <0.01 | 0.14 | 0.15 | <0.01 | 0.05 | 0.07 | <0.01 |
| **Fixed effects[2]** | | | | | | | | | | | | |
| Effort | -0.11 (0.22) | -0.21 (0.23) | **0.07 (0.04)** | **0.67 (0.46)** | **0.78 (0.50)** | 0.37 (0.37) | -0.10 (0.24) | -0.19 (0.25) | 0.03 (0.05) | -0.23 (0.24) | **-0.27 (0.25)** | -0.15 (0.23) |
| Effort[2] | **0.21 (0.22)** | **0.32 (0.22)** | – | **-0.41 (0.41)** | **-0.48 (0.44)** | -0.21 (0.32) | **0.23 (0.23)** | **0.32 (0.23)** | – | **0.31 (0.22)** | **0.38 (0.22)** | 0.19 (0.21) |
| AICc $w_i$ [a] | 0.86 | 0.98 | 0.99 | 0.88 | 0.90 | 0.66 | 0.86 | 0.97 | 0.38 | 0.98 | 0.99 | 0.72 |
| δAICc [b] | 3.6 | 7.8 | 9.2 | 3.9 | 4.4 | 1.5 | 3.6 | 7.1 | 0.1 | 7.6 | 10.4 | 2.6 |
| $R^2_m$ | 0.48 | 0.52 | 0.32 | 0.22 | 0.29 | 0.13 | 0.37 | 0.44 | 0.10 | 0.36 | 0.35 | 0.13 |
| $R^2_c$ | 0.51 | 0.54 | 0.33 | 0.26 | 0.34 | 0.14 | 0.40 | 0.47 | 0.10 | 0.39 | 0.40 | 0.14 |

Note: Analyses used mixed-effects models where Month and Year were random effects and Park and Effort (including a potential quadratic effect) were fixed effect predictors. Random effects are reported as standard deviations (comparable in magnitude to fixed effect estimates), and fixed effects as scaled coefficients (± 95% CIs). Fixed effects per park are depicted in Figure 1 and listed in Appendix S3. Bold values are significantly different ($p < .05$) from zero. AICc[1] weights, δAICc values for the next-ranked model, and the marginal (i.e., fixed effects; $R^2_m$) and conditional (i.e., fixed + random effects; $R^2_c$) trigamma pseudo-$R^2$ values are also reported. See Appendix S3 for park coefficients per each model.

[a] Akaike information criterion (AIC) weight. AIC weights describe the probability that a model is most plausible among those analyzed (Burnham and Anderson, 2002).

[b] δAICc is for the next-ranked model, where a rule-of-thumb is that values >2 indicate a clear top-ranked model.
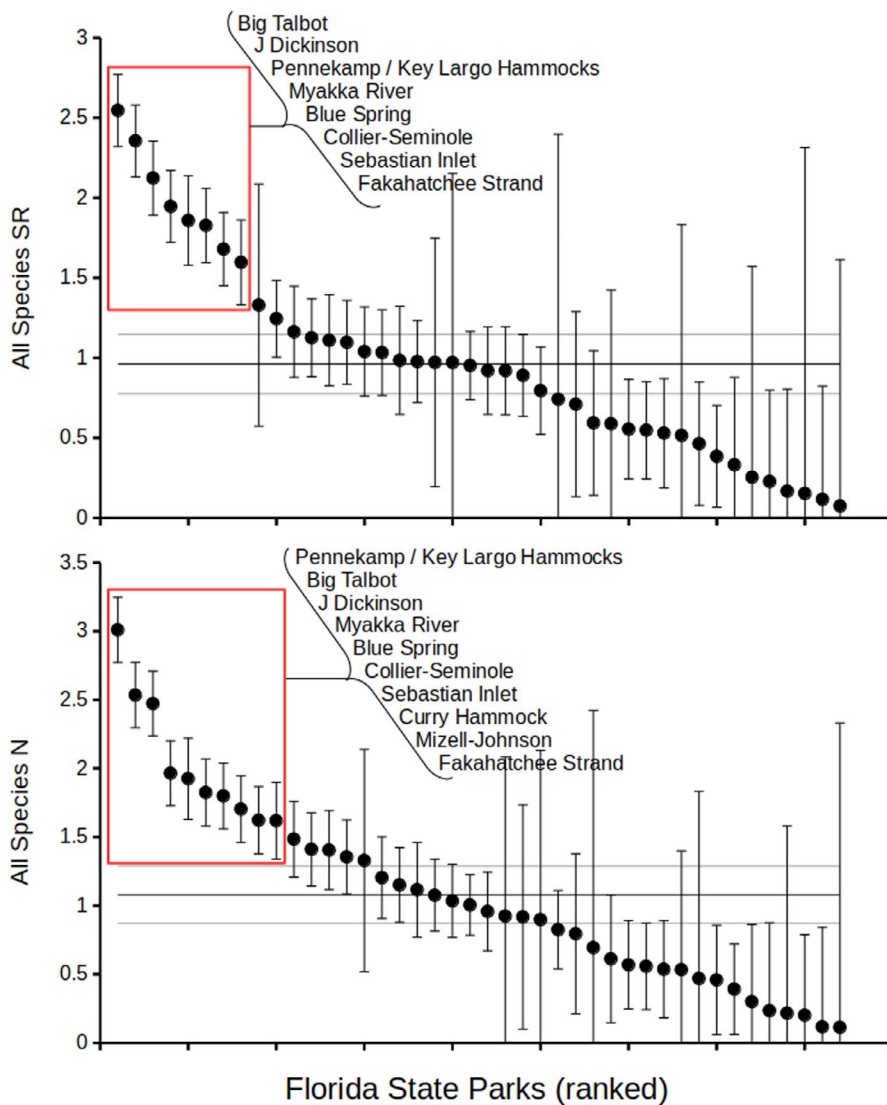
**FIGURE 2** Florida State Parks, ranked for overall species richness (SR) and abundance (N) of wildlife killed as a result of wildlife-vehicle collisions on roads in, through, and adjacent to parks, 2005–2015. Values are model estimates per park after statistically accounting for differences in sampling effort and time. See Appendix S3 for details

here represented geography, climate ecoregions, and human effects (Table 1), and obtained coefficients represent scaled effect sizes after accounting for effects of sampling effort and timing among parks.

Overall SR, N, and D were most plausibly fit by park area, longitude (as easting), park attendance, and (for D) maximum speed limit on through roads (all three AIC $w_i$ ≥ 0.78; δAICc ≥ 2.6; adjusted $R^2$ values ≥ 0.53; Table 4). In general, diversity and abundance of wildlife killed on roads at state parks increased with park size (though not road lengths or road densities), proximity to the East coast, and more in-park vehicles and/or faster traffic on through roads. The scaled predictors in the model were not autocorrelated (maximum variable inflation factor (VIF) = 2.4). More traffic on through roads was retained in most plausible N and D models and listed in Table 4 for transparency, but not significant and discounted in interpretations below.

Compared to other taxa evaluated here, birds in WVC among Florida State Parks were again modeled least effectively (as expected). A null model was most plausible for bird species richness, and only easting plausibly fit bird N, and did so poorly (adjusted $R^2$

= 0.10; Table 4). Only a negative latitude effect plausibly fit bird D (adjusted $R^2$ = 0.22; Table 4).

In contrast to birds, all metrics of mammal WVCs were significantly and strongly modeled by park area and easting (Table 4). All mammal models had fairly strong fits to data (adjusted $R^2$ values = 0.36–0.46; Table 4), but AIC-based details discounted the importance of some predictors. For example, traffic on through roads significantly and negatively "explained" mammal D, but the reported model was not clearly more plausible than a model that lacked the traffic effect (δAICc = 0.3; Table 4)—we discounted that effect in our interpretations but show it in Table 4 for transparency. Similarly, maximum number of annual freezing degree days during the study interval strongly and positively fit mammal SR and N, but did not do so for other taxa or measures (Table 4). Again, those two models were not clearly more plausible than those lacking a thermal effect (δAICc = 0.0.7 and 1.7; Table 4)—we again discounted that effect.

Reptile SR, D, and N were all significantly and strongly fitted by park area, without significant or strong contributions from other variables (though a few were retained in most plausible models;

**TABLE 3** Top five Florida State Parks for wildlife-vehicle collision (WVC) species richness (SR), overall abundance (N). Also see Appendix S3 for details that formed these ranks

| Florida State Parks | Overall SR rank | Overall N rank |
|---|---|---|
| Big Talbot | 1 | 2 |
| Jonathan Dickinson | 2 | 3 |
| John Pennekamp/Key Largo Hammocks | 3 | 1 |
| Myakka River | 4 | 4 |
| Blue Spring | 5 | 5 |

**TABLE 4** Summary of most plausible regression results for Florida State Park effect sizes after accounting for sampling effort and repeated measures (see Table 2)

| | All taxa | | | Birds | | | Mammals | | | Reptiles | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | SR | N | D | SR | N | D | SR | N | D | SR | N | D |
| Intercept | **0.95** (0.13) | **1.04** (0.14) | **0.70** (0.09) | **0.62** (0.10) | **0.72** (0.11) | **0.37** (0.05) | **0.64** (0.12) | **0.73** (0.15) | **0.36** (0.08) | **0.43** (0.12) | **0.50** (0.14) | **0.26** (0.06) |
| Log(area) | **0.34** (0.16) | **0.32** (0.17) | **0.24** (0.10) | | | | **0.30** (0.14) | **0.31** (0.16) | **0.14** (0.10) | **0.23** (0.12) | **0.20** (0.13) | **0.16** (0.07) |
| Easting | **0.18** (0.15) | **0.33** (0.17) | **0.14** (0.10) | | 0.12 (0.11) | | **0.22** (0.12) | **0.28** (0.15) | **0.11** (0.08) | 0.16 (0.15) | | |
| Latitude | | | | | | −0.08 (0.04) | | | | | | |
| Max. freezing degree days | | | | | | | 0.19 (0.12) | 0.18 (0.13) | | | | |
| Mean precip. | | | | | | | | | | | | 0.07 (0.07) |
| Attendance | **0.19** (0.15) | **0.16** (0.16) | **0.11** (0.10) | | | | | 0.05 (0.14) | | | 0.08 (0.14) | |
| Speed limit | 0.16 (0.19) | 0.16 (0.21) | **0.14** (0.13) | | | | | | 0.09 (0.09) | | | |
| Traffic | | −0.11 (0.15) | −0.08 (0.09) | | | | | | **−0.10** (0.08) | | | |
| AICc $w_i$[a] | 0.81 | 0.81 | 0.78 | 0.56 | 0.56 | 0.50 | 0.46 | 0.56 | 0.49 | 0.96 | 0.62 | 0.55 |
| δAICc[b] | 3.7 | 4.3 | 2.6 | 1.6 | 2.1 | 0.3 | 0.7 | 1.7 | 0.3 | 6.7 | 2.1 | 1.6 |
| Adjusted $R^2$ | 0.54 | 0.53 | 0.60 | – | 0.10 | 0.22 | 0.46 | 0.45 | 0.36 | 0.24 | 0.19 | 0.43 |

*Note:* Park means for park species richness (SR), abundance (N), and effective diversity (D) were modeled as functions of biogeography, climate, ecoregions, human effects, and combinations. Combination models were simplified to reduce collinearity and for parsimony using AICc. All effect sizes are scaled for comparability. Bold values are significantly different from zero. No coefficients are listed for Bird SR because a null model was most plausible (as indicated by AICc weight; $w_i$). Predictors are sorted in descending order of frequency listed. See *Methods* for details.

[a]Akaike information criterion (AIC) weight. AIC weights describe the probability that a model is most plausible among those analyzed (Burnham and Anderson, 2002).

[b]δAICc is for the next-ranked model, where a rule-of-thumb is that values >2 indicate a clearly top-ranked model.

Table 4). In contrast to our expectations, thermal variables poorly predicted data for poikilothermic reptiles. Adjusted $R^2$ values ranged from 0.19 to 0.43 (Table 4).

To answer our second question, characteristics of parks (area, location) as well as traffic-related effects of park attendance and speed limits were often the most plausible predictors of WVC diversity and abundance. Overall diversity (measured as SR, D, or N) was more predictably modeled than subsets and emphasized below, though park area was again consistently predictive for diversity measures of mammals and reptiles.

## 4 | DISCUSSION

Results here represent a regional analysis of wildlife-vehicle collisions (WVCs) at Florida State Parks of the Florida peninsula, based on data collected by Florida State Park personnel. The substantial spatio-temporal scale and taxonomic breadth help fill two knowledge gaps for WVCs (diversity and regional scales) and may serve as a basis for similar and improved work in other regions. Important predictors (park area, location) clearly cannot be controlled, but traffic in and adjacent to parks may also be managed to reduce

WVCs in and around Florida State Parks to better maintain wildlife diversity.

## 4.1 | Which parks have more WVC diversity and abundance?

We identified five State Parks as clear WVC "hot spots" (Table 3) and recommend that intervention efforts to reduce WVC impacts on Florida State Park wildlife be first targeted to those parks for the greatest impact. Other parks could also benefit from management aimed to reduce WVCs, especially if the parks are also highly ranked (see Appendix S3) or act as habitats for specific taxa, especially those with small populations prone to WVCs (Harris & Gallagher, 1989). We note that WVC rates reported here may underestimate true rates because the analyses did not fully evaluate detectability differences beyond statistical effects of sampling frequency and temporal effects. However, comparisons among parks were fair here because they used the same data. Florida State Parks should be able to use results here as a basis to target efforts to mitigate WVCs. Likewise, managers at "hot spot" parks will be most able to identify roads or road segments where management would be most effective; our regional analyses precede those potential details.

## 4.2 | What best explains WVC differences among parks?

Florida State Parks with more WVC species, abundance, and effective diversity tend to have more area, be nearer to the Atlantic Coast, have more attendance in parks, and have faster traffic on adjacent roads. All five "hot spot" parks (above) are located on or near the East coast. Of these predictors, area was most important (based on scaled effect sizes in Table 4). Assuming that living diversity is representatively sampled by WVCs (as observed by González-Gallina et al., 2015 and Canova & Balestrieri, 2019), and given that the observed species–area effect fits long-established expectations (Rosenzweig, 1995), then results here may indicate a similar species–area relationship for living wildlife diversity in the parks. Tests of that relationship must await more complete inventories of wildlife living in Florida State Parks, but results here suggest a strong biogeographic effect on habitat "islands" in the midst of rapid human population growth and land use. The habitat island effect may be enhanced for parks as human land use intensifies around parks, which also accentuates the need for mammal and reptiles corridors among parks (Noss, 1983). Larger parks also tend to be further from highest human population density, whereas urban parks tend to be smaller. The combination of park area and location (i.e., greater diversity away from the highly populated Atlantic coast) may indicate a diffuse effect of human land use, population, and traffic loads that was not detected using predictors (US Census data, traffic estimates) in models. Local traffic conditions may greatly affect smaller parks,

whereas larger parks may be more affected by longer-distance traffic conditions (e.g., routes between urban centers). If so, a spatial hierarchy (Wiens, 1989) of anthropogenic processes may affect wildlife diversity and be useful for WVC reduction. We expect that more refined estimates of regional human population effects and traffic (if available) may be more predictive in related analyses.

Park attendance, speed limits, and traffic rates are manageable (unlike park areas and locations). Management options to reduce WVCs often focus on modifying wildlife access to roads, but those options (e.g., fencing, underpasses, ultrasonic whistles) necessarily work better for some taxa than others (Andrews et al., 2015; Forman et al., 2003; van der Ree et al., 2015). Given that traffic-related effects (i.e., park attendance, through-road speed limits) here were most clearly observed for overall diversity, and that natural lands are typically managed for multiple taxa, our results indicate a strong justification for active management of the other participant in WVCs: vehicle drivers.

Parks can reduce wildlife mortality by working with relevant local, county, or state agencies to apply "traffic calming" approaches in those road sections (e.g., Collinson et al., 2019; Garriga et al., 2012; Huijser et al., 2008). Wildlife mortality may be reduced by redirecting heavy traffic loads to other routes. Increased road visibility (Hobday & Minstrell, 2008) may provide a buffer of extra reaction time for drivers but may also encourage counteractive faster speeds. Obstacles (e.g., speed bumps, chicanes) are likely more effective than signage for this purpose (Coulson, 1982; Dique et al., 2003). Park managers may receive complaints, but the purpose of parks is not to make more roadkill.

## 4.3 | Other considerations

Results here identified Florida State Parks that are WVC "hot spots." An alternative is to consider potential "cold-spot" parks with apparently low WVC diversity and abundance (see Appendix S3). Small park area is a factor, but further studies may be especially valuable in these parks because results indicate low wildlife diversity that may be improved by management. Though sampling effort was handled here analytically, it was uneven among parks. Sampling protocols for WVCs that are more consistent among all parks may alter results here to reveal more parks where traffic interventions could be effective. Toward that end, wildlife cameras should be encouraged as a tool to monitor wildlife diversity in Florida State Parks (Ahumada et al., 2011; Smith & van der Ree, 2015). Wildlife cameras could supplement manual surveys, be especially effective in small parks, help educational outreach, track non-native species, evaluate native wildlife adapting to human landscapes, better understand wildlife diversity, and help calibrate WVC censuses in and among parks.

Finally, results here reinforce the value of years of sampling by park personnel on roads that were in, through, and adjacent to parks. A sustained, more robust, statewide WVC monitoring program

would enable analysis and refinement of efforts to reduce wildlife mortality on roads in or adjacent to State Parks, especially if that program used recent smartphone-based technology (e.g., Olson et al., 2014; Shilling & Waetjen, 2015). A citizen science approach that includes public input and park personnel in WVC data collection can provide data in and around state parks to help better manage wildlife diversity. Such a WVC monitoring program should be treated as a long-term research project, with the expectation that delayed wildlife responses are likely for some already-small and slow-growing animal populations.

## 5 | CONCLUSION

Results here support management of human vehicular behavior in and near Florida State Parks to reduce the number and diversity of animals killed in WVCs. Results may translate to other regional park systems. Parks can remind drivers to watch out for wildlife while collecting fees, where applicable. Vertical and/or horizontal lane deflections and perhaps signage should reduce wildlife mortality, especially in or adjacent to highest-ranked parks. Traffic access to select roads within parks may also be managed, and parking lots (a common site of WVCs) may be located at park edges to reduce wildlife casualties. These and other potential interventions may draw complaints but are consistent with the parks' mission. Active management of WVCs will take on greater importance as the Florida human population grows (38% in the 2010–2020 decade) if natural lands are to effectively maintain wildlife populations and diversity.

## AUTHOR CONTRIBUTION
**David G. Jenkins:** Conceptualization (lead); Data curation (equal); Formal analysis (lead); Investigation (lead); Methodology (lead); Project administration (equal); Visualization (lead); Writing-original draft (lead); Writing-review & editing (lead). **Leo Ohyama:** Data curation (equal); Formal analysis (equal); Methodology (equal); Validation (equal); Visualization (equal); Writing-review & editing (equal). **Federico López-Borghesi:** Data curation (equal); Formal analysis (equal); Methodology (equal); Validation (equal); Writing-review & editing (equal). **Jacob D. Hart:** Data curation (equal); Formal analysis (equal); Methodology (equal); Validation (equal); Writing-review & editing (equal). **Juan D. Bogotá-Gregory:** Data curation (equal); Formal analysis (equal); Methodology (equal); Validation (equal); Writing-review & editing (equal). **Rhett M. Rautsaw:** Data curation (equal); Methodology (equal); Validation (equal); Writing-review &

editing (equal). **Vanessa Correa Roldán:** Data curation (equal); Writing-review & editing (equal). **Kevin Guilfoyle:** Data curation (equal); Writing-review & editing (equal). **Anik Jarvis:** Data curation (equal); Writing-review & editing (equal). **Jennifer Loch:** Data curation (equal); Writing-review & editing (equal). **Kathryn Mercier:** Data curation (equal); Writing-review & editing (equal). **Olivia Myers:** Data curation (equal); Writing-review & editing (equal). **Rachel Shaw:** Data curation (equal); Writing-review & editing (equal). **Daniel Volk:** Data curation (equal); Writing-review & editing (equal). **Alice M. Bard:** Conceptualization (equal); Data curation (equal); Project administration (equal); Writing-review & editing (equal).

## ORCID
*David G. Jenkins*   iD   https://orcid.org/0000-0002-0363-2260

## REFERENCES
Ahumada, J. A., Silva, C. E., Gajapersad, K., Hallam, C., Hurtado, J., Martin, E., McWilliam, A., Mugerwa, B., O'Brien, T., Rovero, F., & Sheil, D. (2011). Community structure and diversity of tropical forest mammals: Data from a global camera trap network. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *366*, 2703–2711.

Andrews, K. M., Nanjappa, P., & Riley, S. P. (Eds.) (2015). *Roads and ecological infrastructure: Concepts and applications for small animals*. Johns Hopkins University Press.

Arnold, T. W. (2010). Uninformative parameters and model selection using Akaike's Information Criterion. *Journal of Wildlife Management*, *74*, 1175–1178. https://doi.org/10.1111/j.1937-2817.2010.tb01236.x

Bard, A. M., Smith, H. T., Egensteiner, E. D., Mulholland, R., Harber, T. V., Heath, G. W., Miller, W. J. B., & Weske, J. S. (2002). A simple structural method to reduce road-kills of Royal Terns at bridge sites. *Wildlife Society Bulletin*, *30*, 603–605.

Bar-Massada, A., Radeloff, V. C., & Stewart, S. I. (2014). Biotic and abiotic effects of human settlements in the wildland–urban interface. *BioScience*, *64*, 429–437. https://doi.org/10.1093/biosci/biu039

Bartoń, K. (2018). *MuMIn: Multi-model inference*. R Package Version 1.42.1. https://CRAN.R-project.org/package=MuMIn

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*, 1–48.

Beebee, T. J. (2013). Effects of road mortality and mitigation measures on amphibian populations. *Conservation Biology*, *27*, 657–668. https://doi.org/10.1111/cobi.12063

Bennett, V. J. (2017). Effects of road density and pattern on the conservation of species and biodiversity. *Current Landscape Ecology Reports*, *2*, 1–11. https://doi.org/10.1007/s40823-017-0020-6

Bolker, B., & R Development Core Team (2017). *bbmle: Tools for general maximum likelihood estimation*. R Package Version 1.0.20. https://CRAN.R-project.org/package=bbmle

Burnham, K. P., & Anderson, D. R. (2002). *A practical information-theoretic approach. Model selection and multimodel inference* (2nd edn). Springer.

Canal, D., Camacho, C., Martín, B., de Lucas, M., & Ferrer, M. (2019). Fine-scale determinants of vertebrate roadkills across a biodiversity hotspot in Southern Spain. *Biodiversity and Conservation*, *28*, 3239–3256. https://doi.org/10.1007/s10531-019-01817-5

Canova, L., & Balestrieri, A. (2019). Long-term monitoring by road-kill counts of mammal populations living in intensively cultivated landscapes. *Biodiversity and Conservation*, *28*, 97–113. https://doi.org/10.1007/s10531-018-1638-3

Chyn, K., Lin, T. E., Chen, Y. K., Chen, C. Y., & Fitzgerald, L. A. (2019). The magnitude of roadkill in Taiwan: Patterns and consequences revealed by citizen science. _Biological Conservation_, _237_, 317–326. https://doi.org/10.1016/j.biocon.2019.07.014

Coffin, A. W. (2007). From roadkill to road ecology: A review of the ecological effects of roads. _Journal of Transport Geography_, _15_, 396–406. https://doi.org/10.1016/j.jtrangeo.2006.11.006

Collinson, W. J., Marneweck, C., & Davies-Mostert, H. T. (2019). Protecting the protected: Reducing wildlife roadkill in protected areas. _Animal Conservation_, _22_, 396–403. https://doi.org/10.1111/acv.12481

Coulson, G. M. (1982). Road-kills of macropods on a section of highway in central Victoria. _Australian Wildlife Research_, _9_, 21–26.

Dique, D. S., Thompson, J., Preece, H. J., Penfold, G. C., deVilliers, D. L., & Leslie, R. S. (2003). Koala mortality on roads in south-east Queensland: The koala speed-zone trial. _Wildlife Research_, _30_, 419–426. https://doi.org/10.1071/WR02029

Fahrig, L., & Rytwinski, T. (2009). Effects of roads on animal abundance: An empirical review and synthesis. _Ecology and Society_, _14_, 21. https://doi.org/10.5751/ES-02815-140121

Forman, R. T. T., & Alexander, L. E. (1998). Roads and their major ecological effects. _Annual Review of Ecology and Systematics_, _29_, 207–231.

Forman, R. T., Sperling, D., Bissonette, J. A., Clevenger, A. P., Cutshall, C. D., Dale, V. H., Fahrig, L., France, R. L., Heanue, K., Goldman, C. R., & Jones, J. (2003). _Road ecology: Science and solutions_. Island Press.

Garriga, N., Santos, X., Montori, A., Richter-Boix, A., Franch, M., & Llorente, G. A. (2012). Are protected areas truly protected? The impact of road traffic on vertebrate fauna. _Biodiversity and Conservation_, _21_, 2761–2774. https://doi.org/10.1007/s10531-012-0332-0

González-Gallina, A., Benítez-Badillo, G., Hidalgo-Mihart, M. G., Equihua, M., & Rojas-Soto, O. R. (2015). Roadkills as a complementary information source for biological surveys using rodents as a model. _Journal of Mammalogy_, _97_, 145–154. https://doi.org/10.1093/jmammal/gyv165

González-Suárez, M., Zanchetta Ferreira, F., & Grilo, C. (2018). Spatial and species-level predictions of road mortality risk using trait data. _Global Ecology and Biogeography_, _27_(9), 1093–1105. https://doi.org/10.1111/geb.12769

Grilo, C., Bissonette, J. A., & Santos-Reis, M. (2009). Spatial–temporal patterns in Mediterranean carnivore road casualties: Consequences for mitigation. _Biological Conservation_, _142_, 301–313. https://doi.org/10.1016/j.biocon.2008.10.026

Grilo, C., Koroleva, E., Andrášik, R., Bíl, M., & González-Suárez, M. (2020). Roadkill risk and population vulnerability in European birds and mammals. _Frontiers in Ecology and the Environment_, _18_, 323–328. https://doi.org/10.1002/fee.2216

Hampton, S. E., Strasser, C. A., Tewksbury, J. J., Gram, W. K., Budden, A. E., Batcheller, A. L., Duke, C. S., & Porter, J. H. (2013). Big data and the future of ecology. _Frontiers in Ecology and the Environment_, _11_, 156–162. https://doi.org/10.1890/120103

Harris, L. D., & Gallagher, P. B. (1989). New initiatives for wildlife conservation. The need for movement corridors. In G. Mackintosh (Ed.), _Defense of wildlife: Preserving communities and corridors_ (pp. 11–34). Defenders of Wildlife.

Hobday, A. J., & Minstrell, M. L. (2008). Distribution and abundance of roadkill on Tasmanian highways: Human management options. _Wildlife Research_, _35_, 712–726. https://doi.org/10.1071/WR08067

Huijser, M. P., McGowan, P., Hardy, A., Kociolek, A., Clevenger, A. P., Smith, D., & Ament, R. (2008). _Wildlife-vehicle collision reduction study: Report to congress_. US Department of Transportation, Federal Highway Administration. FHWA-HRT-08-034.

Jenkins, D. G., & Rinne, D. (2008). Red herring or low illumination? The peninsula effect revisited. _Journal of Biogeography_, _35_, 2128–2137. https://doi.org/10.1111/j.1365-2699.2008.01943.x

Jost, L. (2006). Entropy and diversity. _Oikos_, _113_(2), 363–375.

Laurance, W. F., Goosem, M., & Laurance, S. G. (2009). Impacts of roads and linear clearings on tropical forests. _Trends in Ecology & Evolution_, _24_, 659–669. https://doi.org/10.1016/j.tree.2009.06.009

Morelli, F., Rodríguez, R. A., Benedetti, Y., & Delgado, J. D. (2020). Avian roadkills occur regardless of bird evolutionary uniqueness across Europe. _Transportation Research Part D: Transport and Environment_, _87_, 102531.

Muhly, T. B., Semeniuk, C., Massolo, A., Hickman, L., & Musiani, M. (2011). Human activity helps prey win the predator-prey space race. _PLoS One_, _6_, e17050. https://doi.org/10.1371/journal.pone.0017050

Noss, R. F. (1983). A regional landscape approach to maintain diversity. _BioScience_, _33_, 700–706. https://doi.org/10.2307/1309350

Olson, D. D., Bissonette, J. A., Cramer, P. C., Green, A. D., Davis, S. T., Jackson, P. J., & Coster, D. C. (2014). Monitoring wildlife-vehicle collisions in the information age: How smartphones can improve data collection. _PLoS One_, _9_, e98613. https://doi.org/10.1371/journal.pone.0098613

R Core Team (2018). _R: A language and environment for statistical computing_. R Foundation for Statistical Computing.

Ricklefs, R. E. (2008). Disintegration of the ecological community. _American Naturalist_, _172_, 741–750. https://doi.org/10.1086/593002

Rosenzweig, M. L. (1995). _Species diversity in space and time_. Cambridge University Press.

Rousset, F., & Ferdy, J.-B. (2014). Testing environmental and genetic effects in the presence of spatial autocorrelation. _Ecography_, _37_, 781–790. https://doi.org/10.1111/ecog.00566

Santos, R. A. L., Santos, S. M., Santos-Reis, M., de Figueiredo, A. P., Bager, A., Aguiar, L. M., & Ascensao, F. (2016). Carcass persistence and detectability: Reducing the uncertainty surrounding wildlife-vehicle collision surveys. _PLoS One_, _11_, e0165608. https://doi.org/10.1371/journal.pone.0165608

Seiler, A. (2004). Trends and spatial patterns in ungulate-vehicle collisions in Sweden. _Wildlife Biology_, _10_, 301–313. https://doi.org/10.2981/wlb.2004.036

Shackelford, N., Standish, R. J., Ripple, W., & Starzomski, B. M. (2018). Threats to biodiversity from cumulative human impacts in one of North America's last wildlife frontiers. _Conservation Biology_, _32_, 672–684. https://doi.org/10.1111/cobi.13036

Shilling, F. M., & Waetjen, D. P. (2015). Wildlife-vehicle collision hotspots at US highway extents: Scale and data source effects. _Nature Conservation_, _11_, 41–60. https://doi.org/10.3897/natureconservation.11.4438

Smith, D. J., & van der Ree, R. (2015). Field methods to evaluate the impacts of roads on wildlife. In R. van der Ree, D. J. Smith, & C. Grilo (Eds.), _Handbook of road ecology_ (pp. 82–95). John Wiley & Sons.

Storch, D., Evans, K. L., & Gaston, K. J. (2005). The species–area–energy relationship. _Ecology Letters_, _8_, 487–492. https://doi.org/10.1111/j.1461-0248.2005.00740.x

Tiedeman, K., Hijmans, R. J., Mandel, A., Waetjen, D. P., & Shilling, F. (2019). The quality and contribution of volunteer collected animal vehicle collision data in ecological research. _Ecological Indicators_, _106_, 105431. https://doi.org/10.1016/j.ecolind.2019.05.062

van Der Ree, R., Smith, D. J., & Grilo, C. (2015). _Handbook of road ecology_. John Wiley & Sons.

Visintin, C., Van Der Ree, R., & McCarthy, M. A. (2017). Consistent patterns of vehicle collision risk for six mammal species. _Journal of Environmental Management_, _201_, 397–406. https://doi.org/10.1016/j.jenvman.2017.05.071

Waetjen, D. P., & Shilling, F. M. (2017). Large extent volunteer roadkill and wildlife observation systems as sources of reliable data. _Frontiers in Ecology and Evolution_, _5_, 89. https://doi.org/10.3389/fevo.2017.00089

Wang, T., Hamann, A., Spittlehouse, D., & Carroll, C. (2016). Locally downscaled and spatially customizable climate data for historical and

future periods for North America. *PLoS One*, *11*, e0156720. https://doi.org/10.1371/journal.pone.0156720

Wiens, J. A. (1989). Spatial scaling in ecology. *Functional Ecology*, *3*, 385–397. https://doi.org/10.2307/2389612

## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.