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RESEARCH ARTICLE

Spatial responses of black vultures to resource pulses during white-tailed deer hunting seasons

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Abstract

Pulsed resources can dramatically influence spatial ecology of wildlife. Black vulture (*Coragyps atratus*) movements depend on habitat structure and foraging opportunities, but their responses to pulsed resources are poorly understood. In contrast, changes to home ranges during large-game hunting seasons are well documented in mammalian predators. Thus, we hypothesized that increased access to carrion would decrease black vulture space use. To test for changes in space use, we quantified home ranges using data from 12 GPS-tagged black vultures during nonhunting, archery-only, and firearms study periods in Indiana and Kentucky, USA. We compared estimated home range size, home range overlap, density of forest edge, and density of roads within each home range. Home range sizes decreased 52.9% from the nonhunting to archery-only period ($t_{35} = 2.77$, $P = 0.024$), then remained stable (increased 9.98%, $t_{35} = -0.25$, $P = 0.967$) throughout the firearms period. Home range overlaps decreased with greater resource pulse intensities. Estimated forest edge and road densities within home ranges did not change across study periods. Black vultures in our study area changed space use in response to pulsed resources associated with deer hunting. Thus, vultures may shift space use in response to other resource pulses, such as afterbirth and stillbirths from livestock. Pulsed resource locations can serve as targeted survey sites for estimating scavenger abundance and distribution. Integrating resource pulse dynamics into wildlife management strategies can improve efforts to monitor disease risks at aggregation sites and address ecological challenges arising from human activities.

KEYWORDS

carrion, *Coragyps atratus*, deer harvest, home range dynamics, human-wildlife conflict, offal, scavenging, spatial ecology

Understanding animal space use is an essential aspect of investigating a species' ecology and behavior. Home ranges estimate the area traveled by animals in their normal activities, such as foraging, mating, and rearing offspring (Burt 1943). By accessing resources within their established home range, animals avoid risks and energetic costs associated with navigating unfamiliar areas (Burt 1943). Home ranges are dynamic and change as a function of animal age, growth, life history, and temporal span selected for investigation (Fieberg and Borger 2012, Powell and Mitchell 2012). Additionally, multiple authors have demonstrated that home range shifts or changes occur in response to resource pulses (Ruth et al. 2003, Koenig and Liebhold 2005, Thomas et al. 2011, Bisi et al. 2018, Ward et al. 2018).

Resource pulses are localized, large-magnitude increases in the availability of food or other resources that can affect the behavior, movements, and population dynamics of species (Thomas et al. 2011, Maruyama et al. 2013, Eichel et al. 2014, Rogerson et al. 2014). Previous studies have indicated that when animals take advantage of resource pulses, the size and location of their home ranges may change. For instance, wild boars (*Sus scrofa*) constrict their home ranges during high mast years (Bisi et al. 2018), and Alaskan brown bears (*Ursus arctos*) congregate near streams during salmon (*Salmo* spp.) spawning events (Wirsing et al. 2018). Similarly, predators like cougars (*Puma concolor*) and scavengers such as grizzly bears have been observed to shift their home ranges during hunting seasons (Ruth et al. 2003). While much of the literature frames resource pulses as presence or absence, they more commonly occur along an intensity gradient (Yang et al. 2010). A notable example of a resource pulse gradient is demonstrated in large-game hunting seasons, where there is often an archery-only season prior to the regular firearms season, creating a gradual increase in carrion availability. Within the eastern United States (U.S.), carrion from white-tailed deer (*Odocoileus virginianus*) hunting seasons provide a resource pulse that may influence many species' movements, as offal (internal organs of a butchered animal) are more likely to be left near forest edges (Candler et al. 2023). Ward et al. (2018) documented that coyotes (*Canis latrans*) decreased their home range sizes in response to deer hunting seasons. Other species, particularly scavengers, might also shift their home ranges in response to this resource pulse.

Since the 1990s, black vulture (*Coragyps atratus*) populations have experienced considerable growth, resulting in an expansion of their range to include the midwestern and northeastern parts of the United States (Avery 2004, Rushing et al. 2020). Recognized as an obligate scavenger in North America, black vulture population expansion has been accompanied by a rise in the frequency of reports of livestock depredation, as they can occasionally predate weak or newborn livestock (Buckley et al. 2022). Understanding black vulture spatial ecology and movement patterns is necessary to address potential conflicts with agricultural interests (Zimmerman et al. 2019). Currently, knowledge relating to black vulture spatial responses to resource pulses is needed (Kluever et al. 2020, Quinby et al. 2022). Vulture movements are known to be influenced by habitat structure, foraging opportunities, and landscape richness (DeVault et al. 2004, Zimmerman et al. 2019, Kluever et al. 2020).

We hypothesized that increased carrion access would decrease black vulture space use. Furthermore, we predicted that both home range size and overlap for the same individual over time would decrease during white-tailed deer hunting seasons due to the resource pulses provided by offal. We also predicted that black vultures would incorporate a higher density of forest edge and lower density of roads within their home ranges during white-tailed deer hunting seasons due to higher use of offal near forest edges and reduced use of roadkill.

METHODS

Study area

We collected location data from black vultures within the Central Hardwoods region of the U.S. Data collection occurred from 2021 to 2023 during mid- to late-September, October, and November, to correspond with white-tailed deer hunting seasons in Indiana (IN) and Kentucky (KY; Table 1). Within both states, our study area included 6 IN counties and 1 KY county (Figure 1). The study area was dominated by forest (41%) and agricultural land (27%; Dewitz 2021), with other land cover types include grasslands/pasture (15%), developed areas (10%), wetlands (3%), and water (3%).

Data Analysis

We trapped black vultures from October 2020 to June 2023 using walk-in traps baited with a combination of cattle carcasses and roadkill (Humphrey et al. 2000). We attached 40-g solar powered GPS satellite transmitters (GPS/GSM 20–70; Microwave Telemetry Inc., Columbia, MD, USA) to 25 black vultures (12 females and 13 males, all adult or subadult) using Teflon tape backpack harnesses (Humphrey and Avery 2014). All transmitters were less than 2.25% of each bird's body weight. Transmitters recorded latitude-longitude in variable fix intervals, collecting 222 (±239, min = 16, max = 1,599) points per day.

We collected white-tailed deer harvest data from the Indiana Department of Natural Resources and the Kentucky Department of Fish and Wildlife Resources (IDNR 2024, KDFWR 2024). We calculated harvest intensity for each season and year by dividing county-level harvest data by the area of each county. We assigned each bird used in the analysis a harvest intensity based on the primary county of residence.

TABLE 1 Study periods for vulture spatial ecology analysis in Indiana (IN) and Kentucky (KY), USA during 2021–2023.

Year	Study period	Dates
2021	Nonhunting	13–29 Sept
2021	Archery-Only	13–29 Oct
2021	Firearms	13–29 Nov
2022	Nonhunting	12–28 Sept
2022	Archery-Only	12–28 Oct
2022	Firearms	12–28 Nov
2023	Nonhunting	18 Sept–03 Oct
2023	Archery-Only	18 Oct–03 Nov
2023	Firearms	18 Nov–03 Dec

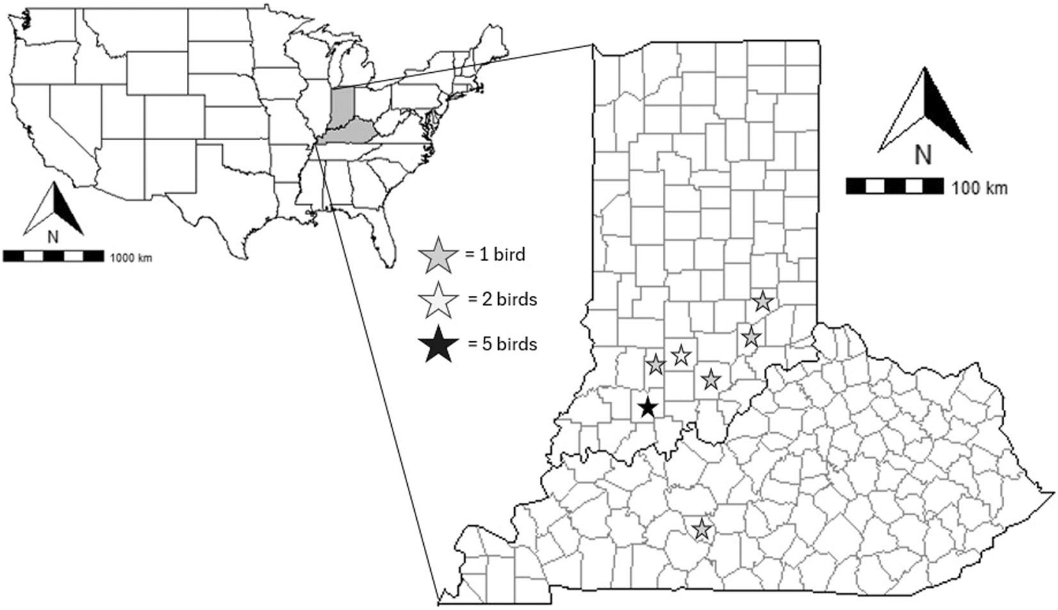

FIGURE 1 A map of space use by GPS-tagged black vultures in Indiana and Kentucky, USA from 2021 to 2023. The location of stars depicts the primary counties in which vultures spent time.

We established 3 study periods for data analysis: nonhunting, archery-only, and firearms (Table 1). All study periods were separated by one month. To define these periods, we first identified the 2-week firearms hunting season for each state, then selected a corresponding 2-week period one month prior, during the archery-only season. Finally, we repeated this process to select a 2-week period outside of hunting season.

For each of the 25 GPS-tracked black vultures, we calculated 3 separate home ranges (one for each study period) using the ctmm package in R (v.4.3.3; Fleming et al. 2023, R Core Team 2023). We used weighted autocorrelated 95% kernel density estimation (wAKDE) to account for correlation in the tracking data and variation in the sampling intervals (Silva et al. 2021). We then created variograms for visual tests of range residency during each study period for each bird. We restricted further analyses to black vultures that were range residents (remained within their home ranges) during all 3 study periods in the same year. This focus on vultures with stable home ranges was necessary to avoid obscuring variation in response to the resource pulse with movement patterns driven by other motivations. Following our initial analyses, we identified 12 black vultures (4 males and 8 females) with stable home ranges. For these individuals, we used the previously calculated home range estimates to determine the percent overlap between home ranges for each study period. We defined home range overlap as the amount of one study period's home range that intersected with another study period's home range for the same individual (Figure 2).

We investigated forest edge and roads as 2 covariates expected to influence black vulture interactions with the landscape. Both forest edge and roads are of interest, as hunters often leave offal at forest edges (Candler et al. 2023). The additional source of carrion could result in less use of roadkill by scavengers. We used ArcGIS (ESRI 2023) to combine all forest data from the national landcover database (NLCD; Dewitz 2021), then calculated forest edge by finding the boundary of all forest pixels within the NLCD raster using the terra and exactextractr packages in R (v. 4.3.3; Baston 2023, R Core Team 2023, Hijmans et al. 2024). We then estimated the density of forest edge within each vulture's home range. We also calculated the density of roads within each bird's home range using all roads from the TIGER/Line database (United States Census Bureau 2023).

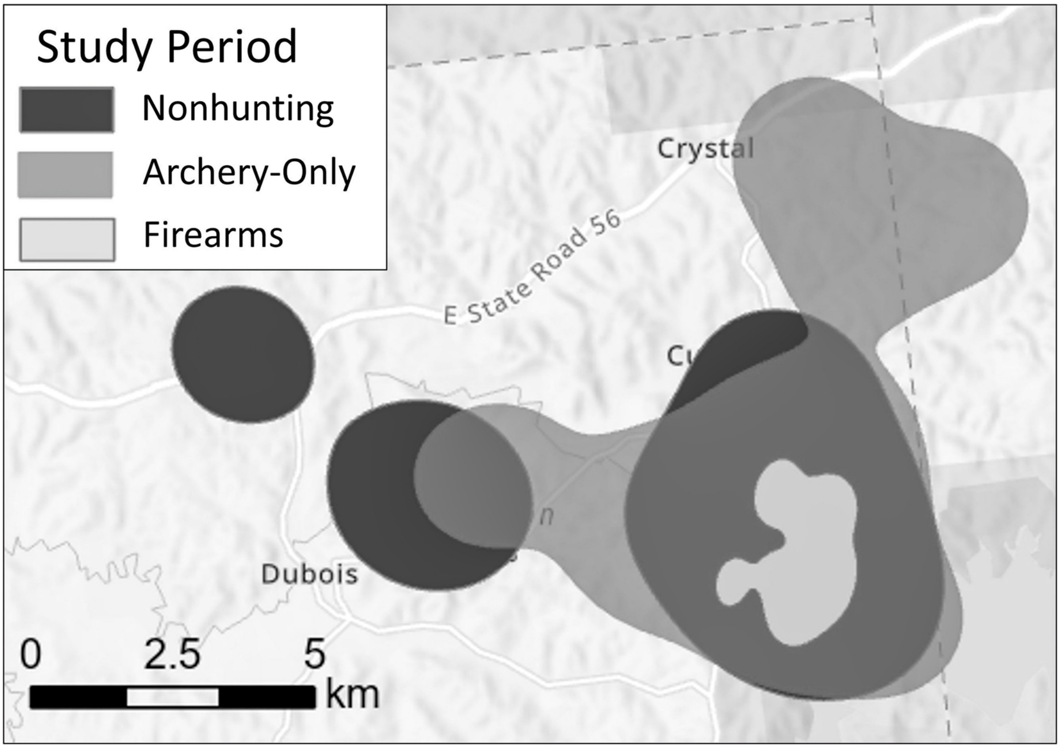

FIGURE 2 An example map indicating one black vulture's home range in nonhunting, archery-only, and firearms deer hunting seasons. In this example, nonhunting and archery-only season overlap 84.1%, nonhunting and firearms season overlap 94.8%, and archery-only and firearms season overlap 98.6%.

For home range comparisons, we used a GLMM with Bird ID as a random effect to account for birds with multiple years of data. We conducted an analysis of variance (ANOVA) to assess differences in response variables between study periods, followed by a Tukey HSD post hoc test to examine pairwise comparisons. We tested the independence, normality, and constant variance assumptions using the Durbin-Watson, Shapiro-Wilk, and Flinger tests, respectively. Study periods were the nonhunting period (mid- to late-Sept.), archery-only period (mid- to late-Oct.), and firearms period (mid- to late-Nov.; Table 1). Response variables included home range size, home range overlap, density of forest edge within a home range, and density of roads within a home range. For the home range size and home range overlap response variables, we conducted multi-factor ANOVAs to determine if there was a significant interaction with harvest intensities before interpreting the individual responses.

RESULTS

Within our study area, an annual average of 1,404.9 ± 378.8 deer were harvested: 345.7 ± 94.2 during archery-only season and 1,059.2 ± 300.1 during firearms season. The average annual harvest intensity was 1.12 ± 0.29 deer/km^2, varying from a low of 0.59 deer/km^2 to a high of 1.65 deer/km^2. The average harvest intensity for archery-only season was 0.33 ± 0.09 deer/km^2, while the average harvest intensity for firearms season was 0.99 ± 0.23 deer/km^2 (IDNR 2024, KDFWR 2024).

We collected 127,401 location points across the 12 birds used in analysis. The average number of observations for nonhunting, archery-only, and firearms periods were 3,735.7 ± 1,558.5, 3,074.2 ± 1,369.4, and 960.6 ± 808.2

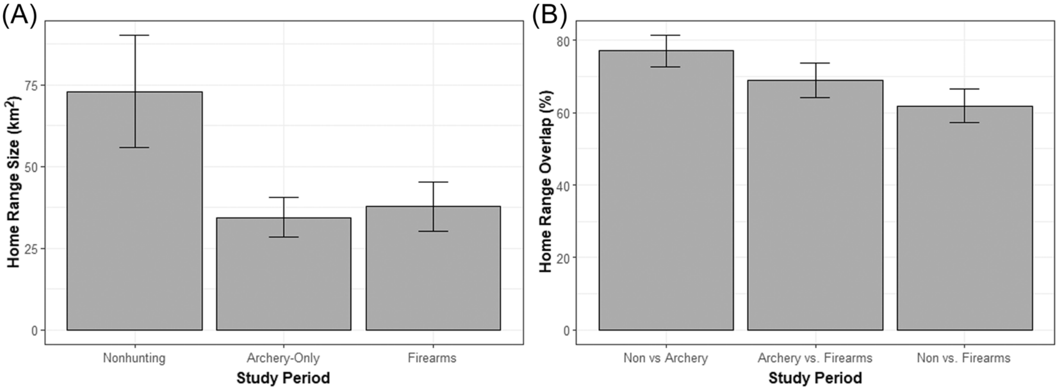

FIGURE 3 Space use by GPS-tagged black vultures in Indiana and Kentucky, USA from 2021 to 2023. Panel A depicts the average home range size between nonhunting, archery-only, and firearms study periods. Panel B depicts pairwise comparisons of home range overlap between study periods. Error bars depict the standard error for each estimate.

points, respectively. Within the nonhunting period home ranges, the land cover consisted of 6.3 ± 11.0% crops, 8.7 ± 6.7% developed land, and 49.6 ± 16.9% forest. Within the archery-only period home ranges, land cover was similar at 6.2 ± 13.4% crops, 9.2 ± 8.6% developed land, and 51.4 ± 13.4% forest. In the firearms period home ranges, there were 6.3 ± 13.4% crops, 10.2 ± 8.7% developed land, and 53.5 ± 15.1% forest cover.

The mean home range size across all periods was 48.35 ± 49.19 km^2 while the mean home range overlap among all periods was 69.40 ± 19.60%. When comparing home range sizes across study periods, we found that nonhunting period home ranges ($\bar{x} = 72.92 \pm 70.90\ \text{km}^2$) were larger than both archery-only ($t_{35} = 2.77$, $P = 0.024$; $\bar{x} = 34.35 \pm 24.91\ \text{km}^2$) and firearms periods ($t_{35} = 2.53$, $P = 0.042$; $\bar{x} = 37.77 \pm 30.77\ \text{km}^2$; Figure 3). The standard deviation for the random effect of Bird ID was 23.79 in the home range size analysis. The home range overlap between hunt periods also differed significantly ($F_{2,35} = 6.89$, $P = 0.003$). The home range overlap between nonhunting and archery-only periods ($\bar{x} = 77.10 \pm 18.40\%$) was larger ($t_{35} = 3.267$, $P = 0.007$) than that between nonhunting and firearms periods ($\bar{x} = 61.90 \pm 19.40\%$). However, no other home range overlaps between periods were significantly different ($t_{35} = 1.93$, $P = 0.145$, $t_{35} = 1.25$, $P = 0.435$; Figure 3). The standard deviation for the random effect of Bird ID was 11 in the home range overlap analysis.

Within each bird's home range, the mean density of forest edge across all periods was 640.49 ± 660.37 km/km^2, while the mean density of roads was 2.27 ± 2.04 km/km^2. Both the density of forest edge ($F_{2,35} = 0.50$, $P = 0.614$) and density of roads ($F_{2,35} = 0.819$, $P = 0.449$) within home ranges remained stable across all periods.

DISCUSSION

We found that changes in black vulture space use aligned with our expectations based on resource pulses, similar to patterns observed in other species. We found less overlap in home ranges, indicating that the intensity of a resource pulse influences the magnitude of response. Previous studies have also detected shifts in home range overlap due to resource pulses (Ruth et al. 2003, Ward et al. 2018, Wirsing et al. 2018). Within our study, home ranges during the nonhunting period overlapped more with archery-only period home ranges than with firearms period home ranges. Our results are incongruent with our home range size results, which indicated that black vulture home range size significantly decreases from the nonhunting to archery-only period, then remains stable throughout the firearms period. These incongruent results could indicate a shift in home range location, rather than a concentration within the same area. Ward et al. (2018) observed habitat shifts and reductions in size in coyote home ranges during white-tailed deer hunting season; black vultures may respond in a similar way. Interestingly, the SD of the random effect associated with Bird ID was twice as large for our analysis of home range size as it was for home range overlap. This observation that variation among individual birds was much greater for changes in home range size across study periods than for home range overlap suggests that studies of space use responses to resource pulses for other wildlife species might benefit from looking for similar patterns.

Contrary to our hypothesis, our results failed to support our prediction of increased use of forest edge density and decreased use of road density within archery-only and firearms period home ranges. Forest edge and road densities within home ranges remained stable among all periods. Overall, this lack of significance could be driven by large amounts of interindividual variation in space use. Alternatively, the amount of time vultures require to consume offal may be so brief that the majority of our locations represent locations collected during roosting, loafing, and soaring activities.

Within our study, the spatial resolution of hunter harvest data available to us was limited to ensure privacy. However, finer scale information on the spatial distribution of carrion could improve the predictive power of models. We had no subset of birds without access to offal, meaning that we had no true control group. Further studies in areas with low hunting pressure could provide comparisons of responses to minimal resource pulses. Additionally, as vultures are the only obligate terrestrial scavengers in North America, facultative scavengers, such as corvids, eagles, or caracaras, might respond differently to hunting based resource pulses (DeVault et al. 2003, Wenting et al. 2022).

As black vulture distributions continue to expand, researchers and land managers need to understand their spatial ecology and minimize potential livestock depredation (Zimmerman et al. 2019). Our study demonstrates that black vultures shift space use at a time that is associated with increased carrion, which could change when and where people are encountering them. Generally, studies considering human-wildlife conflict with vultures consider their behavior and competition, rather than their space use (Blackwell et al. 2007, Avery et al. 2011, Hill et al. 2021). However, understanding black vulture space use can assist with mitigating human-wildlife conflict. As black vultures shift their space use in response to livestock afterbirth and stillbirths, producers may be able counteract this by aligning birthing seasons with carrion resource pulses and reducing attraction to vulnerable livestock (Quinby et al. 2022).

MANAGEMENT IMPLICATIONS

Understanding black vulture space use at a time associated with resource pulses from white-tailed deer hunting season may help to reduce human-wildlife conflict. Ensuring proper disposal of offal can minimize unintentional congregation of vultures near human infrastructure or livestock production areas. Furthermore, as a similar resource pulse occurs during times of synchronous livestock birthing, livestock producers can use this knowledge to predict or reduce potential interactions with black vultures. As disposal of livestock afterbirth is often not feasible, livestock producers can anticipate the need to implement mitigation measures during birthing seasons to reduce the likelihood of livestock predation. Additionally, understanding scavenger response to carrion availability may be useful in the event of wildlife disease outbreaks where scavengers could serve as disease vectors.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHIC STATEMENT

All animal handling and sampling procedures were approved by the Purdue Animal Care and Use Committee (protocol 2004002035) as well as a scientific purposes license from the state of Indiana. The capture, handling and tagging of the birds used in this study were consistent with the recommendations of The Ornithological Council (Fair et al. 2023).

DATA AVAILABILITY STATEMENT

All black vulture location data used in this paper are available in the MoveBank data archive. All data are available in Movebank (Wikelski et al. 2023); please contact author with questions.

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