Biomass of mammal carrion available to Turkey Vultures (*Cathartes aura*) and Black Vultures (*Coragyps atratus*) along a commuter railway in New York, USA.

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Abstract

With 227,000 km of railways in the United States, wildlife-train collisions are more common than generally recognized and could be an important carrion source for Black Vultures (*Coragyps atratus*) and Turkey Vultures (*Cathartes aura*). We conducted a five-year study (2018-2022) in Dutchess and Putnam Counties, New York, USA to 1) estimate the biomass of mammal carrion available to vultures along 32.6 km of commuter railway, and 2) determine if vultures utilize train-killed wildlife as a food resource. During our study we recorded 154 individual mammals of 12 species killed by commuter trains. The number of train-killed mammals averaged 30.8/yr (SD ±13.1 mammals/yr), but varied widely, ranging from 13 to 45 individuals/yr. White-tailed Deer (*Odocoileus virginianus*) contributed the most to this total, followed by Raccoon (*Procyon lotor*), Virginia Opossum (*Didelphis virginiana*), and Coyote (*Canis latrans*). We estimated that 6722.0 kg of mammal carrion resulted from train-wildlife collisions during our five-year study, and of this total, 4778.3 kg were potentially available for consumption by vultures. We estimated that 29.3 kg of mammal carrion per km of railway was available for consumption by vultures each year. During our five-year study, we found evidence that vultures fed on >90% of the train-killed mammal carcasses. Our results suggest the commuter railway is attractive to foraging vultures because 1) carrion occurs at high concentrations relative to the adjacent "natural habitat", 2) the massive traumatic injuries associated with train-wildlife collisions facilitate utilization of carrion, and 3) disturbance is minimal owing to the infrequent passage of trains (ca. 1 train/hr). Given that train-killed birds, frogs, snakes, and turtles were not included in our analysis, the total biomass of carrion available to foraging vultures along the commuter railway may be considerably greater than we estimated in this study.

Introduction

North American Cathartid vultures (Turkey Vulture *Cathartes aura* and Black Vulture *Coragyps atratus*) are near-obligate scavengers that opportunistically feed on a wide variety of carrion (Buckley 2020, Kirk & Mossman 2020). Although Black Vultures and Turkey Vultures are known to consume birds, reptiles, amphibians, fish, invertebrates (including insects and crustaceans), and even fruit and vegetation, mammal carrion comprises the bulk of the diet for both species (Yahner *et al.* 1986, Hiraldo *et al.* 1991, Buckley 2020, Kirk & Mossman 2020, Hill *et al.* 2022). Important sources of mammal carrion include livestock and wild ungulate carcasses, offal from slaughtering operations, stranded marine mammals, and road-killed wildlife (Bent 1937, Jennelle *et al.* 2009, Platt *et al.* 2016, Gunderson 2018). Wildlife-vehicle collisions are an especially important source of mammal carrion for vultures (Thiel 1976, Lambertucci *et al.* 2009, Platt *et al.* 2016, Hill *et al.* 2018, Smith 2020, Hill *et al.* 2022), and the widespread availability of road-killed wildlife may be one of the drivers underlying the on-going range expansion of Turkey Vultures and Black Vultures in North America (Bull 1974, Raebenold 1989).

In contrast to what is known about road ecology and wildlife-vehicle collisions (e.g., Forman *et al.* 2003), studies of wildlife mortality along railways are comparatively few (Heske 2015, Popp & Boyle 2017, Santos *et al.* 2017). However, scattered reports suggest that mammals, especially large ungulates, are at high risk of being struck and killed by trains (van der Grift 1999, Andreassen *et al.* 2005, Santos *et al.* 2017, Backs *et al.* 2022). With 227,000 km of railways in the United States (Heske 2015), wildlife-train collisions are likely more common than generally recognized and potentially constitute an important carrion source for Black Vultures and Turkey Vultures. We here report the results of a multi-year investigation into the availability of mammal carrion along a commuter railway in New York, USA. Our objectives were twofold: 1) estimate the biomass of mammal carrion potentially available to foraging vultures (*C. aura* and *C. atratus*) along the railway, and 2) determine if vultures utilize train-killed wildlife as a food resource.

Methods

Our investigation of mammal carrion availability was conducted concurrently with on-going studies of turtle mortality and nesting (Platt *et al.* 2021, 2022, unpubl. data) along the Metro-North Railway in Putnam and Dutchess Counties, New York, USA. The Metro-North Railway links the New York City metropolitan area with the suburban and rural counties to the north. Our study area includes 32.6 km of the railway from Southeast Station (south) to Dover Plains (north) (Figure 1). Habitat along the Metro-North Railway within our study area consists of a mosaic of deciduous woodland and pastures with scattered houses and farmsteads. Approximately 20 km of the railway that we monitored traverses the Great Swamp on a north-south axis. The Great Swamp encompasses 30,000 ha of upland and swamp forest, open marsh, and fens and as such, constitutes the largest freshwater wetland in New York (Siemann 1999, Holt *et al.* 2006).

One commuter train per hour passes along the railway from Southeast Station to Dover Plains except during peak traffic hours (0600-0900 h and 1600-2000 h) when two trains (sometimes more) pass every hour. However, from 13 April 2020 to 31 August 2021, weekday (Monday through Friday) train service was curtailed, with one train passing every two hours and no trains operating on the weekend. This reduction in rail traffic was in response to dramatically reduced ridership during the COVID-19 pandemic. Regular train service was restored on 1 September 2021. Commuter trains typically consist of one or two diesel-powered locomotives towing 5–10 passenger cars. The maximum speed of commuter trains is approximately 115 km/hr. The Metro-North Railway roughly parallels New York State Highway 22; the distance between the road and railroad varies from <100 m to ca. 2.5 km. Black Vultures and Turkey Vultures are considered “Breeding Summer Residents” (8 March to 15 November) and “Breeding Permanent Residents”, respectively, in southeastern New York (DeOrsey & Butler 2006).

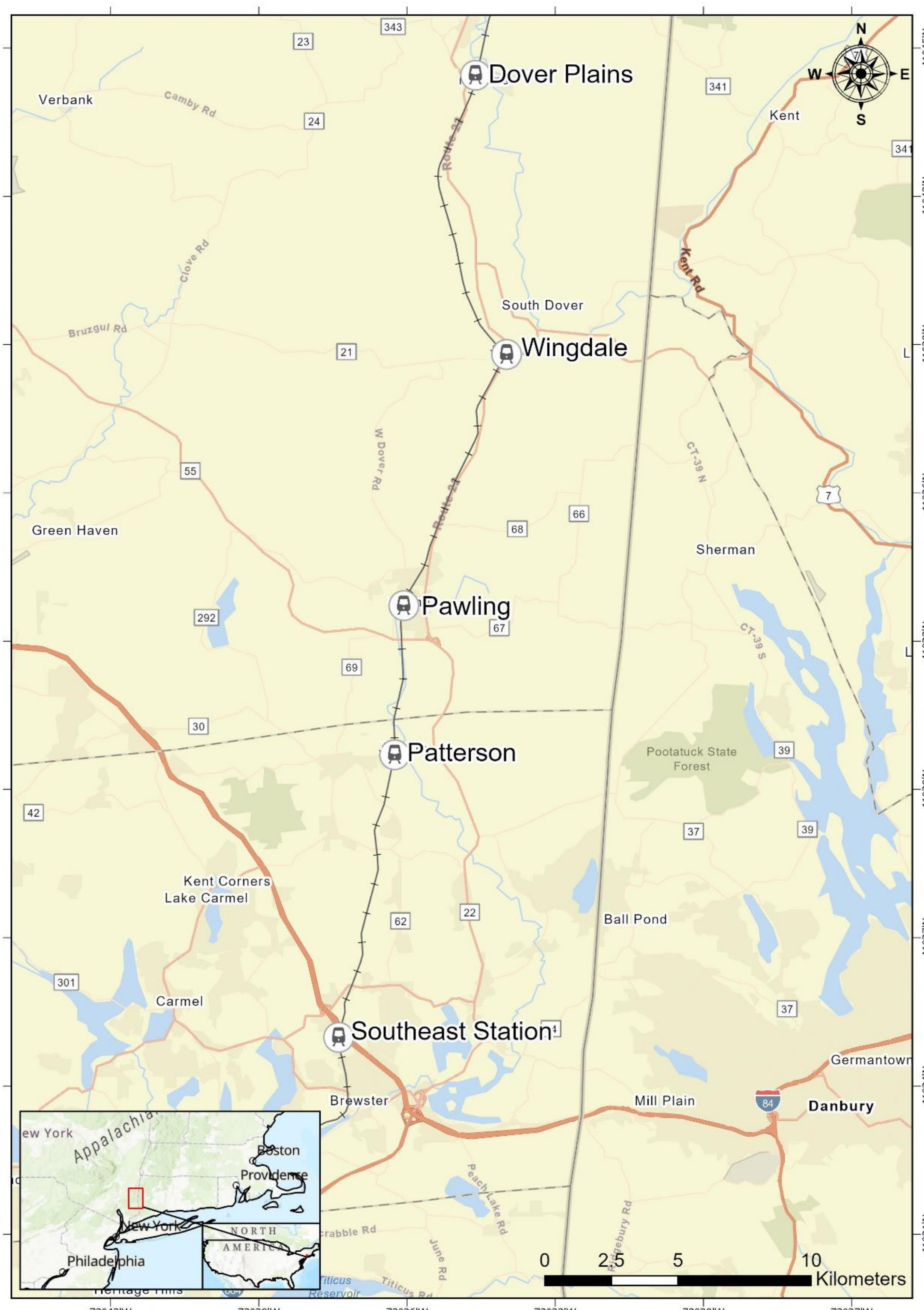

Figure 1: The study was conducted along 32.6 km of the Metro-North Commuter Railway between Southeast Station (south) and Dover Plains (north) in New York, USA. Inset shows location of the study area within New York.

We initiated this study in August 2017 by first clearing mammal remains from the railway between Southeast Station and Dover Plains while searching for turtle nesting sites (Platt *et al.* 2022). In subsequent years (2018–2022), we searched for carcasses and other remains of train-killed wildlife from late July through mid-September (Table 1). We required four days each year to survey the railway between Southeast Station and Dover Plains. Owing to the distance involved, we surveyed the railway in four segments: Southeast Station to Patterson (10.8 km), Patterson to Pawling (5.3 km), Pawling to Wingdale (8.3 km), and Wingdale to Dover Plains (8.2 km). We excluded short segments (ca. 1 km) of the railway within the town limits of Patterson (Putnam County) and Pawling (Dutchess County) from our study for safety reasons.

During our surveys, a single observer (SGP) walked slowly along the tracks and recorded all vertebrate remains found on the railroad tracks or the adjacent ballast. Following Heske (2015), we assumed that vertebrate remains found on the railroad tracks or adjacent ballast resulted from train-wildlife collisions. To avoid potentially double-counting during future surveys, we removed (>10 m from tracks) wildlife remains from the railroad tracks after carefully examining them. When wildlife remains were fresh, evidence of vulture feeding was obvious (Platt *et al.* 2016). For older remains, we forensically determined if vultures had utilized carcasses by noting the presence of dried bits of twisted tissue adhering to bones, scratch marks on bones, inverted skin on smaller mammals, and vulture scats and feathers at the kill site (Figure 2A-F; Reeves 2009, Platt *et al.* 2016).

To quantify the amount of mammal carrion potentially available to foraging vultures, we first estimated carcass biomass for each species using publicly available data on body mass from the New York Department of Environmental Conservation (www.dec.ny.gov/animals). For those species not listed in the New York Department of Environmental Conservation database, we used body mass values from Nowak (1999). In most cases we used mean values for body mass; however, when only a range of values was given (or mean values were presented separately for males and females), we followed Platt *et al.* (2016) and calculated body mass based on the mid-point of these values.

We next estimated the total carcass biomass for each species of mammal found along the railway during our five-year study. For larger species (*Ursus americanus*, *Canis latrans*, *Lynx rufus*, *Odocoileus virginianus*, and *Castor canadensis*) this calculation was straightforward; we multiplied the number of carcasses of a particular species by the estimated individual body mass of that species and summed these values. However, preliminary observations we made in New York suggested that carcasses of smaller mammals persisted for ≤6 months (Platt & Rainwater, unpubl. data). Therefore, we first multiplied the total number of carcasses of smaller species (*Urocyon cinereoargenteus*, *Vulpes fulva*, *Procyon lotor*, *Mephitis mephitis*, *Ondatra zibethicus*, *Sciurus carolinensis*, *Didelphis virginiana*) by two, assuming that 1) our annual sample only represented a six-month period, and 2) species-specific kill rates remain constant throughout the year. We next multiplied the adjusted total number of carcasses by the appropriate biomass value and summed these values.

Our observations from on-going feeding trials (August–September during 2020–2022) at a "Vulture Cafeteria" (Dover Plains), where road-killed wildlife carcasses are weighed, deployed, and then reweighed after being consumed by vultures, suggest Black Vultures and Turkey Vultures are able to utilize approximately 80% (range = 66 to 94%) of the biomass of small mammal carcasses (N = 19; *Procyon lotor*, *Urocyon cinereoargenteus*, *Sciurus carolinensis*, *Sylvilagus floridanus*, *Didelphis virginiana*). Because skeletal mass is proportionally greater in larger mammals (Bonner 2011), we estimated that 70% of the carcass biomass from these species (*Ursus americanus*, *Odocoileus virginianus*, *Canis latrans*, *Lynx rufus*, *Castor canadensis*) is available for consumption by vultures. Therefore, to estimate the biomass of each carcass available and likely to be consumed by vultures, we multiplied the total body mass of small mammal and large mammal carcasses by 0.80 and 0.70, respectively. Lastly, we summed the values for each species to estimate the total biomass of mammal carrion potentially available to foraging vultures during the five-year study period.

Results

During our five-year study (2018-2022) we found the remains of 154 individual mammals of 12 species killed by trains along 32.6 km of the Metro-North Railroad (Table 2). The number of train-killed mammals found each year averaged 30.8 (0.94 mammals/km of railway) but varied widely among years (SD = ±13.1), ranging from a low of 13 to a high of 45 (Table 2). The lowest number of train-killed mammals was recorded during our survey in August-September 2021 (Table 1), a period coinciding with reduced commuter rail traffic during the COVID-19 pandemic (April 2020 through August 2021). White-tailed Deer contributed the most numerically and proportionally to this total, followed by Raccoon, Virginia Opossum, and Coyote; other species were recorded 10 or fewer times (Table 2). After adjusting for the truncated persistence times of small carcasses, we estimated that 6722.0 kg of mammal carrion resulted from train-wildlife collisions during our five-year study, and of this total, 4778.3 kg were potentially available for consumption by vultures (Table 3). White-tailed Deer contributed 76.3% of the carrion biomass available to foraging vultures. Taking into account the linear distance of our study area (32.6 km), we estimate that 29.3 kg of mammal carrion per km of railway was available for consumption by vultures each year during our five-year study. Fresh carcasses of train-killed wildlife typically exhibited extensive traumatic injuries (e.g., multiple broken bones, decapitation, internal hemorrhaging, and ruptured abdominal and thoracic cavities) that facilitated feeding by vultures (Figures 3A-D). We found evidence of vulture feeding on >90% of mammal remains examined during this study. We observed vultures feeding on carcasses of train-killed wildlife or soaring directly overhead on at least 20 occasions during our annual surveys; only Turkey Vultures were observed on 18 (90.0%) occasions (Figure 4A-B), while Black Vultures were observed together with Turkey Vultures on two (10.0%) occasions in 2019 (Figure 4C-D).

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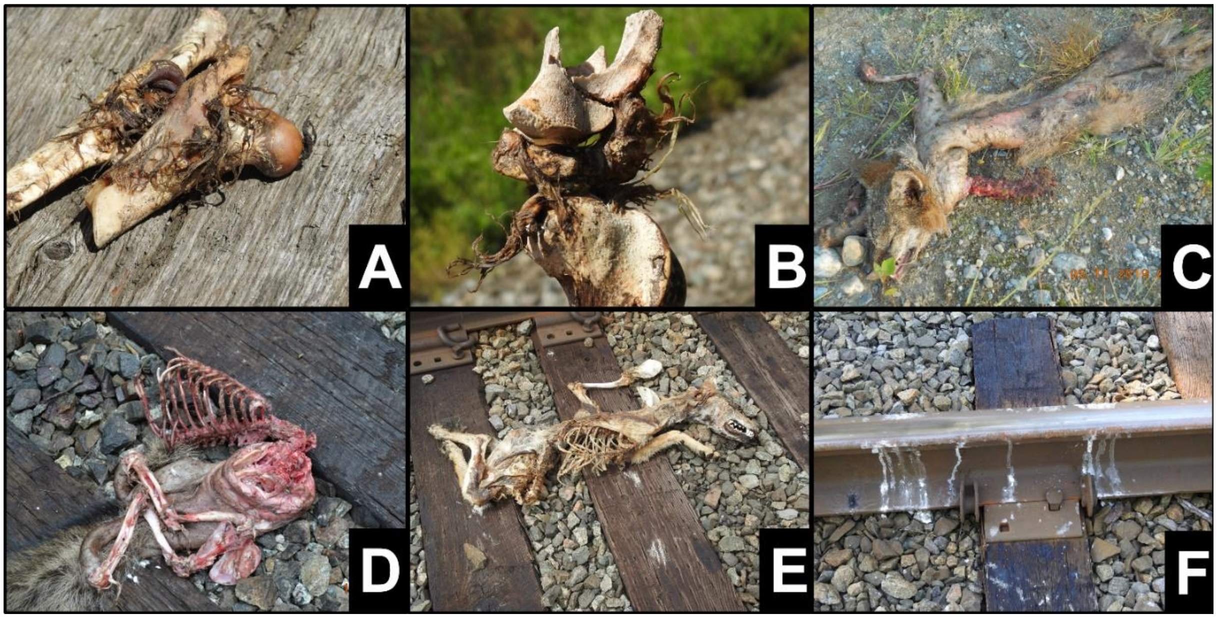

Figure 2: Evidence of vulture feeding. Twisted bits of dried tissue adhering to the femur of a recently killed White-tailed Deer (A). These characteristic pieces of dried tissue also persist on older, weathered bones of train-killed wildlife (B). Inverted skin on carcasses of train-killed Gray Fox (C) and Raccoon (D). Older carcasses desiccate and mummify, but vulture feeding sign remains visible as on this Coyote (E). Vulture "whitewash" (scat) present on rails adjacent to a White-tailed Deer carcass (F).

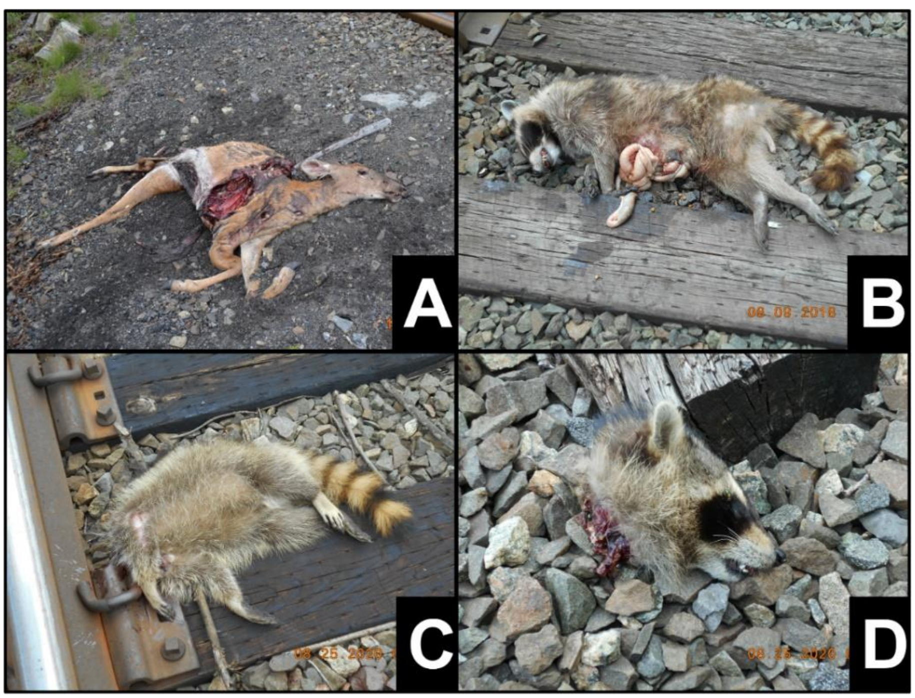

Figure 3: White-tailed Deer were the most frequently found train-killed mammal along a commuter railway in New York and contributed the majority of carrion biomass available to foraging vultures (A). Injuries obvious on this carcass include numerous broken bones and ruptured thoracic cavity. Other examples of traumatic injuries frequently observed in train-killed wildlife include ruptured abdominal cavity (B) and decapitation (C-D) as seen in these Raccoon carcasses. These traumatic injuries facilitate access to the interior of carcasses and increase the efficiency of carrion use by feeding vultures.

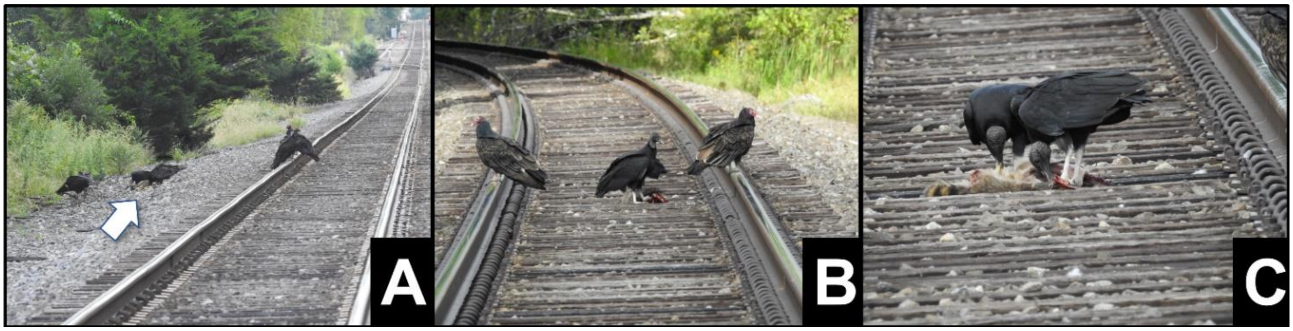

Figure 4: Turkey Vultures feeding on the carcass of a train-killed White-tailed Deer; white arrow denotes approximate location of deer carcass on ballast adjacent to railroad tracks (A). Two Black Vultures feeding together with two Turkey Vultures on the carcass of a train-killed Raccoon (B). Additional Turkey Vultures are present, but not visible in photograph. Close-up of Black Vultures feeding on the Raccoon carcass (C).

Table 1: Dates of surveys conducted for train-killed mammals along four segments of the Metro-North Commuter Railway between Southeast Station and Dover Plains (32.6 km) in Putnam and Dutchess counties, New York, USA (2018–2022). Railway segments: 1 = Southeast Station to Patterson (10.8 km); 2 = Patterson to Pawling (5.3 km); 3 = Pawling to Wingdale (8.3 km); 4 = Wingdale to Dover Plains (8.2 km).

Year	**Railway Segment**			
	1	2	3	4
2018	30 August	23 August	5 August	29 July
2019	13 September	15 September	27 August	26 August
2020	24 August	22 August	20 August	18 August
2021	7 September	8 September	25 August	24 August
2022	7 September	31 August	21 August	25 August

Table 2: Train-killed mammals found along 32.6 km of a commuter railway line in Putnam and Dutchess counties, New York, USA (2018–2022).

Species (Common and scientific name)	**2018**	**2019**	**2020**	**2021**	**2022**	**Total (%)**
Black Bear (*Ursus americanus*)	1	0	1	0	1	3 (1.9)
Coyote (*Canis latrans*)	2	2	2	3	6	15 (9.7)
Gray Fox (*Urocyon cinereoargenteus*)	0	1	1	0	0	2 (1.3)
Red Fox (*Vulpes fulva*)	0	0	0	0	1	1 (0.6)
Bobcat (*Lynx rufus*)	0	0	0	0	1	1 (0.6)
Raccoon (*Procyon lotor*)	3	13	5	4	6	31 (20.1)
Striped Skunk (*Mephitis mephitis*)	1	0	0	0	0	1 (0.6)
White-tailed Deer (*Odocoileus virginianus*)	10	19	8	3	14	54 (35.0)
North American Beaver (*Castor canadensis*)	4	3	1	2	0	10 (6.4)
Muskrat (*Ondatra zibethicus*)	1	1	1	0	0	3 (1.9)
Eastern Gray Squirrel (*Sciurus carolinensis*)	2	0	1	0	1	4 (2.5)
Virginia Opossum (*Didelphis virginiana*)	6	6	4	1	12	29 (18.8)
Total train-killed mammals	**30**	**45**	**24**	**13**	**42**	**154**

Table 3: Estimated biomass of train-killed wildlife available to foraging vultures along a commuter railway in Putnam and Dutchess counties, New York (2018–2022). Scientific names provided in Table 1. We estimated the total number of smaller mammal carcasses (species denoted with asterisk) by multiplying the number of carcasses found during surveys by 2.0 (see text). Biomass for each species was estimated by multiplying the total number of carcasses by body mass. The biomass available to foraging vultures was calculated by multiplying the biomass values for smaller (denoted by asterisk) and larger species by 0.80 and 0.70, respectively (see text).

Species (Common name)	Body mass (kg)	Total carcasses	Biomass (kg)	Biomass available to vultures (kg)
Black Bear	107.0	3	321.0	224.7
Coyote	17.0	15	255.0	178.5
Gray Fox*	5.3	4	21.2	16.9
Red Fox*	5.2	2	10.4	8.3
Bobcat	8.0	1	8.0	6.4
Raccoon*	6.8	62	421.6	337.2
Striped Skunk*	4.0	2	8.0	6.4
White-tailed Deer	96.5	54	5211.0	3647.7
North American Beaver	20.4	10	204.0	142.8
Muskrat*	1.4	6	8.4	6.7
Eastern Gray Squirrel*	0.5	8	4.0	3.2
Virginia Opossum*	4.3	58	249.4	199.5
Total			**6722.0**	**4778.3**

Discussion

Our study found that 1) significant mammal carrion biomass is made available to vultures each year as the result of wildlife-train collisions along the Metro-North commuter railway in New York, USA and 2) vultures (primarily Turkey Vultures) utilize this carrion as a food resource. Although several previous reports quantified mammal mortality along railways (Ito *et al.* 2008, Kušta *et al.* 2011, Heske 2015), our study appears to be the first to estimate the biomass of carrion made available to vultures (and other scavengers) from train-wildlife collisions. Caution is in order however, because our estimate of carrion availability is based in part on survey data collected during the COVID-19 pandemic when decreased rail traffic appeared to result in a concomitant decline in train-killed wildlife. Thus, the biomass of train-killed mammals more typically available to foraging vultures may be somewhat higher than we estimate. In captivity, Turkey Vultures require 140-200g of food per day for maintenance (Hatch 1970, Prather *et al.* 1976). Assuming the energetic requirements of wild vultures are at the upper end of this range, the biomass of carrion that we estimate is available per km of railway each year (29300 g), could theoretically sustain an individual Turkey Vulture for approximately 146 days.

Our results suggest that White-tailed Deer are the most important carrion source for vultures along the Metro-North Railway. White-tailed Deer are common to abundant in our study area and moreover, like other ungulates, exhibit certain behaviors that contribute to the likelihood of a fatal collision with trains (Santos *et al.* 2017). For example, ungulates frequently intercept and travel along railroads, especially when the adjacent terrain is densely vegetated, flooded, or covered in deep snow (Child 1983, Santos *et al.* 2017). This appears to be the case in the Great Swamp where our observations suggest White-tailed Deer avoid thickly vegetated wetlands by traveling on the railway (SGP, pers. obs.). A typical mortality event occurs when an ungulate attempts to outrun an approaching train rather than leave the railway (Child 1983; Santos *et al.* 2017). Furthermore, trains running at night, early morning, late evening, and during a full moon are more likely to kill ungulates than at other times (Gundersen & Andreassen 1998). For these reasons, ungulates are among the mammals most frequently involved in fatal train-wildlife collisions (Kušta *et al.* 2011, Santos *et al.* 2017).

Our estimate of ≤ 6 months seems a reasonable approximation of the persistence time for smaller mammal carcasses on the Metro-North Railroad. That said, studies of road-killed wildlife suggest that persistence times of small mammal and carnivore carcasses on roads are relatively brief, often less than two weeks (Santos *et al.* 2011). Road-killed wildlife are usually crushed and dismembered by passing traffic or removed by scavengers, and therefore likely to escape detection unless monitoring is conducted at frequent intervals (Slater 2002, Antsworth *et al.* 2005, Santos *et al.* 2011). Unfortunately, there are no studies comparing persistence times of road-killed and train-killed wildlife (Santos *et al.* 2017). However, our observations suggest different taphonomic processes occur on railroads where after the initial fatal collision, wildlife carcasses are deposited between the rails or on the adjacent ballast and not subject to further damage by passing trains. Typically, carcasses are rapidly detected and consumed by vultures, the remains are then cleaned by necrophagous insects and thereafter rapidly desiccate and mummify, resulting in considerably longer persistence times than is generally the case with wildlife killed on roads. Nonetheless, we readily acknowledge that scavengers other than vultures (e.g., Jennelle *et al.* 2009, Platt *et al.* 2010) probably remove a few carcasses and others are lost to weathering. In the event that our estimates of the persistence times of smaller mammal carcasses are inflated, the biomass of train-killed wildlife available to vultures would be even greater than we predicted.

There are several reasons why the Metro-North Railway (and probably other railways) appears to be an attractive and important foraging habitat for vultures. First, similar to roads, scavenging is presumably more profitable along the railroad because wildlife mortality occurs at greater rates than the adjacent "natural habitat" leading to the concentration of a highly ephemeral food resource (carrion) that can be readily detected and exploited by foraging vultures (Antsworth *et al.* 2005, Lambertucci *et al.* 2009). Second, because Black and Turkey Vultures are incapable of penetrating the skin of most mammals when feeding (Wallace & Temple 1987, Houston 1988, Platt *et al.* 2016), the massive traumatic injures associated with wildlife-train collisions allow vultures ready access to the interior of carcasses, thereby facilitating utilization of the available carrion. Third, because trains pass infrequently (ca. one train/hour), vultures may prefer to feed along the railway owing to minimal levels of disturbance. The location of a carcass in relation to human disturbance is an important determinant of scavenging, with vultures preferring less disturbed feeding sites (Lambertucci *et al.* 2009). Anecdotally at least, this seems to be the case in our area; over the same five-year study period we made only a single observation of Turkey Vultures scavenging on nearby State Highway 22 despite an abundance of road-killed wildlife. Moreover, none of the wildlife carcasses we collected from the highway exhibited evidence of vulture feeding. We speculate the high traffic volume deters vultures from scavenging on the highway, especially when an alternate supply of carrion is readily available on the railway a short distance away.

While mammal carrion undoubtedly comprises the most significant component of vulture diets in our area, train-killed birds, amphibians (frogs), snakes, and turtles were also recorded during our study and much of this carrion is consumed by foraging vultures. Indeed, exclusive of Turkey Vultures, we recorded the remains of 18 species of birds (raptors, waterfowl, wading birds, gallinaceous birds, corvids, and passerines), including larger species (e.g., Wild Turkey *Meleagris gallopavo*, Great Blue Heron *Ardea herodias*, Canada Goose *Branta canadensis*) that displayed evidence of vulture feeding. Additionally, we recorded four species of anurans, at least two species of snakes (most snake remains consisted of disarticulated vertebrae that could not be identified), and four species of turtles killed by trains (SGP & TRR, unpubl. data). We observed vultures feeding on fresh snakes and most turtle remains (particularly shells of Common Snapping Turtles *Chelydra serpentina*) exhibited evidence of vulture feeding. However, we limited the focus of our study to mammals because amphibian, reptile (excepting large turtles; see Dodd 1995), and bird carcasses generally persist < 7days (Peterson *et al.* 2001, Slater 2002, Antsworth *et al.* 2005, Santos *et al.* 2011). Collectively these additional observations suggest considerably more carrion is available to foraging vultures along the Metro-North Railway than estimated by our study.

The abundance of carrion resulting from wildlife-train collisions along the Metro-North Railroad clearly provides attractive foraging opportunities for vultures. However, scavenging along the railroad also involves a certain degree of risk (DeVault *et al.* 2014), and vultures are occasionally killed by passing trains (SGP & TRR, unpubl. data) with as yet undetermined population-level impacts. Therefore, decreasing the availability of train-killed wildlife is an obvious first step in reducing the likelihood of vulture mortality. Because our study found that White-tail Deer are the single largest source of carrion available to vultures along the Metro-North Railway, mitigation efforts would be well-served to focus on this common ungulate. The spatial distribution of wildlife-train collisions is not random (Gunson *et al.* 2011) and "risk zones" or "hotspots" where deer-train collisions occur most frequently should first be identified (Danks & Porter 2010, Eberhardt *et al.* 2013). Strategically placed fencing is the most consistently effective method to reduce or prevent ungulate access to roads (Glista *et al.* 2009, Backs *et al.* 2022), and would presumably be useful in mitigating the risk of deer-train collisions along the Metro-North Railway. Likewise, clearing or modifying vegetation along roadways has proven effective in reducing the attractiveness of these habitats to deer (Meisinget *et al.* 2014) and should be investigated as a potential mitigation measure along the Metro-North Railway. Lastly, while we recognize that removing every carcass of train-killed wildlife from the Metro-North Railway is impractical, whenever possible work crews should collect and dispose of carrion (especially large mammal carcasses) during routine railroad maintenance operations.

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References

Andreassen, H.P., Gunderson, H. & Soraas, T. 2005. The effect of scent-marking, forest clearing, and supplemental feeding on moose-train collisions. *Journal of Wildlife Management* 69: 1125–1132.

Antsworth, R.L., Pike, D.A. & Stevens, E.E. 2005. Hit and run: Effects of scavenging on estimates of roadkilled vertebrates. *Southeastern Naturalist* 4: 647–656.

Backs, J.A.J., Nychka, J.A., & St. Clair, C.C. 2022. Low audibility of trains may contribute to increased collisions with wildlife. *Transportation Research Interdisciplinary Perspectives* 13: 100516.

Bent, A.C. 1937. *Life histories of North American birds of prey*. *Order Falconiformes*. *Part 1*. United States Government Printing Office, Washington, D.C.

Bonner, J.T. 2011. *Why size matters: From bacteria to blue whales*. Princeton University Press, Princeton.

Buckley, N.J. 2020. Black Vulture (*Coragyps atratus*). Version 1.0. In: Poole, A.F. & Gill, F.B. (Eds.). *Birds of the World*. Cornell Lab of Ornithology, Ithaca.

Bull, J. 1974. *Birds of New York State*. Doubleday Publishers, Garden City.

Child, K. 1983. Railways and Moose in the central interior of BC: A recurrent management problem. *Alces* 19: 118–135.

Danks, Z.D., & Porter, W.F. 2010. Temporal, spatial, and landscape habitat characteristics of moose-vehicle collisions in Western Maine. *Journal of Wildlife Management* 74: 1229–1241.

DeOrsey, S. & Butler, B.A. 2006. *The Birds of Dutchess County*, *New York*. Grinnell and Lawton Publishing, Millbrook, New York.

DeVault, T.L., Blackwell, B.F., Seamans, T.W., Lima, S.L. & Fernández-Juric, E. 2014. Effects of vehicle speed on flight initiation by Turkey Vultures: Implications for bird-vehicle collisions. *PLoS ONE* 9:e87944.

Dodd, C.K., Jr. 1995. Disarticulation of turtle shells in north-central Florida: How long does a shell remain in the woods? *American Midland Naturalist* 134: 378–387.

Eberhardt, E., Mitchell, S., & Farhig, L. 2013. Road kill hotspots do not effectively indicate mitigation locations when past road kill has depressed populations. *Journal of Wildlife Management* 77: 1353–1359.

Forman, R.T.T., Sperling, D., Bisonette, J.A., Clevenger, A.P., Cutshall, C.D., Dale, V.H., Fahrig, L., France, R., Goldman, C.R., Heanue, K., Jones, J.A., Swanson, F.J., Turrentine, T. & Winters, T.C. 2003. *Road ecology: Science and solutions*. Island Press, Washington, D.C.

Glista, D.J., DeVault, T.L., & DeWoody, J.A. 2009. A review of mitigation measures for reducing wildlife mortality on roadways. *Landscape and Urban Planning* 91: 1–7.

Gundersen, H. & Andreassen, H.P. 1998. The risk of moose *Alces alces* collision: a predictive model for Moose-train collisions. *Wildlife Biology* 4: 103–110.

Gunderson, K. 2018. Turkey Vultures *Cathartes aura* scavenging on floating marine mammal carcass in Big Sur, California. *Vulture News* 75: 36–38.

Gunson, K.E., Mountrakis, G., & Quackenbush, L.J. 2011. Spatial wildlife-vehicle models: a review of current work and its application to transportation mitigation projects. *Journal of Environmental Management* 92: 1074–1082.

Hatch, D.E. 1970. Energy conserving and heat dissipating mechanisms of Turkey Vultures. *Auk* 87: 111–124.

Heske, E.J. 2015. Blood on the tracks: Track mortality and scavenging rate in urban nature preserves. *Urban Naturalist* 4: 1–13.

Hill, J.E., DeVault, T.L., Beasley, J.C, Rhodes, O.E., Jr., & Belant, J.L. 2018. Roads do not increase carrion use by a vertebrate scavenging community. *Scientific Reports* 8: 16331.

Hill, J.E., Holland, A.E., Brohl, L.K., Kluever, B.M., Pfeiffer, M.B., DeVault, T.L. & Belant, J.L. 2022. Diets of Black Vultures and Turkey Vultures in coastal South Carolina, USA with a review of species' dietary information. *Southeastern Naturalist* 21 :11–27.

Hiraldo, F., Delibes, M. & Donazar, J.A. 1991. Comparison of diets of Turkey Vultures in three regions of northern Mexico. *Journal of Field Ornithology* 62: 319–324.

Holt, T.V., Murphy, D.M. & Chapman, L. 2006. Local and landscape predictors of fish-assemblage characteristics in the Great Swamp, New York. *Northeastern Naturalist* 13: 353–374.

Houston, D.C. 1988. Competition for food in Neotropical vultures in tropical forest. *Ibis* 130:402–417.

Ito, T.Y., Okada, A., Buuveibaatar, A., Lhagvasuren, B., Takatsuki, S. & Tsunekawa, A. 2008. One-sided barrier impact of an international railroad on Mongolian Gazelles. *Journal of Wildlife Management* 72: 940–943.

Jennelle, C.S., Samuel, M.D., Nolden, C.A. & Berkley, E.A. 2009. Deer carcass decomposition and potential scavenger exposure to chronic wasting disease. *Journal of Wildlife Management* 73: 655–662.

Kirk, D. A. & Mossman, M.J. 2020. Turkey Vulture (*Cathartes aura*). Version 1.0. In: Poole, A.F. & Gill, F.B. (Eds.). *Birds of the World*. Cornell Lab of Ornithology, Ithaca.

Kušta, T., Ježek, M. & Keken, Z. 2011. Mortality of large mammals on railway tracks. *Scientia Agriculturae Bohemica* 42: 12–18.

Lambertucci, S.A., Speziale, K.L., Rogers, T.E. & Morales, J.M. 2009. How do roads affect the habitat use of an assemblage of scavenging raptors. *Biodiversity Conservation* 18: 2063–2074.

Meisinget, E.L., Loe, L.E., Brekkum, O., & Mysterud, A. 2014. Targeting mitigation efforts: the role of speed limit and road edge clearance for deer-vehicle collisions. *Journal of Wildlife Management* 78: 679–688.

Nowak, R.M. 1999. *Walker's Mammals of the World. 6th Edition*. The Johns Hopkins University Press, Baltimore.

Peterson, C.A., Lee, S.L., & Elliot, J.E. 2001. Scavenging of waterfowl carcasses by birds in agricultural fields of British Columbia. *Journal of Field Ornithology* 72: 150–159.

Platt, S.G., Measures, E.A., Rohr, D.M., Kyaw Thu Zaw Wint & Rainwater, T.R. 2022. *Chelydra serpentina* (Snapping Turtle) and *Chrysemys picta* (Painted Turtle). Nesting habitat. *Herpetological Review* 53: 112–114.

Platt, S.G., Rainwater, T.R. & Miller, S.M. 2016. An observational study of carrion use by foraging Turkey Vultures (*Cathartes aura*) in west Texas. *Bulletin of the Texas Ornithological Society* 49: 65–74.

Platt, S.G., Salmon, G.T., Miller, S.M. & Rainwater, T.R. 2010. Scavenging by a bobcat, *Lynx rufus*. *Canadian Field-Naturalist* 124: 265–267.

Platt, S.G., Walde, A.D. & Rainwater, T.R. 2021. *Glyptemys insculpta* (Wood Turtle). Railroad Mortality. *Herpetological Review* 52: 126–127.

Popp, J.N. & Boyle, S.P. 2017. Railway ecology: Underrepresented in science? *Basic and Applied Ecology* 19: 84–93.

Prather, I.D., Conner, R.N. & Adkisson, C.S. 1976. Unusually large vulture roost in Virginia. *Wilson Bulletin* 88: 667–668.

Raebenold, P.P. 1989. Black and Turkey Vultures expand their range northwards. *Eyas* 2: 11–15.

Reeves, N.M. 2009. Taphonomic effects of vulture scavenging. *Journal of Forensic Science* 54: 523–528.

Santos, S.M., Carvalho, F. & Mira, A. 2011. How long do the dead survive on the road? Carcass persistence probability and implications for road-kill monitoring surveys. *PLoS ONE* 6(9):e25383.

Santos, S.M., Carvalho, F. & Mira, A. 2017. Current knowledge on wildlife mortality in railways. In: Borda-de-Água, L., Barrientos, R., Beja, P. & Pereira, H.M. (Eds). *Railway Ecology* 1st Edition, pp. 11–22. Springer, New York.

Siemann, D. 1999. *The Great Swamp: A watershed conservation strategy*. The Nature Conservancy, Pawling, New York.

Smith, P. 2020. Notes on vultures (Cathartidae) in Paraguay with a supporting bibliography. *Vulture News* 79: 11–31.

Slater, F.M. 2002. An assessment of wildlife road casualties – the potential discrepancy between numbers counted and numbers killed. *Web Ecology* 3: 33–42.

Thiel, P.P. 1976. Activity patterns and food habits of southeastern Wisconsin Turkey Vultures. *Passenger Pigeon* 38: 137–143.

van der Grift, E.A. 1999. Mammals and railroads: Impacts and management implications. *Lutra* 42: 77–98.

Wallace, M.P. & Temple, S.A. 1987. Competitive interactions within and between species in a guild of avian scavengers. *Auk* 150: 402–417.

Yahner, R.H., Storm, G.L. & Wright, A.L. 1986. Winter diets of vultures in southcentral Pennsylvania. *Wilson Bulletin* 98: 157–160.

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