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COVID-19 PANDEMIC IMPACTS ON MAMMALIAN CARNIVORE ACTIVITY IN THE EASTERN UNITED STATES

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ABSTRACT

Lockdowns and restrictions associated with the 2020 Covid-19 pandemic altered human activity, with potential impacts on wildlife. In particular, the activity of reclusive mammalian carnivores, which often avoid humans, may have been affected with ramifications for population connectivity and viability. Here, I evaluate changes in the capture rates of humans and mammalian carnivores between 2019 and 2020 across 31 sites in the Eastern United States. Site-specific capture records were obtained from the Snapshot USA camera trapping survey. Differences in carnivore activity were modelled as a response to human activity changes and the development level of the site (urban, suburban, rural or wild) using generalized linear models. Results indicated that, when compared with 2019, there was an overall decrease in human activity at camera sites in 2020, but human activity at urban and wild sites increased slightly. The mean capture rates of all carnivores examined did not change significantly between 2019 and 2020. Capture rates of all individually examined carnivore species varied significantly among development types, with most showing the lowest activity in urban areas. Of seven species modelled individually, only fisher (*Martes pennanti*) activity responded positively to decreases in human activity between years. Overall, with limited exceptions, changes in human activity caused by the COVID-19 pandemic may not have impacted mammalian carnivore activity as much as expected. This lack of a relationship with human activity could imply that some reclusive carnivore species make more use of human-occupied landscapes than was previously thought, but simply go undetected.

INTRODUCTION

In global ecological systems, wildlife and humans are inextricably interconnected, meaning that wildlife activity impacts humans, and human activity – including our use of and

mere presence within landscapes – has a variety of effects on wildlife populations. In particular, reclusive species such as mammalian carnivores may avoid areas of high human activity altogether, which can cause issues for the connectivity and viability of such species' populations in a world dominated by an ever-increasing human population and footprint. Recently, the pandemic caused by the SARS-CoV-2 Coronavirus had such large-scale impacts on the behavior and activity of the global human population that the period of government-induced lockdowns and mobility restrictions to contain the spread of the virus was coined “the Anthropause” (Rutz et al. 2021, Corradini et al., 2021; Pepe et al., 2020; Rupani et al., 2020). Given the mix of impacts human activity can have on wildlife, it seems likely that such drastic changes in the global activity of humans could affect mammalian carnivores. Indeed, there were a series of reports in the public media about purportedly increased sightings of wildlife – including large carnivores – in urban areas during 2020 (BBC, 2020; Radhika, 2020; The Guardian, 2020). While it is unclear if these reports are accurate, it is possible that the reductions in human activity during the COVID-19 pandemic could have led to an increase in mammalian carnivore activity overall, with some variation among species and across different landscapes.

The most immediate effects of the COVID-19 pandemic were on the global human population, with significant alterations in human activity due to the variety of lockdowns and restrictions put in place to limit the spread of the virus. Globally, over 100 countries put some restrictions in place at the start of the pandemic in 2020 (Montgomery et al., 2021). In the United States, 95% of the population had their mobility restricted in the spring of 2020, when most state governments issued some version of a stay-at-home order starting with California on March 19th and ending with South Carolina on April 6th, 2020 (Mervosh *et al.*, 2020). These stay-at-home orders remained in effect through the beginning of the summer of 2020, with states having a

variety of other restrictions in their “reopening” plans that likely altered human mobility for the remainder of 2020 (Washington Post Staff; AJMC Staff).

Human activity also changed differently across different locations, with mobility in the U.S. decreasing at transit stations, recreation facilities like restaurants, workspaces, and grocery stores and pharmacies, while increasing in parks and residential spaces throughout 2020 (Ritchie *et al.*, 2020). Around the world, human activity tended to increase in parks and natural spaces, with a 151% increase in visitors noted in forest areas studied in the Czech Republic (Soga *et al.*, 2021; Cukor *et al.*, 2021). Additionally, one UK survey found a significant increase in the number of people walking outside during the pandemic, with 81% of respondents noting the importance of nature to that outdoor activity (Hockenhull *et al.* 2021). In the U.S., the number of visitors to parks and outdoor spaces increased to a peak of around 60% above baseline levels in the summer of 2020 (Ritchie *et al.* 2020). Overall, human mobility decreased during the pandemic, with some increases in residential and outdoor spaces as people stayed-home and avoided densely populated areas as a part of government instituted orders and social-distancing policies (Soga *et al.*, 2021; Hockenhull *et al.*, 2021; Cukor *et al.*, 2021).

The widespread reduction in human mobility during the pandemic was also indicated by a variety of effects on the global environment, such as a global reduction in consumption of fossil fuels and greenhouse gas production, with an observed 17% decrease in daily global emissions compared to 2019 levels (Le Quéré *et al.*, 2020). There was also a marked reduction in general air pollution: in Bangalore, India there was a 49% decrease in nitrogen dioxide (NO₂) among other gas pollutant reductions from 2019 levels, and the city of Ghaziabad saw an 85.1% reduction in particulate matter concentrations (PM_{2.5}) just from January to April of 2020 (Gouda *et al.*, 2021; Lokhandwala & Gautam, 2020). Water pollution also appeared to decrease during

the “Anthropause;” for example, the Ganges river exhibited an 8 ppm increase in dissolved oxygen and a 3 ppm decrease in biochemical oxygen demand (Lokhandwala & Gautam, 2020). Urban areas also saw a reduction in noise pollution, such as in Colombia, where sound pressure levels increased 128% in urban spaces when mobility restrictions lightened in May and June 2020 (Ulloa *et al.*, 2021). Boston, MA showed sound levels in central urban protected areas 1-3 decibels lower than pre-pandemic conditions, and in San Francisco noise levels during the shutdown markedly decreased in response to traffic returning to levels observed in the 1950s (Terry *et al.*, 2021; Derryberry *et al.*, 2020).

These changes in human mobility and the environment also had consequences for wildlife. For example, in San Francisco, the previously mentioned observed reduction in noise pollution appeared to impact the songs and therefore reproductive success of the white-crowned sparrow (*Zonotrichia leucophrys*). In the past, researchers recorded the species as having higher frequency calls in urban areas with higher ambient noise levels, which resulted in lower bandwidth and vocal performance. This meant songs to which urban birds were less responsive, which could reduce mating opportunities while increasing challenges for territory (Luther *et al.*, 2016). But when ambient noise levels in San Francisco significantly decreased during the COVID-19 shutdown, the songs of the white-crowned sparrow decreased in frequency which means longer and higher communication distances and vocal performance. This could reverse the potential negative impacts human noise levels have on the reproductive success of this species, by potentially increasing mating opportunities and reducing conflict over territory (Derryberry *et al.*, 2020).

The reproductive success of some species was also negatively affected by the large reduction in human mobility. For example, when tourists stopped visiting a seabird colony in the Baltic

Sea during 2020, white-tailed eagles (*Haliaeetus albicilla*) had maximum numbers increase 760% in 2020 compared to 2019, largely due to the reduction of tourists – which the eagles tend to avoid. This increase in eagle numbers led to a sevenfold increase in disturbances of common murrelets (*Uria aalge*), which then experienced a 26% reduction in breeding productivity (Hentati-Sundberg *et al.*, 2021). So, the changes in human activity during the pandemic did not result in solely positive impacts for wildlife.

Wildlife survival rates were also negatively impacted by the COVID-19 pandemic. First, some species have directly contracted the SARS-CoV-2 virus, including: domestic cats and dogs, agriculturally-farmed mink, captive lions, tigers and gorillas, and wild white-tailed deer populations (Ekstrand *et al.*, 2021; USDA APHIS, 2021; Schulz *et al.*, 2021; Sit *et al.*, 2020; Oude-Munnink *et al.*, 2021; McAloose *et al.*, 2020; Hale *et al.* 2021). Additionally, the global COVID-19 shutdowns resulted in reductions in conservation actions and enforcement, which could have resulted in reduced management of potentially destructive invasive species and increased illegal hunting (Manenti *et al.* 2020; Lo Parrino *et al.* 2021; Bates *et al.* 2021; Battisti, 2021; Corlett *et al.*, 2020). Finally, anthro-dependent species that typically rely on human sources of food may have been negatively impacted by the reductions in human activity, especially in urban areas. For example, feral pigeons in Singapore had reduced abundance in the open urban areas and food hotspots they normally inhabit as human-generated food availability decreased (Soh *et al.* 2021). Likewise, the Torresian crow in Australia, which depends on human sources of food, appears to have moved from urban areas to natural beaches, and likely increased predation of smaller beach animals and other bird eggs while outcompeting native scavengers, causing a rippling effect through the entire ecosystem (Gilby *et al.* 2021).

Wildlife survival rates were also positively affected by the reduction in human mobility during the COVID-19 shutdowns. Roadkill rates decreased around the globe – such as in Chelm, Poland, where road mortality levels of the northern, white-breasted hedgehog (*Erinaceus roumanicus*) decreased by 50% during COVID-19 lockdowns (Łopucki *et al.*, 2021). Similarly, roadkill of amphibians and lizards in Italy, where some sites saw 80-100% reductions in road traffic, decreased in 2020 compared to 2019 (Manenti *et al.* 2020). Additionally, overall animal mortalities from collisions with vehicles and water vessels were reported to decrease by 19% in South Korea, and 42% in the United States from their respective baseline levels (Bates *et al.*, 2021). Within the United States, the shelter-in-place COVID-19 orders resulted in a range of 63-73% decreases in driving in California, Idaho, Maine, and Washington. Daily wildlife-vehicle collision rates 4 weeks after restrictions were enacted were reported to decrease by 34% from levels at 4 weeks prior to those restrictions, and in California, a 58% reduction in road mortality was recorded for mountain lions (*Puma concolor*) alone (Shilling *et al.* 2021). These reductions in mortalities could have lasting impacts on these wildlife populations, as more individuals were able to survive, move through and among habitat territories, and potentially reproduce (Łopucki *et al.*, 2021; Manenti *et al.* 2020).

Human mobility shifts during COVID-19 lockdowns also impacted wildlife activity patterns in a variety of ways. For example, in a camera trap study of forested areas in the Czech Republic, human visitor activity was observed to peak between 8 – 11 AM and 4 – 7 PM during 2020, while in comparison, wildlife activity peaked from 4 – 7 AM and 9 – 12 PM, indicating that wildlife were avoiding human visitors temporally, and so were negatively impacted by the increased human disturbance in these outdoor spaces (Cukor *et al.*, 2021). At the same time, where human activity decreased, the effects on wildlife activity patterns appeared more positive.

For example, in urban areas in Spain, a variety of bird species had significantly higher detectability in the early morning in 2020 compared to levels from a baseline of 2015-2019, indicating that these animals may have altered their activity schedules to sing earlier in the day than they did pre-pandemic (Gordo *et al.*, 2021). Similarly, the number of diurnal cottontail (*Sylvilagus floridanus*) records at a site in Italy were higher in 2020 compared to levels in 2014, 2016, and 2018, implying a potential release from the “landscape-of-fear” induced by typical levels of human presence and activity (Manenti *et al.*, 2020). These shifts in the activity patterns of wildlife indicate their ability to adjust their behavior rapidly and flexibly in response to changes in their environment, such as the widespread reductions in human activity during the COVID-19 lockdowns (Gordo *et al.*, 2021).

A final impact of the reductions of human activity during the COVID-19 lockdowns was on the connectivity of wildlife populations. The aforementioned reduction in road-collision mortalities for wildlife populations likely meant roads were less of a barrier to moving animals; so, the reduction in human mobility likely allowed more species to roam to more areas and increased the connectivity of their populations. This was documented in Italy for the brown bear (*Ursus arctos*), which appeared to approach and occupy human-dominated spaces and “hotspots” for road crossings more during 2020 compared to rates in 2016-2019 (Corradini *et al.*, 2021). This could imply that wildlife, specifically large mammalian carnivores, had increased connectivity and were better able to crossroads during the pandemic. Additionally, the same study found that brown bears were reported in 2020 at locations further from their core population area compared to their occurrences in 2019, indicating that they may have been expanding their habitat range during the reduction in human mobility during lockdown (Corradini *et al.*, 2021).

The potential use of new spaces by wildlife in 2020 may be indicative of their increased connectivity during the “Anthropause.” For example, a study analyzing citizen scientist observations on the iNaturalist app during the pandemic reported that there were many large mammal species observed in new locations in 2020 where they had not been previously sighted, although these new sites were not always in the urban areas sensationalized by the news media (Vardi *et al.* 2021; iNaturalist; BBC, 2020; Lanzoni & Almond, 2020; Manenti *et al.*, 2020; Mervosh *et al.*, 2020; Radhika, 2020; The Guardian, 2020). This result could indicate that wildlife may have taken advantage of new spaces that humans vacated during the beginning of the pandemic (Vardi *et al.* 2021). The same study also reported an increase in puma (*Puma concolor*) observations deeper into urban spaces, a finding which is also supported by a study in California specifically, where GPS-collared mountain lions also appeared to lose some of their aversion to urban boundaries and venture into densely populated areas (Vardi *et al.* 2021; Wilmers *et al.* 2021). In other words, the reduction in human mobility during the pandemic may have allowed wildlife species, like mammalian carnivores, to venture into or at least wander through, new spaces that are normally dominated by human activity.

Terrestrial mammalian carnivores are the particular focus of this study for a variety of reasons. First, they are charismatic and tend to attract a lot of public attention and interest. Despite this, they are also quite reclusive and difficult to detect, tend to have low population densities, and typically have large habitat requirements (Bateman *et al.*, 2012; Tucker *et al.*, 2018). Also, as predators, any changes in the activity or populations of these species can have rippling effects on the trophic levels below them (Smith *et al.* 2017). And there is a lot of evidence that these species are greatly affected by humans, who they generally tend to avoid both spatially and temporally (Doherty *et al.*, 2021; Gaynor *et al.*, 2018; Ordeñana *et al.*, 2010; Tigas *et al.*,

2002; George & Crooks, 2006; Flores-Morales *et al.*, 2019; Smith *et al.*, 2017; Nickel *et al.*, 2020; Martin *et al.*, 2010; Lamb *et al.*, 2020; Obreosler *et al.*, 2017; Nisi *et al.*, 2022). Human activity is directly responsible for some of the mortality of carnivores through vehicle-collisions: for example, road-kills were once the primary source of mortality for all large vertebrates in the state of Florida (Coffin, 2007; Tigas *et al.*, 2002). The construction of roads and other human infrastructure through the process of urbanization also destroys and fragments the large habitat spaces carnivores rely upon (Benson *et al.*, 2015; Whittington *et al.*, 2005; Crooks *et al.*, 2002).

Different carnivore species react in a variety of ways to human disturbance. Some carnivore species, such as the coyote (*Canis latrans*) and Northern raccoon (*Procyon lotor*) can live in areas of high human development and even take advantage of the anthropogenic food sources available there, while other species, such as the fisher (*Martes pennanti*) and bobcat (*Lynx rufus*), have been shown to avoid those spaces due to the intensity of the infrastructure and high human presence (Batemen *et al.*, 2012; Suraci *et al.*, 2021; Ordeñana *et al.*, 2010; Kordosky *et al.*, 2021; Šálek *et al.*, 2015). There is also ample evidence for carnivores temporally avoiding humans by altering their diel patterns to become more active at night when humans are not (Gaynor *et al.*, 2018). Such shifts in activity patterns can take place rapidly in response to changes in human disturbance, as was observed in the Czech Republic the during the COVID-19 pandemic when the number of humans visiting parks suddenly increased (Cukor *et al.*, 2021). So, it is feasible that mammalian carnivores could respond to widespread changes in human activity such as those occasioned by the pandemic by adjusting the amount, location, and timing of their activity.

As discussed above, there is already some preliminary evidence that carnivores may have shifted their activity patterns in response to human activity changes during the COVID-19 pandemic (Cuckor *et al.*, 2021), and there is also some anecdotal evidence that carnivores may

have been using new spaces during the “Anthropause,” including sites in developed areas like cities. For example, in the spring of 2020, there were a variety of reports in social and news media about wildlife “reclaiming” and “roaming” cities during lockdowns around the world. Specific to carnivores, there were reports of jackals in Tel Aviv, Israel, pumas in Santiago, Chile, and red fox in Toronto, Canada, among many others (BBC, 2020; Lanzoni & Almond, 2020; Manenti *et al.*, 2020; Mervosh *et al.*, 2020; Radhika, 2020; The Guardian, 2020). A few studies seem to support these observations so far: one by Vardi *et al.* that analyzed iNaturalist observations in North America during the pandemic found that more animals were observed in new locations during 2020, although these new locations were not very urbanized, except in the case of the mountain lion (Vardi *et al.*, 2021). One study that occurred in two cities in Chile, observed several carnivore species, including some that are endangered, in urban spaces although it is unknown if these are novel sightings as there was no data prior to 2020 (Silva-Rodríguez *et al.*, 2021). A study on brown bears in the Italian Alps found that bears did appear closer to human settlements and roads, and so potentially used road-crossing hotspots to get to new habitat and increase their range (Corradini *et al.*, 2021). Finally, a radio-collaring telemetry study of mountain lions in California found that, during the pandemic, some cats did venture farther into urban boundaries than they had pre-pandemic (Wilmers *et al.*, 2021).

While these studies of changes in wildlife activity are interesting, they often relied on anecdotal observations and/or lacked a variety of mammalian carnivore species and a large geographic scale. To truly determine if these sightings were “novel,” a systematic non-invasive dataset collected by researchers experienced in carnivore identification is needed. Without such data, it is difficult to tell if the sightings of carnivores in unusual and/or human dominated spaces

during the pandemic were due to true changes in the activity of carnivore populations, or if they were simply the result of humans becoming increasingly interested in the natural world.

This study analyses data from the Snapshot USA project – a national, yearly camera trapping survey effort in all 50 states to non-invasively collect data on mammal species, including carnivores, across the country (Cove *et al.* 2021). Using Snapshot USA data, I aimed to address gaps in our understanding of how mammalian carnivores in the Eastern United States were impacted by changes in human activity associated with the COVID-19 pandemic. I did this by examining differences in the mean photographic capture rates of carnivores between 2019 and 2020 and among different levels of human development (including urban, suburban, rural and wild) in response to human activity change. In general, I predicted that carnivore activity would be negatively related to human activity. I had two central hypotheses:

- I. Human activity decreased in 2020 due to the government enforced lockdowns, restrictions, and social distancing during the COVID-19 Pandemic, with some variation among landscape development levels.
- II. Mammalian carnivore activity increased overall in 2020 in response to lower human activity due to their general reclusiveness and aversion to humans, with some variation among species and across development types.

METHODS

Study Design

This study analyzed data from the 2019 and 2020 Snapshot USA Projects, which are part of an annual camera trapping survey of terrestrial wildlife across the United States. The inaugural 2019 14-week survey included 1,509 camera trap sites across all 50 states and took

place from August 17 to November 24, 2019. The survey effort resulted in 166,036 detections of 83 different species of mammals (Cove *et al.*, 2021). The 2020 Snapshot USA Project also took place from August to November and consisted of 1,456 camera deployments that detected 81 mammal species (Kays, 2021). In both surveys, camera sites were categorized into one of four types of anthropogenic development zones: Wild, Urban, Rural, and Suburban. Additionally, camera sites were classified as being in one of seven habitat types: Forest, Grassland, Anthropogenic, Riparian, Desert, Alpine, or Wetlands (Cove *et al.*, 2021).

Each national survey consisted of sub-projects in each state that deployed cameras at 351 and 359 field sites in 2019 and 2020, respectively, for a goal of 400-500 total trap nights per sub-project. To meet the Snapshot USA Project requirements, all cameras were to be placed at least 200 meters apart but no greater than 5 km apart and set facing North or South on medium-sized trees at a 50 cm height off the ground. No specific model of camera trap was required, but cameras needed a high trigger sensitivity and were set to only capture photographs, not videos. Cameras were set on a fast trigger setting of less than 0.5 seconds, used infrared flash, and were placed in a burst mode of 3-5 pictures per trigger, with no delay between triggers. No bait was used to attract animals to the camera sites. While setting cameras up, field researchers ensured that the camera was aimed parallel to the ground, and recorded detection distance (how far away the camera could detect movement), date and time, the latitude and longitude of the deployment, and any additional information, such as if there was a trail nearby. All photographs for both surveys were uploaded to and processed through the Smithsonian's eMammal camera trap data repository, with each photo being reviewed at least twice: once by the researchers of each individual sub-project and once by an expert reviewer (Cove *et al.* 2021; Kays, 2021).

Statistical Analyses

For this analysis of mammalian carnivore activity, I downloaded 2019 and 2020 Snapshot data for all sub-projects East of the Mississippi River in the United States from the eMammal camera trap data repository (**Figure 1**). Within Program R, any sub-projects that were West of the Mississippi River or were not a part of both the 2019 and 2020 Snapshot USA surveys were excluded (**Figure 2**; R Core Team, 2021). Additionally, sub-projects or deployments that lacked a designated development zone of Rural, Suburban, Wild, or Urban, were excluded. Only mammal species in the order Carnivora were included in this analysis, but any observations that were unidentifiable to a specific genus and species were excluded. Observations of both Non-staff humans (or humans who were not identified as field researchers) and vehicles were considered observations of humans in this analysis. Species that were observed at least 40 times in both years were modeled individually, including the American black bear (*Ursus americanus*), Bobcat (*Lynx rufus*), Coyote (*Canis latrans*), Fisher (*Martes pennanti*), Gray Fox (*Urocyon cinereoargenteus*), Northern Raccoon (*Procyon lotor*), and Red Fox (*Vulpes vulpes*) (**Table 1**). Separate models were also fit to the human data and to the sum of all 16 mammalian carnivore species observed across deployments. The mean capture rate and standard error was calculated for each of these seven species, humans, and all 16 carnivore species captured across all deployments (**Table 2**).

I summed the captures observed at each camera deployment for each mammal species analyzed. The sum of all mammalian carnivore captures and the sum of all individual human (either non-staff or vehicle) captures were also calculated for each camera deployment. I then fit generalized linear models assuming a Poisson distribution to the combined human counts to quantify a difference in the number of captures of humans between years and among the

anthropogenic development levels of the sub-projects analyzed. A multi-variable model examined “Year” and “Development” as predictors (**Tables 3 & 4**), while the “Year: Development” model was an interaction model with both survey year and the sub-project development type serving as interacting predictors (**Tables 3 & 5**). Both models exhibited overdispersion with the Poisson distribution, so new generalized linear models assuming a quasi-Poisson distribution were fit to the data with the same predictors and goals. These quasi-Poisson count models were also fit to a sum of all 16 mammalian carnivore species captured and the seven individual carnivore species listed above, with the same predictors (**Tables 3, 4, & 5**).

In addition to the count models, I ran eight generalized linear models assuming a binomial distribution of the sum of all mammalian carnivore captures (known as the multi-species carnivore model), and of the captures of the seven species specified above. These models aimed to quantify how much mammalian carnivore captures in 2020 varied as a function of changes in human observations between 2019 and 2020, and among the different development levels of the sub-projects. For each individual species and the multi-species carnivore models, two proportion models assuming binomial distributions were run, a “Human-Change” model with the difference in total human counts between 2020 and 2019 as a predictor (**Tables 3 & 6**), and a “Human Change: Development” interaction model which had the interacting predictors of the difference in human counts between years and sub-project development level (**Tables 3 & 7**). Except for the Fisher and Gray Fox models, all binomial generalized linear models exhibited overdispersion (as evidenced by large residual deviance values in comparison to the degrees of freedom), and so, models with the quasi-binomial distribution were used for all but those two species, with the same predictors and aims outlined above. ANOVA type II F-tests were run on all models outlined above (**Table 3**).

RESULTS

Sub-project Sample Summary Statistics

A total of 31 sub-projects located in 21 states East of the Mississippi River met the criteria for inclusion in this analysis. From these sub-projects, there were a total of 351 camera deployments from 2019 and 359 camera deployments from 2020 (or 710 camera deployments total). In 2019, each deployment had a range of 3 to 89 trap nights (mean \pm SD = 43.19 ± 15.587 , $n = 351$). In 2020, this range was 3 to 74 trap nights (mean \pm SD = 35.26 ± 16.314 , $n = 359$). There were 9,184 and 4,928 “non-staff” humans and vehicles observed in 2019 and 2020, respectively, at the camera deployments included in this analysis. In 2019 and 2020, 3,995 and 2,318 mammalian carnivores of 16 species were observed respectively at the camera deployments included in this analysis. Seven species met the requirement of having over 40 observations in both 2019 and 2020, and so were individually modeled in the analysis (**Table 1**). The mean capture rate across all the sub-projects analyzed varied widely among each of these seven species (**Table 2**).

Human Capture Rate Models

The quasi-Poisson human count models indicated that human capture rates in 2020 were significantly lower than in 2019 ($\beta_{2020} = -0.43 \pm 0.116$, $t_{5675} = -3.69$, $P < 0.001$), implying that human activity decreased between the two years (**Table 4**). Additionally, human capture rates varied significantly with the development level of each sub-project ($F_{3, 5675} = 135.45$, $P < 0.001$), with activity lower in urban areas than elsewhere (**Table 3, 4; Figure 3**). Furthermore, the human count interaction model indicated that the differences in human activity between 2019 and 2020 depended on development status ($F_{3, 5672} = 4.21$, $P = 0.006$; **Table 3**). Specifically,

urban and wild areas had slight increases in human activity whereas rural and suburban areas had reduced human activity (**Table 5; Figure 3**).

Mammalian Carnivore Capture Rate Models

The multi-species carnivore model indicated that overall mammalian carnivore capture rates in 2020 were not significantly different compared to 2019 ($\beta_{2020} = -0.02 \pm 0.145$, $t_{705} = -0.153$, $P = 0.878$), implying that carnivore activity did not change between 2019 and 2020 (**Table 4**). Carnivore capture rates, did however, vary significantly among development levels ($F_{3, 705} = 8.896$, $P < 0.001$), with activity lower overall in urban areas than elsewhere (**Table 3, 4, 5; Figure 3**). The quasibinomial multi-species proportion model indicated that overall carnivore activity did not change in response to the decrease in human capture rates between 2020 and 2019 ($\beta_{2020/2019} = -0.03 \pm 0.046$, $t_{29} = -0.602$, $P = 0.552$; **Table 6**). Furthermore, this finding was unaltered by the consideration of human development level as a predictor ($F_{3, 23} = 1.48$, $P = 0.246$; **Tables 3 & 7**).

All the single carnivore species quasi-Poisson count models had similar results as the multi-species count model, in that capture rates that did not significantly differ between 2019 and 2020 but did vary across development level with lower species activity in urban areas than elsewhere (**Table 3, 4, 5**). Additionally, most quasibinomial single-species proportion models indicated that carnivore species activity did not change in response to the change of human capture rates between 2020 and 2019 (**Table 6; Figure 4**). Only the fisher proportion model indicated otherwise, implying that fisher activity did respond positively to the negative change in human capture rates between years ($\beta_{2020/2019} = -0.89 \pm 0.351$, $z_{10} = -2.545$, $P = 0.011$; **Table 6**). In other words, fisher activity increased in response to the decrease in human activity in 2020.

The effect of the change in human activity between 2019 and 2020 on species' capture rates did not vary across development levels for species modeled (**Table 7**). The quasibinomial interaction proportion models for the coyote and gray fox proved exceptions, however, indicating that the effect of change in human activity on the coyote activity did depend on development status ($F_{3, 23} = 3.32$, $P = 0.038$). The same is true for the gray fox interaction model ($F_{3, 6} = 8.31$, $P = 0.015$; **Table 7**). Specifically, decreases in human activity were correlated with decreased gray fox and coyote activity in urban areas, and increased activity of these species in rural, suburban and wild areas (**Table 7**). However, the estimates of parameters for the interactions between each development status and human activity were very uncertain and not statistically significant.

DISCUSSION

As predicted, the start of the COVID-19 pandemic in 2020 was associated with an overall decrease in human activity at our camera survey locations in the Eastern United States, with some variations among areas of differing development levels. This trend does not appear to have had a substantial impact on the activity levels of most mammalian carnivores in the eastern half of the United States. While there was some variation among species, my results indicate that rates of carnivore activity generally did not vary between years or with the decrease in human activity in 2020. This could indicate that carnivores are more tolerant of human activity than expected or that carnivores responded in another manner that was not explored in this study. Either way, these results give us important insight into the factors influencing broader carnivore activity patterns across both space and time in the Eastern United States.

My first prediction that human activity would decrease overall in 2020 with some variation among development levels was supported by my results, and this observed trend is

most likely due to the various stay-at-home orders and other mobility restrictions enacted around the Eastern U.S. during the COVID-19 pandemic (Mervosh *et al.*, 2020; AJMC Staff). Mean human capture rates did, however, increase slightly at urban and wild camera sites in 2020 (**Table 4**). This could be for a few reasons: first, human activity increased at more remote locations as humans generally tried to avoid densely populated areas during the pandemic and spent increased time outdoors in natural settings (Hockenhull *et al.*, 2021). For example, increased human visitation was observed in parks in both the U.S. and around the world, and so if “wild” camera sub-projects had deployments within public parks, the uptick in human activity in those spaces could be due to the larger trend of people increasingly spending time in more “natural” spaces (Ritchie *et al.* 2021; Cukor *et al.*, 2021). The same could be true in the urban sites that had increased human activity: if camera traps were set up in urban parks or greenspaces, then it is likely those data reflect increased human mobility in the few natural spaces available in highly developed areas where humans may have gone to avoid each other during the pandemic. The possible increase in human activity observed at urban locations is very slight however and should not be relied upon with much confidence.

The overall observed decrease in human activity in 2020 does not appear to have impacted mammalian carnivore activity as I originally predicted. The multi-species carnivore model, as well as most individual species models, showed no variation between 2019 and 2020, but did show significant variation in carnivore capture rates across different development levels (**Tables 3 & 4**). Carnivore activity was generally the lowest at urban sites in both years, which fits the general characterization of carnivores as reclusive, human-averse species that likely avoid areas of intense human activity (Flores-Morales *et al.*, 2019). There was some variation in terms of where individual species activity was the highest: overall carnivore activity was highest

in suburban areas, as was gray fox activity (**Table 4**). Black bears were the only species with the highest activity levels at wild sites, while bobcats, coyotes, red fox, and fisher all had highest activity levels at rural sites (**Table 4**). Such variation could imply that gray fox are more acclimated to human developed spaces, while black bears are especially averse to human infrastructure, for which there is some evidence in the literature (Crooks *et al.*, 2002; Suraci *et al.*, 2021; Oberosler *et al.*, 2017).

Aside from varying with development types, carnivore activity levels, except for the fisher, did not show any significant variation of mean carnivore capture rates with the change in human activity between 2020 and 2019. This result may have been observed for a variety of reasons: first, it could be that human activity and disturbance alone is not the primary factor in determining carnivore activity in an area. For example, physical human infrastructure, and its effects on prey bases and other habitat quality metrics for carnivores, could be more impactful than human activity patterns (Riley *et al.* 2003; Ordeñana *et al.*, 2010). Or it could be that the carnivore species modelled, except for the fisher, are less sensitive to humans than expected, and so did not alter their activity patterns much in response to the widespread decline in human activity in 2020. Many studies in the literature have documented species like the gray fox, Northern racoon, red fox, and the coyote as existing in higher densities in urban areas, and even taking advantage of anthropogenic food sources, indicating they might be more behaviorally adapted to coexisting with humans (Bateman *et al.*, 2012; Suraci *et al.*, 2021; Tigas *et al.* 2002; Ordeñana *et al.*, 2010).

Indeed, a variety of studies have already documented different carnivore species (the bobcat and coyote especially) altering their diel activity patterns to avoid humans in developed spaces and reducing the risk of human-carnivore conflicts and/or mortality (Gaynor *et al.*, 2018;

Tigas *et al.*, 2002; Riley *et al.* 2003). These studies suggest another explanation for my results: carnivores may have avoided humans by shifting the daily timing of their activity rather than reducing their activity overall; detecting such a shift was beyond the scope of this study. There is already some evidence that wild mammals shifted activity patterns in response to higher human presence in parks during the pandemic (Cukor *et al.* 2021). For example, cottontails (*S. floridanus*) in Italy became more diurnal in response to decreased human activity (Manenti *et al.*, 2020). Therefore, it is possible that carnivores also adjusted the timing of their activity patterns in response to large changes in human activity.

As for the fisher, there could be a few reasons why it was the only species to show the predicted significant positive response to the decrease in human activity during the pandemic. There is limited literature about fisher responses to human activity, but there is evidence that the Pacific fisher (*Pekania pennanti*) tend to prefer habitat in more mature forests with high canopy cover that are far from human development or disturbance (Kordosky *et al.*, 2021). Anecdotal evidence suggests that fisher (*Martes pennanti*) can be observed near roads, but that fishers do run from humans when spotted (Johnson and Todd, 1985). Fishers might be more sensitive to human activity levels and therefore more human-averse than some of the other carnivore species evaluated here, so it makes sense that fishers might have a stronger response to human activity decreasing during the pandemic.

My findings indicate that overall carnivore activity did not increase during the pandemic, which contradicts the anecdotes of increased sightings of carnivores in urban areas during the “Anthropause.” One potential explanation could be that humans were more observant of their surroundings and experienced an increased interest in nature while at home during lockdowns. There is some evidence of this from other studies: for example, Roll *et al.* (2021) documented

increased human interest in common bird species in Europe, Soga *et al.* (2021) and Cukor *et al.* (2021) saw increased human visitation to forests, and Hockenhull *et al.* (2021) reported more people in the UK walking in the countryside to engage with nature. Additionally, a study analyzing citizen science iNaturalist app observations during the start of the pandemic found some wildlife species occurring in novel areas during the pandemic, but most of these unique occurrences were not in urban areas (Vardi *et al.*, 2021; iNaturalist). Furthermore, the volume of observations increased in more urban areas during the onset of the pandemic, implying that people in cities became more observant of their surroundings. This means that more urban residents could have seen pre-existing wildlife species than they did pre-pandemic and assumed that wildlife had changed their activity patterns rather than humans altering the focus of their attention. Or, if wildlife did become more active during the day, their activity may have been more visible to humans than before the pandemic, and so they were thought to be “reclaiming” habitat that they normally use at night.

There are a few limitations to my study that should be considered: first, the Snapshot USA project which provided these data started in 2019, only one year prior to the COVID-19 pandemic. As a result, there is limited data to document the status quo for mammalian carnivore activity prior to the pandemic and associated human activity changes. It is difficult know if the 2019 data are representative of typical carnivore activity prior to the pandemic or ascertain if 2020 patterns represent a departure from “normal” patterns. Continuing the Snapshot USA project to monitor mammalian activity for more years should build a better baseline that could fill this gap for future studies comparing carnivore activity patterns in the United States. Another important limitation for this study was that only two of the included sub-projects had an “urban”

development level, so data for carnivore activity in urban areas was limited. Expanding the Snapshot USA project to include more urban sites could remedy this issue for future studies.

Finally, because the camera trap data were collected in September and October, they did not coincide with the most severe restrictions on human mobility during the COVID-19 pandemic in the U.S. (Mervosh *et al.*, 2020). Depending on the state of each sub-project, the 2020 data were collected approximately 4-6 months after stay-at-home orders were lifted (Miller, 2020; Washington Post Staff, 2020). As a result, if carnivore species reacted more dramatically to the most restrictive period of human mobility earlier in 2020, this study would not have observed such responses. In that case, the results of this study could document the rapid shift of carnivore activity back to pre-pandemic levels that occurred in response to the loosening human mobility restrictions as state economies reopened. Some restrictions on human activity continued into the fall of 2020, however, so it seems unlikely that any changes in carnivore activity due to the pandemic would have been completely reversed at that time. Regardless, future studies should attempt to document carnivore responses to changing human activity immediately and continue monitoring for a prolonged period to determine how long those effects may last.

Despite these limitations, datasets like the Snapshot USA data used here represents a valuable resource for tracking mammalian carnivores going forward and could be used in future studies to fill the gaps outlined above. Future studies using this dataset could include investigating carnivore diel activity pattern changes rather than overall capture rates in response to the COVID-19 pandemic. While it would neither be feasible nor desirable to recreate the pandemic conditions that resulted in the altered human activity patterns of 2020, future study on the responses of carnivores to human activity could be conducted on smaller scales - perhaps in locations with regular seasonal change in human activity, such as campgrounds and tourist

towns. Finally, long-term analysis of citizen observations of wildlife, should be continued to see how human interest in the wildlife around them may vary overtime.

CONCLUSIONS

In conclusion, overall mammalian carnivore activity appears to be largely unimpacted by decreases in human activity during the COVID-19 pandemic in the Eastern United States. While the fisher does appear to respond positively to reductions in human mobility, overall carnivore activity appears to vary more with the level of human development in habitats than with changes in levels of human activity. As a result, future studies should explore factors aside from human activity levels – such as human infrastructure or prey-availability – that could impact carnivore activity levels across space or examine how carnivore activity patterns may change over time in response to human activity changes. Nonetheless, these results provide important insight into carnivore activity patterns based on systematically collected data on a large-scale that was not possible before the Snapshot USA Project. Even if the widespread changes in human activity were not enough to improve carnivore connectivity and free up new habitat for them to “reclaim” during the COVID-19 pandemic, periods of reduced human mobility might be important to increasing human interest in wildlife, and perhaps indirectly, their conservation.

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APPENDICES

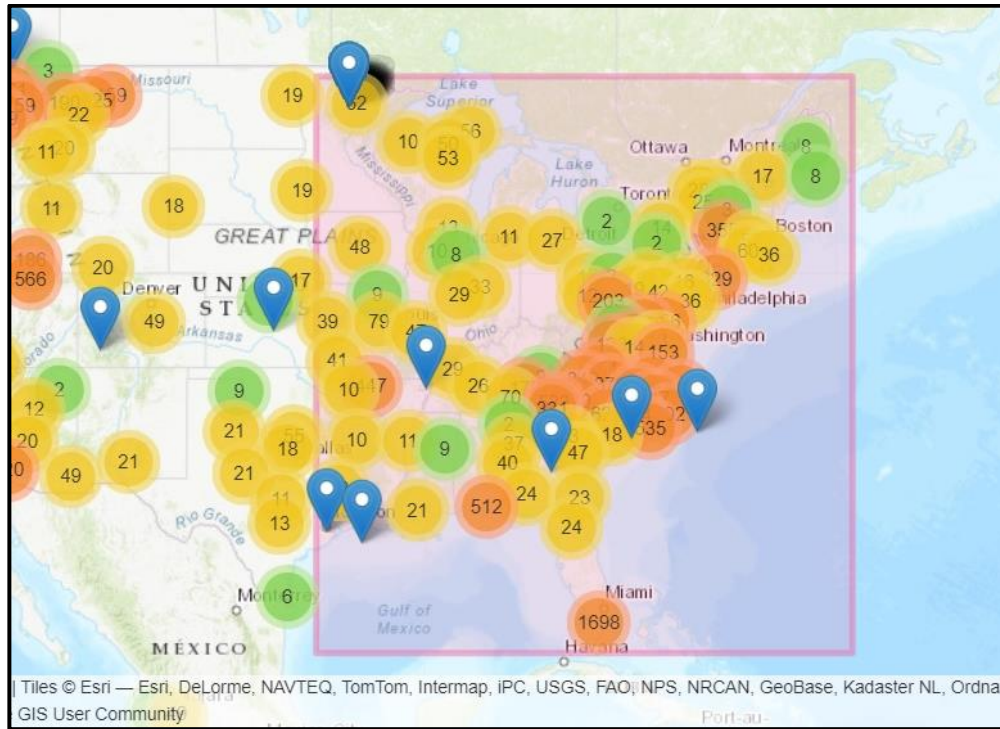


Figure 1. Map of all eMammal projects east of the Mississippi River from which Snapshot USA data was downloaded. The project markers within the red box indicates the projects from which data were selected.



Figure 2. Map of the locations of the camera arrays of sub-projects from the Snapshot USA 2019 and 2020 projects that were analyzed in this study, broken out by development level. All sub-projects included were east of the Mississippi River and were a part of both the 2019 and 2020 Snapshot USA projects.

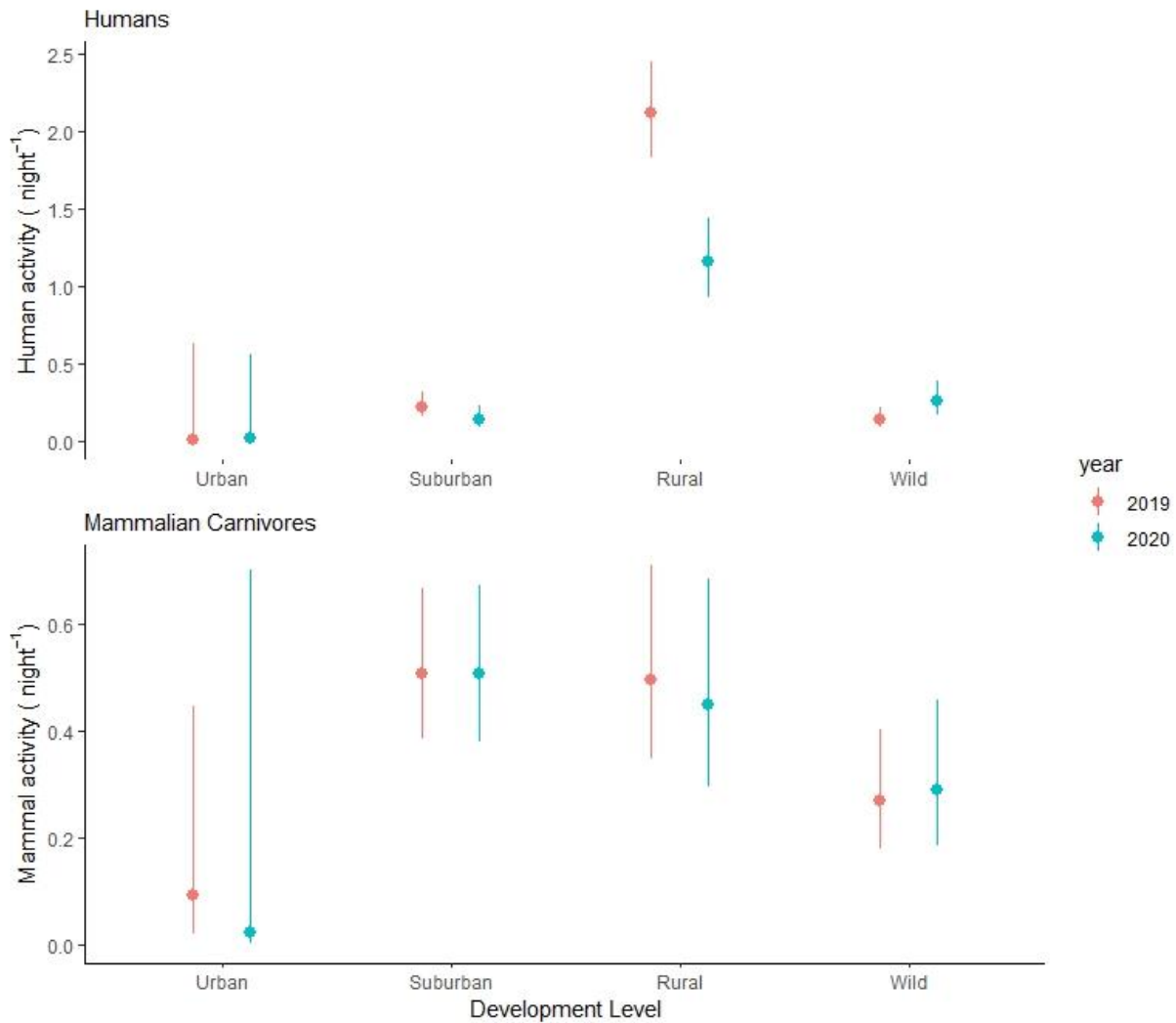


Figure 3. Plots of mean human and overall mammal capture rates between years 2019 and 2020 across four development levels: urban, suburban, rural, and wild. For the top human plot, mean human capture rate appears to have decreased overall in 2020, especially in rural areas, but it also increased in 2020 at wild sites. Overall mammalian carnivore capture rates appear to not have differed significantly between 2019 and 2020 at all development levels.

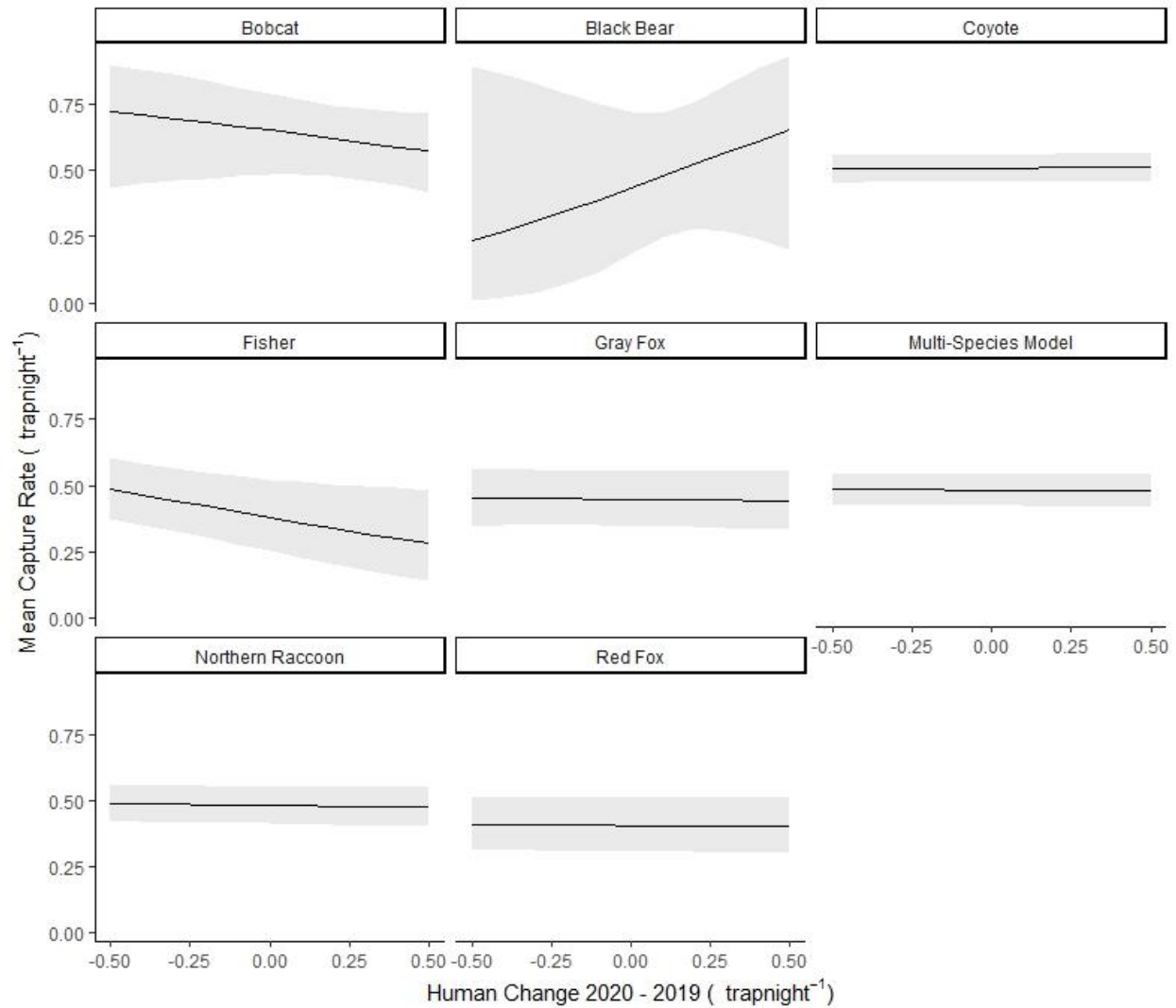


Figure 4. Prediction plots of mean capture rates of different species as a function of the change in human activity in 2020 compared to 2019 (which was negative overall). The multi-species model refers to the capture rates for all 16 carnivore species observed. Only the fisher result was statistically significant.

Table 1. Species Occurrence

Number of human and mammalian carnivore species captures summed across the Snapshot USA camera deployments in the Eastern U.S. that were used in this study. The number of human captures was calculated as the sum of the number of human non-staff (or non-camera trappers) and vehicle observations. Bolded species were captured at least 40 times in both 2019 and 2020 and so were modeled individually.

| <i>Species</i> | <i>Year</i> | |
|----------------------------|-------------|-------------|
| | 2019 | 2020 |
| American Badger | 1 | 0 |
| American Black Bear | 68 | 49 |
| American Marten | 10 | 7 |
| American Mink | 8 | 5 |
| Bobcat | 60 | 78 |
| Canada Lynx | 1 | 0 |
| Coyote | 535 | 459 |
| Ermine | 4 | 6 |
| Fisher | 53 | 44 |
| Gray Wolf | 11 | 43 |
| Grey Fox | 99 | 82 |
| Long-tailed Weasel | 8 | 4 |
| North American Otter | 12 | 36 |
| Northern Raccoon | 3699 | 3250 |
| Red Fox | 688 | 476 |
| Striped Skunk | 39 | 29 |
| Human non-staff | 3312 | 2899 |
| Vehicle | 1027 | 728 |

Table 2. Mean Species Capture Rates

The mean capture rate per trap night across all deployments in 2019 and 2020 for each species modeled. In 2019 the total number of trap nights was 27,819, while in 2020 it was 12,658 trap nights. The “Multi-Species Carnivore” row includes the capture rates of all 16 carnivore species observed in the Snapshot USA project across both years. The “Human” capture rates include captures of both non-camera trapping humans and vehicles.

| Species | Mean Capture Rate 2019 \pm SE | Mean Capture Rate 2020 \pm SE |
|--------------------------------|---------------------------------------|--------------------------------------|
| <i>Humans</i> | 0.606 \pm 0.2335 | 0.360 \pm 0.0936 |
| <i>Multi-Species Carnivore</i> | 0.420 \pm 0.0473 | 0.431 \pm 0.0456 |
| <i>American Black Bear</i> | 0.004 \pm 0.0011 | 0.008 \pm 0.0024 |
| <i>Bobcat</i> | 0.004 \pm 0.0008 | 0.008 \pm 0.0024 |
| <i>Coyote</i> | 0.034 \pm 0.0040 | 0.040 \pm 0.0048 |
| <i>Fisher</i> | 0.004 \pm 0.0011 | 0.003 \pm 0.0012 |
| <i>Gray Fox</i> | 0.007 \pm 0.0013 | 0.007 \pm 0.0017 |
| <i>Northern Raccoon</i> | 0.314 \pm 0.0434 | 0.293 \pm 0.0418 |
| <i>Red Fox</i> | 0.0471 \pm 0.0147 | 0.045 \pm 0.0083 |

Table 3. All Models ANOVA Type II F-tests

Results from ANOVA tests on generalized linear models that examined effects of year or human activity change and development status, and their interaction if statistically supported, on species capture rates. The “Multi-Species Carnivore” model examined the capture rates of all 16 mammalian carnivore species detected in both years of the Snapshot USA project, not just those that had enough observations to be modeled individually. Bolded values are statistically significant.

| Species | Coefficient | Sum of Squares | Degrees of Freedom | Residual Degrees of Freedom | F-value | P(>F) |
|--------------------------------|----------------------------------|----------------|--------------------|-----------------------------|----------------|------------------|
| <i>Human</i> | Year | 4881 | 1 | 5675 | 14.114 | <0.001 |
| | Development | 140536 | 3 | 5675 | 135.450 | <0.001 |
| | Year: Development | 4168 | 3 | 5672 | 4.205 | 0.006 |
| <i>Multi-Species Carnivore</i> | Year | 1 | 1 | 705 | 0.024 | 0.878 |
| | Development | 1532 | 3 | 705 | 8.896 | <0.001 |
| | Year: Development | 47 | 3 | 702 | 0.2769 | 0.8421 |
| | Human Change: Development | 179.09 | 3 | 23 | 1.4801 | 0.2462 |
| <i>Black Bears</i> | Year | 0.58 | 1 | 705 | 0.213 | 0.645 |
| | Development | 255.50 | 3 | 705 | 31.009 | 0.645 |
| | Year: Development | 6.70 | 3 | 702 | 0.9568 | 0.4126 |
| | Human Change: Development | 0.000 | 1 | 4 | 0.0000 | 1.0000 |
| <i>Bobcats</i> | Year | 6.81 | 1 | 705 | 1.823 | 0.177 |
| | Development | 59.61 | 3 | 705 | 5.322 | 0.001 |
| | Year: Development | 8.04 | 3 | 702 | 0.804 | 0.492 |
| | Human Change: Development | 2.07 | 2 | 12 | 0.294 | 0.751 |
| <i>Coyotes</i> | Year | 1.20 | 1 | 705 | 0.197 | 0.657 |
| | Development | 82.00 | 3 | 705 | 4.413 | 0.004 |
| | Year: Development | 14.00 | 3 | 702 | 0.755 | 0.519 |
| | Human Change: Development | 23.29 | 3 | 23 | 3.317 | 0.038 |
| <i>Fisher</i> | Year | 0.00 | 1 | 705 | 0.001 | 0.980 |
| | Development | 47.79 | 3 | 705 | 5.495 | 0.001 |
| | Year: Development | 11.96 | 3 | 702 | 1.347 | 0.258 |
| | Human Change: Development | 9.422 | 3 | 4 | 3.123 | 0.150 |

| | | | | | | |
|-------------------------|----------------------------------|---------------|----------|------------|---------------|------------------|
| <i>Gray Fox</i> | Year | 0.59 | 1 | 705 | 0.173 | 0.678 |
| | Development | 157.07 | 3 | 705 | 15.329 | <0.001 |
| | Year: Development | 10.95 | 3 | 702 | 1.126 | 0.338 |
| | Human Change: Development | 17.86 | 3 | 6 | 8.312 | 0.015 |
| <i>Northern Raccoon</i> | Year | 2 | 1 | 705 | 0.029 | 0.865 |
| | Development | 1246 | 3 | 705 | 6.115 | <0.001 |
| | Year: Development | 55 | 3 | 702 | 0.275 | 0.843 |
| | Human Change: Development | 124.93 | 3 | 22 | 1.021 | 0.402 |
| <i>Red Fox</i> | Year | 19.3 | 1 | 705 | 0.688 | 0.407 |
| | Development | 631.6 | 3 | 705 | 7.5236 | <0.001 |
| | Year: Development | 31.2 | 3 | 702 | 0.401 | 0.752 |
| | Human Change: Development | 50.33 | 2 | 16 | 2.247 | 0.138 |

Table 4. Species Count Models Across Year and Habitat

Results from generalized linear models with quasi-Poisson distributions examining the changes in mean species capture rate between 2019 and 2020 and across different development levels. The “Multi-Species Carnivore” model examined the capture rates of all 16 mammalian carnivore species detected in both Snapshot USA projects, not just those that had enough observations to be modeled individually. Bolded values are statistically significant.

| Species | Coefficient | Estimate | Standard Error | t-value | P(> t) | Degrees of Freedom |
|--------------------------------|------------------|----------------|----------------|---------------|------------------|--------------------|
| <i>Human</i> | Intercept | -4.2613 | 1.435 | -2.969 | 0.003 | 5675 |
| | Year 2020 | -0.43 | 0.116 | -3.690 | <0.001 | 5675 |
| | Suburban | 2.73 | 1.442 | 1.895 | 0.057 | 5675 |
| | Rural | 4.95 | 1.436 | 3.448 | <0.001 | 5675 |
| | Wild | 2.72 | 1.444 | 1.887 | 0.059 | 5675 |
| <i>Multi-Species Carnivore</i> | Intercept | -2.79 | 0.732 | -3.809 | <0.001 | 705 |
| | Year 2020 | -0.02 | 0.145 | -0.153 | 0.878 | 705 |
| | Suburban | 2.12 | 0.736 | 2.875 | 0.004 | 705 |
| | Rural | 2.05 | 0.742 | 2.767 | 0.006 | 705 |
| | Wild | 1.51 | 0.745 | 2.032 | 0.043 | 705 |
| <i>Black Bears</i> | Intercept | -7.5440 | 1.6636 | -4.535 | <0.001 | 705 |
| | Year 2020 | 0.1350 | 0.2920 | 0.462 | 0.6439 | 705 |
| | Suburban | -1.8396 | 2.3435 | -0.785 | 0.4327 | 705 |
| | Rural | 0.1577 | 1.9137 | -0.082 | 0.9343 | 705 |
| | Wild | 3.2420 | 1.6640 | 1.948 | 0.0518 | 705 |
| <i>Bobcats</i> | Intercept | -20.95 | 879.624 | -0.024 | 0.981 | 705 |
| | Year 2020 | 0.44 | 0.327 | 1.343 | 0.180 | 705 |
| | Suburban | 15.15 | 879.624 | 0.017 | 0.986 | 705 |
| | Rural | 16.22 | 879.624 | 0.018 | 0.985 | 705 |
| | Wild | 15.07 | 879.624 | 0.017 | 0.986 | 705 |
| <i>Coyotes</i> | Intercept | -4.62 | 0.591 | -7.819 | <0.001 | 705 |
| | Year 2020 | 0.07 | 0.153 | 0.445 | 0.657 | 705 |
| | Suburban | 1.28 | 0.599 | 2.132 | 0.033 | 705 |
| | Rural | 1.64 | 0.603 | 2.721 | 0.007 | 705 |
| | Wild | 1.30 | 0.603 | 2.149 | 0.032 | 705 |

| | | | | | | |
|-------------------------|------------------|---------------|--------------|----------------|------------------|------------|
| <i>Fisher</i> | Intercept | -4.78 | 0.467 | -10.225 | <0.001 | 705 |
| | Year 2020 | 0.01 | 0.343 | 0.025 | 0.980 | 705 |
| | Suburban | -1.91 | 0.633 | -3.011 | 0.003 | 705 |
| | Rural | -0.181 | 0.509 | -0.356 | 0.722 | 705 |
| | Wild | -1.00 | 0.548 | -1.830 | 0.068 | 705 |
| <i>Gray Fox</i> | Intercept | -6.044 | 0.931 | -6.490 | <0.001 | 705 |
| | Year 2020 | -0.11 | 0.269 | -0.415 | 0.678 | 705 |
| | Suburban | 1.831 | 0.936 | 1.956 | 0.051 | 705 |
| | Rural | 0.533 | 0.998 | 0.534 | 0.593 | 705 |
| | Wild | -1.04 | 1.159 | -0.895 | 0.371 | 705 |
| <i>Northern Raccoon</i> | Intercept | -3.31 | 1.033 | -3.200 | 0.001 | 705 |
| | Year 2020 | -0.03 | 0.185 | -0.170 | 0.865 | 705 |
| | Suburban | 2.32 | 1.038 | 2.233 | 0.026 | 705 |
| | Rural | 2.28 | 1.045 | 2.178 | 0.028 | 705 |
| | Wild | 1.67 | 1.050 | 1.592 | 0.112 | 705 |
| <i>Red Fox</i> | Intercept | -18.66 | 905.870 | -0.021 | 0.984 | 705 |
| | Year 2020 | -0.26 | 0.314 | -0.824 | 0.410 | 705 |
| | Suburban | 16.14 | 905.870 | 0.018 | 0.986 | 705 |
| | Rural | 15.665 | 905.871 | 0.017 | 0.986 | 705 |
| | Wild | 14.27 | 905.871 | 0.016 | 0.987 | 705 |

Table 5. Species Count Models of Interaction between Year and Habitat

Results from generalized linear models with quasi-Poisson distributions examining the potential changes in species capture rate between 2019 and 2020 and across different development levels. The “Year” coefficient refers to changes in species captures between 2019 and 2020 at urban sites which were used as a reference for the other coefficients. The “Multi-Species Carnivore” model examined the capture rates of all 16 mammalian carnivore species detected in both Snapshot USA projects, not just those that had enough observations to be modeled individually. Bolded values are statistically significant.

| Species | Coefficient | Estimate | Standard Error | t-value | P(> t) | Residual Degrees of Freedom |
|------------------------------------|---------------|----------|----------------|---------|---------|-----------------------------------|
| <i>Human</i> | Year | 0.46 | 2.834 | 0.161 | 0.872 | 5672 |
| | 2020:Suburban | -0.90 | 2.849 | -0.315 | 0.753 | 5672 |
| | 2020:Rural | -1.06 | 2.837 | -0.374 | 0.709 | 5672 |
| | 2020:Wild | 0.18 | 2.852 | 0.0630 | 0.950 | 5672 |
| <i>Multi-Species Carnivore</i> | Year | -1.38 | 1.910 | -0.721 | 0.471 | 702 |
| | 2020:Suburban | 1.37 | 1.920 | 0.716 | 0.474 | 702 |
| | 2020:Rural | 1.28 | 1.930 | 0.662 | 0.508 | 702 |
| | 2020:Wild | 1.45 | 1.935 | 0.751 | 0.453 | 702 |
| <i>Black Bears</i> | Year | -15.96 | 2937.104 | -0.005 | 0.996 | 702 |
| | 2020:Suburban | 30.30 | 3162.036 | 0.010 | 0.992 | 702 |
| | 2020:Rural | 0.14 | 3346.756 | 0.000 | 1.000 | 702 |
| | 2020:Wild | 16.14 | 2937.104 | 0.005 | 0.996 | 702 |
| <i>Bobcats</i> | Year | -0.06 | 1732.168 | 0.000 | 1.000 | 702 |
| | 2020:Suburban | 1.31 | 1732.169 | 0.001 | 0.999 | 702 |
| | 2020:Rural | 0.17 | 1732.169 | 0.000 | 1.000 | 702 |
| | 2020:Wild | 0.25 | 1732.169 | 0.000 | 1.000 | 702 |
| <i>Coyotes</i> | Year | -1.09 | 1.408 | -0.771 | 0.441 | 702 |
| | 2020:Suburban | 1.34 | 1.430 | 0.938 | 0.349 | 702 |
| | 2020:Rural | 0.90 | 1.436 | 0.627 | 0.531 | 702 |
| | 2020:Wild | 1.22 | 1.436 | 0.853 | 0.394 | 702 |
| <i>Fisher</i> | Year | -0.53 | 0.942 | -0.558 | 0.577 | 702 |
| | 2020:Suburban | 0.30 | 1.323 | 0.224 | 0.823 | 702 |
| | 2020:Rural | 1.286 | 1.085 | 1.185 | 0.237 | 702 |
| | 2020:Wild | -0.40 | 1.234 | -0.325 | 0.745 | 702 |

| | | | | | | |
|-----------------------------|---------------|--------|----------|--------|---------|-----|
| <i>Gray Fox</i> | Year | -14.34 | 772.376 | -0.019 | 0.985 | 702 |
| | 2020:Suburban | 14.14 | 772.376 | 0.018 | 0.985 | 702 |
| | 2020:Rural | 15.24 | 772.376 | 0.020 | 0.984 | 702 |
| | 2020:Wild | 13.75 | 772.370 | 0.018 | 0.986 | 702 |
| <i>Northern Raccoon</i> | Year | -2.30 | 3.815 | -0.603 | 0.547 | 702 |
| | 2020:Suburban | 2.34 | 3.823 | 0.613 | 0.54023 | 702 |
| | 2020:Rural | 2.162 | 3.831 | 0.564 | 0.573 | 702 |
| | 2020:Wild | 2.29 | 3.836 | 0.596 | 0.552 | 702 |
| <i>Red Fox</i> | Year | -0.06 | 1776.603 | 0.000 | 1.000 | 702 |
| | 2020:Suburban | -0.42 | 1776.603 | 0.000 | 1.000 | 702 |
| | 2020:Rural | 0.12 | 1776.604 | 0.000 | 1.000 | 702 |
| | 2020:Wild | 0.59 | 1776.604 | 0.000 | 1.000 | 702 |

Table 6. Human Change Proportion Models

Summary of binomial and quasibinomial proportion models on mean carnivore capture rates as a function of change in mean human capture rates between 2020 and 2019. All mammal species models assume a quasi-binomial distribution, except for the fisher which assumes a binomial distribution and so the reported “t-value” is a z-value. Bolded values are statistically significant.

| Species | Coefficient | Estimate | Standard Error | t-value or z-value (z value = #) | P(> t) | Residual Degrees of Freedom |
|------------------------------------|--------------|---------------|----------------|--|--------------|-----------------------------------|
| <i>Multi-Species Carnivore</i> | Human Change | -0.028 | 0.046 | -0.602 | 0.552 | 29 |
| <i>Black Bear</i> | Human Change | 1.790 | 2.493 | 0.720 | 0.495 | 7 |
| <i>Bobcat</i> | Human Change | -0.671 | 0.689 | -0.974 | 0.346 | 16 |
| <i>Coyote</i> | Human Change | 0.026 | 0.074 | 0.346 | 0.732 | 29 |
| <i>Fisher</i> | Human Change | -0.890 | 0.351 | -2.545[#] | 0.011 | 10 |
| <i>Gray Fox</i> | Human Change | -0.049 | 0.182 | -0.267 | 0.794 | 12 |
| <i>Northern Raccoon</i> | Human Change | -0.059 | 0.074 | -0.794 | 0.434 | 28 |
| <i>Red Fox</i> | Human Change | -0.026 | 0.037 | -0.702 | 0.491 | 20 |

Table 7. Models of Proportional Changes in Human Activity Across Developments

Results from generalized linear interaction models examining the potential interaction of human change and development type on species capture rates. All mammal species models assume a quasi-binomial distribution, with the exception of the fisher and gray fox, which assume a binomial distribution and so have z-values as indicated by the # symbol. The “All Carnivores” model examined the capture rates of all 16 mammalian carnivores detected in both Snapshot USA projects, not just those that had enough observations to be modeled individually. Bolded values are statistically significant.

| Species | Coefficient | Estimate | Standard Error | T or z-value (z value = #) | P(> t) | Residual Degrees of Freedom |
|------------------------------------|------------------------|------------|----------------|-------------------------------|---------|--------------------------------|
| <i>Multi-Species Carnivore</i> | Intercept | 25.23 | 54.61 | 0.462 | 0.648 | 23 |
| | Human change: Suburban | 4932.95 | 10184.02 | 0.484 | 0.633 | 23 |
| | Human change: Rural | 4932.36 | 10184.02 | 0.484 | 0.633 | 23 |
| | Human change: Wild | 4935.37 | 10184.02 | 0.485 | 0.633 | 23 |
| <i>Black Bears</i> | Intercept | -1.740e+01 | 1.430e+04 | -0.001 | 0.999 | 4 |
| | Human change: Suburban | N/A | N/A | N/A | N/A | 4 |
| | Human change: Rural | -1.343e+00 | 1.653e+04 | 0.000 | 1.000 | 4 |
| | Human change: Wild | N/A | N/A | N/A | N/A | 4 |
| <i>Bobcats</i> | Intercept | -49639.4 | 8253428.5 | -0.006 | 0.995 | 12 |
| | Human change: Suburban | 2.45 | 3.452 | 0.710 | 0.491 | 12 |
| | Human change: Rural | N/A | N/A | N/A | N/A | 12 |
| | Human change: Wild | 0.914 | 3.184 | 0.287 | 0.779 | 12 |
| <i>Coyotes</i> | Intercept | 257.0 | 42846.3 | 0.006 | 0.995 | 23 |
| | Human change: Suburban | 49639.1 | 8253428.5 | 0.006 | 0.995 | 23 |
| | Human change: Rural | 49639.5 | 8253428.5 | 0.006 | 0.995 | 23 |
| | Human change: Wild | 49642.2 | 8253428.5 | 0.006 | 0.995 | 23 |
| <i>Fisher</i> | Intercept | -13.41 | 18.106 | -0.741 [#] | 0.459 | 4 |
| | Human change: Suburban | -2403.32 | 3371.281 | -0.713 [#] | 0.476 | 4 |
| | Human change: Rural | -2422.14 | 5977.593 | -0.405 [#] | 0.685 | 4 |
| | Human change: Wild | -2391.02 | 3371.299 | -0.709 [#] | 0.478 | 4 |
| <i>Gray Fox</i> | Intercept | -1.403e+01 | 1.641e+06 | 0 [#] | 1 | 6 |
| | Human change: Suburban | 1.804e+03 | 3.039e+08 | 0 [#] | 1 | 6 |
| | Human change: Rural | 1.776e+03 | 3.039e+08 | 0 [#] | 1 | 6 |
| | Human change: Wild | 1.234e+03 | 3.039e+08 | 0 [#] | 1 | 6 |

| | | | | | | |
|-------------------------|------------------------|---------|----------|--------|-------|----|
| <i>Northern Raccoon</i> | Intercept | 42.24 | 159.03 | 0.266 | 0.793 | 22 |
| | Human change: Suburban | 8104.28 | 28993.74 | 0.280 | 0.782 | 22 |
| | Human change: Rural | 8103.38 | 28993.74 | 0.279 | 0.782 | 22 |
| | Human change: Wild | 8109.22 | 28993.74 | 0.280 | 0.782 | 22 |
| <i>Red Fox</i> | Intercept | -0.45 | 0.661 | -0.686 | 0.503 | 16 |
| | Human change: Suburban | -0.72 | 2.608 | -0.276 | 0.786 | 16 |
| | Human change: Rural | N/A | N/A | N/A | N/A | 16 |
| | Human change: Wild | 6.55 | 4.313 | 1.518 | 0.149 | 16 |

REFERENCES CITED:

- AMJC Staff. A Timeline of COVID-19 Developments in 2020. AJMC. (1 January 2021).
- Bateman, P. W., and P. A. Fleming. 2012a. Big city life: Carnivores in urban environments. *Journal of Zoology* **287**(1):1-23.
- Bates, A. E., R. B. Primack, P. Moraga, and C. M. Duarte. 2020. COVID-19 pandemic and associated lockdown as a “Global Human Confinement Experiment” to investigate biodiversity conservation. *Biological Conservation* **248**: 108665.
- Battisti, C. 2021. Not only jackals in the cities and dolphins in the harbours: less optimism and more systems thinking is needed to understand the long-term effects of the COVID-19 lockdown. *Biodiversity* 1-5.
- BBC. Coronavirus: Wild animals enjoy freedom of a quieter world. BBC News. (29 April 2020).
- Benson, J. F., P. J. Mahoney, and B. R. Patterson. 2015. Spatiotemporal variation in selection of roads influences mortality risk for canids in an unprotected landscape. *Oikos* **124**(12):1664-1673.
- Coffin, A. W. 2007. From roadkill to road ecology: A review of the ecological effects of roads. *Journal of Transport Geography* **15**(5): 396-406.
- Corradini, A., W. Peters, L. Pedrottic, M. Hebblewhite, N. Bragalantie, C. Tattonig, M. Ciollia, and F. Cagnacci. 2021. Animal movements occurring during COVID-19 lockdown were predicted by connectivity models. *Global Ecology and Conservation* **32**: e01895.
- Corlett, R. T., R. B. Primack, V. Devictor, B. Maas, V. R. Goswami, A. E. Bates, L. P. Koh, T. J. Regan, R. Loyola, R. J. Pakeman, G. S. Cumming, A. Pidgeon, D. Johns, and R. Roth. 2020a. Impacts of the coronavirus pandemic on biodiversity conservation. *Biological Conservation* **246**: 108571.
- Cove, M. V., R. Kays, H. Bontrager, C. Bresnan, M. Lasky, T. Frerichs, R. Klann, T. E. Lee Jr., S. C. Crockett, A. P. Crupi, K. C. B. Weiss, H. Rowe, T. Sprague, J. Schipper, C. Tellez, C. A. Lepczyk, J. Fantle-Lepczyk, S. LaPoint, J. Williamson, M. Fisher-Reid, S. M. King, A. J. Bebeko, P. Chrysafis, A. J. Jensen, D. S. Jachowski, J. Sands, K. A. MacCombie, D. J. Herrera, M. van der Merwe, T. W. Knowles, R. V. Horan III, M. S. Rentz, L. S. E. Brandt, C. Nagy, B. T. Barton, W. C. Thompson, S. P. Maher, A. K. Darracq, G. Hess, A. W. Parsons, B. Wells, G. W. Roemer, C. J. Hernandez, M. E. Gompper, S. L. Webb, J. P. Vanek, D. J. R. Lafferty, A. M. Bergquist, T. Hubbard, T. Forrester, D. Clark, C. Cincotta, J. Favreau, A. N. Facka, M. Halbur, S. Hammerich, M. Gray, C. Rega-Brodsy, C. Durbin, E. A. Flaherty, J. M. Brooke, S. S. Coster, R. G. Lathrop, K. Russell, D. A. Bogan, R. Cliché, H. Shamon, M. T. R. Hawkins, S. B. Marks, R. C. Lonsinger, M. T. O'Mara, J. A. Compton, M. Fowler, E. L. Barthelmess, K. E. Andy, J. L. Belant, D. E. Beyer Jr., T. M. Kautz, D. G. Scognamillo, C. M. Schalk, M. S. Leslie, S. L. Nasrallah, C. N. Ellison, C. Ruthven, S. Fritts, J. Tleimat, M. Gay, C. A. Whittier, S. A. Neiswenter, R. Pelletier, B. A. DeGregorio, E. K. Kuprewicz, M. L. Davis, A. Dykstra, D. S. Mason, C. Baruzzi, M. A. Lashley, D. R. Risch, M. R. Price, M. L. Allen, L. S. Whipple, J. H. Sperry, R. H. Hagen, A. Mortelliti, B. E. Evans, C. E. Studds, A. P. K. Sirén, J. Kilborn, C. Sutherland, P. Warren, T. Fuller, N. C. Harris, N. H. Carter, E. Trout, M. Zimova, S. T. Giery, F. Iannarilli, S. D. Higdon, R. S. Revord, C. P. Hansen, J. J. Millsaugh, A. Zorn, J. F. Benson, N. H. Wehr, J. N. Solberg, B. D. Gerber, J. C. Burr, J. Sevin, A. M. Green, Ç H. Şekercioğlu, M. Pendergast, K. A. Barnick, A. J. Edelman, J. R. Wasdin, A. Romero, B. J. O'Neill, N. Schmitz, J.

- M. Alston, K. M. Kuhn, D. B. Lesmeister, M. A. Linnell, C. L. Appel, C. Rota, J. L. Stenglein, C. Anhalt-Depies, C. Nelson, R. A. Long, K. Jo Jaspers, K. R. Remine, M. J. Jordan, D. Davis, H. Hernández-Yáñez, J. Y. Zhao, and W. J. McShea. 2021a. SNAPSHOT USA 2019: a coordinated national camera trap survey of the United States. *Ecology* **102**(6): e03353.
- Crooks, K. R. 2002. Relative sensitivities of mammalian carnivores to habitat fragmentation. *Conservation Biology* **16**(2): 488-502.
- Cukor, J., R. Linda, K. Mahlerová, Z. Vacek, M. Faltusová, P. Marada, F. Havránek, and V. Hart. 2021. Different patterns of human activities in nature during Covid-19 pandemic and African swine fever outbreak confirm direct impact on wildlife disruption. *Scientific Reports* 2021 **11**:11(1):1-11.
- Derryberry, E. P., J. N. Phillips, G. E. Derryberry, M. J. Blum, and D. Luther. 2020b. Singing in a silent spring: Birds respond to a half-century soundscape reversion during the COVID-19 shutdown. *Science* **370**(6516): 575-579.
- Doherty, T. S., G. C. Hays, and D. A. Driscoll. 2021a. Human disturbance causes widespread disruption of animal movement. *Nature Ecology and Evolution* **5**(4): 513-519.
- Ekstrand, K., A. J. Flanagan, I. E. Lin, B. Vejseli, A. Cole, A. P. Lally, R. L. Morris, and K. N. Morgan. 2021. Animal Transmission of SARS-CoV-2 and the Welfare of Animals during the COVID-19 Pandemic. *Animals: an Open Access Journal from MDPI* **11**(7): 2044.
- Flores-Morales, M., J. Vázquez, A. Bautista, L. Rodríguez-Martínez, and O. Monroy-Vilchis. 2019. Response of two sympatric carnivores to human disturbances of their habitat: the bobcat and coyote. *Mammal Research* **64**(1): 53-62.
- Gaynor, K. M., C. E. Hojnowski, N. H. Carter, and J. S. Brashares. 2018a. The influence of human disturbance on wildlife nocturnality. *Science* **360**(6394):1232-1235.
- George, S. L., and K. R. Crooks. 2006. Recreation and large mammal activity in an urban nature reserve. *Biological Conservation* **133**(1):107-117.
- Gilby, B., C. Henderson, A. Olds, J. Ballantyne, E. Bingham, B. Elliott, T. Jones, O. Kimber, J. Mosman, and T. Schlacher. 2021. Potentially negative ecological consequences of animal redistribution on beaches during COVID-19 lockdown. *Biological Conservation* **253**: 108926.
- Gordo, O., L. Brotons, S. Herrando, and G. Gargallo. 2021. Rapid behavioural response of urban birds to COVID-19 lockdown. *Proceedings of the Royal Society B* **288**: 20202513.
- Gouda, K., P. Singh, P. Nikhilasuma, M. Benke, R. Kumari, G. Agnihotri, K. Hungund, M. Chandrika, B. Kantha Rao, V. Ramesh, S. Himesh. 2021. Assessment of air pollution status during COVID-19 lockdown (March–May 2020) over Bangalore City in India. *Environmental Monitoring and Assessment* **193**(7): 1-13.
- Hale, V.L., P.M. Dennis, D.S. McBride, J.M. Nolting, C. Madden, D. Huey, M. Ehrlich, J. Grieser, J. Winston, D. Lombardi, S. Gibson, L. Saif, M.L. Killian, K. Lantz, R. M. Tell, M. Torchetti, S. Robbe-Austerman, M. I. Nelson, S. A. Faith, and A. S. Bowman. 2022. SARS-CoV-2 infection in free-ranging white-tailed deer. *Nature* **602**: 481–486.

- Hentati-Sundberg, J., Berglund, P. A., Hejdström, A., & Olsson, O. (2021). COVID-19 lockdown reveals tourists as seabird guardians. *Biological Conservation*, 254, 108950.
- Hockenhull, J., K. Squibb, A. Cameron, J. M. Williams, H. Randle, and D. Marlin. 2021. How Has the COVID-19 Pandemic Affected the Way We Access and Interact with the Countryside and the Animals within It? *Animals* 2021, Vol. 11, page 2281 **11**(8):2281.
- iNaturalist. Available from <https://www.inaturalist.org>. Accessed [May 9, 2022].
- Johnson, W.A., and A.W. Todd. 1985. Fisher, *Martes pennanti*, behavior in proximity to human activity. *The Canadian Field Naturalist*, **99**: 367-369.
- Kays, Roland. eMammal. (Producer). (2021). *Snapshot 2021 Welcome Webinar*. [Video]. https://ncsu.zoom.us/rec/play/4eVJhsmiGCYuJMBwuYijnoXTYfv2Kf2O8s7EBn7VXc4GYjPVjoT2ijoI4hI5UQwBksbP4PXaXqHcZMfG.cFzMgbmrpuZkKwqv?startTime=1628269066000&x_zm_rtaid=2x2MMNM1TKWo6puIsD1VRg.1628523364536.a8a2075143346fafc473d72bd032a403&x_zm_rhtaid=578
- Kordosky, J.R., E. M. Gese, C. M. Thompson, P. A. Terletzky, K. L. Purcell, and J.D. Schneiderman. 2021. Landscape use by fishers (*Pekania pennanti*): core areas differ in habitat than the entire home range. *Canadian Journal of Zoology* **99**: 289-297.
- Lamb, C. T., A. T. Ford, B. N. McLellan, M. F. Proctor, G. Mowat, L. Ciarniello, S. E. Nielsen, and S. Boutin. 2020. The ecology of human–carnivore coexistence. *Proceedings of the National Academy of Sciences of the United States of America* **117**(30):17876-17883.
- Lanzoni, W. and K. Almond. With cities on lockdown, animals are finding more room to roam. CNN. (1 May 2020).
- Le Quéré, C., R. B. Jackson, M. W. Jones, A. J. P. Smith, S. Abernethy, R. M. Andrew, A. J. De-Gol, D. R. Willis, Y. Shan, J. G. Canadell, P. Friedlingstein, F. Creutzig, and G. P. Peters. 2020. Temporary reduction in daily global CO₂ emissions during the COVID-19 forced confinement. *Nature Climate Change* **10**(7): 647-653.
- Lo Parrino, E., M. Falaschi, R. Manenti, and G. F. Ficetola. 2021. Lockdown policy effects on invasive species: a perspective. *Biodiversity* **22**(1-2): 35-40.
- Lokhandwala, S., and P. Gautam. 2020a. Indirect impact of COVID-19 on environment: A brief study in Indian context. *Environmental research* **188**:109807.
- Łopucki, R., I. Kitowski, M. Perlińska-Teresiak, and D. Klich. 2021a. How Is Wildlife Affected by the COVID-19 Pandemic? Lockdown Effect on the Road Mortality of Hedgehogs. *Animals* **11**:10.3390/ani11030868.
- Luther, D. A., J. Phillips, and E. P. Derryberry. 2016. Not so sexy in the city: urban birds adjust songs to noise but compromise vocal performance. *Behavioral Ecology* **27**(1): 332-340.
- Manenti, R., E. Mori, V. Di Canio, S. Mercurio, M. Picone, M. Caffi, M. Brambilla, G. F. Ficetola, and D. Rubolini. 2020a. The good, the bad and the ugly of COVID-19 lockdown effects on wildlife conservation: Insights from the first European locked down country. *Biological Conservation* **249**: 108728.

- Martin, J., M. Basille, B. van Moorter, J. Kindberg, D. Allainé, and J. E. Swenson. 2010. Coping with human disturbance: Spatial and temporal tactics of the brown bear (*Ursus arctos*). *Canadian Journal of Zoology* **88**(9): 875-883.
- McAloose, D., M. Laverack, L. Wang, M. L. Killian, L.C. Caserta, F. Yuan, P. K. Mitchell, K. Queen, M. R. Mauldin, E. D. Cronk, S.L. Bartlett, J. M. Sykes, S. Zec, T. Stokol, K. Ingeman, M. A. Delaney, R. Fredrickson, M. Ivančić, M. Jenkins-Moore, K. Mozingo, K. Franzen, N. H. Bergeson, L. Goodman, H. Wang, Y. Fang, C. Olmstead, C. McCann, P. Thomas, E. Goodrich, F. Elvinger, D.C. Smith, S. Tong, S. Slavinski, P. P. Calle, K. Terio, M. K. Torchetti, and D. G. Diel. 2020. From People to *Panthera*: Natural SARS-CoV-2 Infection in Tigers and Lions at the Bronx Zoo. *American Society for Microbiology mBio* **11**(5).
- Mervosh, S., D. Lu, and V. Swales. See Which States and Cities Have Told Residents to Stay at Home. The New York Times. (20 April 2020).
- Miller, H. Reopening America: A state-by-state breakdown of the status of coronavirus restrictions. CNBC. (9 July 2020).
- Montgomery, R. A., J. Raupp, and M. Parkhurst. 2021. Animal Behavioral Responses to the COVID-19 Quietus. *Trends in Ecology & Evolution* **36**(3): 184-186.
- Nickel, B. A., J. P. Suraci, M. L. Allen, and C. C. Wilmers. 2020a. Human presence and human footprint have non-equivalent effects on wildlife spatiotemporal habitat use. *Biological Conservation* **241**: 108383.
- Nisi, A. C., J. P. Suraci, N. Ranc, L. G. Frank, A. Oriol-Cotterill, S. Ekwanga, T. M. Williams, and C. C. Wilmers. 2022. Temporal scale of habitat selection for large carnivores: Balancing energetics, risk and finding prey. *Journal of Animal Ecology* **91**(1): 182-195.
- Oberosler, V., C. Groff, A. Iemma, P. Pedrini, and F. Rovero. 2017a. The influence of human disturbance on occupancy and activity patterns of mammals in the Italian Alps from systematic camera trapping. *Mammalian Biology* **87**: 50-61.
- Ordeñana, M. A., K. R. Crooks, E. E. Boydston, R. N. Fisher, L. M. Lyren, S. Siudyla, C. D. Haas, S. Harris, S. A. Hathaway, G. M. Turschak, A. K. Miles, and D. H. Van Vuren. 2010. Effects of urbanization on carnivore species distribution and richness. *Journal of Mammalogy* **91**(6): 1322-1331.
- Oude-Munnik, B.B., R.S. Sikkemadavid, F. Nieuwenhuijse, R. J. Molenaar, E. Munger, R. Molenkamp, A. Van Der Spek, P. Tolsma, A. Rietveld, M. Brouwer, N. Boumeester-Vincken, F. Harders, R. Hakze-Van Der Honing, M. C. A. Wegdam-Blans, R. J. Bouwstra, C. Geurtsvankessel, A. A. Van Der Eijk, F. M. Velkers, L. A. M. Smit, A. Stegeman, W. H. M. Van Der Poel, and M. P. G. Koopmans. 2020. Transmission of SARS-CoV-2 on mink farms between humans and mink and back to humans. *Science* **371**(6525): 172-177.
- Pepe, E., P. Bajardi, L. Gauvin, F. Privitera, B. Lake, C. Cattuto, and M. Tizzoni. 2020b. COVID-19 outbreak response, a dataset to assess mobility changes in Italy following national lockdown. *Scientific Data* **7**(1): 230.
- Radhika, C. Photos: Wildlife roams during the coronavirus pandemic. ABC News. (22 April 2020).

- Riley, S. P. D., R. M. Sauvajot, T. K. Fuller, E. C. York, D. A. Kamradt, C. Bromley, and R. K. Wayne. 2003. Effects of urbanization and habitat fragmentation on bobcats and coyotes in Southern California. *Conservation Biology* **17**(2): 566-576.
- Ritchie, H., E. Mathieu, L. Rodés-Guirao, C. Appel, C. Giattino, E. Ortiz-Ospina, J. Hasell, B. Macdonald, D. Beltekian and M. Roser (2020) - "Coronavirus Pandemic (COVID-19)". Published online at *OurWorldInData.org*. Retrieved from: 'https://ourworldindata.org/coronavirus' [Online Resource]
- Roll, U., I. Jarić, P. Jepson, A. L. da Costa-Pinto, B. R. Pinheiro, R. A. Correia, A. C. M. Malhado, and R. J. Ladle. 2021. COVID-19 lockdowns increase public interest in urban nature. *Frontiers in Ecology and the Environment* **19**(6): 320-322.
- Rupani, P. F., M. Nilashi, R. A. Abumalloh, S. Asadi, S. Samad, and S. Wang. 2020. Coronavirus pandemic (COVID-19) and its natural environmental impacts. *International Journal of Environmental Science and Technology* **17**(11): 4655-4666.
- Rutz, C., M. Loretto, A. E. Bates, S. C. Davidson, C. M. Duarte, W. Jetz, M. Johnson, A. Kato, R. Kays, T. Mueller, R. B. Primack, Y. Robert-Coudert, M. A. Tucker, M. Wikelski, and F. Cagnacci. 2020b. COVID-19 lockdown allows researchers to quantify the effects of human activity on wildlife. *Nature Ecology & Evolution* **4**(9): 1156-1159.
- Šálek, M., L. Drahníková, and E. Tkadlec. 2015. Changes in home range sizes and population densities of carnivore species along the natural to urban habitat gradient. *Mammal Review* **45**(1):1-14.
- Schulz, C., B. Martina, M. Mirolo, E. Müller, R. Klein, H. Volk, H. Egberink, M. Gonzalez-Hernandez, F. Kaiser, M. von Köckritz-Blickwede, and A. Osterhaus. 2021. SARS-CoV-2–Specific Antibodies in Domestic Cats during First COVID-19 Wave, Europe. *Emerging Infectious Diseases*, **27**(12): 3115-3118.
- Silva-Rodríguez, E. A., N. Gálvez, G. J. F. Swan, J. J. Cusack, and D. Moreira-Arce. 2021a. Urban wildlife in times of COVID-19: What can we infer from novel carnivore records in urban areas? *Science of the Total Environment* **765**: 142713.
- Shilling, F., T. Nguyen, M. Saleh, M. Kyaw, K. Tapia, G. Trujillo, M. Bejarano, D. Waetjen, J. Peterson, G. Kalisz, R. Sejour, S. Croston, and E. Ham. 2021. *Biological Conservation* **256**:109013.
- Sit, T.H.C., C.J. Brackman, S.M. Ip, S.M., K.W.S. Tam, P.Y.T. Law, E. M. W. To, V. Y. T. Yu, L. D. Sims, D. N. C. Tsang, D. K. W. Chu, R. A. P. M. Perera, L. L. M. Poon, and M. Peiris. Infection of dogs with SARS-CoV-2. 2020. *Nature* **586**: 776–778.
- Smith, J. A., J. P. Suraci, M. Clinchy, A. Crawford, D. Roberts, L. Y. Zannette, and C. C. Wilmsers. 2017. Fear of the human ‘super predator’ reduces feeding time in large carnivores. *Proceedings of the Royal Society B: Biological Sciences* **284**: 20170433.
- Soga, M., M. J. Evans, D. T. C. Cox, and K. J. Gaston. 2021. Impacts of the COVID-19 pandemic on human–nature interactions: Pathways, evidence and implications. *People and Nature* **3**(3): 518-527.

- Soh, M.C.K., R. Y. T. Pang, B. X. K. Ng, B. P.Y.H. Lee, A. H.B. Loo, and K.B.H. Er. 2021. Restricted human activities shift the foraging strategies of feral pigeons (*Columba livia*) and three other commensal bird species. *Biological Conservation* **253**: 108927.
- Suraci, J. P., K. M. Gaynor, M. L. Allen, P. Alexander, J. S. Brashares, S. Cendejas-Zarelli, K. Crooks, L. M. Elbroch, T. Forrester, A. M. Green, J. Haight, N. C. Harris, M. Hebblewhite, F. Isbell, B. Johnston, R. Kays, P. E. Lendrum, J. S. Lewis, A. McInturff, W. McShea, T. W. Murphy, M. S. Palmer, A. Parsons, M. A. Parsons, M. E. Pendergast, C. Pekins, L. R. Prugh, K. A. Sager-Fradkin, S. Schuttler, Ç H. Şekercioğlu, B. Shepherd, L. Whipple, J. Whittington, G. Wittemyer, and C. C. Wilmers. 2021. Disturbance type and species life history predict mammal responses to humans. *Global Change Biology* **27**(16):3718-3731.
- Terry, C., L. Zipf, M. Dietze, R. Primack. 2021. Effects of the COVID-19 pandemic on noise pollution in three protected areas in metropolitan Boston (USA). *Biological Conservation* **256**: 109039.
- Tigas, L. A, D.H. Van Vuren, and R.M. Sauvajot. 2002. Behavioral responses of bobcats and coyotes to habitat fragmentation and corridors in an urban environment. *Biological Conservation* **108**(3): 299-306.
- Tucker, M. A., Katrin Böhning-Gaese, W. F. Fagan, J. M. Fryxell, V. M. Bram, S. C. Alberts, A. H. Ali, A. M. Allen, N. Attias, T. Avgar, Hattie Bartlam-Brooks, B. Bayarbaatar, J. L. Belant, A. Bertassoni, D. Beyer, L. Bidner, F. M. v. Beest, S. Blake, N. Blaum, C. Bracis, D. Brown, Nico de Bruyn, P. J., F. Cagnacci, J. M. Calabrese, Constança Camilo-Alves, Simon Chamaillé-Jammes, A. Chiaradia, S. C. Davidson, T. Dennis, S. DeStefano, D. Diefenbach, Iain Douglas-Hamilton, J. Fennessy, C. Fichtel, W. Fiedler, C. Fischer, I. Fischhoff, C. H. Fleming, A. T. Ford, S. A. Fritz, B. Gehr, J. R. Goheen, E. Gurarie, M. Hebblewhite, M. Heurich, A. J. Mark Hewison, C. Hof, E. Hurme, L. A. Isbell, René Janssen, F. Jeltsch, P. Kaczensky, A. Kane, P. M. Kappeler, M. Kauffman, R. Kays, D. Kimuyu, F. Koch, B. Kranstauber, S. LaPoint, P. Leimgruber, D. C. L. John, Pascual López-López, A. Catherine Markham, J. Mattisson, P. M. Emilia, U. Mellone, E. Merrill, Guilherme de Miranda Mourão, R. G. Morato, N. Morellet, T. A. Morrison, Samuel L. Díaz-Muñoz, A. Mysterud, D. Nandintsetseg, R. Nathan, A. Niamir, J. Odden, Robert B. O'Hara, Luiz Gustavo R. Oliveira-Santos, K. A. Olson, B. D. Patterson, d. P. Rogerio Cunha, L. Pedrotti, Björn Reineking, M. Rimmler, T. L. Rogers, M. R. Christer, C. S. Rosenberry, D. I. Rubenstein, K. Safi, Sonia Saïd, N. Sapir, H. Sawyer, M. S. Niels, N. Selva, A. Sergiel, E. Shiilegdamba, P. S. João, N. Singh, E. J. Solberg, O. Spiegel, O. Strand, S. Sundaresan, W. Ullmann, U. Voigt, J. Wall, D. Wattles, M. Wikelski, C. C. Wilmers, J. W. Wilson, G. Wittemyer, Filip Zięba, Tomasz Zwijacz-Kozica, and T. Mueller. 2018b. Moving in the Anthropocene: Global reductions in terrestrial mammalian movements. *Science* **359**(6374):466-469.
- The urban wild: animals take to the streets amid lockdown – in pictures. The Guardian. (22 April 2020).
- Ulloa, J., A. Hernández-Palma, O. Acevedo-Charry, B. Gómez-Valencia, C. Cruz-Rodríguez, Y. Herrera-Varón, M. Roa, S. Rodríguez-Buriticá, and J. Ochoa-Quintero. 2021. Listening to cities during the COVID-19 lockdown: How do human activities and urbanization impact soundscapes in Colombia?. *Biological Conservation* **255**: 108996.
- USDA APHIS, 2021. *Confirmed Cases of SARS-CoV-2 in Animals in the United States*, <https://www.aphis.usda.gov/aphis/dashboards/tableau/sars-dashboard>.

- Vardi, R., O. Berger-Tal, and U. Roll. 2021. iNaturalist insights illuminate COVID-19 effects on large mammals in urban centers. *Biological Conservation* **254**:108953.
- Washington Post Staff. Where states reopened and cases spiked after the U.S. shutdown. The Washington Post. (11 September 2020).
- Whittington, J., C. C. St. Clair, and G. Mercer. 2005. Spatial responses of wolves to roads and trails in mountain valleys. *Ecological Applications* **15**(2): 543-553.
- Wilmers, C.C., A.C. Nisi, and N. Ranc. COVID-19 suppression of human mobility releases mountain lions from a landscape of fear. 2021. *Current Biology* **31**(17): 3952-3955e3.