Behavioral responses of terrestrial mammals to COVID-19 lockdowns

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COVID-19 lockdowns in early 2020 reduced human mobility, providing an opportunity to disentangle its effects on animals from those of landscape modifications. Using GPS data, we compared movements and road avoidance of 2300 terrestrial mammals (43 species) during the lockdowns to the same period in 2019. Individual responses were variable, with no change in average movements or road avoidance behavior, likely due to variable lockdown conditions. However, under strict lockdowns, 10-day 95th percentile displacements increased by 73%, suggesting increased landscape permeability. Animals' 1-hour 95th percentile displacements declined by 12%, and animals were 36% closer to roads in areas of high human footprint, indicating reduced avoidance during lockdowns. Overall, lockdowns rapidly altered some spatial behaviors, highlighting variable but substantial impacts of human mobility on wildlife worldwide.

In 2020, governments around the world introduced lockdown measures in an attempt to curb the spread of the novel SARS-CoV-2 virus (COVID-19). This resulted in a drastic reduction in human mobility including human confinement to living quarters, closure of recreation and protected areas, and reductions in the movement of vehicles and their associated by-products (e.g., noise and pollutants) (*1*). This 'anthropause' provides a unique opportunity to quantify the effects of human mobility on wildlife by decoupling these from landscape modification effects (e.g., roads) (*2*, *3*). It is established that anthropogenic landscape modifications impact how animals use habitats (*4*) and interact with each other (*5*). For example, human infrastructure may induce various behavioral responses in animals, including avoidance (*6*), shifts in movement speed or habitat selection near roads (*7*), and altered diurnal patterns of habitat use (*8*). In addition to these landscape modification effects, animals can react directly to the presence and activity of humans (*9*). These often are perceived as a risk (*10*), which can lead to changes in habitat use due to the avoidance of areas heavily used by humans, increased energetic costs and physiological stress (*11*), and altered demography (e.g., reduced fecundity) (*12*). As large-scale, high-resolution human mobility data are rare, our ability to decouple the effects of landscape modification and human mobility has been limited. In particular, little is known about the overall impact of human mobility on terrestrial mammalian behavior across species and continents. Here, we make use of the quasi-experimental alteration of human mobility during COVID-19 lockdowns in early 2020 to study the effect of human mobility on animal behavior, specifically on movement and road avoidance in terrestrial mammals.

Using animal tracking data to study behavioral changes during lockdowns

We used Global Positioning System (GPS) tracking data to evaluate how 2,300 individual terrestrial mammals, representing 43 species across 76 studies (Fig. 1 and Table S1), changed their spatial behavior during the initial 2020 COVID-19 lockdowns compared to the same time period a year earlier. For the initial 2020 lockdown period we included the date of the first government mandated lockdown in each study area (between 1 February and 28 April, 2020) until 15 May, 2020. We used matching time periods from 2019 as a baseline for comparison. Individuals were tracked for an average of 59 days per observation period (range: 10 – 72 days). We focused on two behaviors: displacement distance (straight-line distance between two consecutive GPS locations) and distance to the nearest road. As changes in displacement might be scale-dependent, we considered displacements at 1-hour and 10-day intervals based on Tucker *et al.* (*13*). Changes in 1-hour displacements reflect immediate responses to altered human mobility (*14*). We expected that reduced human mobility during strict lockdowns would lead to an overall reduction in 1-hour displacements due to fewer avoidance and escape responses, or easier access to foraging areas due to reduced disturbance as has been previously shown for red deer (*14*). For the 10-day displacements, we expected a different response because previous analyses of the effects of land-modifications on mammal movements (*13*) have shown longer displacement distances in areas with low human footprint. Accordingly, displacement distances at the 10-day scale might be longer under lockdown conditions as animals might be able to cross barriers linked to human mobility during lockdowns (e.g., roads with lower traffic volumes during lockdowns). For each time scale, we evaluated the 50th (median) and 95th percentiles of the displacements. Median displacements represent a suite of behaviors including resting and sleeping (1-hour scale) or residency in the same area (10-day scale). The 95th percentile eliminates stationary behaviors and represents longer and more directed movements such as avoidance behaviors on the 1-hour time scale and long-distance displacements at the 10-day time scale (*13*). Because longer displacements generally have a greater probability of encountering humans or infrastructure, we expected stronger responses for the 95th-percentile displacements.

While roads may benefit some species by providing foraging opportunities or movement corridors (*15*), their effects are more often negative as they not only create barriers but also increase mortality and facilitate human access to remote areas (*16*). We expected that declines in vehicular traffic during the early 2020 lockdowns (*17*) would reduce the perceived risk level and mammals would therefore be closer to roads.

To evaluate possible changes in displacements or distance to the nearest roads between the lockdown and baseline periods, we calculated log response ratios for each measure (medians and 95th percentiles of the 1-hour and 10-day displacements, and distance to roads) and each individual. Our analyses of the response ratios involved a two-step process following previous work (*18*). First, we used Bayesian mixed-effects models to examine the overall effect of lockdowns on movement distance and distance to the nearest road (i.e., intercept-only model) (*19*). Second, we used Bayesian mixed-effects models to examine possible relationships between the response ratios and various covariates indicative of environmental context (i.e., lockdown strictness, human footprint and productivity) and species traits (i.e., body mass, diet, activity and relative brain size) (*19*). For both steps of the analyses, we included random effects for species-study combined to account for non-independence between effect sizes from the same study and/or species. For the second step of the analysis, we included the Oxford COVID-19 Government Response Tracker Stringency Index (SI, (*20*)) in our models to examine country-level variation in lockdown strictness, ranging from 0 (no lockdown) to 100 (very strict lockdown; e.g., confined to home). We used the Human Footprint Index (HFI, 1-km resolution, (*21*)) as a proxy of direct and indirect human activities including roads, agriculture and human population density. The HFI values range from 0 to 50, where low values represent areas relatively undisturbed by humans and high values represent areas with high human development levels. We expected stronger behavioral responses to lockdowns in areas with a higher human footprint and in countries with stricter lockdowns for both displacement distances and distance to roads. To account for movement capacity, differences in movements related to diet, activity cycle and behavioral flexibility, we included body mass (range: 10 – 4000 kg), diet (carnivore, omnivore, herbivore), activity (diurnal or nocturnal) and relative brain size as additional explanatory variables. Finally, we also included the between-year difference in Normalized Difference Vegetation Index (NDVI) between 2019 and 2020 to account for potential differences in seasonality and productivity. We fit models for the median and 95th percentile of the 1-hour and 10-day displacements, and for distance to road including all covariates for lockdown strictness, environmental context and species traits (*19*). We report our results as the percentage increase or decrease in movement distance or distance to roads by back-transforming the response ratios (*19*) and reporting the 95% credible intervals (CI).

Changes in movement displacements during lockdowns

We found an average 12% reduction in 1-hour 95th-percentile displacements when evaluating the impact of only the lockdown itself (intercept only model, 95% CI: 1 – 22%, Fig. 2, Table S2). This may indicate reduced avoidance and escape behavior of humans (e.g., no need to travel longer distances to avoid humans (*22*, *23*)) as a result of altered human mobility levels during lockdowns. When exploring potential correlates of this response, no covariates had an effect that differed from zero (Table S3). For the 1-hour median displacements, we found no overall effect (Table S2) and again, no effect of the covariates (Table S4). Taken together, these results suggest that responses at the 1-hour scale were highly variable and not dependent on the selected species traits (body mass, diet, activity or relative brain size) or on the variables describing the local context (lockdown stringency or HFI).

The overall lockdown response was not different from zero for the 10-day 95th-percentile or long-distance displacements (15%, 95% CI; -30–5%, Fig. 2B, Table S2). However, when exploring the covariates that might explain variation in response ratios, the 95% credible intervals of the Stringency Index did not overlap zero (Table S5), with displacements increasing 73% on average in areas of stricter lockdown (i.e., areas with an SI of 90; Fig. 3A). This may indicate that tighter restrictions on human movements, including confinement to living spaces and reduced human mobility in green spaces (e.g., Italy and France; Fig. 1) led to increased landscape permeability for mammals. This effect of human mobility is similar in magnitude to previous work that used the same displacement metric but examined the effect of permanent landscape alterations (land conversion and infrastructure) on terrestrial mammal movements (*13*). While this work used a spatial comparison rather than comparing changes over time within the same individuals, they found a decline of 67% of the 10-day 95th-percentile displacements in areas where the human footprint is high (*13*). We found no effect of the remaining covariates (HFI, body mass, diet, activity or relative brain size) (Tables S5).

We found that the 10-day 95th-percentile displacements in areas with lower lockdown stringency (SI values 50 to 70) were actually shorter (on average 22–72%) than during the lockdown than in 2019 (Fig. 3A). The movement reductions may reflect increased human mobility in semi-natural areas such as parks and other green spaces (*24*, *25*). In fact, green space use by people in some areas of intermediate lockdown increased up to 350% (*25*). In addition to the lockdown effects, seasonality played a role in determining 10-day movement distances. The 10-day median (Fig. S1) and 95th percentile (Fig. 3B) displacements were longer during 2020, when we observed higher NDVI values compared to 2019, which may have led some individuals to begin their spring migration or reproduction earlier in 2020. For the 10-day median displacements, we found no overall lockdown effect (Table S2), no effect of lockdown stringency, and no effects of the other covariates (HFI, body mass, diet, activity or relative brain size) (Tables S6). This difference in responses between 95% and median movements suggests that lockdown stringency may have impacted mainly wide-ranging behavior, such as migratory movements, long-distance dispersal, exploratory excursions or long displacements within individuals' home ranges.

Mammals were closer to roads during lockdowns

We found no overall lockdown response in the distance of individuals to roads (-1%, 95% CI; -5 – 3%, Table S2) nor a relationship with the Stringency Index, NDVI difference or species traits (Table S7). However, the response ratios were negatively related to HFI, showing that animals in areas with a high human footprint were on average 36% closer to roads during lockdown (HFI = 36, Fig. 4). In many parts of the world, traffic volume was significantly reduced during lockdowns (*26*, *27*), which in turn lessened the impact of roads on animals, including reduced barrier effects (*15*, *28*) and road-kill numbers (*17*, *29*). Our findings add context to these previous results by demonstrating that not only were road-kill numbers lower during lockdown (*17*, *29*), but also animals were closer on average to roads in human-modified areas, indicating reduced avoidance.

Overall, we detected three main signals of a lockdown effect on terrestrial mammal behavior, although they were heterogeneously distributed across species and populations. These were (i) reductions in 1-hour 95th-percentile displacements suggesting relaxed avoidance behavior, reduced disturbance, and/or fewer escape responses, (ii) increased 10-day 95th-percentile displacements under strict lockdown conditions, suggesting increased landscape permeability, and (iii) closer proximity to roads in areas heavily used by humans, suggesting a reduction in traffic disturbance. A number of species-specific case studies are consistent with these findings. For example, evidence suggests that during the lockdowns, mountain lions' (*Puma concolor*) usual aversion to urban edges ceased (*9*), crested porcupine (*Hystrix cristata*) abundance increased in urban areas (*30*), diurnal activity of invasive Eastern cottontails (*Sylvilagus floridanus*) increased (*30*), and brown bears (*Ursus arctos*) exploited novel connectivity corridors (*12*).

Despite these three general responses to the lockdowns, considerable variation in responses existed across species and study regions (Fig. 2). This variability highlights that lockdown impacts are highly context dependent. For example, mountain lions explored more urban areas during the lockdown, while other species including American black bears (*Ursus americanus*), bobcats (*Lynx rufus*) and coyotes (*Canis latrans*) in the same areas did not (*31*). In addition, in our study, lockdown stringency was only measured at the country-level and did not account for local variability in restrictions. We also note that our data were predominantly from Europe and North America, so our results should be interpreted with caution for other regions. Finally, we note that a given movement metric could capture different behaviors in different species, especially at the 10-day scale, whereas displacements could capture behaviors ranging from within home range movements to dispersal.

We show that human mobility is a key driver of some terrestrial mammal behaviors, with a magnitude potentially similar to that of landscape modifications. Therefore, when evaluating human impacts on animal behavior, or designing mitigation measures, it is important that both physical landscape alteration and human mobility are considered (see also (*32*)). Disentangling the effects of human mobility and landscape modification will allow the implementation of conservation measures specifically targeted at mitigating the impacts of human mobility, such as enticements to adjust timing, frequency and volume of traffic in areas important for animal movement. Mammals have been living with human disturbance for a long time. Yet, we demonstrate that many wildlife populations retain the capacity to respond to changes in human behavior, providing a positive outlook for future mitigation strategies designed to maintain animal movement and the ecosystem functions they provide.

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Competing Interests: H.H.T.P is a Member of the Welgevonden Scientific Advisory Committee and A.D.M. is a Senior Advisor for Wildlife Conservation for the US Department of Agriculture. C.R. is the President of the International Bio-Logging Society, a member of an expert group providing advice on animal culture and social complexity to the Convention on the Conservation of Migratory Species of Wild Animals (CMS), and member of the advisory committee of a WILDLABS research program aimed at identifying research and funding priorities in movement ecology

Data and materials availability: The full dataset used in the final analyses (33) and associated code (34) are available at datadryad.org. A subset of the spatial coordinate datasets is available from Zenodo (34). Certain datasets of spatial coordinates will be available only through requests made to the authors due to conservation and Indigenous sovereignty concerns (see Table S1 for more information on data use restrictions and contact information for data requests). These sensitive data will be made available upon request to qualified researchers for research purposes, provided that the data use will not threaten the study populations, such as by distribution or publication of the coordinates or detailed maps. Some datasets, such as those overseen by government agencies, have additional legal restrictions on data sharing, and researchers may need to formally apply for data access. Collaborations with data holders are generally encouraged, and in cases where data are held by Indigenous groups or institutions from regions that are under-represented in the global science community, collaboration may be required to ensure inclusion.

Supplementary Materials

This PDF file includes:

Materials and Methods

Fig. S1

Tables S1 to S15

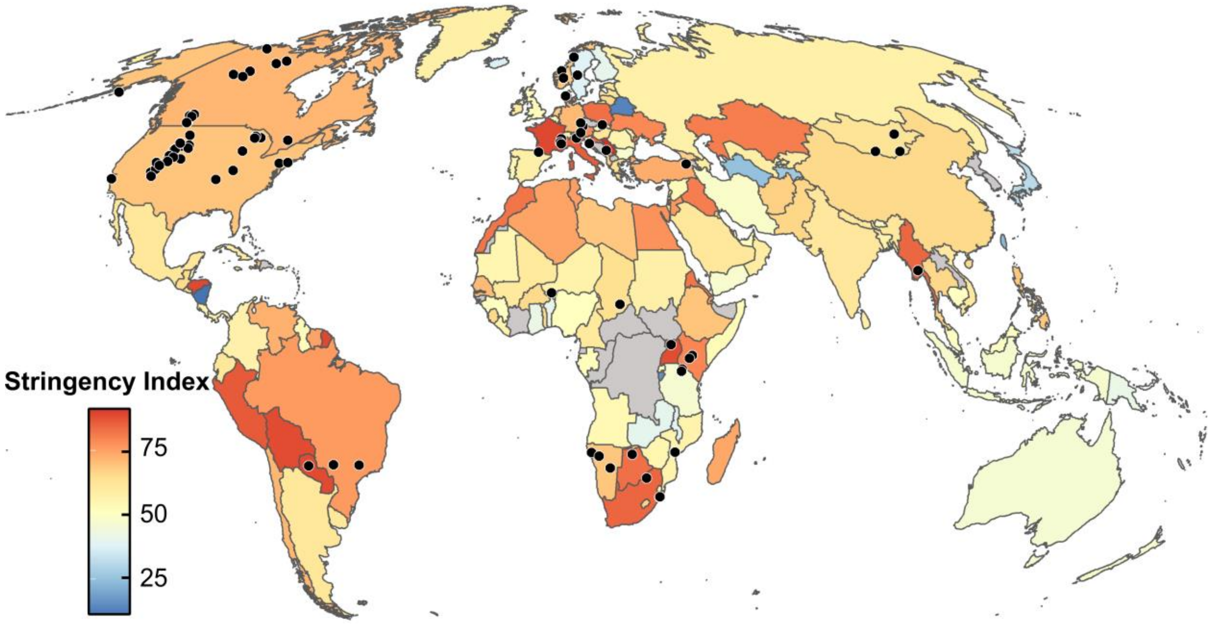

Fig. 1 Distribution of GPS data from 43 terrestrial mammal species. The map represents the mean Oxford COVID-19 Government Response Tracker Stringency Index (SI, (*20*)), which measures lockdown strictness, ranging from 0 (no lockdown) to 100 (very strict lockdown). Values are presented per country during the 2020 study period (i.e., initial lockdown date to 15 May, 2020), where higher values (red) represent countries with a stricter lockdown policy. Light grey represents countries with no SI data. SI values range from 10 to 92. Black points represent the centroids of each study-species combination (n = 90). Map in Mollweide projection.

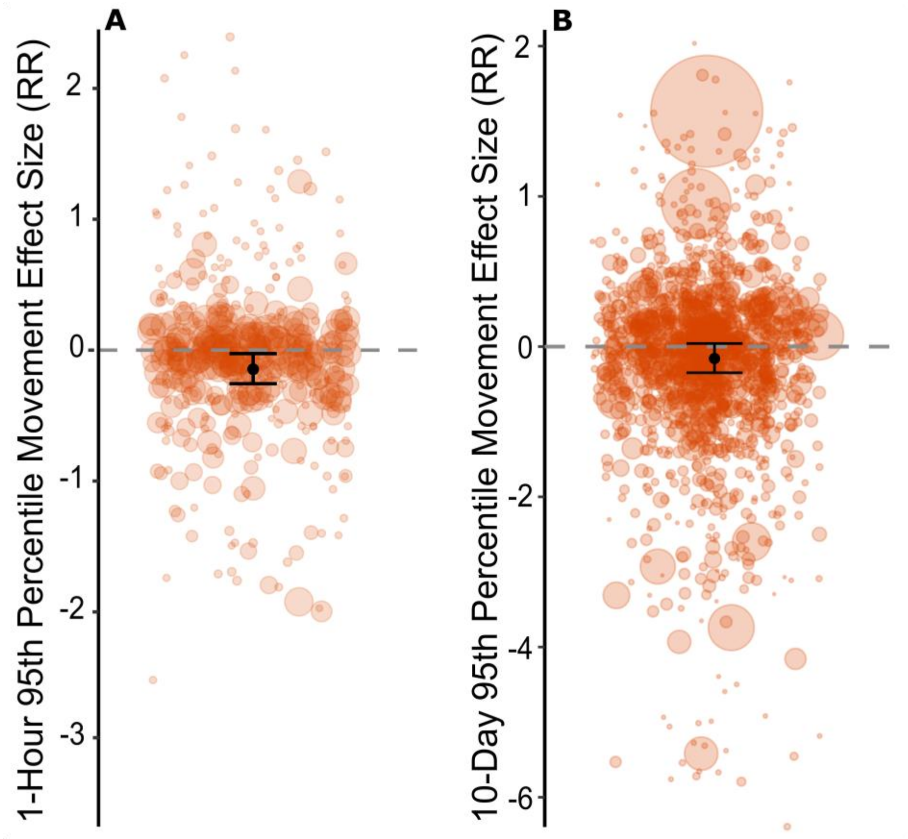

Fig. 2 Changes in 1-hour animal movement during the COVID-19 lockdowns. (**A**) Overall reduction in the 1-hour 95th-percentile displacements (intercept-only model). (**B**) Overall reduction in the 10-day 95th-percentile displacements (intercept-only model). Colored points represent individuals (n = 423 and 1,725), with point sizes proportional to the inverse sampling variance of the response ratio for each individual. The black points and error bars indicate the overall effect with 95% credible intervals. The 1-hour 95% credible intervals do not overlap 0 (-0.25 to -0.01), but the 10-day credible intervals did overlap 0 (-0.36 to 0.05). Negative values indicate reduced movement distances during the early 2020 lockdowns, while positive values indicate increased movement distances during the lockdowns.

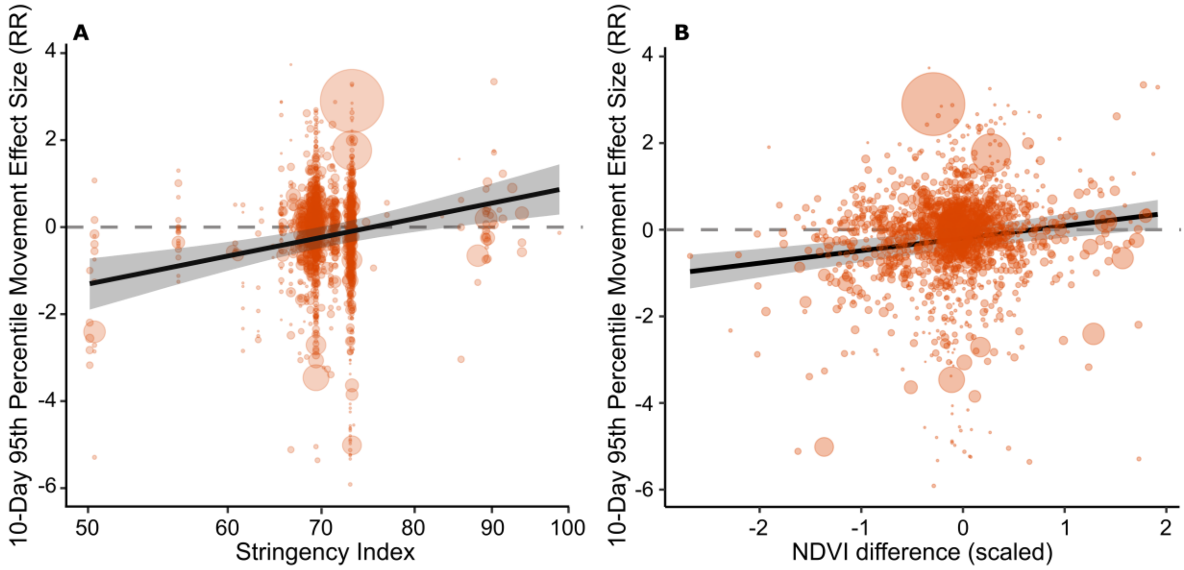

Fig. 3 Changes in 10-day animal movement during the COVID-19 lockdowns. (**A**) Increasing 10-day 95th-percentile displacements in response to the Stringency Index, and (**B**) 10-day 95th-percentile displacements were longer during 2020 when we observed higher NDVI values compared to 2019. Colored points represent individuals (n = 1,725), with point size proportional to the inverse sampling variance of the response ratio for each individual. The black line is the fitted effect size (response ratio; RR). The shaded area indicates 95% credible intervals, and the dashed grey line at zero illustrate no change. Negative values indicate reduced movement distances during the early 2020 lockdowns, while positive values indicate increased movement distances during the lockdowns.

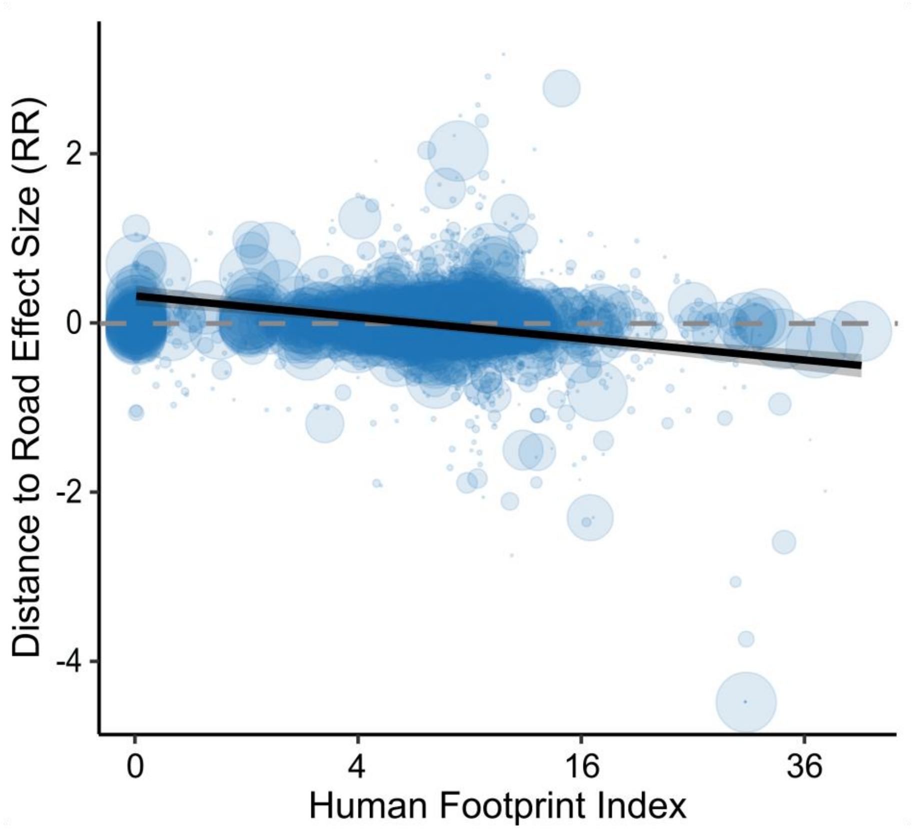

Fig. 4 Changes in animal distance to roads during the COVID-19 lockdowns. Decreasing distance to roads in response to the Human Footprint Index. Colored points represent individuals (n = 2,160), with point size proportional to the inverse sampling variance of the response ratio for each individual. The black line is the predicted effect size (response ratio; RR). The shaded area indicates 95% credible intervals, and the dashed grey line at zero illustrates no change. Negative values indicate closer proximity to roads during the early 2020 lockdowns, while positive values indicate increased distance from roads during the lockdowns.