

1 Behavioral responses of terrestrial mammals to COVID-19 lockdowns

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

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

349

350 **Using animal tracking data to study behavioral changes during lockdowns**

351 We used Global Positioning System (GPS) tracking data to evaluate how 2,300 individual terrestrial
352 mammals, representing 43 species across 76 studies (Fig. 1 and Table S1), changed their spatial
353 behavior during the initial 2020 COVID-19 lockdowns compared to the same time period a year
354 earlier. For the initial 2020 lockdown period we included the date of the first government mandated

355 lockdown in each study area (between 1 February and 28 April, 2020) until 15 May, 2020. We used
356 matching time periods from 2019 as a baseline for comparison. Individuals were tracked for an
357 average of 59 days per observation period (range: 10 – 72 days). We focused on two behaviors:
358 displacement distance (straight-line distance between two consecutive GPS locations) and distance to
359 the nearest road. As changes in displacement might be scale-dependent, we considered displacements
360 at 1-hour and 10-day intervals based on Tucker *et al.* (13). Changes in 1-hour displacements reflect
361 immediate responses to altered human mobility (14). We expected that reduced human mobility
362 during strict lockdowns would lead to an overall reduction in 1-hour displacements due to fewer
363 avoidance and escape responses, or easier access to foraging areas due to reduced disturbance as has
364 been previously shown for red deer (14). For the 10-day displacements, we expected a different
365 response because previous analyses of the effects of land-modifications on mammal movements (13)
366 have shown longer displacement distances in areas with low human footprint. Accordingly,
367 displacement distances at the 10-day scale might be longer under lockdown conditions as animals
368 might be able to cross barriers linked to human mobility during lockdowns (e.g., roads with lower
369 traffic volumes during lockdowns). For each time scale, we evaluated the 50th (median) and 95th
370 percentiles of the displacements. Median displacements represent a suite of behaviors including
371 resting and sleeping (1-hour scale) or residency in the same area (10-day scale). The 95th percentile
372 eliminates stationary behaviors and represents longer and more directed movements such as
373 avoidance behaviors on the 1-hour time scale and long-distance displacements at the 10-day time
374 scale (13). Because longer displacements generally have a greater probability of encountering humans
375 or infrastructure, we expected stronger responses for the 95th-percentile displacements.

376

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

382

383 To evaluate possible changes in displacements or distance to the nearest roads between the lockdown
384 and baseline periods, we calculated log response ratios for each measure (medians and 95th
385 percentiles of the 1-hour and 10-day displacements, and distance to roads) and each individual. Our
386 analyses of the response ratios involved a two-step process following previous work (18). First, we
387 used Bayesian mixed-effects models to examine the overall effect of lockdowns on movement
388 distance and distance to the nearest road (i.e., intercept-only model) (19). Second, we used Bayesian
389 mixed-effects models to examine possible relationships between the response ratios and various
390 covariates indicative of environmental context (i.e., lockdown strictness, human footprint and
391 productivity) and species traits (i.e., body mass, diet, activity and relative brain size) (19). For both

392 steps of the analyses, we included random effects for species-study combined to account for non-
393 independence between effect sizes from the same study and/or species. For the second step of the
394 analysis, we included the Oxford COVID-19 Government Response Tracker Stringency Index (SI,
395 (20)) in our models to examine country-level variation in lockdown strictness, ranging from 0 (no
396 lockdown) to 100 (very strict lockdown; e.g., confined to home). We used the Human Footprint Index
397 (HFI, 1-km resolution, (21)) as a proxy of direct and indirect human activities including roads,
398 agriculture and human population density. The HFI values range from 0 to 50, where low values
399 represent areas relatively undisturbed by humans and high values represent areas with high human
400 development levels. We expected stronger behavioral responses to lockdowns in areas with a higher
401 human footprint and in countries with stricter lockdowns for both displacement distances and distance
402 to roads. To account for movement capacity, differences in movements related to diet, activity cycle
403 and behavioral flexibility, we included body mass (range: 10 – 4000 kg), diet (carnivore, omnivore,
404 herbivore), activity (diurnal or nocturnal) and relative brain size as additional explanatory variables.
405 Finally, we also included the between-year difference in Normalized Difference Vegetation Index
406 (NDVI) between 2019 and 2020 to account for potential differences in seasonality and productivity.
407 We fit models for the median and 95th percentile of the 1-hour and 10-day displacements, and for
408 distance to road including all covariates for lockdown strictness, environmental context and species
409 traits (19). We report our results as the percentage increase or decrease in movement distance or
410 distance to roads by back-transforming the response ratios (19) and reporting the 95% credible
411 intervals (CI).

412

413 **Changes in movement displacements during lockdowns**

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

424

425 The overall lockdown response was not different from zero for the 10-day 95th-percentile or long-
426 distance displacements (15%, 95% CI; -30–5%, Fig. 2B, Table S2). However, when exploring the
427 covariates that might explain variation in response ratios, the 95% credible intervals of the Stringency
428 Index did not overlap zero (Table S5), with displacements increasing 73% on average in areas of

429 stricter lockdown (i.e., areas with an SI of 90; Fig. 3A). This may indicate that tighter restrictions on
430 human movements, including confinement to living spaces and reduced human mobility in green
431 spaces (e.g., Italy and France; Fig. 1) led to increased landscape permeability for mammals. This
432 effect of human mobility is similar in magnitude to previous work that used the same displacement
433 metric but examined the effect of permanent landscape alterations (land conversion and infrastructure)
434 on terrestrial mammal movements (13). While this work used a spatial comparison rather than
435 comparing changes over time within the same individuals, they found a decline of 67% of the 10-day
436 95th-percentile displacements in areas where the human footprint is high (13). We found no effect of
437 the remaining covariates (HFI, body mass, diet, activity or relative brain size) (Tables S5).

438

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

453

454 **Mammals were closer to roads during lockdowns**

455 We found no overall lockdown response in the distance of individuals to roads (-1%, 95% CI: -5 –
456 3%, Table S2) nor a relationship with the Stringency Index, NDVI difference or species traits (Table
457 S7). However, the response ratios were negatively related to HFI, showing that animals in areas with a
458 high human footprint were on average 36% closer to roads during lockdown (HFI = 36, Fig. 4). In
459 many parts of the world, traffic volume was significantly reduced during lockdowns (26, 27), which
460 in turn lessened the impact of roads on animals, including reduced barrier effects (15, 28) and road-
461 kill numbers (17, 29). Our findings add context to these previous results by demonstrating that not
462 only were road-kill numbers lower during lockdown (17, 29), but also animals were closer on average
463 to roads in human-modified areas, indicating reduced avoidance.

464

465

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

477

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

488

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

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776 of Wild Animals (CMS), and member of the advisory committee of a WILDLABS research program
777 aimed at identifying research and funding priorities in movement ecology

778
779 **Data and materials availability:** The full dataset used in the final analyses (33) and associated code
780 (34) are available at datadryad.org. A subset of the spatial coordinate datasets is available from
781 Zenodo (34). Certain datasets of spatial coordinates will be available only through requests made to
782 the authors due to conservation and Indigenous sovereignty concerns (see Table S1 for more
783 information on data use restrictions and contact information for data requests). These sensitive data
784 will be made available upon request to qualified researchers for research purposes, provided that the
785 data use will not threaten the study populations, such as by distribution or publication of the
786 coordinates or detailed maps. Some datasets, such as those overseen by government agencies, have
787 additional legal restrictions on data sharing, and researchers may need to formally apply for data
788 access. Collaborations with data holders are generally encouraged, and in cases where data are held by
789 Indigenous groups or institutions from regions that are under-represented in the global science
790 community, collaboration may be required to ensure inclusion.

791

792

793 **Supplementary Materials**

794 **This PDF file includes:**

795 Materials and Methods

796 Fig. S1

797 Tables S1 to S15

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809 **Figure Captions**

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

817

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

827

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

836

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

844