



## ANIMAL MOVEMENT

# Behavioral responses of terrestrial mammals to COVID-19 lockdowns

Marlee A. Tucker<sup>1\*</sup>, Aafke M. Schipper<sup>1</sup>, Tempe S. F. Adams<sup>2</sup>, Nina Attias<sup>3,4</sup>, Tal Avgar<sup>5</sup>, Natarsha L. Babic<sup>6</sup>, Kristin J. Barker<sup>7</sup>, Guillaume Bastille-Rousseau<sup>8</sup>, Dominik M. Behr<sup>9,10</sup>, Jerrold L. Belant<sup>11</sup>, Dean E. Beyer Jr.<sup>11</sup>, Niels Blaum<sup>12</sup>, J. David Blount<sup>13</sup>, Dirk Bockmühl<sup>14</sup>, Ricardo Luiz Pires Boulhosa<sup>15</sup>, Michael B. Brown<sup>16,17</sup>, Bayarbaatar Buuveibaatar<sup>18</sup>, Francesca Cagnacci<sup>19</sup>, Justin M. Calabrese<sup>20,21</sup>, Rok Černe<sup>22</sup>, Simon Chamailé-Jammes<sup>23,24</sup>, Aung Nyein Chan<sup>25,17</sup>, Michael J. Chase<sup>2</sup>, Yannick Chaval<sup>26,27</sup>, Yvette Chenaux-Ibrahim<sup>28</sup>, Seth G. Cherry<sup>29</sup>, Duško Ćirović<sup>30</sup>, Emrah Çoban<sup>31</sup>, Eric K. Cole<sup>32</sup>, Laura Conlee<sup>33</sup>, Alyson Courtemanch<sup>34</sup>, Gabriele Cozzi<sup>9,10</sup>, Sarah C. Davidson<sup>35,36,37</sup>, Darren DeBloois<sup>38</sup>, Nandintsetseg Dejid<sup>39</sup>, Vickie DeNicola<sup>40</sup>, Arnaud L. J. Desbiez<sup>3,41,42</sup>, Iain Douglas-Hamilton<sup>43,44</sup>, David Drake<sup>45</sup>, Michael Egan<sup>8,27</sup>, Jasper A.J. Eikelboom<sup>46</sup>, William F. Fagan<sup>21</sup>, Morgan J. Farmer<sup>47</sup>, Julian Fennessy<sup>16</sup>, Shannon P. Finnegan<sup>48</sup>, Christen H. Fleming<sup>21,49</sup>, Bonnie Fournier<sup>50</sup>, Nicholas L. Fowler<sup>48,51</sup>, Mariela G. Gantchoff<sup>52,53</sup>, Alexandre Garnier<sup>26,54</sup>, Benedikt Gehr<sup>55</sup>, Chris Geremia<sup>56</sup>, Jacob R. Goheen<sup>57</sup>, Morgan L. Hauptfleisch<sup>58</sup>, Mark Hebblewhite<sup>59</sup>, Morten Heim<sup>60</sup>, Anne G. Hertel<sup>61</sup>, Marco Heurich<sup>62,63,64</sup>, A. J. Mark Hewison<sup>26,27</sup>, James Hodson<sup>65</sup>, Nicholas Hoffman<sup>66</sup>, J. Grant C. Hopcraft<sup>67</sup>, Djuro Huber<sup>68</sup>, Edmund J. Isaac<sup>28</sup>, Karolina Janik<sup>69</sup>, Miloš Ježek<sup>70</sup>, ōrjan Johansson<sup>71,72</sup>, Neil R. Jordan<sup>73,74,10</sup>, Petra Kaczensky<sup>75,76</sup>, Douglas N. Kamaru<sup>57,77</sup>, Matthew J. Kauffman<sup>78</sup>, Todd M. Kautz<sup>48</sup>, Roland Kays<sup>79,80</sup>, Allicia P. Kelly<sup>81</sup>, Jonas Kindberg<sup>82,83</sup>, Miha Krofel<sup>84,85</sup>, Josip Kusak<sup>68</sup>, Clayton T. Lamb<sup>86</sup>, Taylor N. LaSharr<sup>87</sup>, Peter Leimgruber<sup>17</sup>, Horst Leitner<sup>88</sup>, Michael Lierz<sup>89</sup>, John D.C. Linnell<sup>60,90</sup>, Purejav Lkhagvaja<sup>91</sup>, Ryan A. Long<sup>92</sup>, José Vicente López-Bao<sup>93</sup>, Matthias-Claudio Loretto<sup>35,94,95</sup>, Pascal Marchand<sup>109,110</sup>, Hans Martin<sup>59</sup>, Lindsay A. Martinez<sup>97</sup>, Roy T. McBride Jr.<sup>98</sup>, Ashley A.D. McLaren<sup>99,100</sup>, Erling Meisingset<sup>101</sup>, Joerg Melzheimer<sup>14</sup>, Evelyn H. Merrill<sup>102</sup>, Arthur D. Middleton<sup>7</sup>, Kevin L. Monteith<sup>87</sup>, Seth A. Moore<sup>28</sup>, Bram Van Moorter<sup>60</sup>, Nicolas Morellet<sup>26,27</sup>, Thomas Morrison<sup>67</sup>, Rebekka Müller<sup>14</sup>, Atle Mysterud<sup>103</sup>, Michael J. Noonan<sup>104</sup>, David O'Connor<sup>105,106,107</sup>, Daniel Olson<sup>38</sup>, Kirk A. Olson<sup>108</sup>, Anna C. Ortega<sup>109,110</sup>, Federico Jossi<sup>19</sup>, Manuela Panzacchi<sup>60</sup>, Robert Patchett<sup>111</sup>, Brent R. Patterson<sup>112,113</sup>, Rogério Cunha de Paula<sup>114</sup>, John Payne<sup>115</sup>, Wilke Peters<sup>116</sup>, Tyler R. Petroelje<sup>48</sup>, Benjamin J. Pitcher<sup>74,117</sup>, Boštjan Pokorny<sup>118,119,120</sup>, Kim Poole<sup>121</sup>, Hubert Potočník<sup>122</sup>, Marie-Pier Poulin<sup>123</sup>, Robert M. Pringle<sup>124</sup>, Herbert H.T. Prins<sup>125</sup>, Nathan Ranc<sup>19,126,26</sup>, Slaven Reljić<sup>68,127</sup>, Benjamin Robb<sup>109</sup>, Ralf Röder<sup>14</sup>, Christer M. Rolandsen<sup>60</sup>, Christian Rutz<sup>111</sup>, Albert R. Salemgareyev<sup>128</sup>, Gustaf Samelius<sup>72,129</sup>, Heather Sayine-Crawford<sup>65</sup>, Sarah Schooler<sup>48</sup>, Çağan H. Şekercioğlu<sup>130,31</sup>, Nuria Selva<sup>131,132</sup>, Paola Semenzato<sup>133,19</sup>, Agnieszka Sergiel<sup>131</sup>, Koustubh Sharma<sup>134,135,136,137</sup>, Avery L. Shawler<sup>7</sup>, Johannes Signer<sup>138</sup>, Václav Silovsky<sup>70</sup>, João Paulo Silva<sup>139,140</sup>, Richard Simon<sup>141</sup>, Rachel A. Smiley<sup>87</sup>, Douglas W. Smith<sup>56</sup>, Erling J. Solberg<sup>60</sup>, Diego Ellis-Soto<sup>142,143,144</sup>, Orr Spiegel<sup>145</sup>, Jared Stabach<sup>17</sup>, Jenna Stacy-Dawes<sup>146</sup>, Daniel R. Stahler<sup>56</sup>, John Stephenson<sup>147</sup>, Cheyenne Stewart<sup>148</sup>, Olav Strand<sup>60</sup>, Peter Sunde<sup>149</sup>, Nathan J. Svoboda<sup>150</sup>, Jonathan Swart<sup>151</sup>, Jeffrey J. Thompson<sup>152,153</sup>, Katrina L. Toal<sup>141</sup>, Kenneth Uiseb<sup>154</sup>, Meredith C. VanAcker<sup>155,17</sup>, Mariana Velilla<sup>152,153,156</sup>, Tana L. Verzuh<sup>87</sup>, Bettina Wachter<sup>14</sup>, Brittany L. Wagler<sup>87</sup>, Jesse Whittington<sup>157</sup>, Martin Wikelski<sup>35,158</sup>, Christopher C. Wilmers<sup>159</sup>, George Wittemyer<sup>160,43</sup>, Julie K. Young<sup>161,162</sup>, Filip Zięba<sup>163</sup>, Tomasz Zwijacz-Kozica<sup>163</sup>, Mark A. J. Huijbregts<sup>1</sup>, Thomas Mueller<sup>39,164,17</sup>

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 severe acute respiratory syndrome coronavirus 2 (SARS CoV-2) virus. 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 pol-

lutants) (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 affect 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 (7), 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

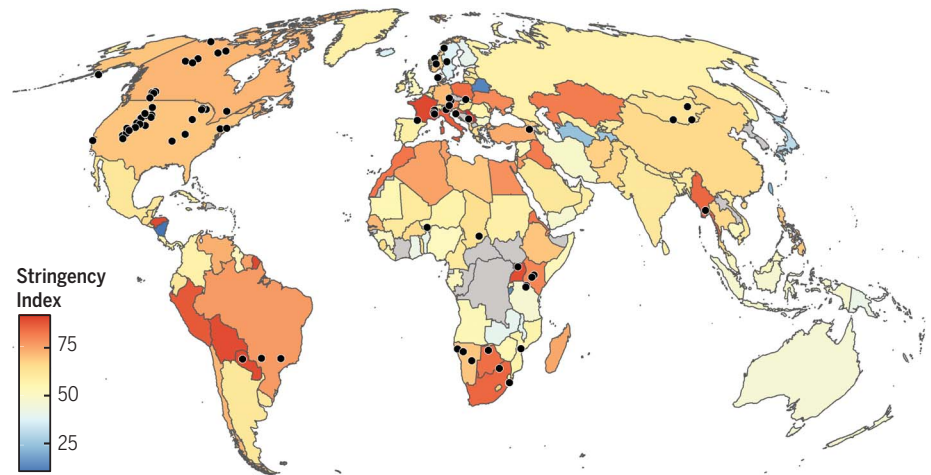
We used global positioning system (GPS) tracking data to evaluate how 2300 individual terrestrial mammals, representing 43 species across 76 studies (Fig. 1 and table S1), changed their spatial behavior during the initial 2020 COVID-19 lockdowns compared with the same time period a year earlier. For 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 to 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

Affiliations are listed at the end of this Research Article.  
\*Corresponding author. Email: marlee.tucker@ru.nl

at the 10-day scale might be longer under lockdown conditions as animals might be able to cross barriers linked to human mobility during such periods (e.g., roads with lower traffic volumes). 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.

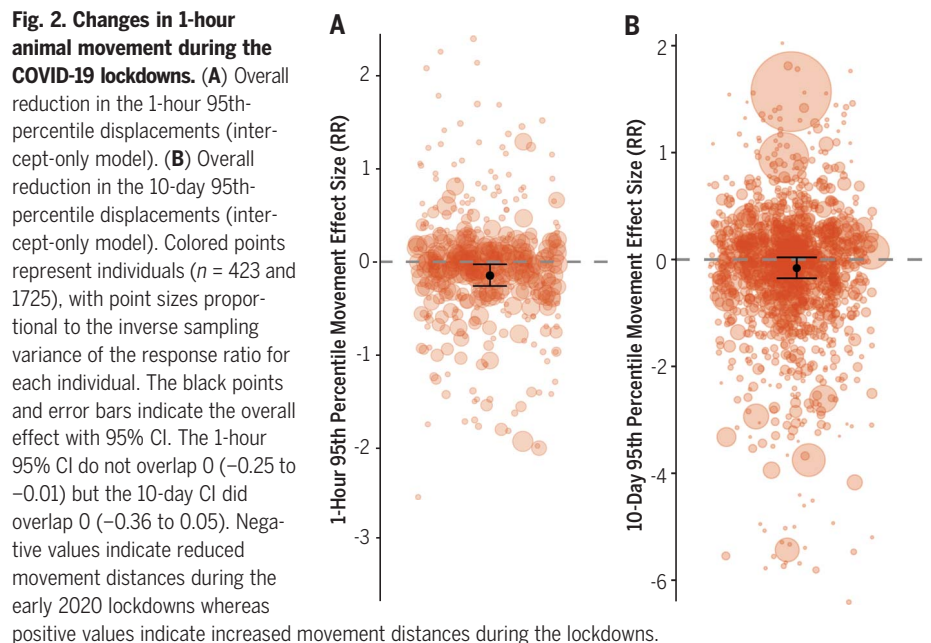
Although roads may benefit some species by providing foraging opportunities or movement corridors (15), their effects are more often negative as they not only create barriers but also increase mortality and facilitate human access to remote areas (16). We expected that declines in vehicular traffic during 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 nonindependence 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 rela-



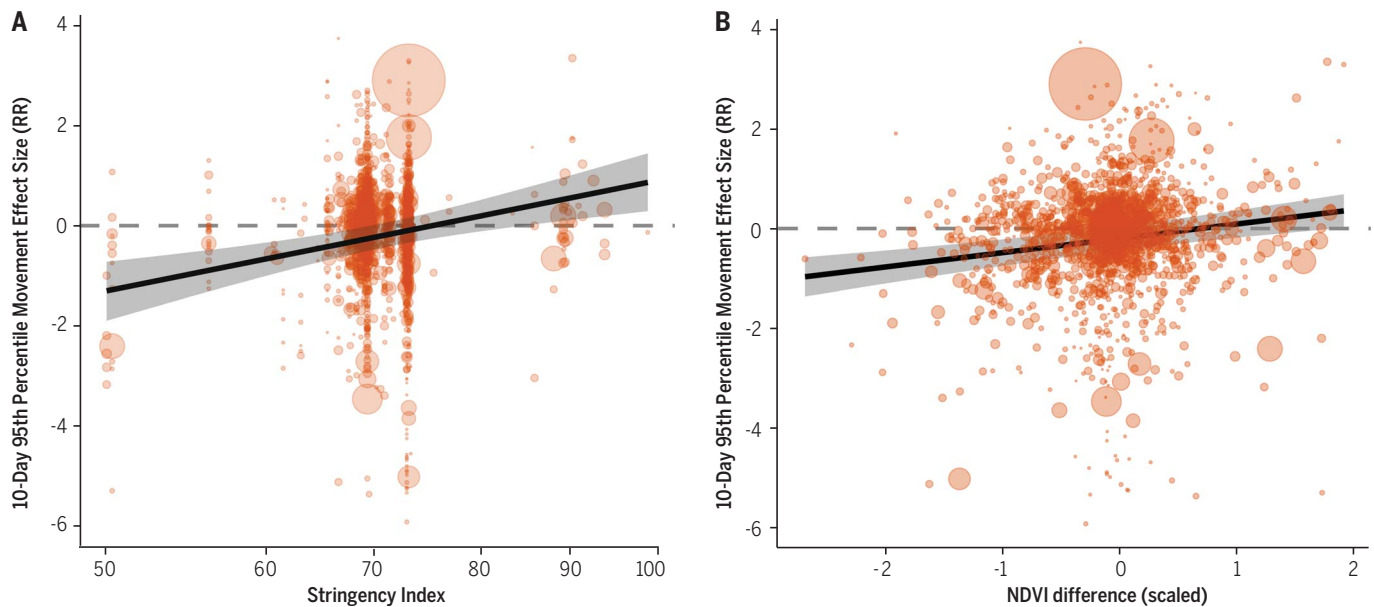
**Fig. 1. Distribution of GPS data from 43 terrestrial mammal species.** The map represents the mean Oxford COVID-19 government response tracker stringency index (SI) (20), which measures lockdown strictness, ranging from 0 (no lockdown) to 100 (very strict lockdown). Values are presented per country 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 gray 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 1725), 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% CI. The 1-hour 95% CI do not overlap 0 ( $-0.25$  to  $-0.01$ ) but the 10-day CI did overlap 0 ( $-0.36$  to  $0.05$ ). Negative values indicate reduced movement distances during the early 2020 lockdowns whereas positive values indicate increased movement distances during the lockdowns.



tively 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 to 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 roads 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).



**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 with 2019. Colored points represent individuals ( $n = 1725$ ), 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% CI, and the dashed gray line at zero illustrates no change. Negative values indicate reduced movement distances during the early 2020 lockdowns whereas positive values indicate increased movement distances during the lockdowns.

### 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 and 22%, Fig. 2 and 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 to 5%; Fig. 2B and table S2). However, when exploring the covariates that might explain variation in response ratios the 95% CI 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). Although 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) (table 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 to 72%) during the lockdown than in 2019 (Fig. 3A). The reduction in movement may reflect increased human mobility in seminatural 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 with 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) (table S6). This difference in responses between 95% and median movements suggests that lockdown stringency may have affected mainly wide-ranging behavior such as migratory movements, long-distance dispersal, exploratory excursions, or long displacements within individuals' home ranges.

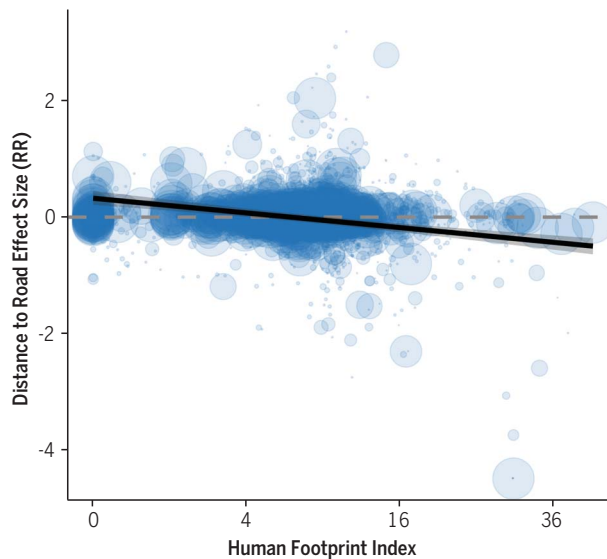
### Mammals were closer to roads during lockdowns

We found no overall lockdown response in the distance of individuals to roads (-1%, 95% CI: -5 to 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 substantially 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;

#### Fig. 4. Changes in animal distance to roads during the COVID-19 lockdowns.

Decreasing distance to roads in response to the human footprint index (HFI). Colored points represent individuals ( $n = 2160$ ), 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% CI, and the dashed gray line at zero illustrates no change. Negative values indicate closer proximity to roads during the early 2020 lockdowns, whereas positive values indicate increased distance from roads during the lockdowns.



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 whereas 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 both physical landscape alteration and human mobility should be taken into consideration [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, but 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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<sup>1</sup>Department of Environmental Science, Radboud Institute for Biological and Environmental Sciences, Radboud University, P.O. Box 9010, 6500, GL Nijmegen, Netherlands. <sup>2</sup>Elephants Without Borders, P.O. Box 682, Kasane, Botswana. <sup>3</sup>Instituto de Conservação de Animais Silvestres (ICAS), Campo Grande, Mato Grosso do Sul, Brazil. <sup>4</sup>Department of Wildlife Ecology and Conservation, University of Florida, Gainesville, FL, USA. <sup>5</sup>Department of Wildland Resources and the Ecology Center, Utah State University, Logan, UT 84322, USA. <sup>6</sup>School of Biological Sciences, Monash University, Clayton, Victoria 3800, Australia. <sup>7</sup>Department of Environmental Science, Policy, and Management, University of California, Berkeley, Berkeley, CA 94720, USA. <sup>8</sup>Cooperative Wildlife Research Laboratory, Southern Illinois University, Carbondale, IL, 62901, USA. <sup>9</sup>Department of Evolutionary Biology and Environmental Studies, University of Zurich, Winterthurerstrasse 190, CH - 8057 Zurich, Switzerland. <sup>10</sup>Botswana Predator Conservation, Private Bag 13, Maun, Botswana. <sup>11</sup>Department of Fisheries and Wildlife, Michigan State University, 480 Wilson Road, East Lansing, MI 48824, USA. <sup>12</sup>University of Potsdam, Plant Ecology and Nature Conservation, Am Mühlberg 3, 14476 Potsdam, Germany. <sup>13</sup>School of Biological Sciences, University of Utah, 257 S 1400 E, Salt Lake City, UT 84112, USA. <sup>14</sup>Department of Evolutionary Biology, Leibniz Institute for Zoo and Wildlife Research, Alfred-Kowalke-Str. 17, 10315 Berlin,

Germany. <sup>15</sup>Instituto Pró-Carnívoros, Atibaia, SP, 12945010 Brazil. <sup>16</sup>Giraffe Conservation Foundation, Eros, PO Box 86099, Windhoek, Namibia. <sup>17</sup>Smithsonian National Zoo and Conservation Biology Institute, Conservation Ecology Center, 1500 Remount Rd, Front Royal, VA, 22630, USA. <sup>18</sup>Wildlife Conservation Society, Mongolia Program, Ulaanbaatar, Mongolia. <sup>19</sup>Animal Ecology Unit, Research and Innovation Center, Fondazione Edmund Mach, Via E. Mach 1, 38010 San Michele all'Adige, Italy. <sup>20</sup>Center for Advanced Systems Understanding (CASUS), Goerlitz, Germany. <sup>21</sup>Department of Biology, University of Maryland, College Park, 4094 Campus Dr, College Park, MA, USA. <sup>22</sup>Slovenia Forest service, Večna pot 2, 1000 Ljubljana, Slovenia. <sup>23</sup>CEFE, CNRS, Univ Montpellier, EPHE, IRD, Montpellier, France. <sup>24</sup>Mammal Research Institute, Department of Zoology and Entomology, University of Pretoria, South Africa. <sup>25</sup>Dept. Fish, Wildlife and Conservation Biology, Colorado State University, Fort Collins, CO 80525, USA. <sup>26</sup>Université de Toulouse, INRAE, CEFS, F-31326 Castanet-Tolosan, France. <sup>27</sup>LTSEZ ZA PYRÉNÉES GARONNE, F-31320 Auzeville-Tolosane, France. <sup>28</sup>Department of Biology and Environment, Grand Portage Band of Lake Superior Chippewa, Grand Portage, MN 55605, USA. <sup>29</sup>Parks Canada Agency, Box 220, Radium Hot Springs, BC, VOA 1M0, Canada. <sup>30</sup>Faculty of Biology, University of Belgrade, Studentski trg 16, 11000 Belgrade, Serbia. <sup>31</sup>KuzeyDoğa Society, Ortakapı Mah. Şehit Yusuf Kad. 69, 36100 Kard. Turkey. <sup>32</sup>U.S. Fish and Wildlife Service, National Elk Refuge, PO Box 510, Jackson, WY 83001, USA. <sup>33</sup>Missouri Department of Conservation, Columbia, MO, 65201, USA. <sup>34</sup>Wyoming Game and Fish Department, Jackson, WY 83001, USA. <sup>35</sup>Department of Migration, Max Planck Institute of Animal Behavior, 78315 Radolfzell, Germany. <sup>36</sup>Department of Biology, University of Konstanz, 78464 Konstanz, Germany. <sup>37</sup>Department of Civil, Environmental and Geodetic Engineering, The Ohio State University, 43210 Columbus, OH, USA. <sup>38</sup>Utah Division of Wildlife Resources. <sup>39</sup>Senckenberg Biodiversity and Climate Research Centre, Senckenberganlage 25, 60325 Frankfurt am Main, Germany. <sup>40</sup>White Buffalo Inc., 26 Davison Road, Moodus, CT 06469, USA. <sup>41</sup>Royal Zoological Society of Scotland (RZSS), Murrayfield, Edinburgh, UK. <sup>42</sup>Instituto de Pesquisas Ecológicas (IPÊ), Nazaré Paulista, São Paulo, Brazil. <sup>43</sup>Save the Elephants, Marula Manor, Marula Lane, Karen, Nairobi 00200, Kenya. <sup>44</sup>Department of Zoology, Oxford University, Oxford OX1 3PS, UK. <sup>45</sup>Department of Forest and Wildlife Ecology, University of Wisconsin-Madison, Madison, WI 53706, USA. <sup>46</sup>Wildlife Ecology and Conservation Group, Wageningen University and Research, Droevendaalsesteeg 3a, 6708 PB, Wageningen, Netherlands. <sup>47</sup>Department of Forest and Wildlife Ecology, University of Wisconsin, 1630 Linden Drive, Madison, WI 53706, USA. <sup>48</sup>Global Wildlife Conservation Center, State University of New York College of Environmental Science and Forestry, 1 Forestry Drive, Syracuse, NY 13210, USA. <sup>49</sup>Smithsonian Conservation Biology Institute, 1500 Remount Rd, Front Royal, VA, USA. <sup>50</sup>Wildlife and Fish Division, Department of Environment and Natural Resources, Government of the Northwest Territories, P.O. Box 1320, Yellowknife, NT, Canada. <sup>51</sup>Alaska Department of Fish and Game, 43961 Kalifornsky Beach Road, Suite B, Soldotna, AK 99669, USA. <sup>52</sup>State University of New York College of Environmental Science and Forestry, Syracuse, NY 13210, USA. <sup>53</sup>Department of Biology, College of Arts and Sciences, University of Dayton, Dayton, OH 45469, USA. <sup>54</sup>Parc National des Pyrénées, 65000 Tarbes, France. <sup>55</sup>Department of Evolutionary Biology and Environmental Studies, University of Zurich, Winterthurerstrasse 190, 8057 Zurich, Switzerland. <sup>56</sup>Yellowstone Center for Resources, P.O. Box 168, Yellowstone National Park, WY 82190, USA. <sup>57</sup>Department of Zoology and Physiology, University of Wyoming, Laramie, WY 82071, USA. <sup>58</sup>Biodiversity Research Centre, Namibia University of Science and Technology Pvt Ltd 13388 Windhoek, Namibia. <sup>59</sup>Wildlife Biology Program, Franke College of Forestry and Conservation, University of Montana, Missoula, MT, 59801, USA. <sup>60</sup>Norwegian Institute for Nature Research, Terrestrial Ecology Department, P.O. Box 5685 Torgarden, 7485 Trondheim, Norway. <sup>61</sup>Behavioural Ecology, Department of Biology, Ludwig Maximilian University of Munich, Großhaderner Str. 2, 82152 Planegg-Martinsried, Germany. <sup>62</sup>Department of Visitor Management and National Park Monitoring, Bavarian Forest National Park, Freyungstr. 2, 94481 Grafenau, Germany. <sup>63</sup>Chair of Wildlife Ecology and Conservation Biology, Faculty of Environment and Natural Resources, University of Freiburg, Tennenbacher Straße 4, 79106 Freiburg, Germany. <sup>64</sup>Institute for forest and wildlife management, Faculty of Applied Ecology, Agricultural Sciences and Biotechnology, Campus Evenstad, Inland Norway University of Applied Science, NO-2480 Koppang, Norway. <sup>65</sup>Wildlife and Fish Division, Department of Environment and Natural Resources, Government of the Northwest Territories, P.O. Box 1320, Yellowknife, NT X1A 2L9, Canada. <sup>66</sup>Ecological Program,

- Pennsylvania Department of Military and Veterans Affairs, Fort Indiantown Gap National Guard Training Center, Annville, PA 17003, USA. <sup>67</sup>Institute of Biodiversity, Animal Health and Comparative Medicine, University of Glasgow, Glasgow G12 8QQ, UK. <sup>68</sup>Veterinary Biology Department, Faculty of Veterinary Medicine, University of Zagreb, Heinzelova 55, HR-10000 Zagreb, Croatia. <sup>69</sup>City of New York Parks and Recreation, Wildlife Unit, 1234 5th Avenue, 5th Floor, NY 10029, USA. <sup>70</sup>Faculty of Forestry and Wood Sciences, Czech University of Life Sciences Prague, Czech Republic. <sup>71</sup>Grimso Wildlife Research Station, Swedish University of Agricultural Sciences, 739 93 Ridrarhyttan, Sweden. <sup>72</sup>Snow Leopard Trust, 4649 Sunnyside Avenue North, Seattle, WA 98103, USA. <sup>73</sup>Centre for Ecosystem Science, School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, NSW, 2052, Australia. <sup>74</sup>Taronga Institute of Science and Learning, Taronga Conservation Society, Sydney, NSW, 2088, Australia. <sup>75</sup>Inland Norway University of Applied Sciences, Department of Forestry and Wildlife Management, Norway. <sup>76</sup>University of Veterinary Medicine Vienna, Research Institute of Wildlife Ecology, Austria. <sup>77</sup>Wildlife Department, Ol Pejeta Conservancy, Private Bag-10400, Nanyuki, Kenya. <sup>78</sup>U.S. Geological Survey, Wyoming Cooperative Fish and Wildlife Research Unit, Department of Zoology and Physiology, University of Wyoming, Laramie, WY 82071, USA. <sup>79</sup>North Carolina Museum of Natural Sciences, Raleigh, NC 27601, USA. <sup>80</sup>Department of Forestry and Environmental Resources, North Carolina State University, Raleigh, NC, 27695, USA. <sup>81</sup>Department of Environment and Natural Resources, Government of the Northwest Territories, P.O. Box 2668, Yellowknife, NT X1A 2P9, Canada. <sup>82</sup>Norwegian Institute for Nature Research, NO-7484 Trondheim, Norway. <sup>83</sup>Department of Wildlife, Fish and Environmental studies, Swedish University of Agricultural Sciences, SE- 901 83 Umeå, Sweden. <sup>84</sup>Department of Forestry, Biotechnical Faculty, University of Ljubljana, Jamnikarjeva 101, SI-1000 Ljubljana, Slovenia. <sup>85</sup>Department of Evolutionary Ecology, Leibniz Institute for Zoo and Wildlife Research, Alfred-Kowalke-Str. 17, 10315 Berlin, Germany. <sup>86</sup>Biological Sciences Centre, University of Alberta, Edmonton, Alberta T6G 2E9, Canada. <sup>87</sup>Haub School of Environment and Natural Resources, Wyoming Cooperative Fish and Wildlife Research Unit, Department of Zoology and Physiology, University of Wyoming, 804 East Fremont, Laramie, WY 82072, USA. <sup>88</sup>Büro für Wildökologie und Forstwirtschaft, Klagenfurt, Austria. <sup>89</sup>Clinic for birds, reptiles, amphibians and fish, Justus-Liebig-University Giessen, Germany. <sup>90</sup>Inland Norway University of Applied Sciences, Department of Forestry and Wildlife Management, Anne Evenstads vei 80, 2480 Koppang, Norway. <sup>91</sup>Snow Leopard Conservation Foundation, Ulaanbaatar, Mongolia. <sup>92</sup>Department of Fish and Wildlife Sciences, University of Idaho, Moscow, ID 83844, USA. <sup>93</sup>Biodiversity Research Institute (CSIC - Oviedo University - Principality of Asturias), Oviedo University, E-33600 Mieres, Spain. <sup>94</sup>Technical University of Munich, TUM School of Life Sciences, Ecosystem Dynamics and Forest Management Group, 85354 Freising, Germany. <sup>95</sup>Berchtesgaden National Park, 83471 Berchtesgaden, Germany. <sup>96</sup>Office Français de la Biodiversité, Direction de la Recherche et de l'Expertise, Unité Ongulés Sauvages, Juvignac, France. <sup>97</sup>Wyoming Cooperative Fish and Wildlife Research Unit, Department of Zoology and Physiology, University of Wyoming, Laramie, WY 82071, USA. <sup>98</sup>Faro Moro Eco Research, Estancia Faro Moro, Departamento de Boquerón, Paraguay. <sup>99</sup>Ontario Ministry of Natural Resources and Forestry, Wildlife Research and Monitoring Section, Trent University, 2140 East Bank Drive, Peterborough, Ontario, K9J 7B8, Canada. <sup>100</sup>Department of Environment and Natural Resources, Government of the Northwest Territories, Highway 5, PO Box 900, Fort Smith, Northwest Territories, X0E 0P0, Canada. <sup>101</sup>Department of Forestry and Forestry resources, Norwegian Institute of Bioeconomy Research, Tingvoll gard, NO-6630 Tingvoll, Norway. <sup>102</sup>Department of Biological Sciences, University of Alberta, Edmonton, Alberta T6G 2E9, Canada. <sup>103</sup>Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biosciences, University of Oslo, P.O. Box 1066 Blindern, NO-0316 Oslo, Norway. <sup>104</sup>Department of Biology, University of British Columbia Okanagan, Kelowna, British Columbia, Canada. <sup>105</sup>Save Giraffe Now, 8333 Douglas Avenue, Suite 300, Dallas, Texas 75225, USA. <sup>106</sup>The Faculty of Biological Sciences, Goethe University, Max-von-Laue-Str. 9, 60438 Frankfurt am Main, Germany. <sup>107</sup>National Geographic Partners, 1145 17th Street NW, Washington, DC 20036, USA. <sup>108</sup>Wildlife Conservation Society, Mongolia Program, Post 20A, Box 21, Ulaanbaatar 14200, Mongolia. <sup>109</sup>Wyoming Cooperative Fish and Wildlife Research Unit, Department of Zoology and Physiology, University of Wyoming, Laramie, WY 82071, USA. <sup>110</sup>Program in Ecology, University of Wyoming, Laramie, WY 82071, USA. <sup>111</sup>Centre for Biological Diversity, School of Biology, University of St. Andrews, Sir Harold Mitchell Building, St. Andrews, KY16 9TH, UK. <sup>112</sup>Department of Environmental and Life Sciences, Trent University, 2140 East Bank Drive, Peterborough, Ontario K9J 7B8, Canada. <sup>113</sup>Ontario Ministry of Natural Resources and Forestry, Wildlife Research and Monitoring Section, Trent University, 2140 East Bank Drive, Peterborough, Ontario K9J 7B8, Canada. <sup>114</sup>Centro Nacional de Pesquisa e Conservação de Mamíferos Carnívoros, Instituto Chico Mendes de Conservação da Biodiversidade, Atibaia, SP, 12952011 Brazil. <sup>115</sup>Research Institute of Wildlife Ecology, University of Veterinary Medicine, Vienna, Austria. <sup>116</sup>Department of Biodiversity, Conservation and Wildlife Management, Bavarian State Institute for Forestry, Hans-Carl-von Carlowitz Platz 1, 85354 Freising, Germany. <sup>117</sup>School of Natural Sciences, Faculty of Science and Engineering, Macquarie University, NSW, 2109, Australia. <sup>118</sup>Faculty of Environmental Protection, Trg mladosti 7, 3320 Velenje, Slovenia. <sup>119</sup>Slovenian Forestry Institute, Večna pot 2, 1000 Ljubljana, Slovenia. <sup>120</sup>Department of Biodiversity, Faculty of Mathematics, Natural Sciences and Information Technologies, University of Primorska, Glagoljaška 8, 6000 Koper, Slovenia. <sup>121</sup>Aurora Wildlife Research, 1918 Shannon Point Rd., Nelson, BC, V1L 6K1, Canada. <sup>122</sup>Department of Biology, Biotechnical Faculty, University of Ljubljana, Jamnikarjeva 101, 1000 Ljubljana, Slovenia. <sup>123</sup>Department of Zoology and Physiology, University of Wyoming, Laramie, WY 82071, USA. <sup>124</sup>Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08544, USA. <sup>125</sup>Department of Animal Sciences, Wageningen University and Research, De Elst 1, 6708 WD, Wageningen, Netherlands. <sup>126</sup>Department of Organismic and Evolutionary Biology, Harvard University, 26 Oxford Street, Cambridge MA 02138, USA. <sup>127</sup>Oikon Ltd, Institute of Applied Ecology, Trg Senjskih uskoka 1-2, HR-10020 Zagreb, Croatia. <sup>128</sup>Association for the Conservation of Biodiversity of Kazakhstan (ACBK), Nur-Sultan, 010000, Kazakhstan. <sup>129</sup>Nordens Ark, 456 93 Hunnebostrand, Sweden. <sup>130</sup>Koç University Department of Molecular Biology and Genetics, Faculty of Sciences, Rumelifeneri, Istanbul, Sarıyer, Turkey. <sup>131</sup>Institute of Nature Conservation Polish Academy of Sciences, Adama Mickiewicza 33, 31-120 Kraków, Poland. <sup>132</sup>Departamento de Ciencias Integradas, Facultad de Ciencias Experimentales, Centro de Estudios Avanzados en Física, Matemáticas y Computación, Universidad de Huelva, 21071 Huelva, Spain. <sup>133</sup>Dimension Research, Ecology and Environment (D.R.E.Am. Italia), Via Garibaldi, 3, 52015 Pratovecchio Stia (AR), Italy. <sup>134</sup>Snow Leopard Trust, Seattle, WA 98103, USA. <sup>135</sup>Global Snow Leopard and Ecosystem Protection Program, Bishkek, Kyrgyzstan. <sup>136</sup>Snow Leopard Foundation, Kyrgyzstan Bishkek, Kyrgyzstan. <sup>137</sup>Nature Conservation Foundation, Mysore 570002, India. <sup>138</sup>Wildlife Sciences, Faculty of Forest Sciences and Forest Ecology, University of Goettingen, Göttingen, Germany. <sup>139</sup>CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, InBIO Laboratório Associado, Campus de Vairão, Universidade do Porto, 4485-661 Vairão, Portugal. <sup>140</sup>BIOPOLIS Program in Genomics, Biodiversity and Land Planning, CIBIO, Campus de Vairão, 4485-661 Vairão, Portugal. <sup>141</sup>City of New York Parks and Recreation, Wildlife Unit, 1234 5th Avenue, 5th Floor, NY, NY 10029, USA. <sup>142</sup>Department of Ecology and Evolutionary Biology, Yale University, New Haven, CT, USA. <sup>143</sup>Center for Biodiversity and Global Change, Yale University, New Haven, CT, USA. <sup>144</sup>Max Planck - Yale Center for Biodiversity Movement and Global Change, Yale University. <sup>145</sup>School of Zoology, Faculty of Life Sciences, Tel Aviv University, Tel Aviv 69978, Israel. <sup>146</sup>San Diego Zoo Wildlife Alliance, 15600 San Pasqual Valley Road, Escondido, CA 92027, USA. <sup>147</sup>Grand Teton National Park, PO Drawer 170, Moose, Wyoming 83012, USA. <sup>148</sup>Wyoming Game and Fish Department, 700 Valley View Dr. Sheridan, WY 82801, USA. <sup>149</sup>Aarhus University, Department of Ecoscience - Wildlife Ecology, C.F. Møllers Allé 4-8, 8000 Aarhus C, Denmark. <sup>150</sup>Alaska Department of Fish and Game, Kodiak, AK 99615, USA. <sup>151</sup>Welgevonden Game Reserve, P.O. Box 433, Vaalwater, South Africa. <sup>152</sup>Guyra Paraguay - CONACYT, Asunción, Paraguay. <sup>153</sup>Instituto Saite, Asunción, Paraguay. <sup>154</sup>Ministry of Environment, Forestry and Tourism, Windhoek, Namibia. <sup>155</sup>Ecology, Evolution and Environmental Biology, Columbia University, NY, NY 10027, USA. <sup>156</sup>School of Natural Resources, University of Arizona, 1064 E Lowell St, Tucson, AZ 85719, USA. <sup>157</sup>Park Canada, Banff National Park Resource Conservation, PO Box 900, Banff, Alberta T1L 1K2, Canada. <sup>158</sup>Centre for the Advanced Study of Collective Behaviour, University of Konstanz, 78457 Konstanz, Germany. <sup>159</sup>Center for Integrated Spatial Research, Environmental Studies Department, University of California, Santa Cruz, CA 95064, USA. <sup>160</sup>Department of Fish, Wildlife and Conservation Biology, Colorado State University, Fort Collins, CO 80523, USA. <sup>161</sup>USDA National Wildlife Research Center, Predator Research Facility, Millville, UT 84326, USA. <sup>162</sup>Department of Wildland Resources, Utah State University, Logan, UT 84322, USA. <sup>163</sup>Tatra National Park, Kuźnice 1, 34-500, Zakopane, Poland. <sup>164</sup>Department of Biological Sciences, Goethe University, Max-von-Laue-Strasse 9, 60438 Frankfurt am Main, Germany.

## SUPPLEMENTARY MATERIALS

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Materials and Methods

Fig. S1

Tables S1 to S15

References (36–59)

MDAR Reproducibility Checklist

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## Behavioral responses of terrestrial mammals to COVID-19 lockdowns

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### Editor's summary

Policies to reduce human movement during the early months of the COVID-19 pandemic produced a kind of natural experiment to observe how human activities affect animal behavior. Using GPS tracking data from 2300 individual mammals of 43 species, Tucker *et al.* documented changes in mammal movement patterns during the spring of 2020 compared with the previous year (see the Perspective by St. Clair and Raymond). In locations with strict lockdown policies, animals traveled longer distances during the lockdown period. In highly populated areas, mammals moved less frequently and were closer to roads than they were before the pandemic. These results demonstrate how human activities constrain animal movement and what happens when those activities cease. —Bianca Lopez

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