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RESEARCH ARTICLE

Human-induced behavioural changes of global threatened terrestrial mammals

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Abstract

Aim: Understanding changes in the behaviour of threatened species responding to rapidly increasing human disturbances is critical for biodiversity conservation. Here, we synthesize a meta-analysis of the cumulative effect of human disturbances on the behaviour of global threatened terrestrial mammals.

Location: Global terrestrial ecosystem.

Time Period: Data collected from 1993 to 2021.

Major Taxa Studied: Terrestrial mammals.

Results: There were significant differences in behavioural changes among categories of human disturbances (i.e. biological invasion, climate change, grazing, habitat degradation, protection management, road traffic and tourism). The effect size of road traffic on behavioural change was the largest and particularly led habitat selection to be more specialized. The effect size for habitat degradation on foraging behaviour was the largest, and the effect mainly led to a shorter time spent in foraging and a change in food selection. Changes to behaviour increased with human disturbance intensity and varied among species according to their functional traits including body mass, food habits, migration and group type. Climate change, grazing, road traffic and tourism had a greater effect on larger species. The effect size for habitat degradation on omnivorous species was the largest, while carnivorous and solitary species were more sensitive to tourism, and migratory species were especially vulnerable to climate changes.

Main Conclusions: The diverse human disturbances interact with disturbance intensity, and some species' functional traits significantly affected the behavioural change in threatened terrestrial mammals. Such behavioural changes away from predisturbance patterns may have consequences for their fitness and community interactions. The management and conservation of threatened species should incorporate knowledge of their behavioural responses to human disturbance and take into account the potential ecological consequences for biodiversity conservation.

KEYWORDS
behavioural change, climate change, human disturbance, migratory mammals, road impacts, threatened mammals, tourism

Chao Zhang, Yumei Li, Xiaoyu Hu and Xiaofan Ma contributed equally to this work.

1 | INTRODUCTION

The accelerated decline in biodiversity due to the global expansion of human development has become a critical current environmental problem, threatening valuable ecosystem services and human well-being (Ceballos et al., 2015; Mace et al., 2012). Threatened species characterized by small population size or highly specialized habits are known to be vulnerable to anthropogenic environmental change (Pimm & Raven, 2000; Zhu et al., 2010), making them indicators of ecosystem health. Understanding how threatened species respond and adapt to human disturbance is essential for biodiversity conservation. Behavioural responses are an important component of animal persistence in ecosystems (Lens et al., 2002). The behavioural plasticity of animals plays an important role in their adaptation to human-induced environmental change, but behavioural changes in response to novel threats may also have negative consequences for fitness, survival and population persistence (Sih, 2013; Tuomainen & Candolin, 2011; Wilson et al., 2020).

Animals adopt spatial or temporal avoidance (e.g. increasing nocturnality) when they perceive direct human presence as a threat (Bouyer et al., 2015; Gaynor et al., 2018). This may be the case even in response to benign activities, such as observational scientific research. Even when not directly present, human disturbance can induce changes in animal behaviour by altering the conditions under which animals make behavioural decisions through human-facilitated chemical and sensory pollution (Parks et al., 2011), infrastructural development (Estrada et al., 2017), habitat degradation (Torres et al., 2016), biological invasion (Zapata-Rios & Branch, 2016) and climate change (Rosenzweig et al., 2008). These diverse human disturbances have been shown to influence different types of behaviour including foraging, movement, habitat selection, social and vigilance (Coleman et al., 2013; Larm et al., 2020; Lehmann et al., 2010; Plante et al., 2018).

The diverse human disturbances represent different levels of risk to animals (Gaynor et al., 2018), and changes in each type of aforementioned behaviour can have different ecological consequences (Wilson et al., 2020). For instance, changes in the movement patterns of animals may modify the transport of nutrients, seeds and pathogens in ecosystems (Dougherty et al., 2018). Also, changes in vigilance can affect individual fitness through changes to physiological stress and susceptibility to predation, resulting in lower reproductive output and offspring survival (Arroyo et al., 2017). Most previous studies have focussed on the effect of human disturbances on specific behaviours (Gaynor et al., 2018) or on the effect of a particular human disturbance on the behaviours of a species or group of taxa (Pilfold et al., 2017; Williams & Behie, 2020). However, a comprehensive assessment of the influence of diverse human disturbances on the behaviour of large-scale threatened mammal species remains unclear.

The magnitude of the changes in animal behaviour may depend on the disturbance intensity and species characteristics. The environmental footprint of humans is a prominent cause of spatial variation in animal behaviour (Stewart et al., 2016), and more intense human disturbance has a greater effect on animal movements (Tucker et al., 2018) and increases nocturnality in previously diurnal species (Gaynor et al., 2018). Functional traits and characteristics such as body size, diets, migration mode and group size and structure are closely related to mammal foraging, movement and sociality (Doherty et al., 2021; Kent & Sherry, 2020; Kerth, 2008). For instance, a landscape-scale experiment demonstrated that large, medium-sized and small mammals displayed changes in different behaviour types in response to human presence (Suraci et al., 2019). In addition, human-induced behavioural changes may vary regionally with different historical disturbance and protected status. Therefore, it is critical to consider how human disturbances interact with multiple factors to shape animal behaviour.

We predict that behavioural changes of threatened terrestrial mammals may differ among categories of human disturbances and affected behaviour types, as a result of the different mechanisms of behavioural response to the diverse disturbances. We also predict a positive relationship between behavioural change and human disturbance intensity. Furthermore, we expect that human-induced behavioural changes vary in effect size according to species with different functional traits, such that large species show stronger behavioural changes. To test these predictions, we conducted a systematic meta-analysis of human-induced changes in the behaviour of globally threatened terrestrial mammals. We reveal how human disturbance types (biological invasion, climate change, grazing, habitat degradation, protection management, road traffic and tourism) and their intensity influence the behavioural response of threatened terrestrial mammals. We also explore how behavioural responses of threatened terrestrial mammals vary among different regional attributes' and species' functional traits.

2 | MATERIALS AND METHODS

2.1 | Literature search

We collated data from a literature search following the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) guidelines (Moher et al., 2010, Figure S1) to systematically compile studies related to human-induced changes in behaviour of threatened terrestrial mammals. We cannot be sure which human disturbances had effects on mammal's behaviour before screening the literatures, so we searched for studies using behaviour-related terms and then discarded studies unrelated to behavioural responses to human disturbances to avoid an incomplete literature search. We first searched for studies on Web of Science core collection database as of December 2021 using the following string of keywords: behav* AND (threatened OR endangered) AND (mammal* OR animal*) AND terrestrial. An additional search for specific behaviour types was conducted using the following string of keywords: ("activity pattern" OR migrat* OR forag* OR budget* OR hiberna* OR vigilance OR anxiety OR reproduct* OR breed* OR social OR "habitat selection" OR "home range" OR movement OR avoiding)

AND (threatened OR endangered) AND (mammal* OR animal*) AND terrestrial. Then, the resulting studies that were not focussed on terrestrial mammals that defined above near-threatened (NT) level by IUCN and unrelated to behavioural responses to human disturbance were discarded by scanning the articles. Finally, we selected 109 articles from 1993 to 2021, including 540 cases involving 12 orders, 30 families and 87 species/subspecies, for qualitative analyses (a list of the data sources reference is found in Appendix A). Locations of the studies were distributed in 39 countries (Figure 1). In 369 of the 540 cases, the full data were available for calculating effect size for quantitative analyses (Figure S1).

2.2 | Data extraction

We extracted numerical parameters from each study to compute the effect sizes, including the sample size, mean, standard error, correlation coefficient r and values of *F* tests, *t* tests and chi-square tests, to assess the effects of human disturbances on animal behaviour. We retrieved these data directly from tables and the main text or from graphs using WebPlotDigitizer (Burda et al., 2017).

We also recorded data on the study attributes: location (continent, country), geographical coordinates, protected area status (protected, unprotected), human disturbance types and intensity. Human disturbance types were classified into biological invasion, climate change, grazing, habitat degradation (habitat loss or fragmentation caused by land use change, mining, anthropogenic landscapes and urbanization), protection management (fire, forage enhancement and fence), road traffic (road, traffic and noise), tourism and others (less studied types including scientific research, artificial lighting, overflights and hunting) through full-text evaluation. We used the human footprint index (HFI) that combines the measures of human population density, land transformation, human access and power infrastructure (Sanderson et al., 2002) as a proxy to quantify human disturbance intensity. We used the location of each study to extract HFI data from the global dataset in the 1993 version (Sanderson et al., 2002) and an annual terrestrial Human Footprint dataset from 2000 to 2018 (Mu et al., 2022) depending on when a study was conducted. For studies during the 1993 and 2000–2018 period, we extracted the mean values of the corresponding years, and for studies beyond this period, we used available HFI data from the nearest year. Studies of climate change that was based on model prediction data were excluded from the HFI analysis.

Additionally, we recorded data on the threatened mammals' affected behaviour types, body size (log-transformed due to the wide range), food habits (carnivores, herbivores and omnivores), migration type (migration and nonmigration), group type (gregarious and solitary) and IUCN threat status. Behaviour types involved in the study were divided into avoiding (including avoiding distance and time), breeding (breeding range, time and reproductive success), foraging (foraging time, frequency, range and food selection), habitat selection (habitat range and preferences), movement (moving time, distance, speed and path, migration and rest time), social (social time, communication and group size), vigilance (vigilance time, distance and frequency) and others (less studied types including anxiety, self-groom and hibernation) following literature included in the study and Wilson et al. (2020). Trait information on mammals was obtained from an online database Animal Diversity Web (https://animaldiversity.org/), and maximum body mass was used as an estimate of body size. Threat status was obtained from the IUCN Red

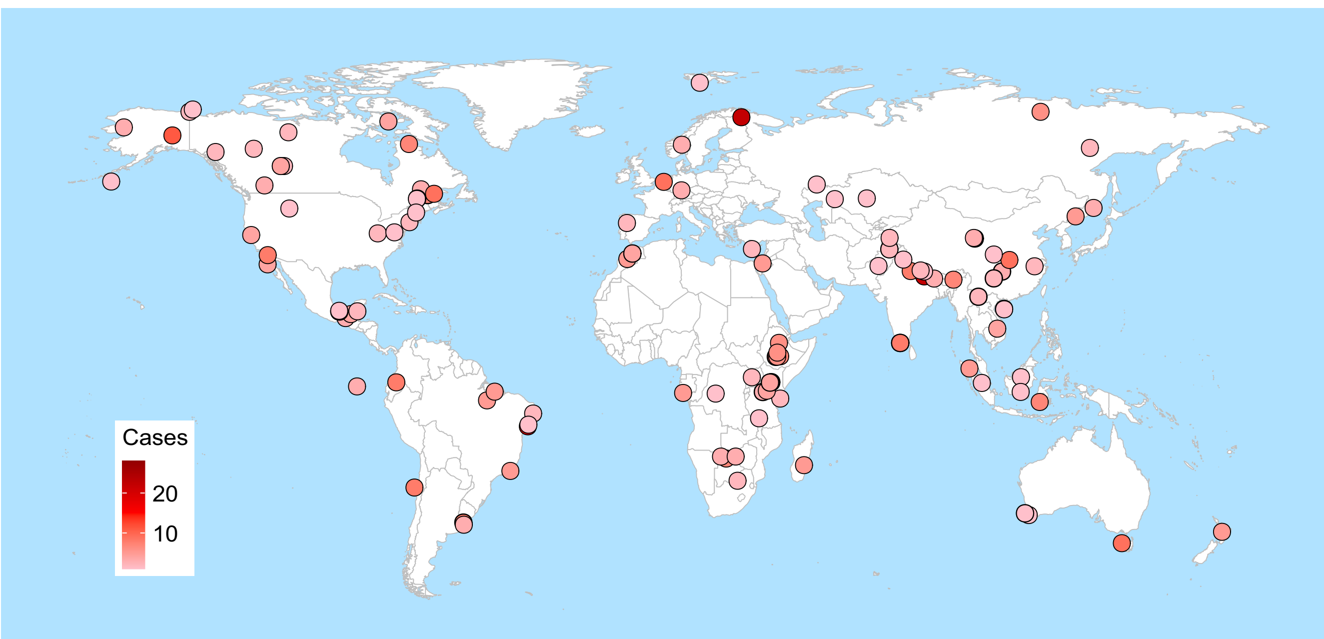

FIGURE 1 Geographical location of the studies included in the analysis. The colour of each point represents the number of study cases from each location.

List of Threatened Species Database (2022.2 version, http://www.iucnredlist.org).

2.3 | Statistical analysis

We performed all the analyses in R (R Core Team, 2023, version 4.2.3) using the '*metafor*' package (Viechtbauer, 2010). We used Cohen's *d*, the standardized mean difference, as the effect size measure across all cases. We calculated the effect size in three ways as in some previous meta-analysis studies (Benitez-Lopez et al., 2017; Carbone et al., 2019; Gunn et al., 2022; Peng et al., 2019). For most of the cases, the response ratio (RR) was calculated from the mean values, sample size and standard deviation of behaviour in both treatment (human disturbance) and control conditions. For cases presenting the presence/absence data of a specific behaviour from observation records of human disturbance and controlled conditions, we calculated the odds ratio (OR) from the two-by-two frequency table. In addition, for cases providing correlational data (e.g. the selection probabilities of a specific habitat in relation to its distance to the road) or the value of the *F* test, *t* test and χ^2 test, we calculated the Fisher's *Z* from these parameters. The response ratio, odds ratio and Fisher's *Z* were mathematically transformed into Cohen's *d* following Borenstein et al. (2009) (Table S1).

In some cases, higher values do not equate to greater behavioural expression. For instance, rest time was used to measure movement behaviour, and longer periods therefore indicate decreases in movement. Also, a lower intake of certain food compared with predisturbance equate to greater change in food selection. Therefore, we multiplied effect sizes by −1 for 48 cases following Gunn et al. (2022) and Moiron et al. (2020) to ensure the biological interpretations were uniform across estimates. Following this standardization, negative values of Cohen's *d* imply a decrease in a certain behaviour under human disturbance, whereas a positive value represents an increase in the behaviour. However, we treated both the increase and decrease in animal behaviours represent behavioural changes away from predisturbance natural patterns. For instance, in conditions with low food availability, some species decrease moving time to conserve energy (Smith et al., 2014), while others increase moving distances to locate high-quality foods (Santhosh et al., 2015). To avoid positive and negative values offsetting each other when calculating the cumulative effect size, we used absolute values of Cohen's *d* to assess the behavioural change intensity. Analyses based on signed Cohen's *d* were provided in the Supporting Information to identify where there is variation in the direction of particular behaviours (Figure S4–S7; Table S2, S4 and S6).

We used funnel plots and Egger's regression analysis (Stuck et al. 1998) to evaluate potential publication bias in our dataset. Egger's regression test $p > 0.05$, indicating that our estimated cumulative effect size was not affected by publication bias (Figure S2).

We used the random-effect meta-analyses restricted maximum likelihood (REML) method (Veroniki et al., 2016) to calculate the cumulative effect size of all cases and assessed the heterogeneity of effect size with *Q* statistics (Hedges & Olkin, 1985). A significant value of Q_t indicated that the effect size varies greatly among all cases and may be influenced by other factors. Hence, we built mixed-effect REML models (Veroniki et al., 2016) to assess the variation in effect size among the different human disturbance types. We also built mixed-effect models to assess the variations in effect size according to several categorical (food habits, group type, migration type, protected area status, distribution continents) and continuous (HFI and body mass) moderators for all and each human disturbance type in the study. The *p* values of Q_m statistics describe the variation in effect size that can be attributed to differences among categories of each predictor variable, and Q_e values describe the residual heterogeneity. Models with categorical factors were also run without the intercept to obtain the parameter estimates (mean effect sizes) of each level. Specifically, we consider an effect to be insignificant if confidence intervals overlap zero. Continuous variables were log-transformed and fitted as quadratic polynomials to account for nonlinear relationships. The models assessed for the relationship between effect size and continuous moderators (HFI and body mass) were also considered the hierarchical dependence in absolute data by including a random effect as a nesting factor. We use reference as a random effect and HFI as a fixed effect in multilevel mixed-effect models to assess the variation in effect size according to HFI. Also, we used the order as a random effect and body mass as a fixed effect in models to assess the variation according to animal body mass. In addition, we assessed effect sizes for climate change based on empirical and model prediction data separately in Figure S9.

3 | RESULTS

3.1 | The pattern of studies on human-induced behavioural changes

Of the 540 cases, those focussed on habitat selection were the most common (220 cases; 40.7% of the total), followed by movement (133; 24.6%), foraging (107; 19.8%), social (27; 5.0%) and vigilance behaviours (26; 4.8%; Figure 2). The representation of human disturbances and focal taxa differed among the different behaviours. In studies of habitat selection, most cases focussed on the effect of habitat degradation (119; 54.1%), road traffic (35; 15.9%) and climate change (29; 13.2%; Figure 2). Studies related to the effect of habitat degradation on habitat selection mainly focussed on Artiodactyla (52; 43.7%) and Carnivora (30; 25.2%; Figure 2). In studies of both movement and foraging behaviours, the effect of habitat degradation on Primates has received the most attention (18.6% and 35.5%, respectively; Figure 2).

3.2 | Effect of human disturbance types and intensity

Overall, the behaviour of threatened terrestrial mammals changed significantly in response to human disturbances (Absolute Cohen's

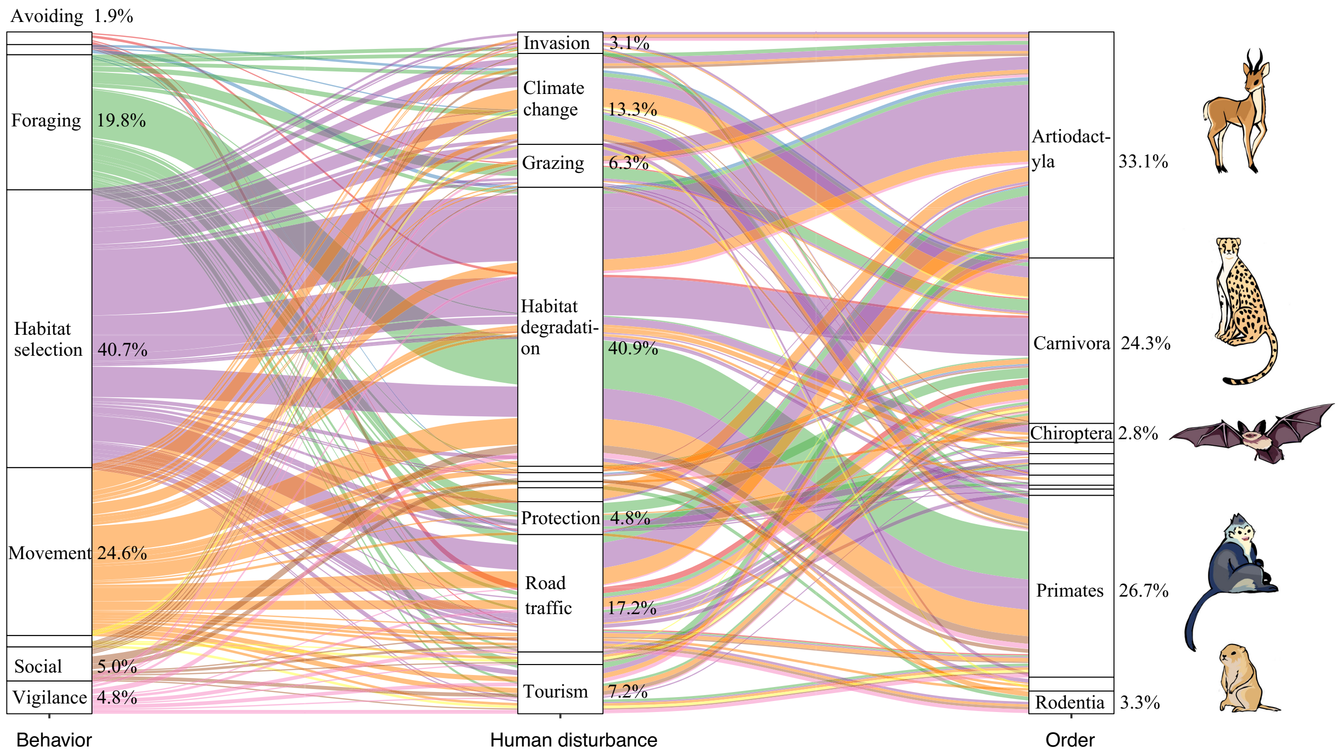

FIGURE 2 Sankey plot for study patterns of different behaviour types with focussed human disturbances and mammal taxa. The line thicknesses represent the number of study cases focussed on different categories of disturbances and orders. The percentage of each category was provided.

$d=1.23$ (95% CI: 1.11–1.34), $p<0.001$; Figure S3), and the total heterogeneity of effect sizes was large and statistically significant ($Q_t=22373.54$, $p<0.001$; Table S2). There was a significant variation in effect sizes between the different human disturbance types ($Q_m=15.64$, $p=0.029$; upper panel of Figure 3a). The effect size for road traffic was the largest (absolute Cohen's $d=1.65$), followed by grazing (1.36), biological invasion (1.35) and habitat degradation (1.23; Figure 3a). However, there was no significant variation between effect sizes for the different behaviours ($Q_m=3.54$, $p=0.738$; lower panel of Figure 3a).

When considering different behavioural responses separately, there was a significant variation between effect sizes for both habitat selection ($Q_m=19.87$, $p=0.006$) and foraging ($Q_m=16.33$, $p=0.022$) with different disturbance types (Figure 3b, Table S3). The effect size for habitat selection induced by road traffic was the largest (absolute Cohen's $d=2.04$; Figure 3b), 92.6% of which became more specialized. The effect size for foraging induced by habitat degradation was the largest (absolute Cohen's $d=2.03$; Figure 3b), which was mostly focussed on changes in feeding habits (50.0%) and foraging time (37.5%). Habitat degradation induced a lower intake proportion of normal foods and higher species diversity in the diet for 87.5% of the feeding habits cases, and shorter foraging time for 66.7% of the time cases. Behavioural change information for the cases is provided in Appendix S2.

Over all studies, there was a significant increase in the effect size of behavioural changes with increasing HFI ($Q_m=12.15$, $p<0.001$; Figure 4a). When considering different human disturbance types separately, the effects of grazing ($Q_m=4.03$, $p=0.045$; Figure 4d) and habitat degradation ($Q_m=166.86$, $p<0.001$; Figure 4e) on behavioural changes were stronger with increasing HFI.

3.3 | Factors influencing human-induced behavioural changes

Species with different functional traits respond to human disturbances differently. The effects of overall human disturbances on behavioural changes showed a significant weak negative correlation with body mass ($Q_m=10.88$, $p=0.001$; Figure 5a). Separate studies on different human disturbance types showed that the effects of climate change ($Q_m=225.66$, $p<0.001$), grazing ($Q_m=38.25$, $p<0.001$), road traffic ($Q_m=55.43$, $p<0.001$) and tourism ($Q_m=128.97$, $p<0.001$) on behavioural changes increased significantly with larger body mass (Figure 5c,d,g,h).

For the effects of habitat degradation ($Q_m=7.93$, $p=0.019$) and tourism ($Q_m=49.93$, $p<0.001$) on behavioural changes, there was a significant variation in different food habits. The effect size for habitat degradation on omnivorous species was the largest (absolute Cohen's $d=1.48$), as did the effect size for tourism on carnivorous species (absolute Cohen's $d=4.19$; Figure 6a). For species with different group types and migration types, the effect size of tourism was significantly greater on solitary species (absolute Cohen's

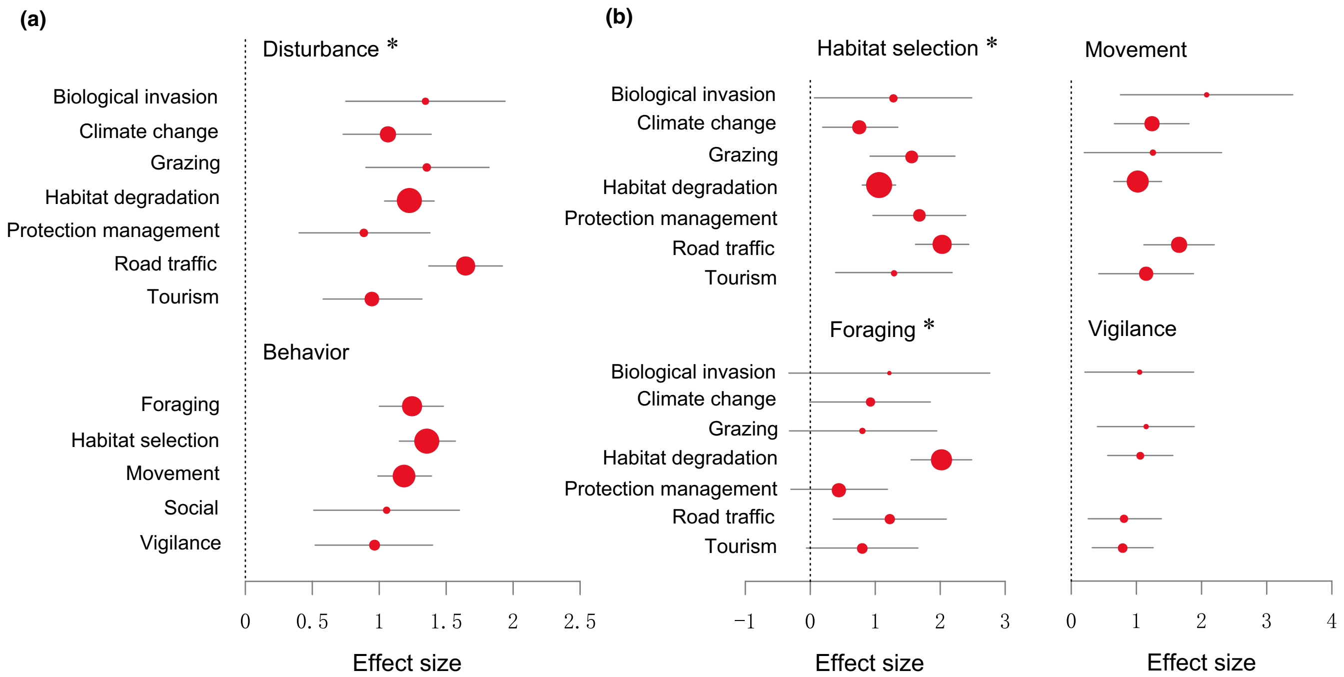

FIGURE 3 Weighted mean effect sizes and 95% confidence intervals showing behavioural changes for (a) human disturbance and behaviour types for overall studies and (b) human disturbances for studies on the four most focussed behaviour types based on absolute Cohen's *d*. The size of symbol is proportional to its sample size for each category. Asterisks denote a significant difference (Q_m) among categories (*$p<0.05$). Sample sizes for each category and parameters of meta-analysis are shown in Table S3. Categories with sample size <10 are not shown in (a).

$d=2.83$; $Q_m=13.73$, $p<0.001$; Figure 6b), and climate change had a significantly greater impact on migratory species (absolute Cohen's $d=1.67$; $Q_m=7.55$, $p=0.006$; Figure 6c). In addition, behavioural changes in response to human-mediated disturbances were not affected by the continent and protected area status of the studied species ($p>0.05$; Figure S8).

4 | DISCUSSION

The studies in our qualitative review focussed mostly on the impact of habitat degradation (40.9%), suggesting that habitat degradation may be the most prevalent study disturbance for threatened mammals. Our quantitative study reveals marked behavioural changes and found that the effect sizes varied across diverse human disturbances. This finding may be due to the different mechanisms of behavioural response to these disturbances. For instance, road traffic typically fragments habitat or acts as a barrier, affecting the distribution and dispersal patterns of animals (Brady & Richardson, 2017; Estrada et al., 2017). While human-facilitated invasive species affect native species by increasing predator and competitor abundance (Gibson et al., 2013; Ripple & Beschta, 2003). In addition, climate change altered animal behaviour by changing the physical environmental conditions (Beever et al., 2017; Harmon & Barton, 2013).

The effect size for behavioural changes of threatened mammals in response to road traffic was the largest, in particular for their habitat selection, consistent with the current understanding that roads and their environmental effects typically act as agents of selection (Brady & Richardson, 2017). Some animals such as the boreal woodland caribou *Rangifer tarandus caribou* adjusted their selection for certain habitats to avoid roads (Beguin et al., 2013), and this avoidance increased with disturbance intensity (Leblond et al., 2013). However, our analysis for road traffic suggested that threatened mammals' behaviour did not change significantly with increasing HFI. The latter finding may be because, in areas of lower disturbance intensity, studies were focussed on larger mammals like Asian elephants *Elephas maximus* (Pan et al., 2009), which tend to be more sensitive to roads due to their larger home range needs and a greater likelihood of vehicle collisions, hunting and harassment (Kerley et al., 2002; Noss et al., 1996). This was confirmed in our result that the effect of road traffic on threatened mammals increased significantly with larger body mass.

Highly specialized habits of threatened species can be the result of adaptive evolution to specific environmental selection pressures. Accordingly, changes to the environment and habitat may lead to reduced habitat suitability for a species. Habitat shifts may also cause niche overlap between species previously occupying separate niches and increase interspecific competition and vulnerability to predators (Smith et al., 2018). Our finding that roads have a relatively large effect size on animal behavioural changes indicates the critical need to design and construct roads carefully, taking into account their effect on the environment and the species therein. We recommend the basic design principles of avoiding dividing habitat by forcing roads through their core, especially where large mammals

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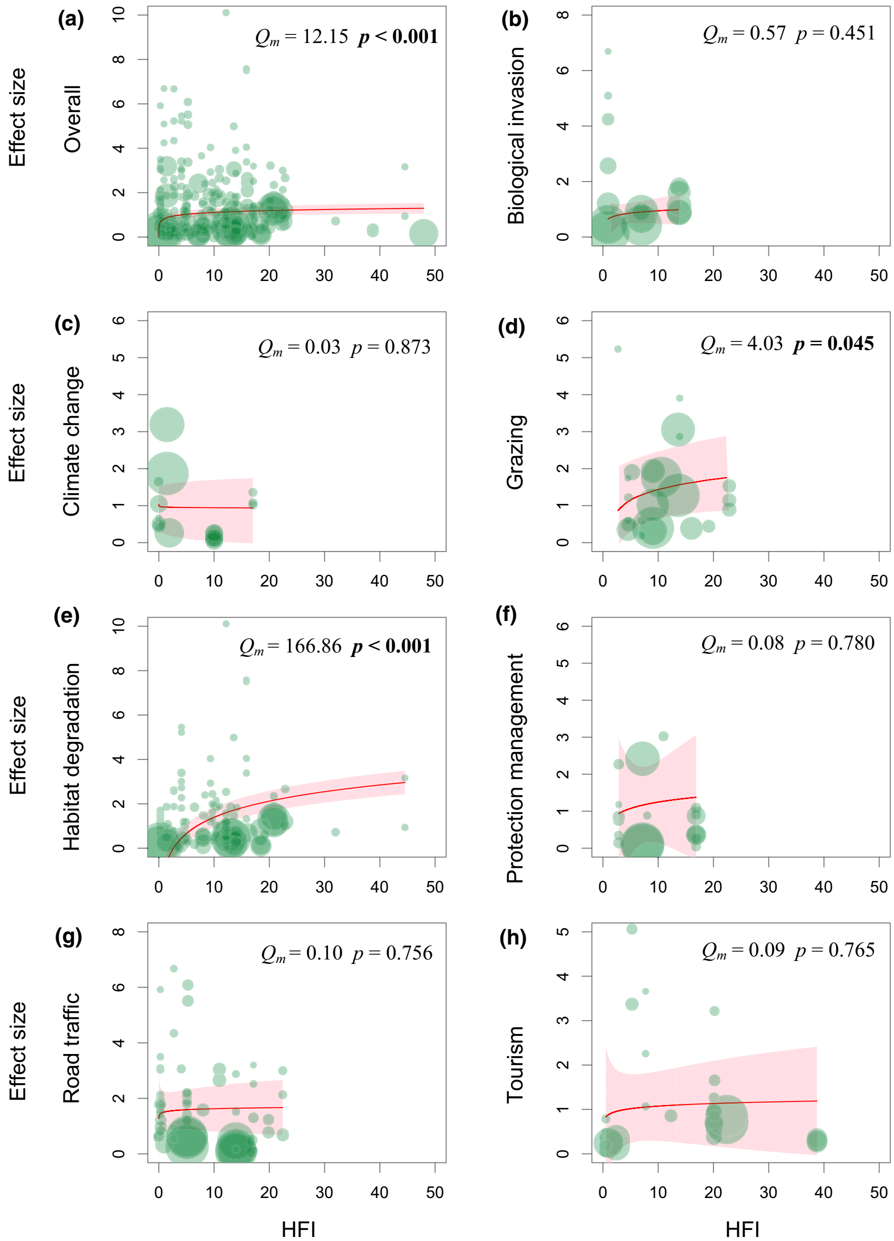

FIGURE 4 Behavioural changes of threatened terrestrial mammals affected by overall and each human disturbance type with human footprint index (HFI) based on absolute Cohen's *d*. Regression lines in red (with 95% CI in pink). Size of data points is inversely proportional to the sampling variance. Parameters and the significance (*p* value) of correlation analysis are provided in each panel and Table S5.

are concerned, and to take steps to maintain access to critical habitat resources (water, mineral licks, seasonal habitat).

The effect size for habitat degradation on the foraging behaviour of threatened mammals was larger than other disturbances. On the one hand, reduced natural resource availability in fragmented habitats is a major cause of change in animals' foraging time. For example, Coimbra-Filho's titi monkeys *Callicebus coimbrai* spent more time foraging in highly fragmented habitats (Souza-Alves et al., 2021). Altering food availability also led to changes in food selection, such as in bale monkeys *Chlorocebus djamdjamensis* that spent significantly more time feeding on non-bamboo plants and insects in fragmented forest in response to the relative scarcity of bamboo (Mekonnen et al., 2018). Animals' select diets are influenced by their energy, nutrients and toxic secondary metabolites concentrations (Villalba & Provenza, 2009), feeding on more low-quality foods may impact fitness. Food selection changes in some animals may also reshape the structure of trophic cascades and lead ultimately to the whole community changes (Hebblewhite et al., 2005).

In our review, habitat degradation affected the behaviour of mammals with a wide range of body mass, ranging from Chiroptera to Proboscidea (0.01–6100 kg). We found that the effect size for habitat degradation on omnivorous species was the largest, which may be because they are more sensitive to the reduction in food resource availability due to their food habits and seasonal differences in time spent foraging, resting and travelling caused by the seasonal phenology (Souza-Alves et al., 2021). Hence, we suggest integrating animal foraging ecology principles into landscape design and management, in particular for omnivore species, to maintain their natural resource acquisition and reproduction success in areas where habitat modification is inevitable. For historically fragmented habitats, improving resource availability such as by restoring vegetation or

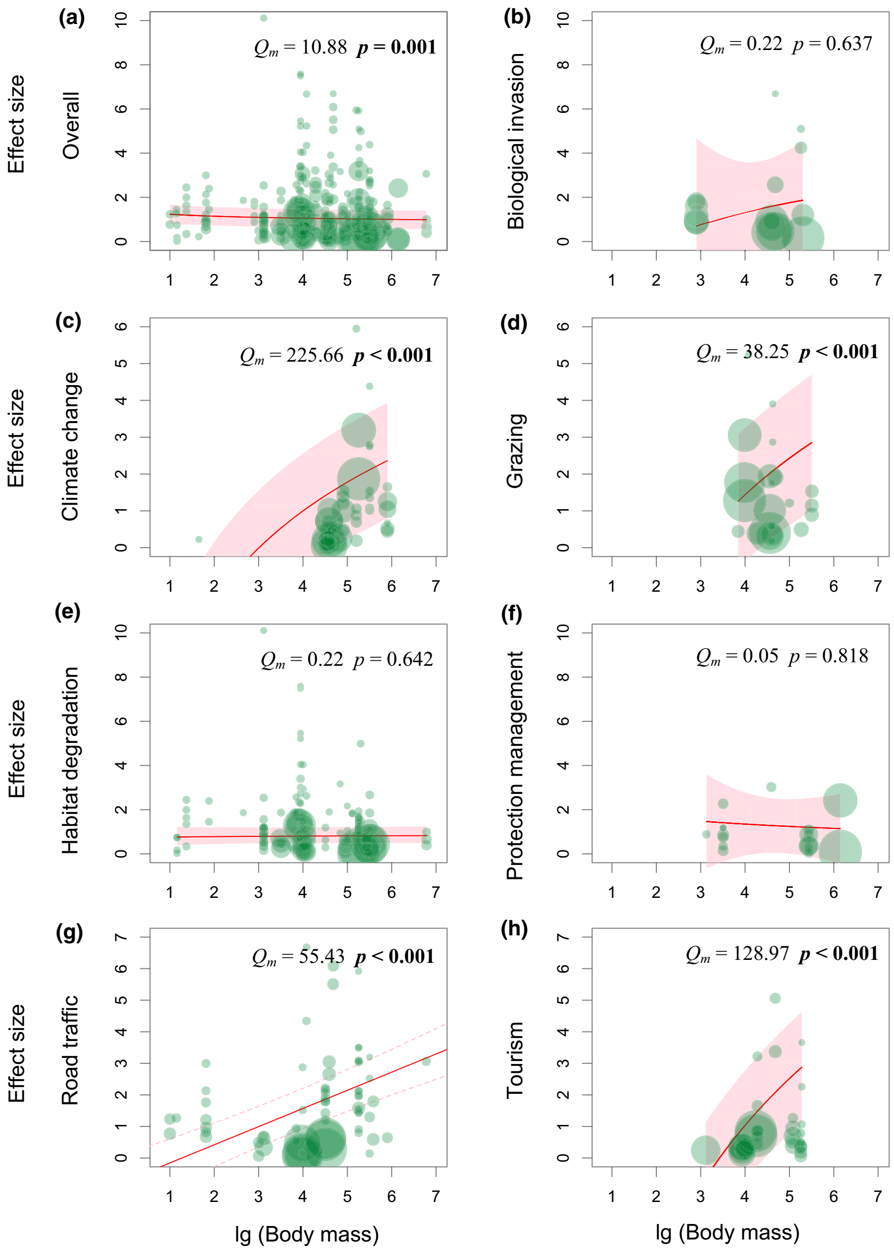

FIGURE 5 Behavioural changes of threatened terrestrial mammals affected by overall and each human disturbance type with their body mass based on absolute Cohen's *d*. Regression lines in red (with 95% CI in pink). Size of data points is inversely proportional to the sampling variance. Result of (g) obtained with linear correlation and others with logarithmic correlation. Parameters and the significance (*p* value) of correlation analysis are provided in each panel and Table S5.

building ecological corridors may be important measures to ensure animal long-term survival (Souza-Alves et al., 2021).

Tourism had a significantly greater influence on larger mammals, likely because their space needs force them into more frequent contact with human (Gaynor et al., 2018). Tourism affected the vigilance time, moving time, foraging time and avoidance distance of carnivore and solitary species, such as the amur leopard *Panthera pardus orientalis* (Yang et al., 2018), indicating these species may be more sensitive to the direct presence of humans with a behavioural response similar to that of actual predation risk (Tadesse & Kotler, 2012). Human-induced time budget imbalance, more time spent in vigilance and less in moving and foraging, may result in substantial fitness costs for threatened species, compromising their reproduction and survival (Doherty et al., 2021; Reimer et al., 2019). Thus, the distribution patterns of large carnivore and solitary species should be carefully considered for tourism attractions planning and management, and tourism activity should be restricted during breeding seasons.

The effect of climate change on animal behaviour was most often raised in terms of suitable habitat range loss and activity time changes caused by global warming (Lehmann et al., 2010; Luo et al., 2015), which were greater for migratory species, consistent with their vulnerability to climate change (Rushing et al., 2020). Increasing nocturnal activity can help animals to cope with high daytime temperatures, but this strategy was confined mainly to moonlit nights for some species like African wild dog *Lycaon pictus* (Rabaiotti & Woodroffe, 2019). Threatened species with a limited ability to increase nocturnal activity may not be able to adapt to increasing global warming via behavioural plasticity. For these species, conservation efforts should be focussed on potential suitable habitats for migratory species under future climate scenarios and especially on maintaining habitat connectivity along historical migration routes.

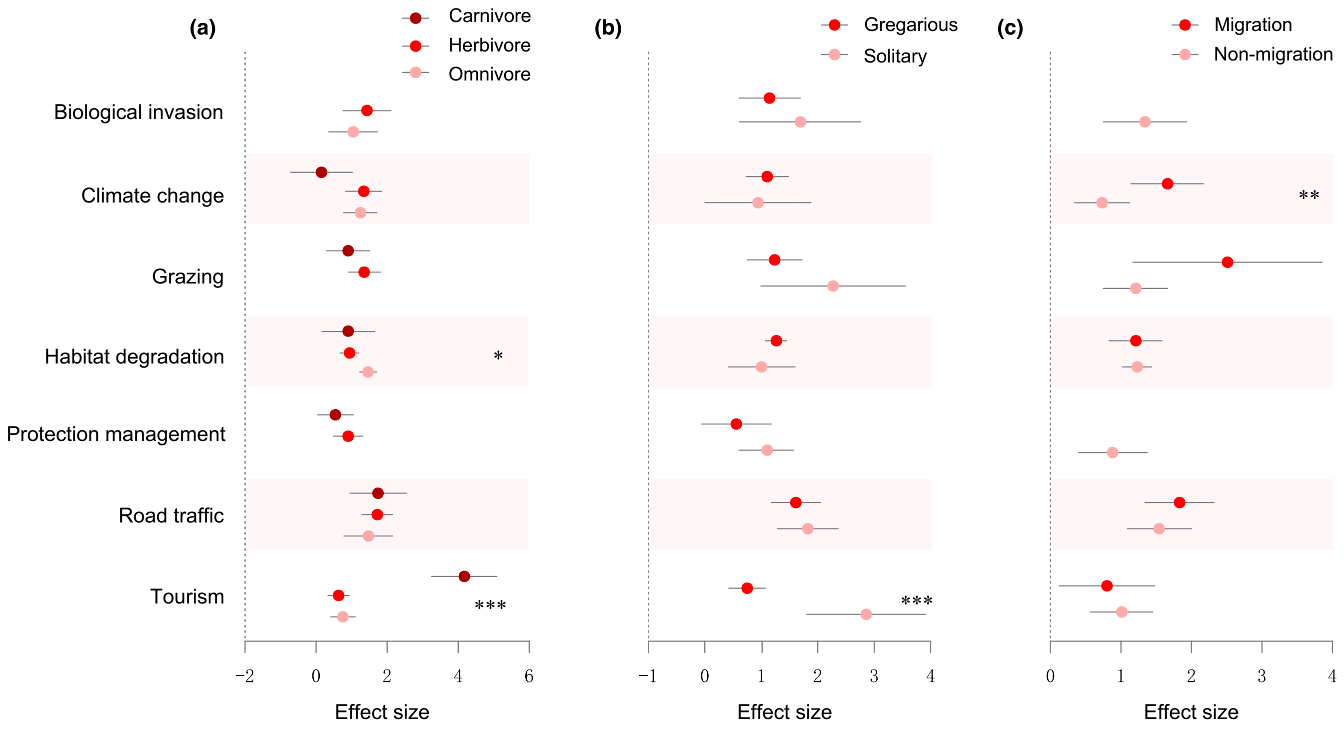

FIGURE 6 Weighted mean effect sizes and 95% confidence intervals showing behavioural changes of threatened terrestrial mammals affected by each human disturbance with their (a) food habits, (b) group type and (c) migration type based on absolute Cohen's *d*. Asterisks denote a significant correlation (***$p<0.001$, **$p<0.01$ and *$p<0.05$). Sample size and parameters of meta-analysis are shown in Table S3. Categories with sample size less than two are not shown in the Figure.

In conclusion, the effects of diverse human disturbances and their intensity significantly affected the behavioural responses of threatened terrestrial mammals. Behavioural responses varied across species with different functional traits including body size, food habits, migration type and group type. In addition, models built to assess the variation in effect size according to each predictor variable had significant Q_e values, suggesting that there are causes of behavioural changes that perhaps unmeasured in this meta-analysis or in the original papers. The management and conservation of threatened species should incorporate knowledge of their behavioural responses to human disturbance and take into account the potential ecological consequences for biodiversity conservation. This study provides a framework for prioritizing the management and conservation of threatened mammals affected by human disturbances.

AUTHOR CONTRIBUTIONS

Yonggang Nie conceived the ideas and designed the methods; Xiaoyu Hu, Xiaofan Ma, Wei Jia and Kai Liu collected the literature and data; Chao Zhang, Yumei Li and Yonggang Nie analysed the data and wrote the manuscript. All authors contributed critically to the drafts and gave the final approval for publication.

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CONFLICT OF INTEREST STATEMENT

There are not any potential sources of conflict of interest.

DATA AVAILABILITY STATEMENT

The authors confirm that all data underlying the findings are fully available without restriction. The datasets used to perform these analyses are available in Supplemental Material.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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APPENDIX A

DATA SOURCES

Abrahms, B., Jordan, N. R., Golabek, K. A., McNutt, J. W., Wilson, A. M., & Brashares, J. S. (2016). Lessons from integrating behaviour and resource selection: Activity-specific responses of African wild dogs to roads. *Animal Conservation*, *19*(3), 247-255.

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