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Antipredator behaviour of African ungulates around human settlements

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Abstract

As human populations grow and come into more frequent contact with wildlife, it is important to understand how anthropogenic disturbance alters wildlife behaviour. Using fine-scale spatial analyses, we examined how proximity to human settlements affects antipredator responses of ungulates. We studied seven common ungulate species (Kirk's dik-dik, Thomson's gazelle, impala, common warthog, common wildebeest, common zebra and Masai giraffe) in the Tarangire–Manyara ecosystem in northern Tanzania. In zebra and giraffe, flight responses to humans were significantly more likely when closer to settlements; however, there was a weak relationship between flight responses and distance to settlement in all other species. While there was largely a weak relationship between proximity to human settlements, the distribution of settlements in the landscape appears to affect wildlife behaviour, suggesting that animals perceive and respond to spatial variation in risk exerted by humans.

Résumé

Alors que les populations humaines croissent et entrent de plus en plus en contact avec la faune sauvage, il est important de bien comprendre comment les perturbations des hommes modifient le comportement de la faune. Par des analyses à échelle spatiale fine, nous avons étudié comment la proximité d'installations humaines affecte les réponses des ongulés contre les prédateurs. Nous avons étudié sept espèces communes d'ongulés, le dik-dik de Kirk, la gazelle de Thompson, l'impala, le phacochère commun, le gnou commun, le zèbre commun et la girafe masaï dans l'Écosystème Tarangire-Manyara au nord de la Tanzanie. Chez le zèbre et la girafe, les réponses de fuite loin des hommes étaient significativement plus probables lorsqu'ils étaient plus proches des installations humaines, mais il n'y avait qu'une faible relation entre les réponses de fuite et la distance par rapport aux installations chez les autres espèces. Même s'il y avait en général peu de relation avec la proximité des installations humaines, la distribution de ces installations dans le paysage semble affecter le comportement de la faune, ce qui suggère que les animaux perçoivent et répondent à la variation spatiale des risques représentés par les hommes.

KEYWORDS

antipredator behaviour, flight initiation distance, landscape of fear, Tarangire–Manyara ecosystem

1 | INTRODUCTION

With the growth of human populations and the expansion of settlements around protected areas, interactions between humans and wildlife are becoming more frequent and widespread (Wittemyer, Elsen, Bean, Burton, & Brashares, 2008). Human activities such as recreation, livestock herding and hunting, and infrastructure such as roads and settlements, may alter patterns of wildlife behaviour. Animals often perceive threats from human presence and activity and adjust their behaviour accordingly (Frid & Dill, 2002). Wildlife risk perception and response varies with spatio-temporal patterns of human activity, creating an anthropogenic “landscape of fear” for wildlife (Laundré, Hernandez, & Ripple, 2010). Perceived risk in human-inhabited areas may lead to greater wariness and stronger reactive responses to human presence and may even lead to complete avoidance of these areas by wildlife, effectively limiting habitat availability and landscape connectivity between protected areas.

Animals associate different human activities with distinct risk levels and respond to minimize perceived risk (Frid & Dill, 2002; Leblond, Dussault, & Ouellet, 2013; Stankowich, 2008). When animals are in an area that they perceive as more dangerous, they typically respond more strongly to the presence of perceived threats, such as people on foot or in vehicles. Reactive antipredator responses to perceived threats include increased vigilance and flight. Changes in patterns of these behaviours occur in response to direct disturbance such as hunting and harassment (Blumstein, Anthony, Harcourt, & Ross, 2003; Matson, Goldizen, & Putland, 2005; Nyahongo, 2008) as well as other types of human activity (Brown et al., 2012; Valcarcel & Fernandez-Juricic, 2009).

The cumulative costs of heightened antipredator behaviours in areas of frequent human contact may be detrimental to individual physiology and fitness (Cooke et al., 2014). Responses may also involve maladaptive habitat selection, with risk trade-offs driving animals to select poor habitats or avoid suitable habitats (Battin, 2004). These responses may scale up to affect population dynamics and community interactions (Cooke et al., 2014; Lima, 1998; Lima & Dill, 1990). Antipredator responses and their associated risk effects should vary across the landscape, corresponding to spatio-temporal patterns of predation risk (Creel, Schuette, & Christianson, 2014). Given that humans have a dominant presence in many African savannah ecosystems (Lindsey et al., 2013; Martin, Caro, & Kiffner, 2013), it is important to understand how different types and patterns of human disturbance affect fine-scale patterns of behaviour of wildlife, and how such patterns vary by species.

To assess the effects of human disturbance, we need to describe and quantify spatial patterns of anthropogenic activity. In many studies, land use is categorized into discrete levels based on protected area status (Kioko, Zink, Sawdy, & Kiffner, 2013; Setsaas, Holmern, Mwakalebe, Stokke, & Roskaft, 2007), urban–rural gradients (Mccleery, 2009; Valcarcel & Fernandez-Juricic, 2009) or the legality and intensity of hunting (Caro, 1999; Donadio & Buskirk, 2006; Kiffner, Stoner, & Caro, 2013). However, such indirect measures of human activity may not accurately reflect the way that animals perceive and respond to disturbance. Remote sensing and GIS technology provide opportunities to quantify spatial patterns of human disturbance, including fine-scale land use classification and identification of small-scale features such as households or farms. Remotely sensed data, combined with the use of GPS technology in wildlife field data collection, allow for a more spatially explicit examination of how animal behaviour is influenced by anthropogenic landscape features.

In this study, we investigated behavioural responses of wildlife to fine-scale spatial patterns of human settlement to better understand spatial patterns of animal wariness of humans. We examined animal responses to human presence as a proxy for fear and assessed how apparent fear varies with distance from human settlement. Human activity occurs in and around households and towns, and wildlife perceives risk from humans as a result of threatening nonlethal anthropogenic stimuli (people, infrastructure and associated noise), and occasionally direct persecution in the form of hunting or chasing animals (Frid & Dill, 2002).

To evaluate landscapes of fear, we assessed how the distance to human settlements (towns and households) affected the flight response behaviour of seven ungulate species in the Tarangire–Manyara ecosystem of Northern Tanzania. The study area is characterized by a fast-growing human population and rapidly changing land use practices (Msoffe et al., 2011). We predicted that wildlife would be more likely to respond to the observer when in closer proximity to a household or a town, due to greater perceived risk in areas near human settlements.

2 | MATERIALS AND METHODS

2.1 | Study Area

The Tarangire–Manyara ecosystem in Northern Tanzania has an area of c. 20,000 km^2 (Foley & Faust, 2010) and receives 600–650 mm of rain annually, spread across the short rains (November to January) and long rains (February to May) (Morrison & Bolger, 2012).

We collected data from three locations within the study area: Lake Manyara National Park (LMNP), Manyara Ranch (MR) and the Mto wa Mbu Game Controlled Area (GCA) (Figure 1). LMNP is characterized by groundwater forests, *Acacia-Commiphora* bushlands and alkaline grassland while MR, and the GCA are primarily *Acacia-Commiphora* bushland and grassland habitat. These three locations are characterized by different types of land management systems and human activity. LMNP is bordered by the steep Rift Valley escarpment to the west and by Lake Manyara to the east, limiting east–west movement in and out of the park for wildlife. The park allows eco-tourism but restricts other land uses including settlement, livestock grazing, farming and resource extraction (Kiffner et al., 2014). Manyara Ranch is managed by the Tanzanian Land Conservation Trust and permits livestock grazing but prohibits

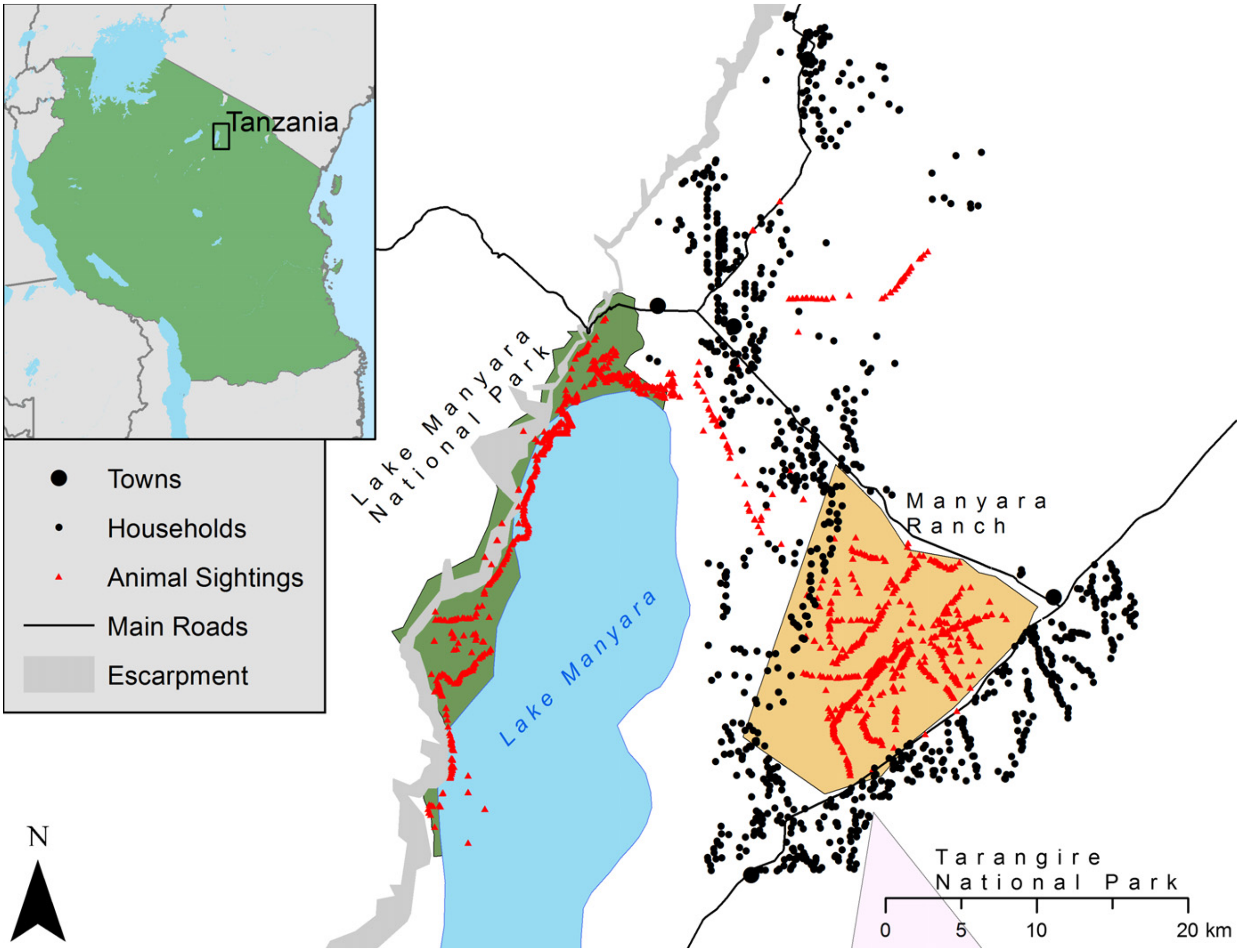


FIGURE 1 Map of the study area in Northern Tanzania showing the boundaries of protected areas, animal sightings and locations of settlements and towns. [Colour figure can be viewed at wileyonlinelibrary.com]

settlement, agriculture and hunting. The GCA is managed by the Wildlife Division and permits diverse land uses (incl. hunting with permits). It is primarily used for agriculture and livestock grazing. There are several towns spread throughout the GCA, although most human settlement occurs in small villages or solitary homesteads that are outside of towns. While hunting is officially banned in LMNP and Manyara Ranch and is restricted in the GCA, it occurs illegally throughout the study area, though mostly in GCA (Kiffner et al., 2014). Hunters primarily hunt with spears or machetes, aided by motorbikes to chase animals. The primary natural predators in this system are lions (*Panthera leo*), spotted hyaenas (*Crocuta crocuta*) and leopards (*Panthera pardus*), which concentrate in protected areas like LMNP in the dry season and spread out during the wet seasons (Koziarski, Kissui, & Kiffner, 2016). While risk from predators may vary and contribute to baseline levels of fear across the landscape, it is unlikely that fear of natural predators would be a strong driver of patterns of behavioural responses to human observers, particularly because predators in this system are mainly active at night (Estes, 2012). Rather, it is more likely that anthropogenic factors would drive patterns of wariness and responses to humans.

2.2 | Assessing flight response

To assess wildlife responses to humans in each of the three study locations, we conducted two-kilometre driving transects. We systematically chose transect locations along tracks and roads that represent all habitats in each location, with a minimum of 0.5 km between transects. We shortened eighteen transects so as not to overlap with other transects. From November 2011 to September 2013, we surveyed each transect at least once in each of the three seasons (short rains, long rains and dry season). We repeated transects up to three times in each season. We conducted 334 transects (total 631.4 km) in LMNP, 346 transects (total 674.5 km) in Manyara Ranch and 347 transects (total 659.9 km) in the GCA.

Upon encountering a group of animals within 500 m of the transect, we recorded location along the road (using a handheld GPS unit), herd size (number of animals within 50 m) and distance from the road/observer (using a laser rangefinder). For each group, we recorded a binary flight response: whether or not the majority of the group moved in a sustained, directed manner away from the observer upon encounter (Kiffner et al., 2014). We also recorded distance to observer, as animals likely perceive greater risk when closer to human stimuli, and our minimum distance to the group was constrained by roads. Herd size generally is an important defence mechanism against predators in many species and may therefore be a predictor of perceived risk and group antipredator responses (Caro, 2005; Pulliam, 1973). Finally, we classified the vegetation type for each sighting as open (grassland or open bushland), closed (closed bushland, woodland and shrubland) or riverine. Habitat generally plays a large role in determining actual predation risk and risk perception, and animals become more vigilant and flee at greater distances in more risky habitats (Riginos, 2015). We evaluated vegetation and herd size because they have been shown to affect antipredator behaviours (Creel et al., 2014; Frid & Dill, 2002). Distance to observers and roads can also play an important role in determining behaviour (Ciuti et al., 2012).

We recorded observations of all wild ungulates with a body mass >0.5 kg and restricted analyses to species which had >100 total observations. The species included (in order of ascending body mass): Kirk's dik-dik [Madaqua kirkii (Günther, 1880), *n* = 173], Thomson's gazelle [Eudorcas thomsonii (Günther, 1884), *n* = 245], impala [Aepyceros melampus (Lichtenstein, 1812), *n* = 441], common warthog [Phacochoerus africanus (Gmelin, 1788), *n* = 159], wildebeest [Connochaetes taurinus (Bulchell, 1823), *n* = 257]), plains zebra [Equus quagga (Boddaert, 1785), *n* = 503] and giraffe [Giraffa camelopardalis (Linnaeus, 1758), *n* = 272; Tables S1, S2].

2.3 | Mapping households and towns

To map households and towns, we analysed Google Earth orthoimagery from 2005 to 2013. While the human population area has grown as some images were taken, the general pattern and spatial orientation of settlements have likely remained similar. We defined households as single-family units, which were characterized by 3–10 small buildings surrounding a livestock enclosure. Household units (*n* = 1019) were generally circular in shape and 30–100 m in diameter. We defined towns as large centres of development containing 100+ buildings in close proximity. Towns (*n* = 6) were much larger than households (approximately 2–4 km in diameter) and more variably shaped. We used centroid points to represent the locations of both households and towns. It was difficult to delineate town edges from the satellite imagery, so we instead used a point as close to the centre as possible.

We digitized all households and towns within 10 km of an animal observation. We did not include households and towns west of the Gregory Rift on the western border of our study area. Movement of people and animals up and down the rift's escarpment is restricted to a few passages, and the escarpment thus serves as a natural barrier to interaction between animals and people living in the highlands (Morrison & Bolger, 2012). We used the "Near" tool in ArcMap 10.2 (Esri, 2014) to calculate the distances between each animal observation and the centroid of the nearest household and town (Table S3).

2.4 | Data analysis

To assess the impact of human settlement on animal flight response to human stimuli, we built species-specific generalized linear models in the software R (R Development Core Team, 2013). We evaluated five predictors in models for the binary flight response variable, including distance to nearest household (metres), distance to nearest town (metres), vegetation type (open, closed and riverine), herd size and distance to observer. Distance to households and towns were used as proxies for relative human disturbance across the study area. Using the logit link in R, we tested models of all permutations of predictors including a null model. To identify the best models, we calculated AICc scores using the MuMIn package (Barton, 2013) and ranked models from lowest AICc (best model fit) to highest (Burnham & Anderson, 2002). We then identified all predictor variables that were present in competitive models (models <2 AICc values of the best model). Using only the competitive models, we averaged with the zero method to estimate the coefficients (Grueber, Nakagawa, Laws, & Jamieson, 2011).

To assess the direction and strength of predictors in determining the likelihood of flight response (yes/no), we estimated odds ratios and their associated 95% confidence intervals using the MuMIn package in R (Barton, 2013). These ratios represent the odds of a flight response given a one unit change in the explanatory variable. We considered the relationship between flight and explanatory variables to be significant (at the $p = .05$ level) when the 95% confidence interval of the odds ratio did not overlap with 1.

3 | RESULTS

Household distance was a predictor of flight behaviour in at least one of the top models for all species except impala (Tables 1, S4). Zebra (Odds Ratio = 0.9998 per m distance from households, 95% CI = 0.9997–0.99995) and giraffe (OR = 0.9999, CI = 0.9997–0.999993) were significantly more likely to flee when nearer to households. For all other species, results were insignificant (Figure 2a).

Town distance was a predictor in at least one of the top models of flight behaviour for all species except zebra (Tables 1, S4), but odds ratios were not significant for any species (Figure 2b).

Vegetation and herd size were present in at least one of the top models (Tables 1, S4). Wildebeest (OR = 1.0008 per capita increase in herd size, CI = 1.0033–1.0143) were more likely to exhibit flight behaviour when in larger groups while in all other species, results were insignificant (Figure 2d). Odds ratios for vegetation were not significant for any species (Figure 2c).

Distance to observer was a predictor of flight in all of the top models for Thomson's gazelle, impala, warthog, wildebeest, zebra and giraffe, and in at least one of the top models for dik-dik (Tables 1, S4). In Thomson's gazelle (OR = 0.9962 per m distance

TABLE 1 Results of generalized linear models showing the predicted responses of species to human observers in the Tarangire–Manyara ecosystem (in order of ascending body mass): dik-dik, Thompson's gazelle, impala, warthog, wildebeest, zebra and giraffe. We report models within two AICc values of the best model, in addition to the null model and global model (all predictor variables), ordered from lowest to highest ΔAICc. For full model list, see Table S4

	Intercept	df	ΔAICc	AICc weight
Dik-dik Model				
Distance to observer	0.7028	2	0	0.074
Town distance, Distance to observer	1.247	3	0.12	0.07
Household distance, Distance to observer	1.116	3	0.27	0.065
Null model	0.5077	1	0.34	0.062
Vegetation, Distance to observer	1.027	3	0.34	0.062
Herd size, Distance to observer	0.9588	3	0.96	0.046
Town distance	0.9191	2	1.07	0.043
Household distance, Herd size, Distance to observer	1.415	4	1.08	0.043
Town distance, Herd size, Distance to observer	1.521	4	1.09	0.043
Town distance, Vegetation, Distance to observer	1.43	4	1.1	0.043
Vegetation, Herd size, Distance to observer	1.266	4	1.42	0.036
Household distance	0.7662	2	1.43	0.036
Vegetation	0.7082	2	1.44	0.036
Herd size	0.7196	2	1.52	0.035
Household distance, Town distance, Distance to observer	1.373	4	1.55	0.034
Household distance, Vegetation, Distance to observer	1.195	4	1.83	0.03
Global model (Household distance, Town distance, Vegetation, Herd size, Distance to observer)	1.735	6	4.13	0.009
Thomson's Gazelle Model				
Distance to observer	−0.1434	2	0	0.142
Herd size, Distance to observer	−0.251	3	0.22	0.127
Vegetation, Distance to observer	−0.1942	3	0.93	0.089
Household distance, Herd size, Distance to observer	−0.5498	4	0.96	0.088
Household distance, Distance to observer	−0.379	3	1.13	0.081
Vegetation, Herd size, Distance to observer	−0.2978	4	1.25	0.076
Household distance, Vegetation, Herd size, Distance to observer	−0.6187	5	1.85	0.056
Town distance, Distance to observer	−0.2748	3	1.87	0.056
Town distance, Herd size, Distance to observer	−0.4567	4	1.88	0.055
Household distance, Vegetation, Distance to observer	−0.4515	4	1.93	0.054
Global model (Household distance, Town distance, Vegetation, Herd size, Distance to observer)	−0.7065	6	3.84	0.021
Null model	−0.5967	1	9.94	0.001
Impala Model				
Vegetation, Distance to observer	0.2023	3	0	0.157
Distance to observer	−0.03756	2	0.25	0.138
Vegetation, Herd size, Distance to observer	0.3327	4	0.4	0.128
Herd size, Distance to observer	0.05631	3	1.04	0.093
Town distance, Vegetation, Distance to observer	0.1056	4	1.84	0.063
Global model (Household distance, Town distance, Vegetation, Herd size, Distance to observer)	0.2526	6	4.08	0.02
Null model	−0.6325	1	28.38	0
Warthog Model				
Household distance, Vegetation, Herd size, Distance to observer	−0.9681	5	0	0.152
Household distance, Vegetation, Distance to observer	−0.5354	4	0.26	0.133
Household distance, Distance to observer	−0.09698	3	0.4	0.124

(Continues)

TABLE 1 (Continued)

	Intercept	df	ΔAICc	AICc weight
Household distance, Herd size, Distance to observer	−0.3616	4	0.93	0.095
Global model (Household distance, Town distance, Vegetation, Herd size, Distance to observer)	−0.732	6	1.06	0.09
Household distance, Town distance, Vegetation, Distance to observer	−0.3195	5	1.6	0.068
Household distance, Town distance, Distance to observer	0.1167	4	1.63	0.067
Household distance, Town distance, Herd size, Distance to observer	−0.1345	5	1.88	0.059
Vegetation, Herd size, Distance to observer	−0.1052	4	1.92	0.058
Null model	−0.7793	1	54.14	0
Wildebeest Model				
Herd size, Distance to observer	−0.4916	3	0	0.188
Household distance, Herd size, Distance to observer	−0.2802	4	0.24	0.166
Vegetation, Herd size, Distance to observer	−0.5254	4	0.62	0.137
Household distance, Vegetation, Herd size, Distance to observer	−0.3058	5	0.69	0.133
Household distance, Town distance, Herd size, Distance to observer	−0.3989	5	1.94	0.071
Town distance, Herd size, Distance to observer	−0.4396	4	2	0.069
Global model (Household distance, Town distance, Vegetation, Herd size, Distance to observer)	−0.413	6	2.47	0.055
Null model	−1.163	1	30.75	0
Zebra Model				
Household distance, Herd size, Distance to observer	−0.1816	4	0	0.32
Household distance, Vegetation, Herd size, Distance to observer	−0.2421	5	0.99	0.195
Household distance, Distance to observer	0.04014	3	1.79	0.131
Global model (Household distance, Town distance, Vegetation, Herd size, Distance to observer)	−0.2112	6	3.02	0.071
Null model	−1.419	1	43.95	0
Giraffe Model				
Household distance, Distance to observer	−0.2809	3	0	0.231
Household distance, Herd size, Distance to observer	−0.5354	4	1.11	0.133
Household distance, Town distance, Distance to observer	0.03093	4	1.48	0.111
Household distance, Vegetation, Distance to observer	−0.2065	4	1.51	0.109
Global model (Household distance, Town distance, Vegetation, Herd size, Distance to observer)	−0.169	6	4.31	0.027
Null model	−2.051	1	17.22	0

from observer, CI = 0.9939–0.9985), impala (OR = 0.9916, CI = 0.9880–0.9952), warthog (OR = 0.9835, CI = 0.9758–0.9911), wildebeest (OR = 0.9952, CI = 0.9932–0.9972), zebra (OR = 0.9941, CI = 0.9920–0.9963) and giraffe (OR = 0.9923, CI = 0.9879–0.9968), animal groups were more likely to flee when closer to the observer while in dik-dik, results were insignificant (Figure 2e).

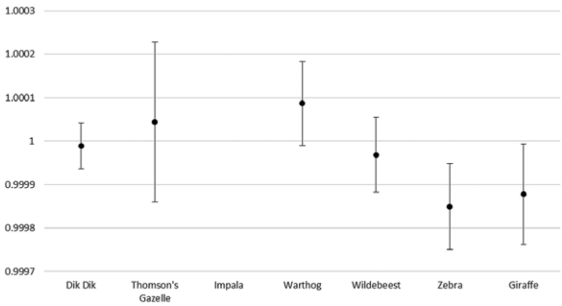
4 | DISCUSSION

Our study provides evidence that human settlements create a landscape of fear for wildlife. Animals likely perceive greater risk when in proximity to households and settlement. They respond with heightened antipredator behaviours such as flight when in the presence of human stimuli, as observed across animal taxa (Bjørvik, Dale, Hermansen, Munishi, & Moe, 2015). Distance to settlements was a predictor of flight behaviour for all species, but was only statistically significant for zebra and giraffe, indicating that distance to settlement alone may not capture the complex trade-offs involved in risk perception and response.

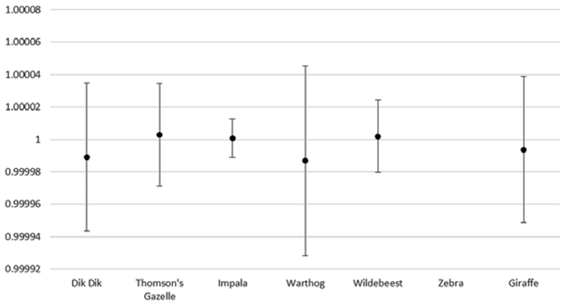
Although our study found weak evidence for increased flight behaviour near settlements, all of the species studied exhibited flight responses to human presence. Flight and other antipredator behaviours are energetically costly (Frid & Dill, 2002) and if human disturbance is frequent, such responses may scale up to have physiological and fitness consequences. The illegal hunting in the area may reinforce fear of humans and fleeing from humans may thus be an adaptive behaviour that allows wildlife to co-exist in this human-dominated landscape (Kiffner et al., 2014). Dik-dik showed the weakest response to households or observers, possibly related to their strong territoriality (Estes, 2012). It is possible that because dik-diks are territorial, those found closer to settlements are habituated to people while all the other species tend to be wider ranging (Estes, 2012).

The lack of strong relationships between human settlements and antipredator behaviour implies that antipredator behaviours may be better explained by smaller-scale, continuous indicators of risk,

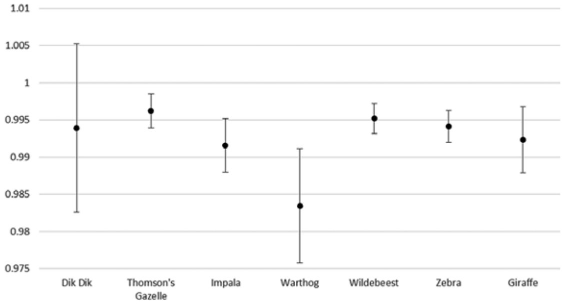
(a) Household Distance



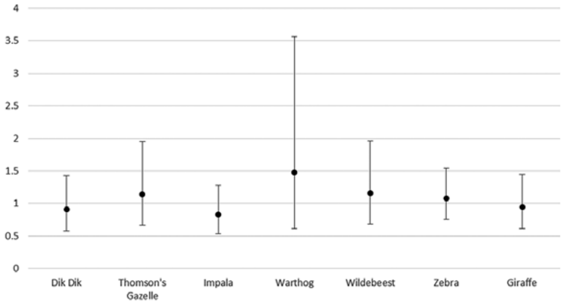
(b) Town Distance



(c) Distance to Observer



(d) Vegetation



(e) Herd Size

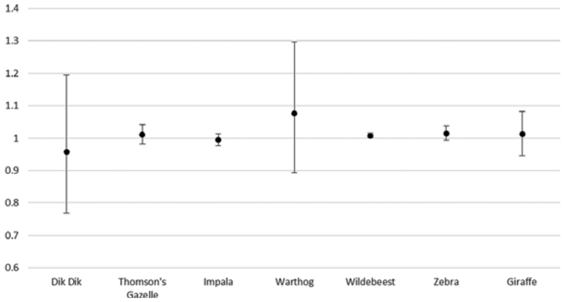


FIGURE 2 Odds ratios (and 95% confidence intervals) for variables affecting likelihood of flight in wildlife species in the Tarangire–Manyara ecosystem, Tanzania. For household distance (a), town distance (b) and distance to observer (c), likelihood of flight per metre increase in distance. For vegetation (d), likelihood of flight in more closed habitats. For herd size (e), likelihood of vigilance when number of individuals increases by 1. Missing odds ratio indicates that the variable was not present in the best models for that species

rather than static settlement location. We did not explicitly evaluate the fine-scale spatial pattern of hunting or other activities in the study area, so we could not directly test how animals perceive risk from different human activities around settlements. Additional research is necessary to quantify and examine the impacts of fine-scale patterns of human activity on wildlife behaviour. Furthermore, animal trade-off opportunity costs of antipredator behaviour when they are engaging in fitness-enhancing activities such as foraging, and their responses to human presence, may not directly reflect their fear or perceived risk in a given area.

It is possible that the density of natural predators also influenced the prey species' landscape of fear, affecting general wariness towards all threats such as human presence. Lions, the dominant predator in the study area, occur at highest densities in LMNP, and lowest densities in human-dominated areas (Lee, 2015). The effects of predator density on fear may therefore offset effects of human density, if prey perceives and responds to all risk similarly.

In this study, we only considered reactive antipredator behaviours to human observers. However, animals also respond proactively to human-inhabited areas through avoidance. Ungulates tend to respond proactively to more predictable, long-term risks and engage in reactive responses for more immediate predation risks (Creel et al., 2014). Through systematic sampling of wildlife and settlements in the Maasai Mara region, Ogutu et al. (2010) found that peak wildlife densities were farther from settlements than from water and were more spread out in the protected reserve than in an adjacent pastoral area.

Potentially, habituation may play a role in tempering behavioural responses to human disturbance and that animals may exhibit weaker behavioural responses to human presence in areas where they are regularly exposed to nonlethal human activity. Ultimately, we require a better understanding of how the physical footprint of human settlements and towns translates into activities that disturb wildlife. Furthermore, we need to examine how different human activities affect wildlife to improve our understanding of human–wildlife interface. For example, human activities such as livestock grazing (herders or dogs often chase wildlife) and hunting are likely to occur throughout the landscape, not just in close proximity to settlements.

5 | CONCLUSION

Our study demonstrates how fine-scale spatial analysis can be used to examine how animals perceive and respond to landscapes of fear created by human infrastructure. We provide insight into previously observed differences in antipredator behaviour on more coarse scales, such as inside vs. outside of protected areas (Blake et al., 2008; Kioko et al., 2013). While we found a weak effect of human activity on wildlife risk responses, our study does not comprehensively address all facets of disturbance or wildlife behaviour. Future research is needed to deeply explore behavioural responses of wildlife to human activity. The incorporation of fine-scale spatial data of both human disturbance and animal movement will help us better understand nuances in human–wildlife interactions.

Understanding small-scale patterns of behavioural variation can reveal where animals may suffer from physiological and fitness costs due to increased energy expenditure on antipredator responses (Cooke et al., 2014). Wildlife may perceive human-inhabited areas as high-risk areas, leading them to avoid those areas and thus limiting available habitats and movement. An improved understanding of anthropogenic effects on wildlife behaviour may ultimately enable us to predict how animals may respond to the expansion of human settlements. This is crucial in promoting human–wildlife coexistence in human-dominated landscapes.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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