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Anthropogenic Environments Are Associated with High Body Surface Temperatures in an Equatorial Mammal, the Banded Mongoose

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Abstract

Global land use is changing rapidly, particularly in the tropics, where human populations have had relatively high growth rates in recent decades. This has resulted in wildlife increasingly living in or using anthropogenic environments, which often have different thermal properties in comparison to natural habitats. For example, materials used for buildings, such as concrete and brick, typically absorb, retain and radiate more heat than vegetated surfaces. The mosaic of man-made and natural areas formed when anthropogenic environments expand is therefore likely to generate microhabitats with different thermal properties. Here, we investigated the association between microhabitats and the body surface temperature of wild banded mongooses (*Mungos mungo*), a social mammal living in equatorial Uganda. After controlling for the significant effects of air temperature, humidity, time of day and body contact, we found that mongooses had the highest body surface temperatures when present on anthropogenic substrates, such as discarded roofing straw and refuse, while mongooses present on building materials, dead vegetation and bare soil had intermediate body surface temperatures. In contrast, mongooses had the lowest body surface temperatures when present in more natural, vegetated habitats. Although our study is relatively small scale and limited in scope, our results indicate that anthropogenic modifications to natural environments may result in hotter microhabitats, which may in turn impact space use, movement and thermoregulation in wildlife. We hope that our study encourages further research into this understudied but emerging topic.

Keywords: thermal microclimate; body surface temperature; anthropogenic change; rural development; banded mongoose

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1. Introduction

Global land use is changing rapidly due to anthropogenic activities, with 17% of the Earth's land surface area having changed use at least once over the past 60 years [1], and approximately three-quarters having been altered by humans in the last 1000 years [2]. In the Global South, recent land use change has been driven by rapid population expansion,

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with sub-Saharan Africa having the greatest population growth rate over the past decade in comparison to other global regions [3]. Larger populations have resulted in land clearance for subsistence farming and associated settlements [1,4], and many previously natural landscapes are now dominated by farms, villages and small towns. However, population growth is not the only factor driving land use change, and the loss of natural ecosystems in Africa has also occurred as a result of commodity crop expansion [4], climate change [5] and urbanisation [6–8].

Land use changes and expanding human populations have resulted in wildlife increasingly living in or using anthropogenic environments. This can have a range of impacts on the wildlife concerned. For example, changes in acoustic and visual environments have been shown to impact communication, distribution, activity patterns, phenology, foraging, physiology and homeostasis across a wide range of taxa [9,10]. Similarly, inhabiting anthropogenic environments is associated with increased infectious disease risk [11] and changes in the microbiome [12], which may present health issues for both wildlife and humans [13].

An understudied disturbance associated with wildlife in anthropogenic landscapes is change in the thermal environment. A built environment is typically made up of low-albedo surfaces (which absorb sunlight), resulting in a reduction in solar radiation being reflected into the atmosphere, and leading to increased surface temperatures [14,15]. Furthermore, urban areas also commonly lack vegetation, which provides shade and reduces heat through evaporation and transpiration [16,17]. Accordingly, cities have been shown to generate ‘heat islands’ that can be up to 10–15 °C higher than the surrounding environments [14,18], potentially posing a risk to the people and wildlife occupying those areas [19–21]. For example, the 2003 European heat wave is estimated to have killed >70,000 people over several months [22], and there is evidence that the death rate from heat waves such as this has been greater in cities compared to rural areas [23,24]. Similarly, heat waves have caused mass mortality across a wide range of animal species [25–27], and these events are likely to increase in frequency with future climate change [28]. However, the combined impact of urbanisation and high temperatures on wildlife has been poorly studied, as the vast majority of studies to date have investigated urban heat islands from a human perspective. The few studies that have been conducted have found: (1) that anthropogenic nesting sites in urban areas are at higher temperatures than those of natural nest sites (for genets *Genetta tigrina* [29] and lizards *Anolis cristatellus* [30]), and (2) negative impacts of urban thermal environments on fitness-related traits in lizards *Anolis cristatellus* [19] and desert-adapted rodents [31].

While we have a good understanding of thermal microclimates in urban areas, we know comparatively little about the thermal impact of human settlements in more rural areas, particularly in lower-income countries [32]. This is despite such landscapes dominating human land use change [1] and therefore occurring at the interface between humans and areas protected for wildlife. Nevertheless, similar to urban areas, hotter rural microclimates are expected to result from the addition of man-made building materials [14] and the removal of vegetation [17]. The expansion of road networks in rural areas are also likely to have thermal impacts on animals, as several species have been recorded to thermoregulate by basking on asphalt, which in turn may increase the likelihood of road collisions [33–36]. Furthermore, rural areas in lower-income countries often lack the infrastructure to deal with refuse [37], with little opportunity for waste sorting or recycling, resulting in mixed waste landfills. Such landfills have been associated with higher temperatures [38] and spontaneous fires [39], and so may have an important impact on thermal environments. Additionally, high-calorie food items found in refuse sites may also attract wild animals [40], therefore posing a particular challenge for wildlife management. Despite the potential for anthropogenic microclimate modification, thermal conditions are rarely considered in management actions for wildlife, making it difficult to understand how anthropogenic changes contribute to the thermal habitat of species [41].

The thermal properties of microhabitats can be measured by investigating their impact on the body surface temperatures of the mammals that inhabit them. For example, body surface temperature has been shown to vary strongly with the temperature of the microclimate in wild vervet monkeys, *Chlorocebus pygerythrus* [42]; howler monkeys, *Alouatta palliata* [43]; and domestic animals [44]. The body surface temperature can therefore provide a biologically relevant representation of a thermal environment as it is experienced by animals in a particular location. This contrasts with the body core temperature, which increases above normal levels only when mammals experience substantial thermal stress and start to become hyperthermic. A high body surface temperature can therefore indicate thermal stress or thermoregulatory challenges occurring before the point at which hyperthermia sets in.

Here, we investigate the impact of anthropogenic and natural microhabitat use on the body surface temperatures of wild banded mongooses, *Mungos mungo*, a social mammal living at the human–wildlife interface in rural Uganda. In our study population, banded mongooses move between anthropogenically modified environments and natural habitats within and between days. We predict that banded mongooses will have higher body surface temperatures when present in anthropogenically modified environments compared to natural habitats. Specifically, we expect that waste products such as refuse and low-albedo materials such as concrete will lead to high body surface temperatures, whilst vegetated areas will have a cooling effect.

2. Materials and Methods

2.1. Study Site and Population

This study was conducted in May 2023 in Queen Elizabeth National Park, Uganda (0°12′ S,27°54′ E). Our study site has an equatorial climate with little seasonal change in temperature (monthly mean maximum daily temperature ± SD = 29.5 ± 1.5 °C) [45]. Rainfall is characterised by two distinct wet seasons, which occur from March to May and September to November [46]. Temperatures have been increasing in Uganda by, on average, 0.3 °C per decade since the 1960s and are predicted to continue to increase by 2–2.5 °C by 2065–2095 [47]. The human population size has also increased dramatically over this period, from a population of 6.5 million people in 1959 to 45.9 million in 2024, leading to substantial anthropogenic changes in land use [48].

Data were collected from a social group of 38 banded mongooses that were habituated to the presence of observers at ~1 m (sufficiently close to obtain body surface temperatures). The group comprised 14 females and 24 males, with ages ranging from 2.5 months to > 7 years old. The home range of the banded mongoose group (Figure 1) consisted of natural areas of grasses and scrubs and also incorporated a village and safari lodge, where the mongooses were exposed to human-modified environments and from which the mongooses could sometimes forage on anthropogenic food sources. The anthropogenically modified areas included several asphalt roads and dirt tracks connecting relatively dispersed buildings; areas of loosely maintained vegetation and dispersed trees in the village; and a well-maintained safari lodge with accommodations, a kitchen and leisure facilities surrounded by lawns, maintenance areas and storage barns. Some vegetation (grass and scrub) was maintained/clipped in the village, air strip and safari lodge for safety reasons or to increase visual appeal. The banded mongooses could access refuse at several sites in the village and at the refuse disposal site. There were also areas close to the safari lodge where waste building materials had been deposited, including wooden planks and straw for thatching. The straw was largely present in a single pile approximately 4 × 4 m and up to 1 m deep.

Figure 1. (**a**) A map of the study site (Google Maps), showing the territory boundary of the social group of banded mongooses in blue, which incorporates Mweya village, along with a refuse site (marked with a pink dot). Also shown are images of banded mongooses in their (**b**) natural habitat and (**c**) anthropogenic habitat.

The individual mongooses were identified in the field using unique shave patterns in their fur which were maintained every 3–6 months. When the individuals were first captured, usually at 1–2 months old, they were anesthetised, visually inspected to determine their sex and fitted with a Passive Integrated Transponder tag (TAG-P-122IJ, Wyre Micro Design Ltd., Blackpool, UK) for permanent identification. A radio collar weighing 27 g (< 2% of body mass; Sirtrack Ltd., Havelock North, New Zealand) with a 20 cm whip antenna was attached to one adult in the group, allowing for the group to be located in the field. To establish ages, their birth dates were recorded based on the absence of previously pregnant females on foraging trips the morning after birth, the start of pup-care behaviour, and abdomen size of pregnant females returning to normal [49].

2.2. Field Data Collection

The animals in our study were well habituated to human observers, allowing us to take measurements of body surface temperatures (T_{bs}) (°C) using a handheld infrared thermometer (Model IRO280H, Perfect Prime, New York, NY, USA). Measurements were taken from ~1 m (the distance recommended by the manufacturer for greatest accuracy) and the emissivity was set to 0.98, which is representative of animal body surfaces [50]. We used the 'body mode' setting on the thermometer, which is highly accurate at the expected T_{bs} for mammals of 32–42 °C (accuracy ± 0.3 °C). Temperatures were taken from the head, as previous studies of mammals under field conditions have found a strong association between facial temperatures and the microclimate [42,43]. We avoided taking temperatures from the nose area as it was often placed in damp or cool areas during foraging, which could have resulted in unrepresentative temperatures. We also avoided taking temperatures when in direct sunlight, minimising the effect of direct solar radiation on the surface measurements [51]. Banded mongooses also usually avoid exposure to direct sunlight, especially during the hotter parts of the day through seeking the shade of vegetation and buildings [52], further minimising the impact of direct sunlight on the T_{bs}.

A total of 827 temperature recordings were taken opportunistically during 164 focal-animal observation sessions, which usually lasted 5 min (range: 2 min 21 s–6 min 47 s). The T_{bs} was measured between 1 and 14 times during each focal, with the number of measurements varying depending on the accessibility and body position of the mongoose. To account for repeated measurements taken during each focal observation session, the mean T_{bs} values per substrate per focal session were used in the subsequent analyses, resulting in 223 datapoints (see Section 2.3). Most individuals (35 of 38) were observed during 3–6 focal observation sessions (median = 4; range: 1–8). However, the number and length of observation sessions varied due to some individuals moving out of sight or to areas where we could not observe them due to accessibility or safety considerations. The focal sessions were conducted during daylight hours between 7:47 and 19:01, which represents approximately 93% of the 12 h of day light during which banded mongooses are active. It was not possible to observe the mongooses at night as they took shelter in inaccessible dens.

For each temperature recording, we noted the substrate that the animal was present on. We classified the substrates into 8 categories (Table 1). Weather variables have been demonstrated to impact the T_{bs} [43]. Therefore, at the start of each focal, measurements of air temperature (T_a, °C) and humidity (%) were taken at ground level using a digital thermometer and humidity monitor (Pitasha, accuracy 1 °C for ambient temperature and 5% for relative humidity). As the body surface in contact with a substrate may influence the T_{bs}, we recorded the position of the mongoose as standing (3), sitting (2) or lying (1) at the time the T_{bs} measurement was taken. Finally, as proximity to other individuals may influence the thermal environment [53], we recorded this as a categorical variable as follows: the focal mongoose was not in body contact with other mongooses (0), or the focal mongoose was in body contact with at least one other mongoose (1) when the T_{bs} was taken.

Table 1. Descriptions of categories of substrates that banded mongooses were found on.

Substrate Category	Description
Tall vegetation	Living vegetation that was taller than the focal mongoose.
Short vegetation	Living vegetation that was shorter than the focal mongoose.
Dead vegetation	Dead, dried plant matter, typically comprising leaves, twigs and/or grasses.
Soil	Bare soil and sand, sometimes with small stones and rocks.
Building material	Concrete (cement or asphalt based) or brick used to pave paths and roads.
Refuse	Human refuse materials, such as cans, glass, textile and plastics, often mixed with biodegradable (e.g., food) waste.
Wooden planks	Wooden planks, likely varnished or treated with preservative.
Straw	Discarded straw used for thatching roofs.

2.3. Statistical Analysis

To analyse our data, we constructed general linear mixed effects models (LMMs) in R 4.5.2 [54] using the lme4 2.0.1 package [55]. The models are described in detail below. We included the identity of the focal and the day as random effect terms in all models to account for pseudoreplication resulting from repeated sampling. It was not possible to include the identity of the individual mongoose as a random effect as this resulted in a singular fit, with zero variance being explained by individual identity, likely because the variance was subsumed by the other random effects—focal and day. The residuals were plotted to confirm that they met model assumptions of normality, homoscedasticity and lack of influential outliers. We determined the significance of each variable using likelihood ratio tests, which were run using the 'drop1' function, which compares models with and without each term included.

Conducting a field study on the impact of the anthropogenic environment on animal body surface temperature has the advantage that the data collected are ecologically relevant, so only the microhabitats that animals are exposed to under natural conditions are incorporated. However, in the field it is not possible to control external variables, such as the weather or mongoose thermoregulatory behaviour, which could potentially impact our results. We therefore began by investigating the relationships between the variables that may influence the impact of substrate type on body surface temperature. First, we tested the possibility that banded mongooses may be more likely to exhibit different body postures on different substrates (which may influence the transfer of heat between themselves and the substrate) by fitting an LMM with the mean body posture score per substrate per focal as the response variable, and the substrate, humidity and air temperature fitted as the explanatory variables. Second, we tested the possibility that banded mongooses may be more likely to be in body contact with each other on different substrates (which may influence the transfer of heat) by fitting an LMM with the mean touching score per substrate per focal as the response variable, and the substrate, humidity and air temperature fitted as the explanatory variables. Finally, we investigated the possibility that banded mongooses may be more likely to be present on different substrates under different weather conditions by fitting a multinomial model in the nnet package [56] with the substrate as the response variable, and the humidity and air temperature fitted as the explanatory variables.

Our preliminary models found associations between the substrate the mongoose was on, the air temperature, their body posture and body contact with other mongooses (see Appendix A Tables A1–A3). Furthermore, a previous study on banded mongoose thermoregulation found that air temperature, humidity and behaviour (incorporating posture and body contact) vary depending on the time of day [52]. Following Franks, Ruxton and Sherratt [57], which addresses the need to thoroughly consider potential biological causality in ecological statistics, we created a directed acyclic graph (DAG) of the likely causal pathways present in our study using the DAGitty web app [58] (Figure A1). The DAG was used to ensure that our model was appropriate for investigating the total impact of substrate on body surface temperature.

To investigate the impact of substrate on the banded mongoose T_{bs}, we constructed a linear mixed effects model with the T_{bs} fitted as the response variable, and the substrate category fitted as an explanatory variable. To address pseudoreplication resulting from multiple T_{bs} measurements taken during each focal, we used mean values of T_{bs} per substrate per focal observation session (which resulted in 223 datapoints taken over 164 focal observation sessions). We fitted the T_a, humidity and time of day in the model, as these represent potentially biasing pathways as indicated by our DAG (Figure A1). As the relationships between T_{bs} and T_a and humidity and time of day may not be linear, we tried incorporating these variables squared into the model. Only the squared relationship with time of day (measured in hours after midnight) was significant and so was retained in the final model. Furthermore, as we also found associations between the substrate and our indexes of body posture and body contact, we ran an additional model also including the average body posture score and average touching score per focal per substrate, and also incorporating the sex and age of the focal mongoose into the model (as these have been suggested to impact T_{bs} in other studies [59]). Only body contact had a significant impact on the mongooses' T_{bs}, so this variable was retained in the final model while the other variables were not retained (sex, p = 0.916; age, p = 0.347; and body posture, p = 0.603). Moreover, our DAG did not indicate that the excluded variables were required to account for biasing pathways (Figure A1).

3. Results

The air temperature, body surface temperature and humidity varied substantially over the course of our study: T_a mean = 30.6 °C, range: 25.3 °C to 37.2 °C; T_{bs} mean = 37.7 °C, range: 34.4 °C to 42.6 °C; humidity mean = 61.3%, range: 45% to 79%. The air temperature range the mongooses experienced during our study is reflective of the normal range of temperatures to which this study population is exposed: of the 7841 records of daily maximum temperatures that we have for our field site, 94.4% were within the range of temperatures that we recorded during our current study [52]. During our 164 focals, the banded mongooses were most often recorded on short vegetation (in 88 focals), followed by soil (in 56 focals), tall vegetation (in 26 focals), straw (in 17 focals), building material (in 15 focals), and dead vegetation (in 12 focals), with the fewest observations on wood (in five focals) and refuse (in four focals).

The banded mongooses' T_{bs} correlated positively with T_a and body contact, negatively with humidity, and displayed a non-linear relationship with time, with the highest T_{bs} in the middle of the day (Table 2, Figure 2). After controlling for the significant impacts of these variables, we found that the T_{bs} of banded mongooses varied with the substrate that they were present on, with the mongooses having the lowest surface temperatures whilst amongst tall vegetation, followed by discarded wood and short vegetation. Building materials, dead vegetation and bare soil were associated with an intermediate T_{bs}, whilst mixed refuse and discarded straw were associated with the highest T_{bs} (Table 2, Figure 3).

Table 2. Summary of a general linear mixed effects model investigating the variables that impact the body surface temperature of banded mongooses. The model coefficients, standard error and t-values are obtained from the model, while *p*-values are obtained from likelihood ratio tests. The reference level of substrate was building material, represented by the intercept.

Term	Level	Model Coefficient	Standard Error	T-Value	*p*-Value
Intercept		29.209	3.528	8.28	
Substrate	Dead vegetation	0.189	0.437	0.433	0.039
	Refuse	0.590	0.650	0.908	
	Straw	0.989	0.419	2.358	
	Soil	0.317	0.324	0.978	
	Short vegetation	−0.001	0.307	−0.004	
	Tall vegetation	−0.212	0.360	−0.588	
	Wood	−0.249	0.578	−0.431	
Air temperature		0.203	0.059	3.447	0.0006
Humidity		−0.046	0.018	−2.535	0.009
Body contact		0.510	0.226	2.255	0.020
Time		0.741	0.345	2.15	0.025
Time squared		−0.027	0.013	−2.091	0.029

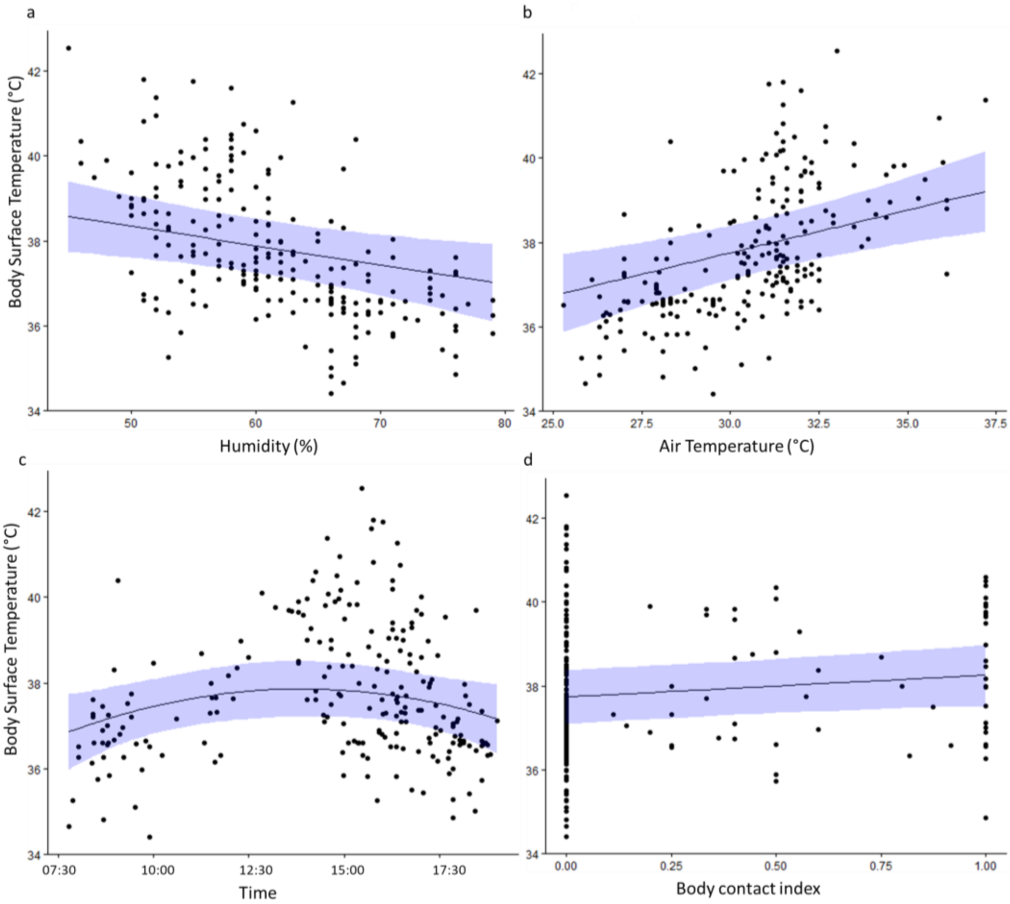

Figure 2. Associations between banded mongoose body surface temperature and (**a**) humidity, (**b**) air temperature, (**c**) time of day and (**d**) body contact. The lines are the predicted relationships from the general linear mixed effects model after taking account of other variables in the model; the shaded areas represent the 95% confidence intervals and the points represent the raw data.

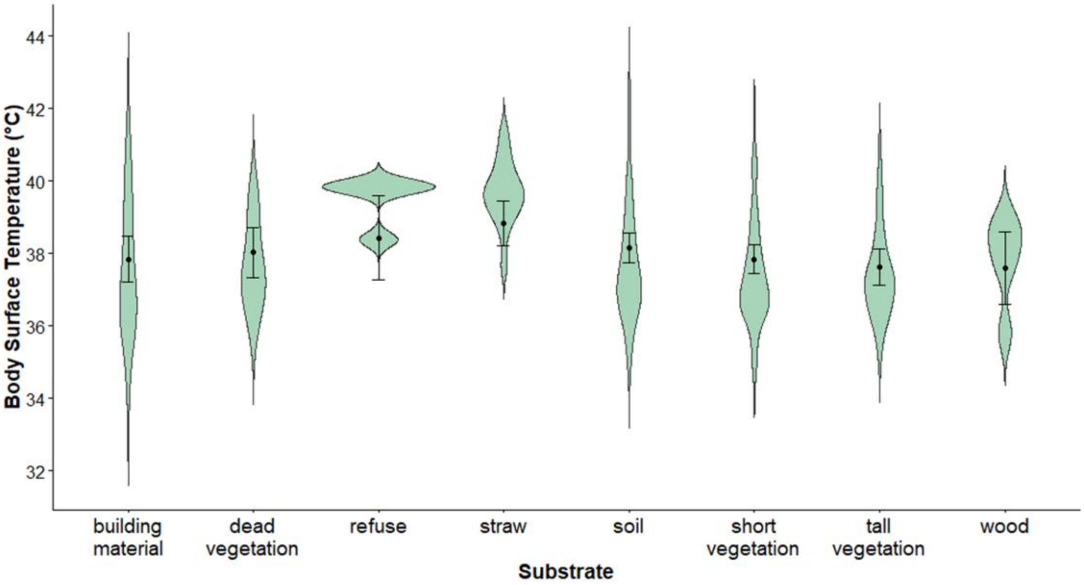

Figure 3. Associations between the banded mongooses' body surface temperatures and the substrate they were present on. The points and error bars represent the predicted means and 95% confidence intervals from the general linear mixed effects model after taking account of other variables in the model, and the violins represent the distribution of the raw data.

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4. Discussion

Here, we investigated the relationships between the body surface temperatures of banded mongooses and the microhabitat that they were present in. In accordance with our prediction, we found that the mongooses had relatively low body surface temperatures when they were present in vegetated areas, particularly when the vegetation was taller than the focal mongoose. This is likely due to a combination of shading and the cooling effects of evaporation and transpiration [17]. The cooling effect of vegetation on a microclimate can be considerable [60]; for example, in the United Kingdom, the presence of grass can reduce maximum surface temperatures by up to 24 °C, while shade provided by trees can reduce them by up to 19 °C [61]. Furthermore, the cooling impact of short vegetation (e.g., grasses) is strongest close to the ground [61]. This may result in a greater reduction in body surface temperatures of relatively small animals, such as banded mongooses, as the underside of their bodies are only approximately 10 cm from the ground. The banded mongooses present on wooden planks also had relatively low surface temperatures. The wooden planks were largely present in a single pile in the deep shade of a building, which may explain the low temperature of this microhabitat. However, we were only able to obtain temperature readings for mongooses present on this substrate during five focal observation sessions, and further data is needed before we can understand how generalizable this pattern is.

As we predicted, the highest body surface temperatures were found when the mongooses were present on anthropogenic waste substrates, comprising mixed refuse and discarded straw. There are two potential reasons for the relatively high temperatures of these microclimates. First, the presence of air spaces in the hollow centre of straw makes it a good insulator [62], potentially impairing the dissipation of body heat by conduction to the ground, which can be an important source of cooling in animals living in hot climates [63–65]. Second, while straw has a similar albedo to grass [66], which did not result in high body surface temperatures in our study, both straw and refuse contain biological material that is likely to be undergoing decomposition and therefore generating heat. The heat generated from decomposition can be substantial; for example, grass snakes (*Natrix natrix*) make use of the warmer temperatures resulting from decomposition in anthropogenic compost and manure heaps to incubate their eggs in the colder, more northernly parts of their range, which can result in temperatures 5.1–15.2 °C higher than in natural nest sites [67,68]. In our study, the decomposition in anthropogenic waste piles may also explain why they were associated with higher body surface temperatures in comparison to natural areas of dead vegetation, which tended to be much smaller in size and therefore had less potential to generate and retain heat as they decompose.

In line with our observations, previous studies have found that anthropogenic refuse sites are associated with high temperatures [38], which sometimes facilitate spontaneous fires [39]. Although some species may benefit from the reliable food source that mixed refuse sites can provide, foraging in human refuse has long been associated with negative effects, including disease spread and exposure to toxic materials [40]. For example, in banded mongooses living in Botswana, refuse feeding was associated with increased infection with tuberculosis, likely due to increased wound acquisition through which bacteria can enter [69]. In contrast, past research on our study population (which is not impacted by tuberculosis) has found that refuse-feeding generally has a positive impact, with refuse-feeding groups being larger with heavier adults that are in better physical condition [70,71], but is also associated with higher pup mortality [71] and inter-group conflict [70]. These contrasting impacts may negate the benefits of anthropogenic features, as has been found in Arabian babblers (*Argya squamiceps*) [72]. In our study, the banded mongooses were only present in mixed refuse during four focal observation sessions, indicating that most foraging occurs on more natural prey. Future studies would therefore benefit from a more extensive exploration of the impact of refuse sites on the thermal environment of banded mongooses. Indeed, the potential for refuse to influence thermal microclimates has rarely been considered in relation to refuse-feeding species [40]. For example, it is possible that animals which rely on access to refuse sites may be particularly vulnerable to the impacts of climate change through being exposed to hotter microclimates or high fire risk.

The banded mongooses had intermediate temperatures when on building materials and soil, which both represent environments without transpiring vegetation, but also without decomposing matter. Both environments are also influenced by anthropogenic activities, with bare soil being created through the presence of dirt paths and roads, and also through removing of vegetation for safety reasons (although some patches of bare soil are present naturally). The thermal properties of soils vary dependent on their minerology, shape, density and water content [73,74]. It was not possible to examine the properties of the soils at our study site, but the intermediate body surface temperatures of the banded mongooses when present on them may indicate that they have an intermediate albedo and/or retain cooling moisture. Building materials such as concrete (particularly asphalt concrete, which was present at our study site) have a very low albedo [75], indicating that they readily absorb heat from the environment. Low-albedo surfaces have been shown to generate hot microclimates, with some anthropogenic surfaces reaching over 60 °C [76]. Even in the United Kingdom, which has a relatively mild climate, concrete surfaces have peaked at around 40 °C in the sun, which was 17 °C higher than the peak air temperature [61]. There is also evidence from other species that these hot microclimates can be used for behavioural thermoregulation, such as basking [34,36]. It is therefore surprising that the banded mongooses did not have particularly high body surface temperatures when present on building materials. However, buildings also create shade, so it is possible that the study animals were generally able to avoid contact with building materials that had recently been exposed to the sun. Consistent with this, the banded mongooses experienced the greatest range of body surface temperatures when present on building materials (from 24.4 C to 41.26 C), indicating highly variable thermal environments. Future studies that involve deploying thermal sensors in different microhabitats in an environment and also attaching sensors to the study animals, in conjunction with collecting detailed movement data, would be able to reveal much more about the impact of movement and behaviour on thermoregulation in relation to microhabitat selection. Future work would also benefit from investigating the structure of different anthropogenic and natural habitats, addressing how these habitats might impact thermal biology.

In addition to finding differences in the banded mongooses' body surface temperatures in relation to the substrate that they were found on, we also found impacts of environmental variables. Their body surface temperature increased with increasing air temperature, in line with previous studies on livestock [77,78] and wild animals [51]. The banded mongooses' surface temperatures decreased as humidity increased, similar to findings from wild blue tits in Scotland [79]. At particularly high temperatures, high humidity may impair evaporative heat loss, leading to hyperthermia [80,81]. However, so long as an animal's surface temperature is above that of surrounding air, as was the case in the current study (see [52]), animals may be able to cool evaporatively in an environment with high humidity levels [50]. Their body surface temperature was higher during the middle of the day, likely due to the impact of solar radiation on T_{bs}, which can increase temperatures through reflection from other surfaces, even when animals are not exposed to direct solar radiation [50]. Finally, their body surface temperature was marginally higher when the mongooses were in direct contact with other individuals. Huddling behaviour has previously been suggested as a form of thermoregulation in response to cool weather for banded mongooses [82]; however, a recent study (supported by the supplementary analysis in the current study) found no association between body contact and T_a in our study population and instead suggested that body contact may have a social function [52].

Our study recorded banded mongoose body surface temperatures under relatively 'typical' conditions in Uganda. For resting banded mongooses under laboratory conditions, the thermoneutral zone is likely between 30.7 and 33.4 °C [83]. However, this has limited applicability to banded mongooses in the wild, where activity levels are higher and preferred temperatures are therefore likely to be lower. The maximum air temperature we recorded during our study was 37.2 °C, and 9% of our datapoints were collected at air temperatures above 33.4 °C (including body surface temperatures of banded mongooses on refuse, straw, soil, dead vegetation, short vegetation, tall vegetation and wood). Therefore, our study provides preliminary information on the impact of anthropogenic environmental modifications on the thermal conditions that banded mongooses are regularly exposed to, including at some relatively high air temperatures. Nevertheless, substantial further work is needed to understand the importance of thermal microclimates under more extreme conditions, such as heat waves or storms, which are becoming more common under climate change. Thermoregulation under extreme conditions may be particularly important in the context of maintaining energy intake, as banded mongooses spend much of their time foraging and the microhabitats containing food supplies may differ from those with the best opportunities for thermoregulation [52].

While our study did not address the fitness consequences of exposure to different thermal environments, previous work has demonstrated that high temperatures have substantial negative impacts on banded mongooses. For example, adult banded mongooses alter their behaviour as air temperature increases, spending less time foraging and more time resting [52], implying that foraging may be constrained under hot conditions. Higher ambient temperatures have also been associated with increases in pup mortality [84] and decreases in pup weight [85]. Once weaned, high temperatures continue to have negative impacts on banded mongoose pups, both directly (for example through inducing thermal stress) and indirectly (through reducing pup care provided by adults) [84]. A similar situation has been found in African wild dogs (*Lycaon pictus*), whereby adults forage less when exposed to high temperatures [86], leading to a reduction in pup care [87] and increased extinction risk under climate change [88]. Comparable negative impacts of high temperatures on fitness have been demonstrated in a wide variety of species, from insects [89–91] to large mammals [92,93]. The impacts on individuals, populations and species are likely to increase with climate change [94], particularly in anthropogenic environments where temperatures can be especially high [31], emphasising the need for further studies exploring anthropogenic impacts on the thermal biology of wildlife.

5. Conclusions

The banded mongooses had relatively high body surface temperatures when present in anthropogenic microhabitats, particularly those containing decomposing materials, but had lower body surface temperatures in more natural vegetated environments. Our results indicate that anthropogenic modifications to natural environments can result in hotter microhabitats, which may in turn have important impacts on activity levels, foraging, offspring care and thermoregulation in wild animals [95]. Very few studies address the thermal impact of anthropogenic habitats outside of highly urbanised areas, but such impacts may be particularly important to understand in the Global South, where land use changes are happening rapidly [1]. While our study is relatively small-scale and limited in scope, we hope that it spurs further research into the impacts of anthropogenic modifications to the environment on the thermal biology, behaviour and fitness of wild animals.

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Abbreviations

The following abbreviations are used in this manuscript:

T_a	Air temperature
T_{bs}	Body surface temperature
LMM	Linear mixed effects model
DAG	Directed acyclic graph

Appendix A

Table A1. Summary of a general linear mixed effects model investigating the variables that are associated with the body posture of banded mongooses. The model coefficients, standard error and t-values are obtained from the model, while the *p*-values are obtained from likelihood ratio tests. The reference level of substrate is the building material, represented by the intercept.

Term	Level	Model Coefficient	Standard Error	T-Value	*p*-Value
Intercept		4.256	1.633	2.606	
Substrate	Dead vegetation	0.346	0.256	1.354	0.00001
	Refuse	−0.218	0.385	−0.566	
	Straw	−0.600	0.245	−2.451	

	Soil	0.163	0.190	0.855	
	Short vegetation	0.408	0.179	2.288	
	Tall vegetation	0.349	0.212	1.651	
	Wood	−0.240	0.338	−0.71	
Air temperature		−0.077	0.036	−2.165	0.028
Humidity		0.005	0.010	0.467	0.669

Table A2. Summary of a general linear mixed effects model investigating the variables that are associated with body contact in banded mongooses. The model coefficients, standard error and t-values are obtained from the model, while the *p*-values are obtained from likelihood ratio tests. The reference level of substrate is building material, represented by the intercept.

Term	**Level**	**Model Coefficient**	**Standard Error**	**T-Value**	***p*-Value**
Intercept		0.050	0.809	0.062	
Substrate	Dead vegetation	−0.193	0.131	−1.465	0.001
	Refuse	0.275	0.196	1.398	
	Straw	0.178	0.126	1.415	
	Soil	0.053	0.099	0.542	
	Short vegetation	−0.094	0.093	−1.008	
	Tall vegetation	−0.167	0.109	−1.529	
	Wood	−0.224	0.175	−1.280	
Air temperature		0.004	0.018	0.200	0.812
Humidity		0.001	0.005	0.256	0.722

Table A3. Summary of a multinomial model investigating the variables that are associated with the substrate the banded mongooses are present on.

Substrate	**Term**	**Model Coefficient**	**Standard Error**	**Z-Value**	***p*-Value**
Dead vegetation	Intercept	2.213	9.393	0.236	
	Air temperature	−0.061	0.211	−0.288	0.773
	Humidity	−0.009	0.063	−0.144	0.886
Refuse	Intercept	−32.694	2.038	−16.041	
	Air temperature	0.857	0.111	7.729	1.09×10^{-14}
	Humidity	0.063	0.061	1.042	0.298
Straw	Intercept	−11.788	8.625	−1.367	
	Air temperature	0.438	0.190	2.302	0.021
	Humidity	−0.034	0.062	−0.543	0.587
Soil	Intercept	24.803	5.895	4.208	
	Air temperature	−0.530	0.140	−3.797	0.0001
	Humidity	−0.119	0.042	−2.846	0.004
Short vegetation	Intercept	22.562	5.369	4.202	
	Air temperature	−0.457	0.127	−3.584	0.0003
	Humidity	−0.111	0.039	−2.841	0.005
Tall vegetation	Intercept	6.000	7.010	0.856	
	Air temperature	−0.058	0.161	−0.362	0.717
	Humidity	−0.059	0.050	−1.192	0.233
Wood	Intercept	−2.236	10.475	−0.213	
	Air temperature	0.154	0.238	0.647	0.518
	Humidity	−0.061	0.080	−0.761	0.447

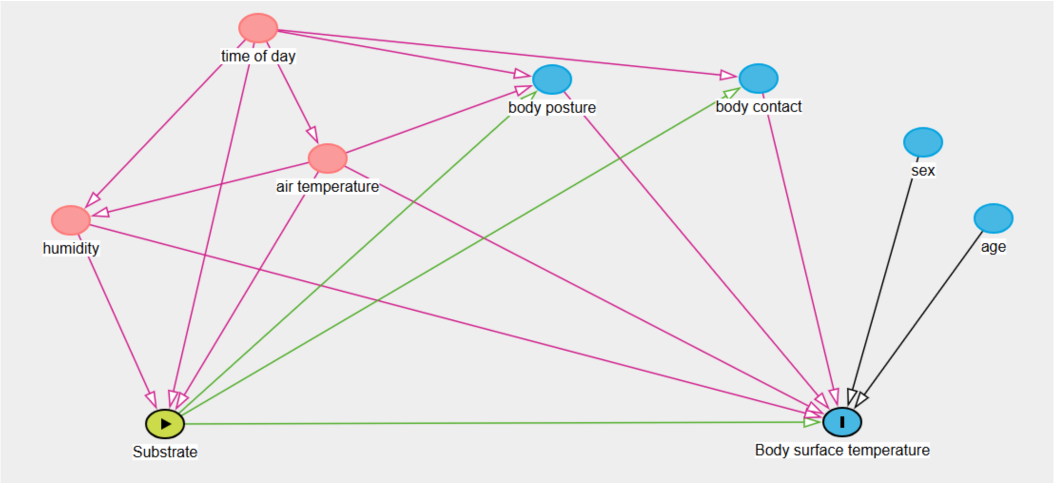

Figure A1. Directed acyclic graph of the likely causal pathways present in our study. We are primarily interested in the impact of substrate (the exposure variable) on body surface temperature (the outcome variable). The humidity, air temperature and time of day (coloured red) are identified as potentially biasing pathways (which impact both the exposure and outcome variables), and hence should be included in a statistical model to allow for estimation of the total effect of substrate on body surface temperature. The remaining explanatory variables (coloured blue) do not represent biasing pathways, so they are not required to be included in the model.

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