The influence of apex predators and humans on the occurrence and temporal activity patterns of crop-raiding mammals in southwestern Ethiopia

A case-study of the leopard (*Panthera pardus*), bushpig (*Potamochoerus larvatus*), and common warthog (*Phacochoerus africanus*)

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Abstract

Human activities, such as land-use change, are altering landscapes at the expense of wildlife habitat, resulting in a global loss of biodiversity. These changes are particularly concerning in the tropics, because this region houses over half of the Earth's biodiversity. One of the most threatened regions is southwestern Ethiopia, as part of the Eastern Afromontane biodiversity hotspot, where many biodiverse Afromontane forest areas have been converted to agricultural land. Here, the local human population is highly dependent on the natural resources that are provided by the forests. In turn, mammals raid crops in the agricultural land outside of the forests, which is a critical disservice for humans. In order to both conserve crop-raiding mammals and improve human-wildlife coexistence, a better understanding is needed of the spatial and temporal behavior of these crop-raiders in relation to their environment, and apex predator and human disturbance. Little is known about the role of humans on these interactions, particularly in the tropics. This study explores these research gaps and aims at understanding the spatiotemporal activity patterns of two crop-raiding mammals, the bushpig and common warthog, and the leopard, which is the apex predator in the region.

Using data from 92 camera traps over 10,894 camera days, generalized linear mixed models (GLMMs) were built for each species to model their spatial activity, as occurrence, in relation to their environment (using forest cover data), apex predator presence, and human presence. Their temporal activity patterns, in relation to human and leopard presence, are modelled using kernel density functions.

GLMMs outcomes showed that there was only one significant relationship between the mammal occurrences and the explanatory variables, which was the positive influence of forest cover on warthog and leopard occurrences. The temporal activity patterns suggest that humans likely influenced the temporal activity of the three mammals, whereas an influence of leopards was again not observed. The latter indicates that the top-down control of leopards on these species was absent. A potential top-down influence of humans was only observed in the temporal activity of the three target species, which suggests that they may separate themselves in time rather than space from human disturbances in southwestern Ethiopia. I discuss the theoretical and practical implications of these results for conservation efforts to improve human-wildlife coexistence and maintain biodiversity, with particular focus on the target species. There may be different mechanisms driving the observed outcomes, which underlines the necessity for future research.

Key words: human-wildlife coexistence | crop-raiding mammals | southwestern Ethiopia | spatiotemporal activity patterns.

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1. Introduction

In the Anthropocene, biodiversity loss accelerated rapidly as a result of human activities of which land-use change exerts the most significant effect (Rockström et al., 2009; Newbold et al., 2016). The conversion of natural areas into agricultural land was the largest contributor to land-use change (Foley et al., 2005; Lambin & Meyfroidt, 2011). As a consequence, declines in the species richness and abundance are observed globally (Dirzo et al., 2014). The expected human population growth will put an increasing pressure on natural ecosystems. In response, the United Nations (2015) addressed halting biodiversity loss and protecting the natural ecosystem as one of their main targets for 2030 in the overarching Sustainable Development Goal 15, *Life on Land*. The magnitude of this challenge will be enormous, especially in the tropical region (e.g. Barlow et al., 2018).

Gibbs et al. (2010) found that in the tropics, between 1980 and 2000 more than half of the intact forests (i.e. forests that are free from anthropogenic degradation) were converted into agricultural land. Because these tropical forests house over half of the Earth's biodiversity (Lewis et al., 2015), substantial changes in biodiversity are projected for the year 2100 if land-use change continues (Sala et al., 2000). Mammal species are particularly threatened by habitat loss, primarily due to their large habitat requirements (Ripple et al., 2016). Dirzo et al. (2014) already observed larger declines of mammal species in tropical regions than in other regions, even after accounting for the greater biodiversity in the tropics. Mammals (particularly carnivores) have an important role in an ecosystem because of their influence on lower trophic levels, e.g. by consuming and trampling vegetation, predation, or even by dispersing seeds (Lacher et al., 2019). Therefore, conserving these mammals is vital for the functioning of an ecosystem.

One of the most threatened regions in the tropics is the Eastern Afromontane biodiversity hotspot, which is largely located in Ethiopia (BirdLife International, 2012). Many Ethiopian Afromontane forest areas have already been converted to agricultural land (Tadesse et al., 2014). Habel et al. (2019) predict that this hotspot will lose all its intact vegetation by 2050 because the demand for agricultural areas is increasing. This will likely precede the loss of many species who are dependent on the undisturbed vegetation. One of these species is the leopard (*Panthera pardus*), which is considered to be the apex predator in the Ethiopian Afromontane forests (Rodrigues et al., 2020). The leopard population is already declining in Ethiopia, which is primarily the result of human interference in their habitat (Stein et al., 2016). Leopards exert top-down control over the ecosystem, which is a very important conservation value. Their control (via predation and instilling fear) cascades through multiple trophic levels (Ripple et al., 2014).

The loss of the Afromontane forest is a concerning trend for the human population as well, because humans are highly dependent on the services that this ecosystem provides (BirdLife International, 2012; Dorresteijn et al., 2017). A variety of resources are obtained from the forests, including the wild Arabica coffee plant (*Coffea Arabica*) that find its origin in southwestern Ethiopia (Tadesse, 2013). Arabica coffee has a high economic value in the region, and it is Ethiopia's most valued export product (Amamo, 2014). To maximize coffee yield, coffee density is increasing at the cost of the amount of forest trees and wildlife habitat (Aerts et al., 2011). The combination of habitat loss and human encroachment into wildlife habitats could potentially increase negative encounters between humans and wildlife. Crop raiding and livestock predation by mammals are already two major disservices for the local population in southwestern Ethiopia (Dorresteijn et al., 2017). Ango et al. (2017) estimate that a quarter of the total crop yield is lost due to crop raiding in this region. Crop damage could increase if the leopard population continues to decline, because crop-raiding mammals are released from predation pressure (Strong & Frank, 2010; Ripple & Beschta, 2012; Lennox et al., 2018).

To conserve these crop-raiding mammals and to improve human-wildlife coexistence simultaneously, a better understanding is needed of their spatiotemporal activity. It is useful to know how the spatial behaviour of crop-raiding mammals relate to their environment, apex predator presence, and human presence. This is particularly important considering the increasing human disturbances in natural areas and the predator-prey relationship that could change in human-dominated landscapes (Dorresteijn et al., 2015). Little is known about the influence of humans on the natural predator-prey interactions and human-induced trophic cascades, particularly in human-dominated landscapes and the tropics (Brodie & Giordano, 2013; Dorresteijn et al., 2015). Furthermore, the temporal activity patterns of these crop-raiders need to be studied to understand if and how these mammals adapt to human and predator disturbances in time. Especially the nonlethal influence of humans on the spatiotemporal behavior of mammals, by instilling fear, is highly understudied (Gaynor et al., 2018).

This study aims to understand the spatiotemporal patterns of the crop-raiding mammals and the leopard (apex predator) in southwestern Ethiopia. I will focus on two common crop-raiders in this region: the bushpig (*Potamochoerus larvatus*) and the common warthog (*Phacochoerus africanus*) (Dorresteijn et al., 2017). The crop-raiders were frequently recorded by camera traps located at the forest edges in southwestern Ethiopia (Rodrigues et al., 2019). The spatial patterns of these crop-raiders will be explained by their occurrence in relation to two environmental variables (forest cover and distance to the forest edge) and to apex predator and human presence. In the second part of this study, mammal temporal activity patterns will be related to apex predator presence and human presence. The leopard is the third target species because it is also useful to know how their spatiotemporal patterns are influenced. Since leopards are the apex predators, their occurrence will only be related to environmental factors and human presence. For their temporal activity patterns, solely the influence of human presence is studied.

The two research questions are: (1) *"How does the occurrence of the target species relate to their environment, apex predator presence, and human presence?",* and (2) *"How are the temporal activity patterns of the target species influenced by apex predator and human presence?"*.

The outcomes of this study will be useful for stakeholders involved in policy implementation, such as the regional Oromia Bureau of Agriculture and Natural Resource and Oromia Forest and Wildlife Enterprise or local kebele leaders. On the one hand, adequate measures should be implemented to ensure forest and wildlife conservation. On the other hand, these stakeholders can improve the coexistence of humans and wildlife. For example, farmers can be supported to alleviate crop raiding, because it is a critical disservice that occurs throughout the day (Ango et al., 2017).

2. Literature review

The central concepts in this research are habitat fragmentation, habitat loss, and the apex predator and human influence on both the spatial and temporal activity patterns of mammals. Habitat fragmentation and habitat loss are the bottom-up factors that cause biodiversity loss, particularly threatening mammal species. Apex predators exert top-down control on both the occurrence and temporal activity of prey mammals, either directly through predation or indirectly by creating a landscape of fear. Humans can influence this natural top-down control and can also exert direct and indirect top-down effects that permeate through trophic levels of ecosystems.

2.1 Bottom-up influence of habitat fragmentation and habitat loss

Already ~40% of the Earth's terrestrial surface is converted to agricultural land (Foley et al., 2005), and there is evidence that only 22% of the Earth's ice-free land is unaltered by humans (Ellis & Ramankutty, 2008). Land-use change is the largest contributor to biodiversity loss in the Anthropocene (Rockström et al., 2009). Sala et al. (2000) project that land-use change will continue to have the largest effect on terrestrial ecosystems until the year 2100. Land-use change typically leads to habitat fragmentation and habitat loss (Fischer & Lindenmayer, 2007). Fahrig (2003) defines habitat fragmentation as habitat area that is breaking apart, without losing habitat amount. Based on this definition, habitat fragmentation can be considered as independent or in addition to habitat loss (i.e. decreasing habitat amount). Habitat fragmentation causes an increased isolation of the habitat areas that remain, which could negatively impact a species' behavior, biology, and interactions with their environment and other species (as reviewed by Fischer & Lindenmayer, 2007). Fahrig's (2003) review study suggests that the effects of habitat fragmentation are as likely to be positive, for example, because some species require multiple habitats (e.g. Law & Dickman, 1998). However, in general, the negative effects of habitat loss on biodiversity clearly outweigh the effects of habitat fragmentation (Fahrig, 2003).

The combination of habitat fragmentation and habitat loss has a major impact in the tropics, because this region houses over half of the Earth's biodiversity (Lewis et al., 2015). Deforestation has already resulted in a dramatic loss of forest cover across the tropics (Gibbs et al., 2010). The biodiversity hotspots, most being located in this region, have already lost ~70% of their original habitat extent (Mittermeier et al., 2011). For one third of the biodiversity hotspots, including the Eastern Afromontane biodiversity hotspot, it is projected that all remaining intact vegetation will be converted into agricultural land by 2030 (Habel et al., 2019). Furthermore, forest fragmentation has caused a greater area of natural forest to be closer to the forest edges, with 70% of the world's forest being within 1 km of the forest edge (Haddad et al., 2015). The edge effects may negatively impact ecosystems in numerous ways, including shifting the community composition and diversity of animals (Broadbent et al., 2008).

Large mammals are particularly vulnerable to forest fragmentation and the loss of forest cover, because they need a larger habitat area to survive (Cardillo et al., 2005). Moreover, intact forest areas are crucial for the survival of most mammal species (Habel et al., 2019), and the ongoing loss of forests could lead to the local or regional extinction of many species. For example, Garmendia et al. (2013) found that the mammals with large habitat requirements, similar to the target species from this study, were the most sensitive to forest fragmentation and habitat loss. In this study, these mammals were observed in a continuous forest, whereas they were nearly absent in a fragmented forest. In particular, large carnivores are susceptible for extinction due to their low population densities and slow life-history traits (e.g. low reproductive rates), in addition to their large area requirements (Cardillo et al., 2005; Wallach et al., 2015; Ripple et al., 2016). Out of the 27 largest terrestrial carnivores, the leopard is one of the 16 species that is threatened with extinction (Ripple et al., 2016). In 2016, the extinction risk of the leopard got updated to Vulnerable on the Red List of Threatened Species, indicating a higher extinction risk than the Near Threatened status of the earlier 2008 report (Henschel et al., 2008; Stein et al., 2016). It should be noted that poaching also contributed to the decline of the leopard.

Both the loss of forest cover and the closer distance to the forest edges indicate that wildlife is losing habitat and are more exposed to human-induced perturbations, which may enhance human-wildlife conflicts. This is highly relevant in the context of this study, because land-use change and semi-managed coffee cultivation has resulted in deforestation, forest simplification, and increasing edge density in southwestern Ethiopia (Aerts et al., 2011; Rodrigues et al., 2019). Crop raiding by mammals could potentially be one of the aggravated conflicts in this region. Interestingly, crop-raiders can also negatively affect forest. Luskin et al. (2017) show this in their case-study of the wild boar (*Sus scrofa*) in a region in Malaysia. Here, the wild boar forage in oil palm plantations, outside of their natural forest habitat. Their reproductive activities increase because the oil palm fruit is an additional accessible food source. As a result, they build more nests in the forest, thereby damaging saplings and ultimately altering forest cover. The observed cascading effects (i.e. cross-boundary subsidy cascades) are particularly relevant for southwestern Ethiopia, where crop-raiding mammals are active, and forest is surrounded by agricultural land. These cascades are an example of the many feedback effects that may be triggered by habitat fragmentation and habitat loss.

In southwestern Ethiopia, the evergreen forests host a diverse mammal community, including bushpigs, warthogs, and leopards (Mertens et al., 2018). Therefore, forest-related variables are suitable to explain the environmental influences on the occurrence of the three mammals. In this research, the variables 'distance to the forest edge' and 'forest cover' are used. These are also commonly used in other studies (e.g. Norris et al., 2008; Rovero et al., 2014; Rodrigues et al., 2018; Cavada et al., 2019). Although these variables are likely positively related to each other, they may indicate separate effects on mammal occurrence. The variable forest cover may be an indicator of how deforestation affects mammal occurrence, whereas distance to the forest edge may be an indicator of how forest fragmentation affects mammal occurrence.

2.2 Top-down influence of apex predators and humans

Vertebrate apex predators are structuring terrestrial ecosystems by both controlling herbivore populations and suppressing predation by mesopredators through intraguild competition (Ripple et al., 2014). The latter trophic cascading effect is beyond the scope of this research, although mesopredators, such as the African civet (*Civettictis civetta*), are present in the study area (Rodrigues et al., 2019). Top predators control herbivore populations and their distribution either directly through predation or indirectly by changing the spatial behavior of herbivores (e.g. Kuijper, 2011). The indirect effect can be ascribed to the landscape of fear, which is predation risk affecting the spatiotemporal use of a landscape by prey species (Laundré et al., 2010). For example, in their review study, Letnic et al. (2012) found that the distribution of some prey species was limited by the dingo, Australia's apex predator.

The regulating role of apex predators via trophic cascades could be exemplified by the reintroduction of the wolf (*Canis lupus*) in Yellowstone National Park. In the first 15 years after wolf reintroduction, direct prey population (elk; *Cervus elaphus*) declined and plant biomass increased (Ripple & Beschta, 2011). Indeed, predators can release plant suppression through the predation of herbivores (i.e. tri-trophic cascades; Strong & Frank, 2010). Furthermore, the distribution of the elk population changed after wolf reintroduction. Ripple & Beschta (2011) found that areas where the wolf became more active were avoided by elk. This predator-prey separation in space could lead to local differences in prey abundance, with abundances being higher where the predator is less active.

Given their important role in ecosystems, the elimination of a top predator from a certain region could be highly concerning. The population of large carnivorous top predators and their geographic range are declining globally, and local extinctions have already been observed (Ripple et al., 2014). In general, the elimination of a top predator will result in higher prey populations because the prey is released from predation (as reviewed by Lennox et al., 2018). In southwestern Ethiopia this could imply that the local extinction of the leopard will lead to higher abundances of the bushpig and warthog. Moreover, it could aggravate crop raiding by these mammals. However, there is evidence that the reduction of apex predator abundance or extirpation would not lead to increasing herbivore (prey) populations in the tropics (Brodie & Giordano, 2013). It is difficult to make a prediction for southwestern Ethiopia, because little is known about apex predator control in human-dominated landscapes outside protected areas (Dorresteijn et al., 2015) and particularly in the tropics (Brodie & Giordano, 2013).

Humans exert top-down control over the natural predator-prey relationships both directly, by predation of predator and prey, and indirectly, by instilling fear (Gaynor et al., 2018). The top-down influence of humans across trophic levels could be stronger than the natural top-down control of apex predators, as shown by Dorresteijn et al. (2015) in their case-study of a human-dominated ecosystem in Transylvania, Romania. Kuijper's (2011) review study on the natural top-down control on ungulates in managed temperate European forest systems suggests that the natural indirect top-down influence, via the landscape of fear that is produced by the natural apex predator, cannot be mimicked by humans (e.g. because human hunting activity was more predictable than the hunting behavior of the natural predator). These different results highlight the uncertainties regarding the top-down effects of humans on wildlife.

Furthermore, carnivores and herbivores could avoid areas where humans are active, similar to the natural predator-prey separation in space as discussed earlier. However, this may be difficult when animals co-occur with humans in a restricted geographical range. Moreover, there is evidence that spatial displacement of animals as a result of human disturbance is not present at the fine spatial scale (i.e. camera trap locations). For example, Carter et al. (2012) found that tigers (*Panthera tigris*) did not avoid camera trap locations where human disturbance was high. Similarly, Oberosler et al. (2017) revealed that human disturbance did not have a significant influence on the spatial activity patterns of mammals (both carnivores and herbivores) in the Italian Alps. An explanation could be that humans did not hunt on these animals. Even if hunting was present, however, the landscape of fear produced by natural predators would be stronger than the one produced by humans (Kuijper, 2011).

In the temperate region and mostly in protected areas, evidence on the effects of top-down control of apex predators on herbivores seems abundant (e.g. the Yellowstone National Park case). However, the top-down control of humans on these predator-prey interactions is understudied, particularly in the tropics. In the context of this study, the bushpig and warthog may alter their spatial behavior in response to human and leopard presence. These crop-raiders may separate themselves more from leopards than humans, because they are foraging the agricultural land outside of the forest where humans are more active. In response to crop raiding, the leopard may also be more active at the forest edges to prey on these species.

2.3 Temporal activity patterns

Naturally, temporal activity patterns are species-specific, although mammals can adapt their temporal activity to either avoid predation or to catch prey (Arias-Del Razo et al., 2011). In human-dominated landscapes where humans and wildlife co-occur, mammals may separate themselves in time rather than in space to minimize predation risk (Gaynor et al., 2018). This could indicate that when humans are present in a certain area, animals will likely be less active at that time. On the other hand, when humans are absent, prey animals will be more active at that time.

The two herbivorous target species from this study, the bushpig and warthog, have an almost opposite temporal activity: bushpigs are predominantly nocturnal (Seydack, 2017), whereas warthogs are highly diurnal (Deribe et al., 2008). The leopard does not seem to have a predominant temporal activity. Asrulsani et al. (2017) found that leopards were crepuscular (i.e. active mostly during twilight) in a protected area in Peninsular Malaysia. Mondal et al. (2012) observed a more nocturnal activity in a national park in Western India, which was also observed by Odden & Wegge (2005) for male leopards in a national park in Nepal.

After monitoring both female and male leopards, Odden et al. (2014) found that in human-dominated landscapes in India, outside protected areas, leopards were nocturnal. In areas where human population density was higher, leopards were even more nocturnal. The same separation in time from human activity was observed for other top predators. For example, Carter et al. (2012) found that tiger activity during the day (between 06:00 and 18:00) was higher inside Nepal’s protected Chitwan National Park than outside the park, where human activity was higher.

Mertens et al. (2018) studied the difference between the communities of large mammals in natural forest and in human-dominated coffee forest in Ethiopia. They found that species richness and diversity of large mammals did not differ between the two forest areas. However, they did observe interesting differences in the temporal activity patterns between the two mammal populations. Mammals in the human-dominated coffee forest were predominantly active during the night, whereas mammal activity in the natural forest was diurnal. The bushpig, one of the observed mammals, also showed a nocturnal activity pattern in the coffee forest, whereas an activity peak around midday was observed in the natural forest. This shift in activity can potentially be explained by human disturbance.

The observed shifts to a more nocturnal activity pattern are in line with findings by Gaynor et al. (2018), who conducted a global-scale meta-analysis on how human disturbance influences wildlife nocturnality. Their findings suggest that all mammals (>1 kg body weight) increase their activity during the night significantly in response to all forms of human presence. Moreover, the increase in nocturnality was found across trophic levels. Gaynor et al. (2018) also found that mammals are less active throughout the day in response to human presence. A more nocturnal activity of the target species would also be a possible response to human activity in southwestern Ethiopia. The warthogs do have to shift their activity because they are diurnal, whereas the bushpig and leopard are already less active during hours of daylight.

2.4 Conceptual framework

Figure 1 represents the conceptual framework of this study, showing the hypothesized interactions between apex predator (leopard) and prey (bushpig and warthog) with the predicted influences of their natural environment (forest cover and distance to the forest edge) and human disturbance. I am aware of the complexity of the ecosystem and the other interactions that may be present (e.g. the influence of humans on forest cover), but these are beyond the scope of this study.

Based on current knowledge complemented with *a priori* knowledge on the case-specific ecosystem, I hypothesize that the leopard negatively influences herbivore occurrence and I expect strong temporal distancing of these prey species. I also predict that both forest cover and distance to the forest edge have a positive effect on the occurrence of the three mammals. Further, I hypothesize that humans have a negative top-down influence on the occurrence of all three mammals. Finally, I predict that human disturbance will have an influence on the temporal activity of these mammals, which will result in a temporal displacement of the mammals. Moreover, I predict an increase in animal nocturnality in areas as a response to the predominant activity of humans during the day, as described by Gaynor et al. (2018).

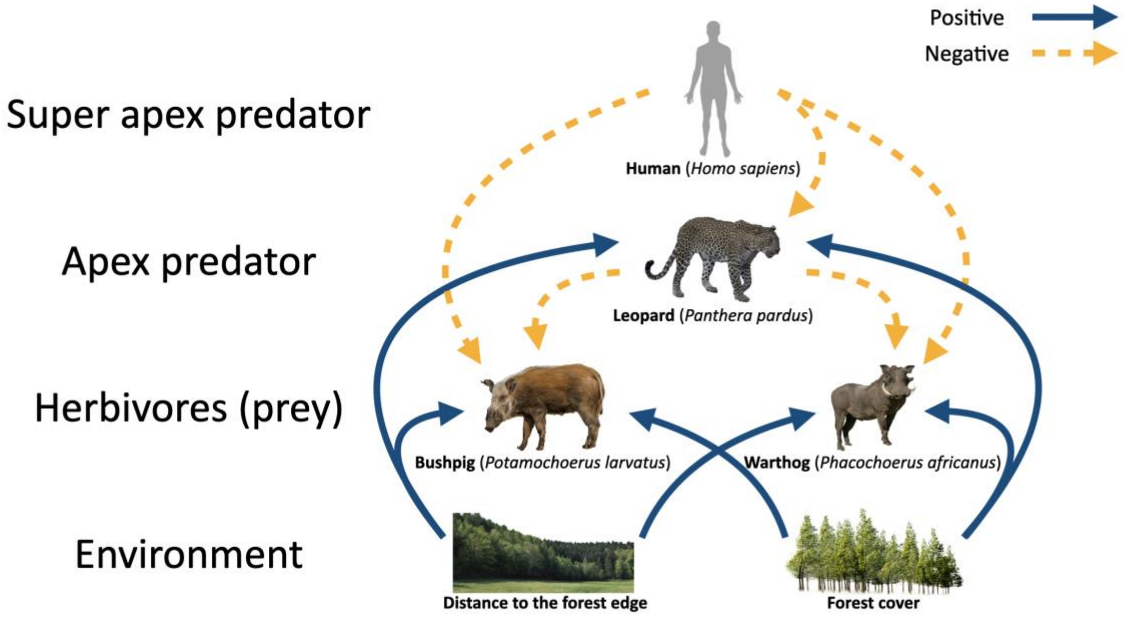

Figure 1. Conceptual diagram illustrating the *a priori* hypothesized apex predator-prey interactions in southwestern Ethiopia, including humans exerting top-down control and the environment having a bottom-up effect. The predicted relationships are represented by arrows, of which solid lines indicate negative relationships and dashed lines represent positive relationships.

3. Methodology

3.1 Research area

The study area is located within the two *woredas* (administrative districts in Ethiopia) Gera and Setema in the southwest of Ethiopia (Figure 2). Within each woreda, two *kebeles* (the smallest administrative unit in Ethiopia) are the focus of this study. The four kebeles, Boricho Deka, Difo Mani, Guido Bere, and Kele Harari, encompass a total area of approximately 158 km^2. This area is located within the Eastern Afromontane forests, which are unique for its undisturbed patches of moist evergreen forest (Shumi et al., 2019). Moreover, southwestern Ethiopia is part of the Eastern Afromontane biodiversity hotspot, encompassing an area of more than 1 million square kilometers. To put this area in perspective; the hotspot is home to around 7,600 plant species, 1,300 bird species, and 500 mammal species (BirdLife International, 2012).

The natural and semi-managed forests in southwestern Ethiopia provide a variety of essential services, with provisioning services being the most important for the local population (Dorresteijn et al., 2017; Shumi et al., 2019). One of the main products that is directly obtained from these areas is coffee. Arabica coffee finds its origin in the Ethiopian Afromontane forests and it is the largest export product of the country, accounting for over 40% in Ethiopia's total export (Amamo, 2014). The wild coffee plants grow at latitudes between 1,000 and 2,000 meters above sea level (Schmitt et al., 2010). The study area itself is located at altitudes ranging between 1,500-2,900 meters above sea level (Dorresteijn et al., 2017). Forest is the dominant land cover in the four kebeles (approximately 90% in Boricho Deka and Kele Harari, 70% in Guido Bere, and 58% in Difo Mani). The forests are surrounded by heterogeneous agricultural land with human settlements (Manlosa et al., 2020).

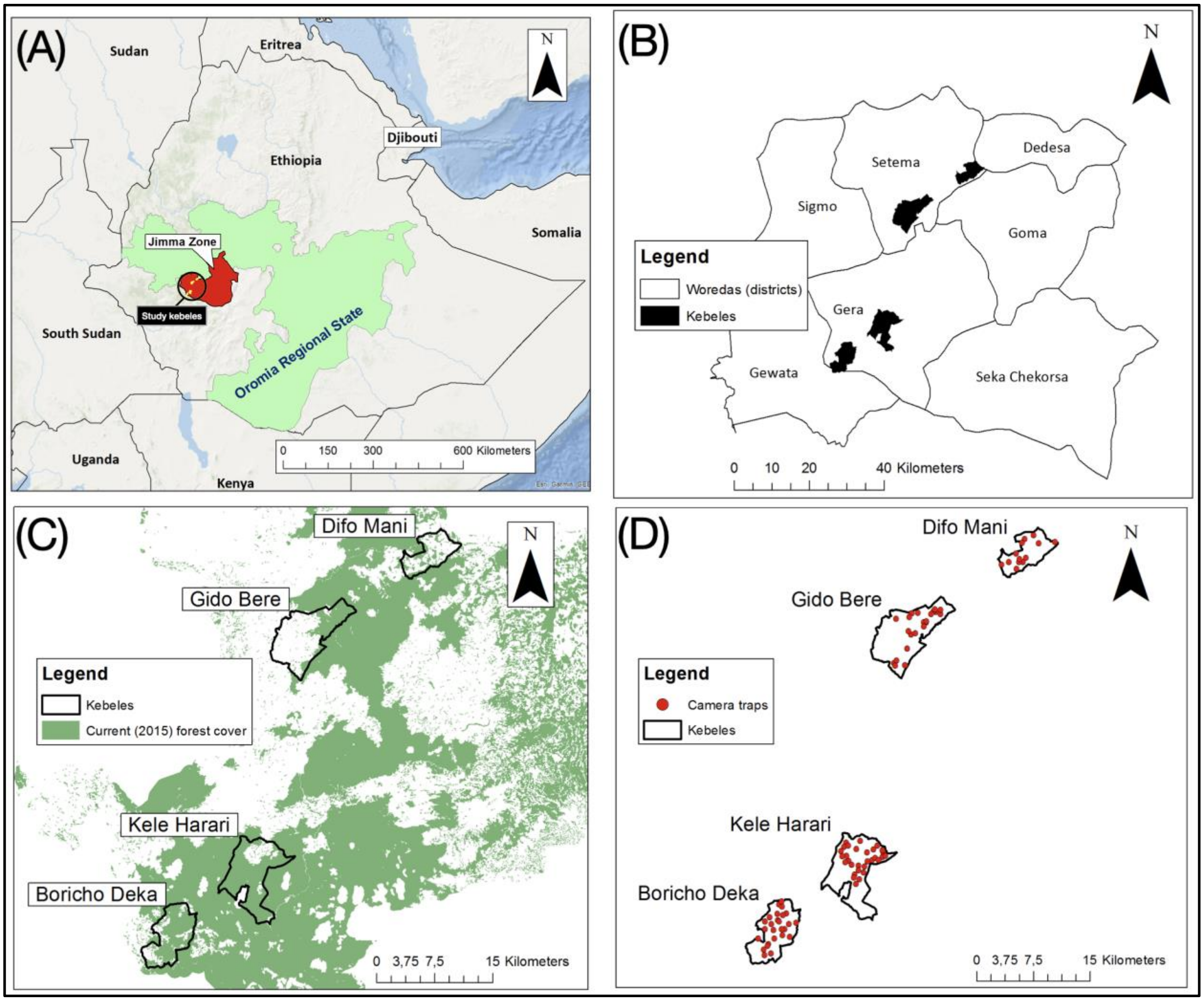

Figure 2. **(A)** The study area in southwestern Ethiopia, which is part of the Jimma Zone within the national state *Oromia Region*. **(B)** The four study kebeles are located within the districts *Gera* and *Setema*. **(C)** These kebeles are Difo Mani, Boricho Deka, Gido Bere, and Kele Harari. The area is part of the Afromontane biodiversity hotspot, which is characterized by undisturbed patches of moist evergreen forest. **(D)** In this study, data is used of 92 camera traps (red dots) that were placed within the kebeles.

3.2 Research design and data collection

This study is based on collected data by Rodrigues et al. (2020), who aimed to map the community of mammals of medium to large body size in southwestern Ethiopia. Besides bushpigs, leopards and warthogs, many other mammals, such as the olive baboon (*Papio anubis*) and white-tailed mongoose (*Ichneumia albicauda*), were registered by the researchers. Rodrigues et al. (2019) mapped 26 mammals in total in an earlier assessment of the mammal community in the region.

Between January 2016 and March 2017, motion-triggered Bushnell Trophy CamHD cameras were positioned at 96 locations in the forests and at the forest edges of the four study kebeles. The cameras were rotated to new sampling locations approximately every three months in 2016. The first set of cameras (29) were placed in January, the second set (34) from mid-June until the second week of July, and the third set (29) from October until the second week of November. Each stage, cameras were randomly placed along a gradient of forest cover and a gradient of edge amount. Distance between camera locations was aimed at 500 m to obtain independent species observations, however, due to logistical constraints this was not always possible. Seasonal influence is assumed to be absent because of data collection in each kebele throughout the year.

The cameras were positioned approximately 50 cm above ground level, away from trails. Some vegetation in front of the cameras was cleared if the natural clearings were not sufficiently large to get clear images of the species passing by. No bait or lure was used. The operating time of the cameras ranged from 5 to 180 days. Because of a short operating time (< 30 days), data of four camera traps were not analyzed. Of the 92 camera traps, 30 were placed in kebele Kele Harari, 26 in Boricho Deka, 23 in Guido Bere, and 13 in Difo Mani, which was proportional to the amount of forest cover in each kebele. There are 91 unique camera sites because at one location two cameras were placed in consecutive periods (stage 2 and 3). There are 10,894 camera trap days in total, with an average camera operating time of 118 days. Each picture was tagged to the specific location (in latitude and longitude), name of the camera trap, and the day and time. If the same species is recorded multiple times by the same camera within one hour, this is classified as one and the same event because it is not considered independent (following Bowkett et al., 2007).

Humans were also recorded. This data is registered as the total number of recordings of humans by each camera trap. It only provides information on how active people are at a certain site, because the specific time of the pictures is not yet registered. After counting all pictures of humans, they were deleted from the database in accordance with the ethics procedure of Leuphana University Lüneburg. The data was manually classified using ExifPRO™ software.

3.3 Variables used for the data analysis

Two top-down variables (human and leopard presence) and two bottom-up variables (forest cover and distance to the forest edge) were used to potentially explain the occurrence of the target species in the research area. For the temporal activity patterns of the target species, only the two top-down effects were used. Naturally, the spatiotemporal patterns of the leopard were not related to their own presence.

3.3.1 Human and apex predator presence

Human presence is the top-down variable that represents the influence of humans on the spatiotemporal patterns of the bushpig, warthog, and leopard. Leopard presence represents the top-down influence of the apex predator on the spatiotemporal patterns of the two crop-raiding mammals. To model the occurrence of the target species, human presence and leopard presence were calculated as a ratio between the total amount of unique events (i.e. independent recordings) and the total number of camera days. For the temporal activity models, camera traps were manually classified according to human presence/absence and leopard presence/absence (see Chapter 3.4).

3.3.2 Environmental variables

The bottom-up variables distance to the forest edge and forest cover were used to potentially explain the effects of the environment on the occurrence of the three target species. The variables were calculated by Rodrigues et al. (2020) using the following steps. First, a forest cover map was derived from remotely sensed RapidEye satellite images from 2015 (5 m resolution), using a Maximum Likelihood classifier in ArcGIS (ESRI, 2013). The map was then used as a basis to calculate forest cover and distance to the forest edge. The forest cover was calculated using a 500 m buffer around each camera site (with an average of 82% and values ranging between 16% and 100%). The distance to the forest edge was calculated as the distance between each camera site and the closest forest edge, using Euclidean distance (with an average of 331 m and values varying between 5 m and 1080 m).

3.4 Data analysis

The data analysis followed a two-step procedure of (1) modelling mammal occurrence and (2) modelling mammal temporal activity patterns. Before modelling, the dataset was separated into two sets of data. One contains the observations per camera site (92 camera sites with observations), which was used to model mammal occurrence. The other contains all the pictures of the three mammals with the exact time each picture was taken from the 91 unique camera trap locations, which was used to model the temporal activity of the mammals. Also prior to modelling, the variables were checked for linear correlation using the Pearson correlation coefficient. Only the environmental variables, forest cover and distance to the forest edge, showed a positive correlation (correlation coefficient r = 0.69). Therefore, forest cover was used as the only environmental factor in the data analysis. All analyses were conducted using the statistical analysis program R *v.4.0.0*.

3.4.1 Mammal occurrence

The R-script that was used to model mammal occurrence can be found in Appendix A. From R-package 'lme4' (Bates et al., 2015), a generalized linear mixed model (GLMM) with a Poisson error distribution was built for each mammal to examine the relationship between the aforementioned variables and the occurrence of that species. A GLMM was chosen because both multiple fixed effects (explanatory variables) and random effects were present in the data (Zuur et al., 2009). The response variables were defined as the total number of independent recordings of each mammal. An offset for the number of camera days was added to the models to account for unequal trapping effort of the mammals. The fixed effects, human and leopard presence and forest cover, were standardized using the 'scale' function to overcome scaling errors due to the different scales of the three variables. The fixed effects were also log-transformed, but the model with the standardized effects performed better (based on AIC). The variables 'kebele' and 'set' were taken as the random effects in the models to account for grouping in experimental units (Shumi et al., 2019) and to account for temporal autocorrelation. In addition, individual site identity ('pointid') was included as a random effect to account for additional model variance because all three models were overdispersed (i.e. the residual deviance is higher than the residual degrees of freedom). Overdispersion was tested using the function 'overdisp_fun' (Bolker, 2020). The models were also tested for spatial autocorrelation using spline correlograms from the R-package ‘ncf’ (Bjornstad, 2020). Spatial autocorrelation was not present in the GLMMs (see Appendix B).

The marginal and conditional coefficient of determination for GLMMs (R^2) from Nakagawa et al. (2017) was used to represent what proportion of variance of each GLMM is explained by the fixed effects and random effects. Marginal R^2 represents the proportion of variance that is explained by the fixed effects, whereas the conditional R^2 provides the variance explained by the entire model, including both fixed and random effects. The values of R^2 range between 0 and 1, with a higher value indicating that a larger proportion of variance of the response variable is explained by these effects.

3.4.2 Mammal temporal activity patterns

Out of the 91 unique camera sites in total, six cameras did not record any of the three mammals. Therefore, they could not be included in the analysis of the temporal activity patterns. The bushpig was recorded at 83 locations, the leopard at 27 locations, and the warthog at 29 camera sites. The dataset containing all the pictures of the three mammals was modified by manually adding classifications of human and leopard presence.

The local human population is highly dependent on forest resources and people will be present in the forests to collect them, especially at the edges. Therefore, human absence at the camera traps is assumed to be unlikely and a classification is used according to low and high human pressure. Human pressure is low at camera sites when at most 5% of the total number of pictures are recordings of humans, other sites are classified as high human pressure. Low human pressure is valid for 31 camera trap locations, of which 17 cameras did not record any humans. Human pressure was high at the other 54 other locations. This classification of human pressure was compared to other classifications to check whether the temporal activity patterns of the three mammals differed or not. Two boundary values were used between low and high human pressure: 10% and 20% of the total number of pictures per camera site. For each of the mammal activity patterns, the same activity peaks and valleys were observed in all three classifications (see Appendix C). The only difference was that some activity peaks and valleys differed in height between the three classifications, but the overall activity patterns remained the same. This justifies using the initial classification of human pressure (with <5%).

In the dataset, camera sites were also manually separated according to leopard presence (at least one recording) and leopard absence. The leopard was recorded at 27 camera sites and absent at the other 58 locations.

The temporal activity patterns are modelled by the following procedure to examine the separate influence of human pressure and leopard presence. At first, the dataset was separated according to the pictures taken of each mammal. Then each set of mammal pictures was separated according to both low/high human pressure and leopard presence/absence. The specific times of all pictures (point data) were converted to radians in a vector. The activity patterns were then calculated using kernel density functions of these activity times. The R-package ‘overlap’ from Meredith & Ridout (2014) was used to make a graphical display of the activity patterns. The y-values of the curve are estimates of the probability of the mammal being active at a certain time (x-value). According to Frey et al. (2017), this novel method provides improved insights in species’ activity patterns. The R-script that was made to model the temporal activity patterns can be found in Appendix D.

4. Results

A total of 1,315 unique activity events were recorded of bushpigs (992), warthogs (266), and leopards (57). Humans were recorded 91,614 times. The relative abundance of the bushpig was 9.11 independent events per 100 camera days. The relative abundance of the warthog was 2.44 independent events per 100 camera days and the leopard's relative abundance was 0.523 independent events per 100 camera days.

4.1 Mammal occurrence

The relationship between human presence and mammal occurrence was negative for all three target species, however, no significance was found. The outcomes of the bushpig model indicate that none of the explanatory variables (forest cover, human presence, and leopard presence) had a significant effect on its occurrence. Bushpig occurrence was negatively related to forest cover and positively related to leopard presence. Leopard presence did have a negative effect on the occurrence of the warthog, whereas forest cover had a positive effect on warthog occurrence. The latter was significant ($p < 0.01$). Forest cover also had a significant positive effect on the occurrence of the leopard ($p < 0.05$).

The marginal R^2 values suggest that the explanatory variables did not explain the variance of the bushpig model ($R^2 = 0.025$), and only slightly the variance of the warthog model ($R^2 = 0.166$). The explanatory variables did explain a large proportion of the variance of the leopard model ($R^2 = 0.810$). The combination of explanatory effects and random effects explained almost all variance of the three models (conditional $R^2 > 0.8$ in all GLMMs). The main results of the GLMMs are presented in Table 1, and Figure 3 represents a diagram with the observed relationships between the explanatory variables and response variables.

Table 1. Generalized linear mixed model results for each of the target species. The estimates, or coefficients, (with standard error) indicate how the response variables will change as a result of a unit change of the fixed effect. Significance levels are indicated by asterisks (*): *P < 0.05; **P < 0.01.

Model	Fixed effects	Estimate ± S.E	P-value	R-squared (marginal/ conditional)
Bushpig	Forest cover	-0.024 ± 0.133	0.857	0.025/0.91
	Human presence	-0.129 ± 0.141	0.360	
	Leopard presence	0.087 ± 0.121	0.474	
Warthog	Forest cover	1.242 ± 0.470	0.008**	0.166/0.99
	Human presence	-0.944 ± 0.613	0.123	
	Leopard presence	-0.053 ± 0.299	0.859	
Leopard	Forest cover	3.372 ± 1.321	0.0107*	0.810/0.810
	Human presence	-0.246 ± 0.331	0.4562	

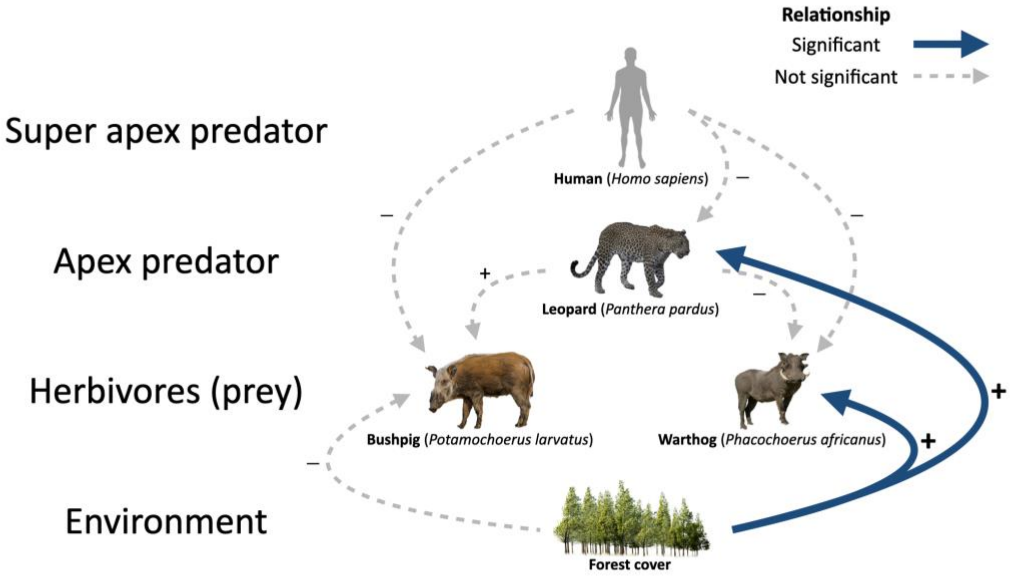

Figure 3. A diagram showing the positive (+) and negative (-) relationships between the explanatory variables and the occurrence of the bushpig, warthog, and leopard, resulting from generalized linear mixed models. Solid lines represent significant relationships, whereas dashed lines indicate relationships that are not significant.

4.2 Mammal temporal activity patterns

At sites where human pressure was low, bushpigs were crepuscular, whereas they were highly nocturnal at sites where human pressure was high (Figure 4A). Although bushpigs were primarily active during twilight at sites with low human pressure, they remained active at hours of daylight and darkness. This was not observed at sites where human pressure was high, because bushpigs were almost inactive between approximately 09.00h and 16.00h. At these sites, there was one large activity peak at around 19.00h. Bushpig activity at sites with leopard presence was similar to the observed activity at sites where the leopard was absent, both showing a higher activity during the night (Figure 4B). Bushpigs were slightly more nocturnal at sites where the leopard was absent.

The temporal activity of the warthog followed a diurnal pattern. Their activity was low during the night and high during the day, both at sites with low and high human pressure (Figure 5A) and at sites with and without leopard presence (Figure 5B). At sites where human pressure was high, warthog activity peaks at around 10.00h and 18.00h. A small peak was observed around midnight. Warthogs were even more diurnal at sites where human pressure was low. Here, warthogs were more active between 09.00h-17.00h and less active between 17.00h-09.00h than at sites where the human pressure was high. Warthog activity at sites with leopard presence was similar to the observed activity at sites where the leopard was absent. There were two activity peaks (one between 09.00h-12.00h and the other one around 18.00h) and warthogs were the least active during the night.

The activity patterns of the leopard were highly fluctuating throughout the day at sites with low and high human pressure (Figure 6). A striking observation is the overall difference in activity patterns between the areas with low/high human pressure, because the patterns were opposing each other. The noticeable top-down influences on the temporal activity of the target species are summarized in Figure 7.

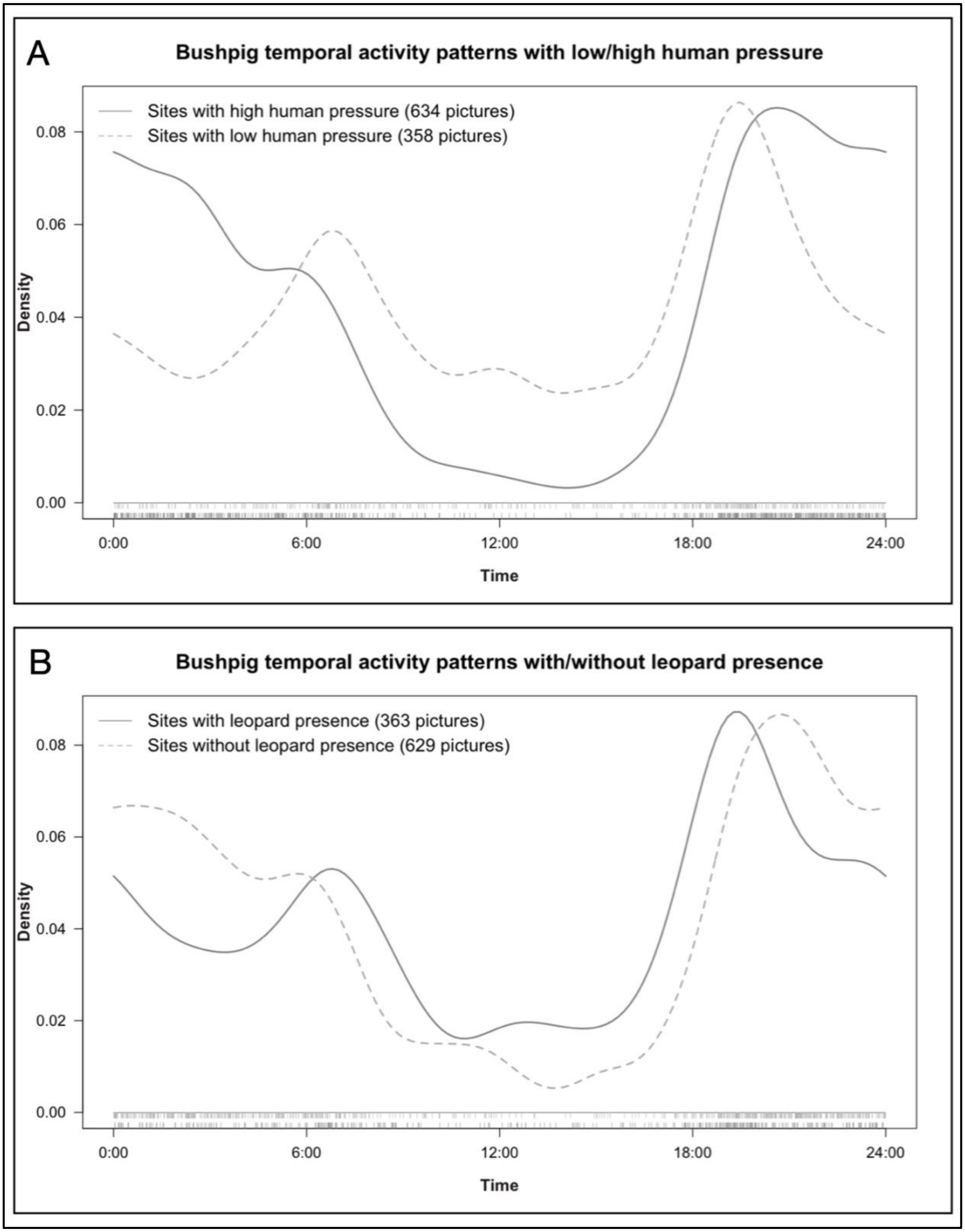

Figure 4. The temporal activity patterns of the bushpig **(A)** at sites with low/high human pressure and **(B)** at sites with and without leopard presence.

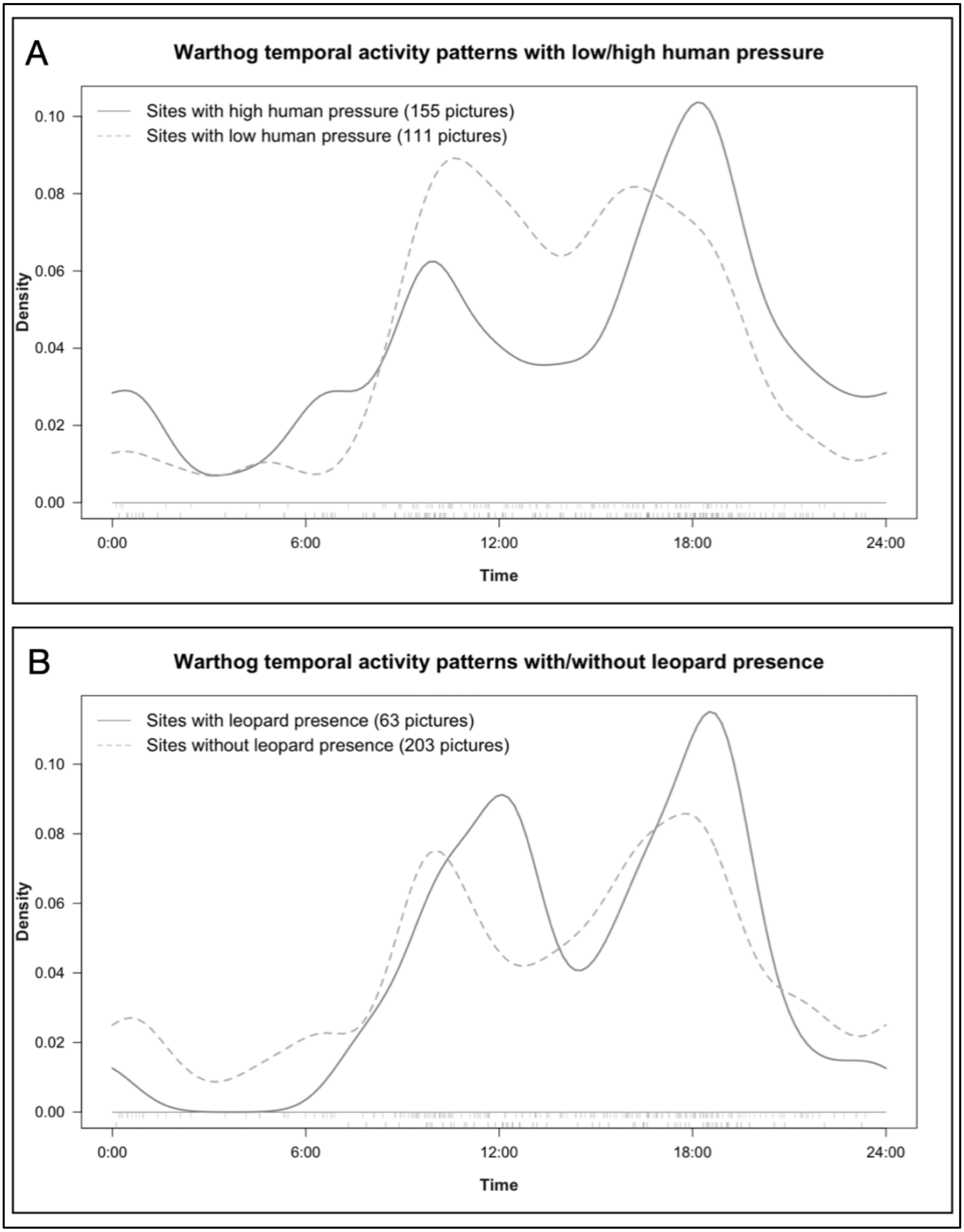

Figure 5. The temporal activity patterns of the warthog **(A)** at sites with low/high human pressure and **(B)** at sites with and without leopard presence.

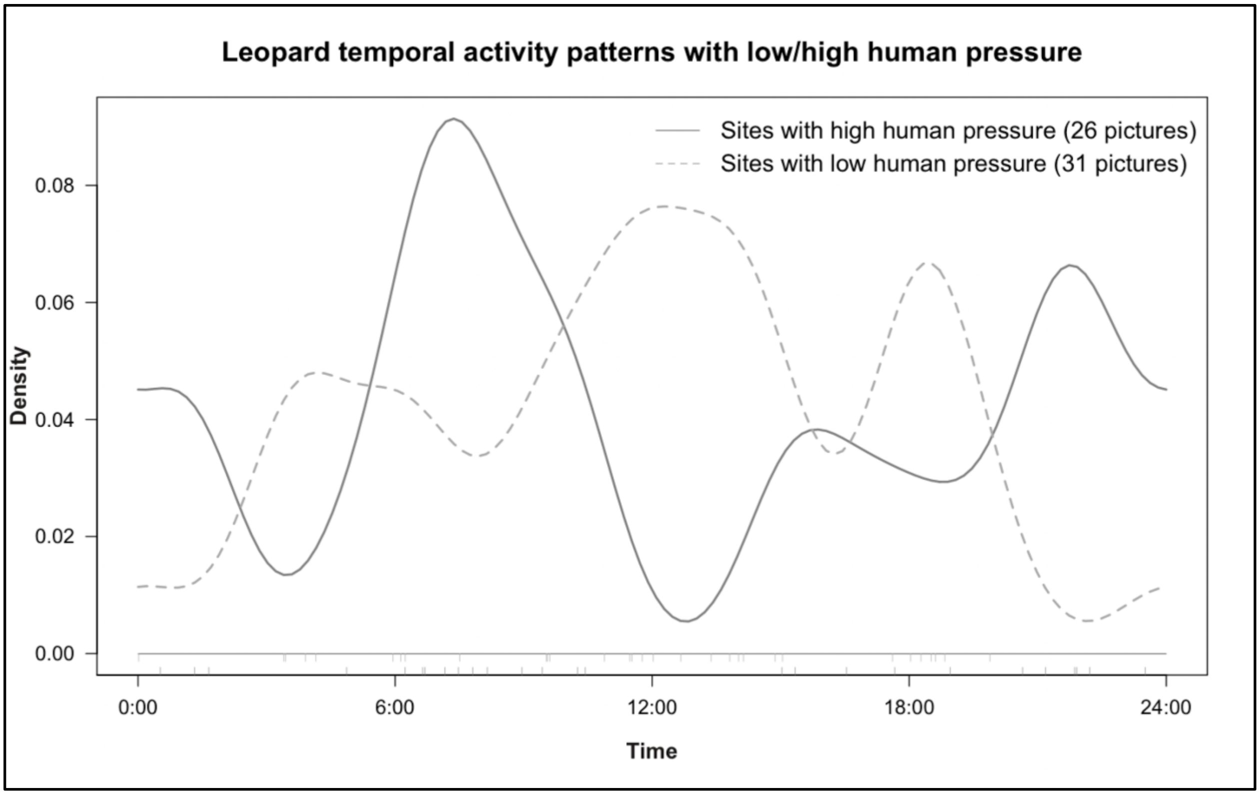

Figure 6. The temporal activity patterns of the leopard at sites with low/high human pressure.

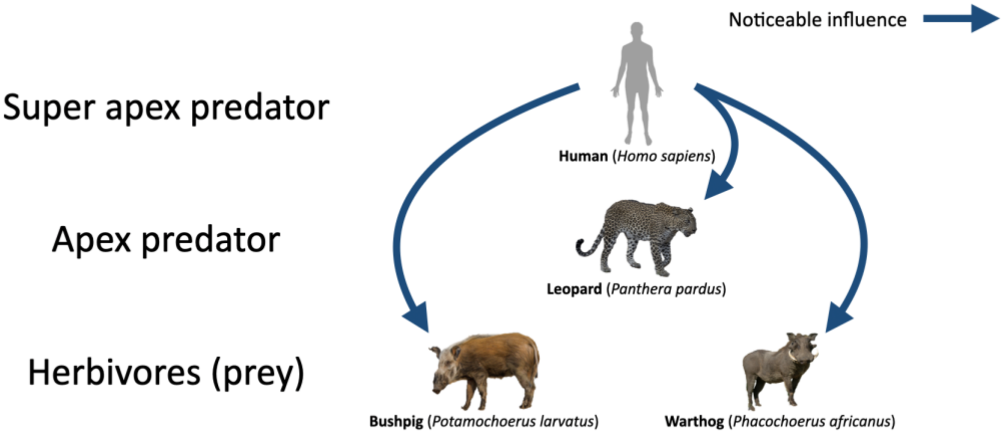

Figure 7. The noticeable top-down influences on the temporal activity of the bushpig, warthog, and leopard, based on the interpretation of the temporal activity patterns (solid lines). The top-down influence of leopard presence on the temporal activity of the two herbivores was less clear.

5. Discussion

This study aims to address how the spatiotemporal patterns of crop-raiding mammals relate to their environment, human presence, and apex predator presence in southwestern Ethiopia. I focused on two crop-raiding mammals: the bushpig and common warthog. The third target species is the leopard, which is considered the apex predator in the region. To conserve these mammals and to improve the coexistence between humans and wildlife, it is important to understand how they respond to anthropogenic disturbances. Furthermore, a better understanding is needed on the predator-prey interactions in human-dominated landscapes (Dorresteijn et al., 2015), which is particularly understudied in the tropics (Brodie & Giordano, 2013). The present study explores those research gaps.

The main outcomes of the GLMMs were that (1) forest cover had a significant positive effect on the occurrence of the warthog and leopard, and (2) there was no top-down effect on the occurrence of the target species. The top-down effect of humans was observed in the temporal activity patterns of the three mammals, whereas leopard presence did also not affect the temporal activity of the crop-raiders. These observations are discussed on the basis of existing literature and empirical evidence. Furthermore, I discuss limitations, practical implications, and suggestions for future research.

5.1 Bottom-up influence and importance of the Afromontane forest cover

The only significant relationship that was found in the GLMMs outcomes was between mammal occurrence and the amount of forest cover. This relationship was significant and positive for both warthog and leopard occurrence, however, it was not positive nor significant for the bushpig occurrence. The latter could be due to the fact that bushpigs forage more in the agricultural land outside of the Afromontane forests than warthogs do (Gobosho et al., 2015; Ango et al., 2017). It is also possible that bushpigs find refuge in areas where humans are more active, because leopards are avoiding those areas (e.g. as observed for prey mammals by Muhly et al., 2011). The observed significant positive bottom-up effect of forest cover on warthog and leopard occurrence was consistent with the predicted positive bottom-up effects. It was also in line with a study by Van Cleave et al. (2018), who showed that leopards in central Kenya were more active in areas where tree cover density was higher. Because the variable forest cover correlated with distance to the forest edge, the latter has an indirect positive effect on the occurrence of the warthog and leopard.

This significant positive effect is an important finding of this study. It emphasizes the necessity to conserve the intact vegetation in southwestern Ethiopia, because these forests are critical for the survival of the warthog and leopard, and many other species. This will be an enormous challenge, especially considering the projected loss of all undisturbed vegetation in this biodiversity hotspot (Habel et al., 2019). Conserving the Afromontane forests could reduce biodiversity loss and prevent the leopard from becoming locally extinct. Besides conserving biodiversity, the Afromontane forests as an intact forest ecosystem has numerous other significant values, such as mitigating climate change by functioning as a carbon sink (Watson et al., 2018). A region-specific incentive for forest conservation is the forest-dependence of the local human population for coffee and other natural resources. This is a controversial incentive, because resource extraction may further degrade the forests if intact forest is not maintained or restored. For example, Hundera et al. (2013) showed that any intensification of coffee production negatively impacted species diversity and structure of the Afromontane forests. If deforestation continues and coffee management intensifies, there will also likely be more negative encounters between humans and the target species as these mammals are more exposed. This could aggravate crop raiding and other human-wildlife conflicts, such as livestock predation or even attacks on humans (Garcia & Feintrenie, 2014).

5.2 Temporal activity adaptation in response to human disturbance

In accordance with the absence of a significant relationship between leopard and mammal occurrence, model results showed that the leopard did not have a clear influence on the temporal activity patterns of the two crop-raiding mammals. Although the relationship between human presence and mammal occurrence was also absent, the model results revealed that humans likely have an influence on the temporal activity of all three mammals. At camera sites where human pressure was high, the mammal activity patterns showed a higher nocturnality. This finding is in line with a review study by Gaynor et al. (2018), who suggest that animals will increase their activity during the night in response to human disturbance. There was a clear difference in bushpig activity between sites with low and high human pressure, which is surprising considering the absence of a positive and significant relationship between human presence and bushpig occurrence. The results of the activity pattern models may suggest that both crop-raiding mammals and the apex predator can adapt to human disturbance by shifting their activity in time. Moreover, in addition to the absence of human influence on mammal occurrence, the target species may prefer to separate their activity in time rather than in space.

On the one hand, this temporal displacement could indicate that the coexistence between humans and wildlife is possible in southwestern Ethiopia. This supports empirical evidence by Carter et al. (2012) from inside and outside a national park in Nepal. They found that humans and tigers spatially overlapped, but that the latter offsets their temporal activity to become more nocturnal. On the other hand, it is possible that this displacement in time precedes a population decline of the target species. This may particularly be plausible for the leopard. The bushpig and warthog benefit from the agricultural land outside of the forests, whereas the leopard is probably more wary towards the forest edges, as indirectly indicated by the significant positive relationship between forest cover and leopard occurrence. The leopard may experience a strong landscape of fear, which could also indicate that they are losing out on feeding opportunities (Laundré et al., 2010).

5.3 Absence of natural top-down control

While the leopard is active in the study area, the top-down control of the apex predator seems absent. This is a striking finding because it was not predicted nor consistent with dominant literature that was reviewed. For example, Dorresteijn et al. (2015) found that apex predators maintained their top-down control in a human-dominated landscape in the temperate region. However, the lack of natural top-down effects on the spatial patterns of prey species was found by Brodie & Giordano (2013), who were one of the first to focus on the apex predator's top-down control in a tropical human-dominated landscape. In their case-study of Malaysian Borneo, no negative correlation was found between the abundance of the apex predator, the Sunda clouded leopards (*Neofelis diardi*), and the abundance of four prey species.

The absence of apex predator top-down control could indicate a lack of predation by leopards and an altered or absent landscape of fear that is created by the leopard. It is plausible that the leopard abundance in the study area is relatively low because most leopards could be avoiding human activity in the area. It is also possible that deforestation and forest fragmentation already caused a local decline of the leopard population. If the leopard abundance indeed declined, this would likely weaken the top-down control of leopards, resulting in less predation and an altered landscape of fear. As a result, herbivores would potentially be released from natural predation pressure (as reviewed by Lennox et al., 2018). Consequently, the abundance of herbivores has already increased, or potentially will increase, in southwestern Ethiopia. However, the results from this study do not indicate if leopard abundance has changed over time. This study does reveal strong evidence that human pressure highly affects the temporal activity patterns of the leopard. Therefore, it is likely that leopards are affected by the landscape of fear that is created by humans. Based on the observed temporal activity patterns of the bushpig and warthog, the landscape of fear that is produced by humans seems stronger than the one produced by the leopard. Differences in bushpig and warthog temporal activity patterns were observed between sites with low human pressure and sites with high human pressure, whereas their temporal activity patterns did not differ between sites where the leopard was present and sites where the leopard was absent. This is a very surprising finding, because the leopard is still active in the area.

The absence of natural top-down control is contradicting the findings from Kuijper's (2011) review study on the top-down apex predator control over ungulates in human-dominated temperate forests. Here, evidence is presented that the indirect top-down effect of the natural apex predator, by the creation of a landscape of fear, cannot even be mimicked by the one resulting from hunting pressure (which is the main threat to biodiversity loss after habitat destruction; see Romero-Muñoz, 2020). This implicates that when the apex predator is present, prey species are more wary of this apex predator than of humans. Therefore, in the context of the present study, it is likely that the leopard is too absent to exert any top-down control.

Thus, the absence of natural top-down control may indeed be the result of a relatively low leopard abundance in the study area. This could cause a trophic release (i.e. the increase in prey abundance following the extirpation or abundance decline of the apex predator), even when hunting replaces the natural lethal top-down regulation of herbivore populations (Kuijper, 2011). Besides, bushmeat and trophy hunting are not common in southwestern Ethiopia (BirdLife International, 2012). A trophic release was not observed on Borneo when Brodie & Giordano (2013) examined the abundances of four prey species with varying apex predator abundance. They related local abundances of prey species to local abundances of the apex predator, without examining changes in local apex predator abundance. If there would be a decline in local apex predator abundance, then one can observe if and how prey population sizes are changing. Therefore, I believe that it is unjustified that Brodie & Giordano (2013) claim that there is a lack of trophic release. In the context of the present study, a potential leopard abundance decline may release herbivore populations from predation, which probably results in more crop raiding and other human-wildlife conflicts.

5.4 Limitations

Before discussing the limitations of this study, a couple of strengths should be mentioned regarding the methodology. One of the strong assets of this research is the research design, which improves the reliability of the data. For the data collection, Rodrigues et al. (2020) used relevant methods from earlier studies by Mertens et al. (2018) and Rodrigues et al. (2019), including the manual classification of camera observations. In the present study, the top-down variables that are used in the GLMMs (human presence and leopard presence) are based on this manually classified count data, which makes them highly reliable. The temporal activity pattern models used classifications of camera sites according to leopard presence and human pressure. Prior to modelling, a sensitivity analysis was applied to check whether different human pressure classifications were creating different outcomes or not. This was not the case (see Appendix C), thereby increasing the robustness of the temporal activity models.

Particularly the GLMMs did not demonstrate results that were in line with the expectations. This may be the result of limitations of the models, which can be ascribed to the model parameters that are used. Explanatory variables might have been missing from these models, which is also indicated by the low marginal R^2 values of the bushpig and warthog GLMMs. For example, instead of using the bottom-up variable distance to the forest edge, a distinction could have been made between the bottom-up variables 'distance to the nearest human settlement' and 'distance to the nearest cropland'. These variables might have provided a more detailed indication of the spatial behavior of the target species towards the forest edge, if a strong correlation between the two variables is absent. A similar distinction was made by Carter et al. (2012), who used the variables 'distance to the forest road' and 'distance to human settlements'. They found that tigers were avoiding human settlements, whereas their spatial activity overlapped with human activity near the forest road. Furthermore, structural equation modelling (SEM) could have been applied to estimate the relative importance of the explanatory variables in the GLMMs, and to examine the direct and indirect relationships between variables based on *a priori* knowledge (Grace, 2008). This approach was also used by Dorresteijn et al. (2015) to examine the trophic network of a human-dominated landscape in Transylvania, Romania.

Furthermore, the theoretical implications of this study are limited by the lack of similar research in human-dominated landscapes, as argued by Dorresteijn et al. (2015), and areas that are not isolated (e.g. national parks or islands), particularly in the tropics (Brodie & Giordano, 2013).

5.5 Practical implications and future research

The GLMMs revealed interesting results that are relevant for stakeholders involved in policy implementation, and conservation policies in particular. The significant positive bottom-up influence of forest cover on the warthog and leopard occurrences demonstrated the importance to maintain a high Afromontane forest cover. Halting both deforestation and forest fragmentation is critical to conserve these target species, and to maintain the services that the forests provide for the local human population. Moreover, 'a failure to act decisively and to act now will greatly increase the risk of unprecedented and irrevocable biodiversity loss in the hyperdiverse tropics' (Barlow et al., 2018, p. 524). The study kebeles are located within two National Forest Priority Areas, however, a constitution is not yet in place (Rodrigues et al., 2020). Recognizing the conservation values of the Afromontane forests and effectively managing the conservation of this region are essential for maintaining biodiversity (e.g. da Silva et al., 2018). The leopard should particularly be conserved to establish a strong top-down control, thereby preventing potential trophic release and cascades that eventually could result in further biodiversity loss (Estes et al., 2011).

Unfortunately, the results from this study may not be useful for the local farmers to alleviate crop raiding. The temporal activity patterns indicated that there was not a time in the day where both of the bushpig and warthog were inactive. Therefore, farmers cannot use time-specific strategies to mitigate crop raiding. Besides, other crop-raiders, such as the olive baboon, are also active in the region (Dorresteijn et al., 2017). The temporal activity patterns of the crop-raiders also revealed a potential response to human pressure. This could indicate that when humans are present in the croplands, crop damage may be less severe. Guarding crops may therefore be an efficient mitigation strategy. However, it is financially and physically not feasible for farmers to guard their crops throughout the day, and other mitigation strategies are not sufficient to minimize crop damage (Ango et al., 2017). Therefore, I recommend that regional governmental bodies, such as the Oromia Bureau of Agriculture and Natural Resource or Oromia Forest and Wildlife Enterprise Jimma Branch Office, set up a funding system to compensate the farmers that experience crop yield loss. If possible, locally, unemployed or landless people could be engaged in crop guarding, in return for food and or income. This could be facilitated by kebele leaders and externally financed by an overarching governmental body, which is also proposed by Ango et al. (2017).

In general, more research is needed on the predator-prey interactions in the tropics and in human-dominated landscapes. In particular, it would be highly relevant to better understand the role of the leopard in southwestern Ethiopia for a couple of reasons. First, it would be relevant to study the spatiotemporal patterns of other mammals in relation to leopard presence in the region. Given this information, we would have a more complete image of the presence of any apex predator top-down control. Second, it would be useful to examine the relative abundance of leopards in other areas in southwestern Ethiopia, and in other regions within the biodiversity hotspot. We can then suggest if the leopard’s top-down control is relatively weak or strong. Third, available data on the local leopard abundance and prey abundances can be analyzed to claim whether a trophic release is present or not. Contrary to Brodie & Giordano (2013), a decline in local leopard abundance should be observed before claiming this. Camera trap data is collected in the period November 2015-March 2017, from Rodrigues et al. (2019) and Rodrigues et al. (2020), respectively. Local leopard abundance could be monitored for a similar period of time, and a comparison can be made with the existing data.

Furthermore, it is plausible that the target species are adjusting their temporal activity in response to human disturbances before they are adjusting their spatial activity. This potential mechanism could also be explored in future research by studying spatiotemporal pattern changes in time. Another interesting topic for future research would be the cross-boundary subsidy cascades that are triggered by crop-raiders. These cascades could negatively impact forest ecosystems (Luskin et al., 2017), hence it is important to study if they are present in southwestern Ethiopia and how they alter the ecosystem. Nevertheless, the existence of these cascades, in general, underlines both the complexity of (indirect) human impacts on ecosystems and the necessity to prevent mammals from foraging outside the forest areas.

6. Conclusions

The objective of this study was to answer the two research questions. The answer to the first research question, “How does the occurrence of the target species relate to their environment, apex predator presence, and human presence?”, is straightforward: the only significant effect that was found in the results of the generalized linear mixed models was the positive bottom-up influence of forest cover on warthog and leopard occurrence. These results highlight the importance of maintaining Afromontane forest cover, because of the forest-dependence of these species, as well as the local human population. The second research question was: *“How are the temporal activity patterns of the target species influenced by apex predator and human presence?”*. In accordance with the occurrence of the crop-raiders, the leopard did also not have a noticeable influence on their temporal activity. These findings suggest that leopards did not exert direct and indirect top-down control on these crop-raiding mammals. In turn, the temporal activity of the leopards seemed to be affected by human presence. A large temporal separation was observed. A temporal separation was also observed in the temporal activity patterns of the crop-raiders. In general, the three mammals increased their nocturnality at sites where human pressure was high. The outcomes of this study indicate that the target species responded to human presence by adjusting their temporal activity rather than spatial activity. What exact role the leopard fulfils as the apex predator in the ecosystem, requires further research.

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Appendix A. R-script for the generalized linear mixed models

The following script is used to estimate bushpig, warthog, and leopard occurrence using generalized linear mixed models (GLMMs). The number signs (#) represent comments, including links to useful websites, that are useful for reproduction purposes.

```
rm(list=ls())
setwd("/Users/merijnderoos/R-script/") #"C:" before already taken into account

library(lme4)           #for the GLMM (glmer function)
library(ggplot2)        #for (gg)plotting
library(labeling)       #for axes labeling
#library(MASS)
#library(arm)
#library(boot)
#library(GGally)
# Install Dependencies for these packages to make them work

# The datasets on this R version = library(help = 'datasets')

my_data <- read.csv("/Users/merijnderoos/R-script/my_data.csv", sep=";", dec=",", header = TRUE)
my_data <- data.frame(my_data, check.rows = FALSE, check.names = TRUE)
str(my_data) #Check data class by using "class(x)" or "str(x)"
names(my_data)
#head(my_data)

## ---------------------------------------------------------------------------------- ##
## --------- Checking for relationship between variables --------- ##
## ---------------------------------------------------------------------------------- ##

# -------- Correlation between the environmental variables -------- #
res <- cor.test(my_data$pfst500m, my_data$distedge, method = "pearson")
#Or just use "cor(my_data$pfst500m, my_data$distedge, method="pearson")", which gives the same
 outcome
res             #0.6897861, pretty strong correlation

# Plot of the correlation
environcorrelation <- ggplot(data = my_data, mapping = aes(pfst500m,distedge)) + geom_point(shape=1,
 size=2.5)
print(environcorrelation + ggtitle("Relation between forest cover and distance to the edge") +
```

```
labs(x="Forest cover (500m buffer)", y="Distance to the forest edge (in m)"))

# ----- Correlation between the environmental variables and human presence ----- #
cor(my_data$npict_withpeople, my_data$pfst500m) #Using the number of pictures of people because the 'Human_presence' column is containing characters ('with' and 'without')
	# coefficient = -0.2627074, weak correlation
cor(my_data$npict_withpeople, my_data$distedge)
	# coefficient = -0.1908303, weak correlation

# Plot of the correlation
x <- my_data$npict_withpeople
y <- my_data$pfst500m
plot(x,y, main="Relation between forest cover and human presence", xlab="Number of human recordings", ylab="Distance to the forest edge (in m)")

# ----- Correlation between the number of mammal pictures and human presence ----- #
cor(my_data$npict_withpeople, my_data$Pota_larv_ev)		#Bushpig and human presence, not correlated
cor(my_data$npict_withpeople, my_data$Phac_afri_ev)		#Warthog and human presence, not correlated
cor(my_data$npict_withpeople, my_data$Pant_pard_ev)		#Leopard and human presence, not correlated
# Also no correlation amongst registered mammal appearances per location.

########################################
##### Generalized Linear Mixed Model #####
########################################
library(DHARMa)		#to simulate the model residuals
library(MuMIn)		#for the r-squared of the models
#library(effects)
#library(sjmisc)

# Response variables (mammal occurrence)
#Using ev instead of uq, that's the right one I think
Bushpig <- (my_data$Pota_larv_ev)
Warthog <- (my_data$Phac_afri_ev)
Pantera <- (my_data$Pant_pard_ev)

# Explanatory factors (scaled, which is necessary for the models to work)
Forest <- scale(my_data$pfst500m)
Human <- scale(my_data$npict_withpeople/my_data$time_field_days) #Adjusted for the amount of camera days
```

```
Leopard <- scale(my_data$Pant_pard_ev/my_data$time_field_days)     #Idem

# Explanatory factors (log transformed)
ForestL <- log((my_data$pfst500m)+1)
HumanL <- log((my_data$npict_withpeople/my_data$time_field_days)+1)
LeopardL <- log((my_data$Pant_pard_ev/my_data$time_field_days)+1)

# Random effect
#kebele <- as.numeric(my_data$kebele) #kebele gave error messages before adding this, but seems unnecessary
#without adding random effect 'pointid', the GLMMs are all highly overdispersed

#Offset#
#Definition: https://www.jmp.com/support/help/en/15.1/index.shtml#page/jmp/poisson-regression-with-offset.shtml
#In the GLMMs in this research we use time_field_days (total camera day length) as offset to account for the differences in length of camera deployment

#Overdispersion#
#Overdispersion is the presence of greater variability (statistical dispersion) in a data set than would be expected based on a given statistical model
#Check: https://cran.r-project.org/web/packages/DHARMa/vignettes/DHARMa.html

# Overdispersion test (overdisp_fun), as described by Ben Bolker and others: https://bbolker.github.io/mixedmodels-misc/glmmFAQ.html
overdisp_fun <- function(model) {
  rdf <- df.residual(model)
  rp <- residuals(model,type="pearson")
  Pearson.chisq <- sum(rp^2)
  prat <- Pearson.chisq/rdf
  pval <- pchisq(Pearson.chisq, df=rdf, lower.tail=FALSE)
  c(chisq=Pearson.chisq,ratio=prat,rdf=rdf,p=pval)
}
#Overdispersed when (e.g., see http://rstudio-pubs-static.s3.amazonaws.com/263877_d811720e434d47fb8430b8f0bb7f7da4.html):
#The residual deviance (chisq) is greater than the residual degrees of freedom (rdf), so the ratio should be smaller than 1
#If the p-value is < 0.05

# Other method for overdispersion:
#Overdisp <- simulateResiduals(m1, refit=T)
```

```r
#testOverdispersion(Overdisp) #Resulting also in more than 11, which is in line with the overdisp_fun calculation.

#Spatial autocorrelation#
#The models need to be checked if observations from different camera trap locations show a correlation because of similar spatial characteristics (longitude/latitude).
#Using longitude and latitude
#check https://www.rdocumentation.org/packages/ncf/versions/1.2-9/topics/correlog
#check https://www.r-bloggers.com/spatial-correlograms-in-r-a-mini-overview/
#check https://cran.r-project.org/web/packages/ncf/ncf.pdf
library(ncf)      #for using the correlog function for spatial autocorrelation

#R-squared#
#Check: https://journals.plos.org/plosone/article/file?type=supplementary&id=info:doi/10.1371/journal.pone.0177614.s003
#Check: https://stats.stackexchange.com/questions/92221/is-it-worth-reporting-small-fixed-effect-r2-marginal-r2-large-model-r
#Marginal R2 provides the variance explained only by fixed effects
#Conditional R2 provides the variance explained by the entire model, i.e., both fixed effects and random effects
#Values between 0 and 1

#Other method for R-squared:
#vars <- insight::get_variance(?)          #fill in m1, m2 or m3 as '?'
#r2_marginal <- vars$var.fixed / (vars$var.fixed + vars$var.random + vars$var.residual)
#r2_conditional <- (vars$var.fixed + vars$var.random) / (vars$var.fixed + vars$var.random + vars$var.residual)
#r2_marginal              #For m3 it is R2m = 0.810
#r2_conditional

## ---------------------------------------- ##
## ----- GLMM for Bushpig ----- ##
## ---------------------------------------- ##
m1 <- glmer(Bushpig ~ Human + Forest + Leopard + offset(log(time_field_days)) + (1|kebele) + (1|set) + (1|pointid), data = my_data, family = "poisson")
#control = glmerControl(optimizer = "bobyqa", optCtrl = list(maxfun = 100000))) tolPwrss = 1e-7))
summary(m1)
r.squaredGLMM(m1)    #left column gives marginal and right column gives conditional values
#confint(m1)

# Checking if the model performs better with log transformations
```

```r
#m1L <- glmer(Bushpig ~ HumanL + ForestL + LeopardL + offset(log(time_field_days)) + (1|kebele) + (1|set) + (1|pointid), data = my_data, family = "poisson")
#anova(m1L, m1)                    #m1 performs better (lower AIC and BIC values)

# Test for overdispersion of m1
overdisp_fun(m1)                   #overdisp_fun function already stated before
#Without the fixed effect pointid, the ratio is far above zero for the three models. With pointid it is far below zero, which is fine and does not indicate overdispersion.

# Quick plot of effects of m1
sim.resid <- simulateResiduals(m1)
plotSimulatedResiduals(sim.resid)
plot(allEffects(m1))
drop1(m1, test="Chi")

# Checking for spatial autocorrelation (by using longitude and latitude)
Correlog <- correlog(x=my_data$long, y=my_data$lat, z=resid(m1), increment=1500, resamp=1000, latlon=T) #only the value of $p changes by repeating this function.
plot(Correlog$correlation, ylim=c(-0.3,0.5))
abline(0,0) #adding a x-axis
#str(Correlog)
#Dorresteijn et al.'s autocorrelation plot:
#plot(Correlog$correlation, pch=sym[(p.adjust(Correlog$p[1:20],"holm")<0.05)+1],ylim=c(-0.3,0.5))

spline.correlog.bushpig <-  spline.correlog(x=my_data$long, y=my_data$lat, z = residuals(m1, type = "pearson"), resamp=100)
plot(spline.correlog.bushpig, main="Autocorrelation test for the bushpig model", cex.main=2, cex.lab=1.4)              #I would say there is no spatial autocorrelation!

## ------------------------------------------ ##
## ----- GLMM for Warthog ----- ##
## ------------------------------------------ ##
m2 <- glmer(Warthog ~ Human + Forest + Leopard + offset(log(time_field_days)) + (1 | kebele) + (1 | set) + (1|pointid), data = my_data, family = "poisson")
#, control = glmerControl(optimizer = "bobyqa", optCtrl = list(maxfun = 100000))) #tolPwrss = 1e-7)
summary(m2)
r.squaredGLMM(m2)
#confint(m2)

# Checking if the model performs better with log transformations
#m2L <- glmer(Warthog ~ HumanL + ForestL + LeopardL + offset(log(time_field_days)) + (1|kebele) + (1|set) + (1|pointid), data = my_data, family = "poisson")
```

```
#anova(m2L, m2)                    #m2 performs better (lower AIC and BIC values)

# Test for overdispersion of m2
overdisp_fun(m2)         #no overdispersion

# Quick plot of effects of m2
sim.resid <- simulateResiduals(m2)
plotSimulatedResiduals(sim.resid)
plot(allEffects(m2))
drop1(m2, test = "Chi")

# Checking for spatial autocorrelation of m2
Correlog <- correlog(x=my_data$long, y=my_data$lat, z=resid(m2), increment=1500, resamp=1000,
 latlon=T)
plot(Correlog$correlation, ylim=c(-0.3,0.5))
abline(0,0)
#str(Correlog)

spline.correlog.warthog <-  spline.correlog(x=my_data$long, y=my_data$lat, z = residuals(m2, type =
 "pearson"), resamp=100)
plot(spline.correlog.warthog, main="Autocorrelation test for the warthog model", cex.main=2,
 cex.lab=1.4)              #Again, there is no spatial autocorrelation.

## --------------------------------------- ##
## ----- GLMM for leopard ----- ##
## --------------------------------------- ##
# Comment: Poisson will not work here because there are very few leopard pictures per camera
m3 <- glmer(Pantera ~ Human + Forest + offset(log(time_field_days)) + (1 | kebele) + (1 | set) +
 (1|pointid), data = my_data, family = "poisson")
#, control = glmerControl(optimizer = "bobyqa", optCtrl = list(maxfun = 100000))) #tolPwrss = 1e-7)
summary(m3)
r.squaredGLMM(m3)
#confint(m3)

# Checking if the model performs better with log transformations
#m3L <- glmer(Pantera ~ HumanL + ForestL + offset(log(time_field_days)) + (1|kebele) + (1|set) +
 (1|pointid), data = my_data, family = "poisson")
#anova(m3L, m3)                    #m3 performs better (lower AIC and BIC values)

# Test for overdispersion of m3
overdisp_fun(m3)         #no overdispersion
```

```
# Quick plot of effects of m3
sim.resid <- simulateResiduals(m3)
plotSimulatedResiduals(sim.resid)
plot(allEffects(m3))
drop1(m3, test = "Chi")

# Checking for spatial autocorrelation of m3
Correlog <- correlog(x=my_data$long, y=my_data$lat, z=resid(m3), increment=1500, resamp=1000,
 latlon=T)
plot(Correlog$correlation, ylim=c(-0.3,0.5))
abline(0,0)
#str(Correlog)

spline.correlog.warthog <-  spline.correlog(x=my_data$long, y=my_data$lat, z = residuals(m3, type =
 "pearson"), resamp=100)
plot(spline.correlog.warthog, main="Autocorrelation test for the leopard model", cex.main=2,
 cex.lab=1.4)               #Again, there is no spatial autocorrelation.


# Checking if binomial distribution works better in the GLMMs
#The response variables are made with cbind when using a binomial distribution family (Rodrigues et al.,
 2020).
Bushpig1 <- cbind(my_data$Pota_larv_ev, my_data$time_field_days - my_data$Pota_larv_ev)
Warthog1 <- cbind(my_data$Phac_afri_ev, my_data$time_field_days - my_data$Phac_afri_ev)
Pantera1 <- cbind(my_data$Pant_pard_ev, my_data$time_field_days - my_data$Pant_pard_ev)

model1 <- glmer(Bushpig1 ~ Human + Forest + Leopard + offset(log(time_field_days)) + (1|kebele) +
 (1|set) + (1|pointid), data = my_data, family = "binomial")
anova(model1,m1)                #m1 performs better
model2 <- glmer(Warthog1 ~ Human + Forest + Leopard + offset(log(time_field_days)) + (1|kebele) +
 (1|set)+ (1|pointid), data = my_data, family = "binomial")
anova(model2,m2)                #model2 performs better
model3 <- glmer(Pantera1 ~ Human + Forest + offset(log(time_field_days)) + (1|kebele) + (1|set) +
 (1|pointid), data = my_data, family = "binomial")
anova(model3,m3)                #m3 performs better
#Conclusion: the poisson distribution family performs better overall, but the values are similar
```

Appendix B. Test results for spatial autocorrelation in the GLMMs

The generalized linear mixed models were tested for spatial autocorrelation using spline correlograms from R-package ‘ncf’ (Bjornstad, 2020). Spatial autocorrelation was not present in the models, because there was no correlation between spatial observations (i.e. values were close to zero; Figure B1).

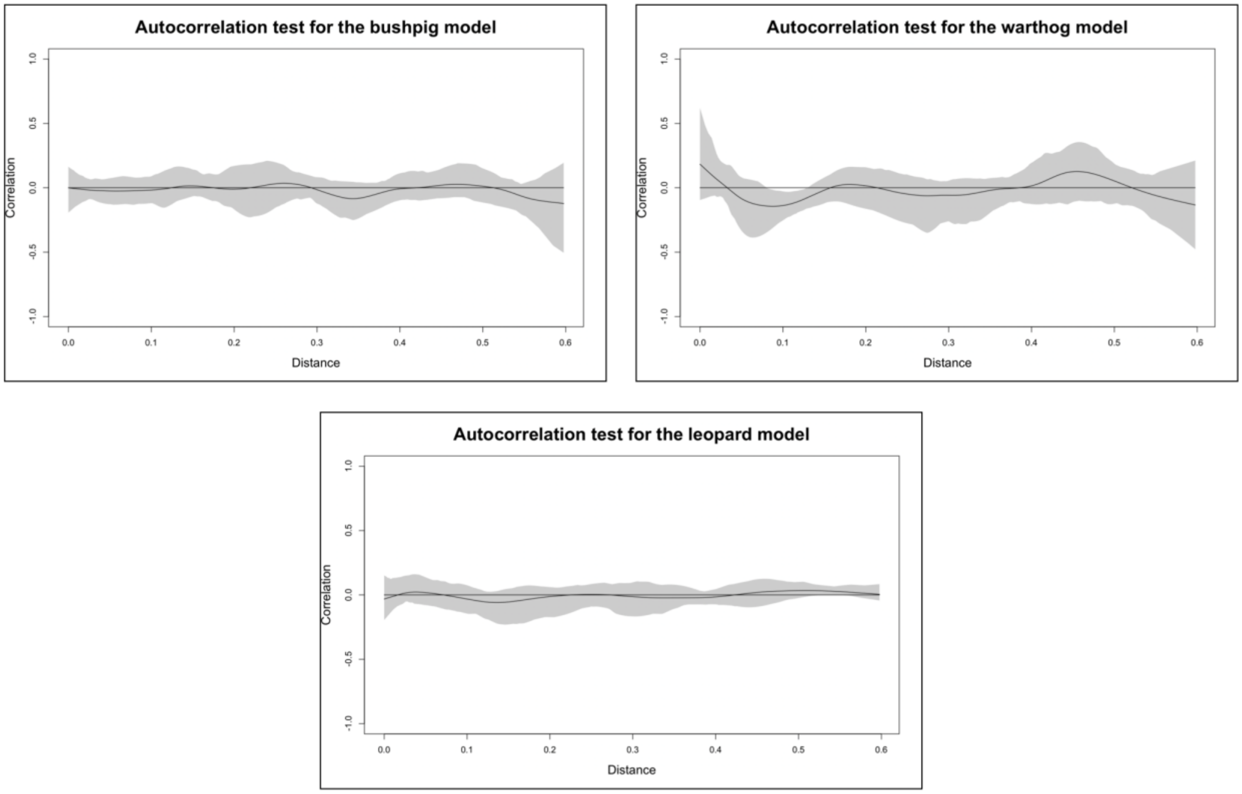

Figure B1. Spline correlogram plots (with 95% confidence intervals) as a test for spatial autocorrelation for the generalized linear mixed models of the bushpig, warthog, and leopard. Correlation values range between -1 and 1, with increasing values indicating a greater correlation.

Appendix C. Mammal temporal activity patterns for different human pressure classes

To model the influence of humans on the temporal activity of the bushpig, warthog, and leopard, a classification of human pressure was used. The human pressure is low at camera sites when at most 5% of the total number of pictures of a camera trap are recordings of humans. To justify using this percentage as a boundary value between low and high human pressure, two additional classifications were made using 10% and 20% (Figures C1, C2, and C3).

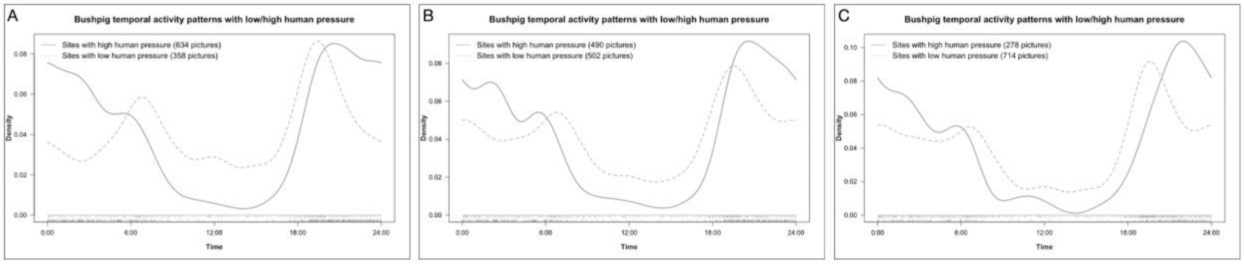

Figure C1. Bushpig activity patterns when high human pressure is classified as (A) at least 5%, (B) at least 10%, and (C) at least 20% of the total number of pictures of a camera trap are recordings of humans.

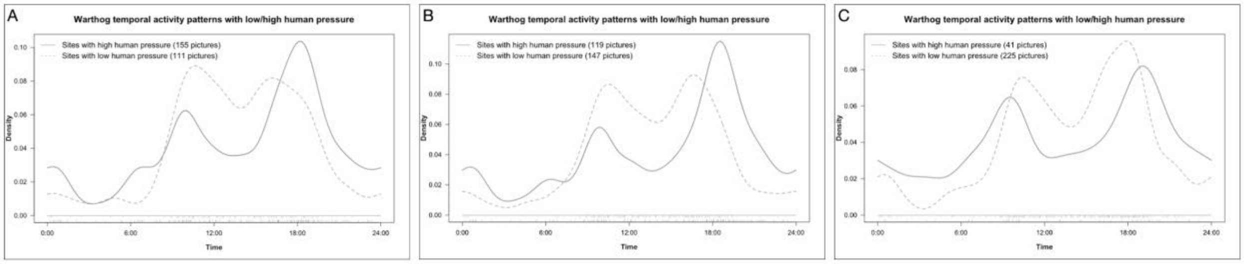

Figure C2. Warthog activity patterns when high human pressure is classified as (A) at least 5%, (B) at least 10%, and (C) at least 20% of the total number of pictures of a camera trap being recordings of humans.

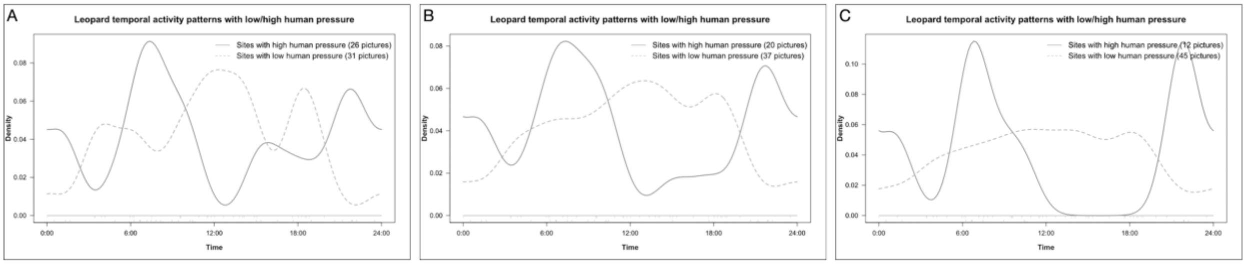

Figure C3. Leopard activity patterns when high human pressure is classified as (A) at least 5%, (B) at least 10%, and (C) at least 20% of the total number of pictures of a camera trap being recordings of humans.

Appendix D. R-script for modelling the temporal activity patterns

The following script is used to estimate bushpig, warthog, and leopard temporal activity patterns. The number signs (#) represent comments that are useful for reproduction purposes.

```
rm(list=ls())
setwd("/Users/merijnderoos/R-script/") #"C:" before already taken into account

#library(lme4)          #for the GLMM
#library(ggplot2)       #for (gg)plotting
#library(labeling)      #for axes labeling

#########################
##### Activity patterns #####
#########################
library(astroFns)       #for converting time in radians
library(overlap)        #for plotting the activity patterns
library(chron)          #for the function 'time'
# Install Dependencies for these packages to make them work

activity.data <- read.csv(file="all_pictures1.csv", sep= ";", h=T, stringsAsFactors = F)
#names(activity.data)

# Picture date
Date <- as.Date(activity.data$Date, format = "%Y-%m-%d") #transfer 'Date' column to date

# Time of pictures
activity.data$Time <- (times(activity.data$Time)) #transfer 'Time' column to time
str(activity.data)

## --------------------------------------------------------- ##
## --------- Mammal activity patterns ---------- ##
## --------------------------------------------------------- ##

# Amount of sites with low human pressure (at most 5 percent of the total number of pictures are
 recordings of humans)
Data_lowHumanP <- activity.data[ which(activity.data$Human_presence=='without'),]
unique(Data_lowHumanP$PointCode) #31 locations
```

```
# Amount of sites with high human pressure (at least 5 percent of the total number of pictures are recordings of humans)
Data_highHumanP <- activity.data[ which(activity.data$Human_presence=='with'),]
unique(Data_highHumanP$PointCode) #54 locations

## ------------------------------------------------ ##
## ------------------ Bushpig ------------------ ##
## ------------------------------------------------ ##
activity.bushpig <- activity.data[ which(activity.data$Common_name=='bushpig'),]
str(activity.bushpig)

# Set human pressure
highHumanP1 <- activity.bushpig[ which(activity.bushpig$Human_presence=='with'),] #only data with high human pressure
lowHumanP1 <- activity.bushpig[ which(activity.bushpig$Human_presence=='without'),] #only data with low human pressure

# Set leopard presence
withLeopard1 <- activity.bushpig[ which(activity.bushpig$Leopard_territory=="Y"),]
withoutLeopard1 <- activity.bushpig[ which(activity.bushpig$Leopard_territory=="N"),]

# Convert time to radians to vector
activity.bushpig$time.rad <- hms2rad(activity.bushpig$Time)
bushpigdat.tot <- as.vector(activity.bushpig$time.rad)
str(bushpigdat.tot) #992 pictures

# Radians to vector for human pressure
highHumanP1$time.rad <- hms2rad(highHumanP1$Time)
bushpigdat.highHumanP <- as.vector(highHumanP1$time.rad)
str(bushpigdat.highHumanP) #634 pictures

lowHumanP1$time.rad <- hms2rad(lowHumanP1$Time)
bushpigdat.lowHumanP <- as.vector(lowHumanP1$time.rad)
str(bushpigdat.lowHumanP) #358 pictures

# Radians to vector for leopard presence
withLeopard1$time.rad <- hms2rad(withLeopard1$Time)
bushpigdat.withLeopard <- as.vector(withLeopard1$time.rad)
str(bushpigdat.withLeopard) #363 pictures

withoutLeopard1$time.rad <- hms2rad(withoutLeopard1$Time)
bushpigdat.withoutLeopard <- as.vector(withoutLeopard1$time.rad)
```

```
str(bushpigdat.withoutLeopard) #629 pictures

# Plotting total bushpig activity
densityPlot(bushpigdat.tot, xscale = 24, xcenter = c("noon", "midnight"),
        add = FALSE, extend= NULL, rug = TRUE, n.grid = 100, kmax = 3, adjust = 1,
        main="Total bushpig activity throughout a day (992 pictures)", col="#7d7d7d", lwd=2, bty="o",
 cex.main=1.5,
        cex.axis=1.1, cex.lab=1.2, font.lab=2, col.lab="#1d1919", las=1, lty="solid")

#add "dev.new()" to see multiple plots in different windows

# Plotting bushpig activity with high human pressure
densityPlot(bushpigdat.highHumanP, xscale = 24, xcenter = c("noon", "midnight"),
        add = FALSE, extend= NULL, rug = TRUE, n.grid = 100, kmax = 3, adjust = 1,
        main="Bushpig activity at camera sites with high human pressure (634 pictures)", col="#7d7d7d",
 lwd=3, bty="o", cex.main=1.5,
        cex.axis=1, cex.lab=1.1, font.lab=2, col.lab="#1d1919", las=1, lty="solid")

# Plotting bushpig activity with low/high human pressure
#Overlapplots: https://www.rdocumentation.org/packages/overlap/versions/0.3.2/topics/overlapPlot
overlapPlot(bushpigdat.highHumanP, bushpigdat.lowHumanP, xscale = 24, xcenter = c("noon",
 "midnight"),
        linetype = c(1, 2), linecol = c("gray50", "darkgrey"), linewidth = c(2, 2), olapcol = "white", rug=TRUE,
 extend=NULL,
        n.grid = 128, kmax = 3, adjust = 1, lwd=3, bty="o", main="Bushpig temporal activity patterns with
 low/high human pressure",
        cex.axis=1.1, cex.lab=1.2, cex.main=1.5, font.lab=2, col.lab="#1d1919", las=1, lty="solid")
legend('topleft', legend=c("Sites with high human pressure (634 pictures)", "Sites with low human
 pressure (358 pictures)"), col=c("gray50", "darkgrey"), lty=1:2, cex=1.3,  box.lty=0)

# Plotting bushpig activity in leopard territory
densityPlot(bushpigdat.withLeopard, xscale = 24, xcenter = c("noon", "midnight"),
        add = FALSE, extend= NULL, rug = TRUE, n.grid = 100, kmax = 3, adjust = 1,
        main="Bushpig activity at camera sites with leopard presence (363 pictures)", col="#7d7d7d",
 lwd=3, bty="o", cex.main=1.5,
        cex.axis=1.1, cex.lab=1.2, font.lab=2, col.lab="#1d1919", las=1, lty="solid")

# Plotting bushpig activity with and without leopard presence
overlapPlot(bushpigdat.withLeopard, bushpigdat.withoutLeopard, xscale = 24, xcenter = c("noon",
 "midnight"),
        linetype = c(1, 2), linecol = c("gray50", "darkgrey"), linewidth = c(2, 2), olapcol = "white", rug=TRUE,
 extend=NULL,
```

```
        n.grid = 128, kmax = 3, adjust = 1, lwd=3, bty="o", main="Bushpig temporal activity patterns with/without leopard presence",
        cex.axis=1.1, cex.lab=1.2, cex.main=1.5, font.lab=2, col.lab="#1d1919", las=1, lty="solid")
legend('topleft', legend=c("Sites with leopard presence (363 pictures)", "Sites without leopard presence (629 pictures)"), col=c("gray50", "darkgrey"), lty=1:2, cex=1.3,  box.lty=0)

## Bushpig activity in leopard territory and leopard activity ##
#overlapPlot(bushpigdat.withLeopard, leoparddat.tot, xscale = 24, xcenter = c("noon", "midnight"),
#       linetype = c(1, 2), linecol = c("gray50", "darkgrey"), linewidth = c(2, 2), olapcol = "white", rug=TRUE, extend=NULL,
#         n.grid = 128, kmax = 3, adjust = 1, lwd=3, bty="o", main="Bushpig and leopard temporal activity patterns",
#         cex.axis=1.1, cex.lab=1.2, cex.main=1.5, font.lab=2, col.lab="#1d1919", las=1, lty="solid")
#legend('topleft', legend=c("Bushpig activity with leopard presence (363 pictures)", "Total leopard activity (57 pictures)"), col=c("gray50", "darkgrey"), lty=1:2, cex=1.3,  box.lty=0)

## ------------------------------------------------ ##
## ----------------- Leopard ----------------- ##
## ------------------------------------------------ ##
activity.leopard <- activity.data[ which(activity.data$Common_name=='leopard'),]
str(activity.leopard)

# Set human pressure
highHumanP2 <- activity.leopard[ which(activity.leopard$Human_presence=='with'),]
lowHumanP2 <- activity.leopard[ which(activity.leopard$Human_presence=='without'),]

# Convert time to radians to vector
activity.leopard$time.rad <- hms2rad(activity.leopard$Time)
leoparddat.tot <- as.vector(activity.leopard$time.rad)
str(leoparddat.tot) #57 pictures

# Radians to vector for human presence
highHumanP2$time.rad <- hms2rad(highHumanP2$Time)
leoparddat.highHumanP <- as.vector(highHumanP2$time.rad)
str(leoparddat.highHumanP) #26 pictures

lowHumanP2$time.rad <- hms2rad(lowHumanP2$Time)
leoparddat.lowHumanP <- as.vector(lowHumanP2$time.rad)
str(leoparddat.lowHumanP) #31 pictures

# Plotting total leopard activity
densityPlot(leoparddat.tot, xscale = 24, xcenter = c("noon", "midnight"),
```

```
        add = FALSE, extend= NULL, rug = TRUE, n.grid = 100, kmax = 3, adjust = 1,
        main="Total leopard activity throughout a day (57 pictures)", col="#7d7d7d", lwd=2, bty="o",
 cex.main=1.5,
        cex.axis=1.1, cex.lab=1.2, font.lab=2, col.lab="#1d1919", las=1, lty="solid")

# Plotting leopard activity with high human pressure
densityPlot(leoparddat.highHumanP, xscale = 24, xcenter = c("noon", "midnight"),
        add = FALSE, extend= NULL, rug = TRUE, n.grid = 100, kmax = 3, adjust = 1,
        main="Leopard activity at camera sites with high human pressure (26 pictures)", col="#7d7d7d",
 lwd=3, bty="o", cex.main=1.5,
        cex.axis=1.1, cex.lab=1.2, font.lab=2, col.lab="#1d1919", las=1, lty="solid")

# Plotting leopard activity with low/high human pressure
overlapPlot(leoparddat.highHumanP, leoparddat.lowHumanP, xscale = 24, xcenter = c("noon",
 "midnight"),
        linetype = c(1, 2), linecol = c("gray50", "darkgrey"), linewidth = c(2, 2), olapcol = "white", rug=TRUE,
 extend=NULL,
        n.grid = 128, kmax = 3, adjust = 1, lwd=3, bty="o", main="Leopard temporal activity patterns with
 low/high human pressure",
        cex.axis=1.1, cex.lab=1.2, cex.main=1.5, font.lab=2, col.lab="#1d1919", las=1, lty="solid")
legend('topright', legend=c("Sites with high human pressure (26 pictures)", "Sites with low human
 pressure (31 pictures)"), col=c("gray50", "darkgrey"), lty=1:2, cex=1.3,  box.lty=0)

#Interesting observation: complete opposite activity patterns in time!

## -------------------------------------------------- ##
## ------------------ Warthog ------------------ ##
## -------------------------------------------------- ##
activity.warthog <- activity.data[ which(activity.data$Common_name=='warthog'),]
str(activity.warthog)

# Set human pressure
highHumanP3 <- activity.warthog[ which(activity.warthog$Human_presence=='with'),]
lowHumanP3 <- activity.warthog[ which(activity.warthog$Human_presence=='without'),]

# Set leopard presence
withLeopard3 <- activity.warthog[ which(activity.warthog$Leopard_territory=="Y"),]
withoutLeopard3 <- activity.warthog[ which(activity.warthog$Leopard_territory=="N"),]

# Convert time to radians to vector
activity.warthog$time.rad <- hms2rad(activity.warthog$Time)
warthogdat.tot <- as.vector(activity.warthog$time.rad)
```

```r
str(warthogdat.tot) #266 pictures

# Radians to vector for human pressure
highHumanP3$time.rad <- hms2rad(highHumanP3$Time)
warthogdat.highHumanP <- as.vector(highHumanP3$time.rad)
str(warthogdat.highHumanP) #155 pictures

lowHumanP3$time.rad <- hms2rad(lowHumanP3$Time)
warthogdat.lowHumanP <- as.vector(lowHumanP3$time.rad)
str(warthogdat.lowHumanP) #111 pictures

# Radians to vector for leopard presence
withLeopard3$time.rad <- hms2rad(withLeopard3$Time)
warthogdat.withLeopard <- as.vector(withLeopard3$time.rad)
str(warthogdat.withLeopard) #63 pictures

withoutLeopard3$time.rad <- hms2rad(withoutLeopard3$Time)
warthogdat.withoutLeopard <- as.vector(withoutLeopard3$time.rad)
str(warthogdat.withoutLeopard) #203 pictures

# Plotting total warthog activity
densityPlot(warthogdat.tot, xscale = 24, xcenter = c("noon", "midnight"),
        add = FALSE, extend= NULL, rug = TRUE, n.grid = 100, kmax = 3, adjust = 1,
        main="Total warthog activity throughout a day (266 pictures)", col="#7d7d7d", lwd=2, bty="o",
 cex.main=1.5,
        cex.axis=1.1, cex.lab=1.2, font.lab=2, col.lab="#1d1919", las=1, lty="solid")

# Plotting warthog activity with high human pressure
densityPlot(warthogdat.highHumanP, xscale = 24, xcenter = c("noon", "midnight"),
        add = FALSE, extend= NULL, rug = TRUE, n.grid = 100, kmax = 3, adjust = 1,
        main="Warthog activity at camera sites with high human pressure (155 pictures)", col="#7d7d7d",
 lwd=3, bty="o", cex.main=1.5,
        cex.axis=1.1, cex.lab=1.2, font.lab=2, col.lab="#1d1919", las=1, lty="solid")

# Plotting warthog activity with low/high human pressure
overlapPlot(warthogdat.highHumanP, warthogdat.lowHumanP, xscale = 24, xcenter = c("noon",
 "midnight"),
        linetype = c(1, 2), linecol = c("gray50", "darkgrey"), linewidth = c(2, 2), olapcol = "white", rug=TRUE,
 extend=NULL,
        n.grid = 128, kmax = 3, adjust = 1, lwd=3, bty="o", main="Warthog temporal activity patterns with
 low/high human pressure",
        cex.axis=1.1, cex.lab=1.2, cex.main=1.5, font.lab=2, col.lab="#1d1919", las=1, lty="solid")
```

```
legend('topleft', legend=c("Sites with high human pressure (155 pictures)", "Sites with low human
 pressure (111 pictures)"), col=c("gray50", "darkgrey"), lty=1:2, cex=1.3,  box.lty=0)

# Plotting warthog activity in leopard territory
densityPlot(warthogdat.withLeopard, xscale = 24, xcenter = c("noon", "midnight"),
          add = FALSE, extend= NULL, rug = TRUE, n.grid = 100, kmax = 3, adjust = 1,
          main="Warthog activity at camera sites with leopard presence (63 pictures)", col="#7d7d7d",
 lwd=3, bty="o", cex.main=1.5,
          cex.axis=1.1, cex.lab=1.2, font.lab=2, col.lab="#1d1919", las=1, lty="solid")

# Plotting warthog activity with and without leopard presence
overlapPlot(warthogdat.withLeopard, warthogdat.withoutLeopard, xscale = 24, xcenter = c("noon",
 "midnight"),
          linetype = c(1, 2), linecol = c("gray50", "darkgrey"), linewidth = c(2, 2), olapcol = "white", rug=TRUE,
 extend=NULL,
          n.grid = 128, kmax = 3, adjust = 1, lwd=3, bty="o", main="Warthog temporal activity patterns
 with/without leopard presence",
          cex.axis=1.1, cex.lab=1.2, cex.main=1.5, font.lab=2, col.lab="#1d1919", las=1, lty="solid")
legend('topleft', legend=c("Sites with leopard presence (63 pictures)", "Sites without leopard presence
 (203 pictures)"), col=c("gray50", "darkgrey"), lty=1:2, cex=1.3,  box.lty=0)

## Warthog activity in leopard territory and leopard activity ##
#overlapPlot(warthogdat.withLeopard, leoparddat.tot, xscale = 24, xcenter = c("noon", "midnight"),
#         linetype = c(1, 2), linecol = c("gray50", "darkgrey"), linewidth = c(2, 2), olapcol = "white", rug=TRUE,
 extend=NULL,
#           n.grid = 128, kmax = 3, adjust = 1, lwd=3, bty="o", main="Warthog and leopard temporal activity
 patterns",
#           cex.axis=1.1, cex.lab=1.2, cex.main=1.5, font.lab=2, col.lab="#1d1919", las=1, lty="solid")
#legend('topleft', legend=c("Warthog activity with leopard presence (63 pictures)", "Total leopard
 activity (57 pictures)"), col=c("gray50", "darkgrey"), lty=1:2, cex=1.3,  box.lty=0)
```