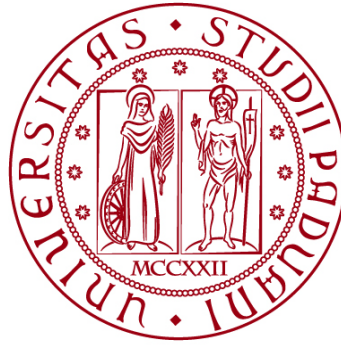


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**TESI DI LAUREA**

# **Wild mammals' sensitivity to the acoustic disturbance along the urbanization gradient**

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## SUMMARY

<b>RIASSUNTO</b> .....	3
<b>ABSTRACT</b> .....	3
<b>INTRODUCTION</b> .....	4
Human as super predator: known effects of human disturbance on animal behaviour.....	4
Responses of mammals living in urbanized environment.....	5
<b>MATERIALS AND METHODS</b> .....	8
Study area.....	8
Study species.....	9
Sampling design.....	9
Urbanization gradient assessment.....	12
Video and behavioural analysis.....	14
Statistical analyses.....	15
<b>RESULTS</b> .....	19
Behavioural models.....	19
Species-specific models.....	21
<b>DISCUSSION</b> .....	25
Inter-species models.....	25
Sensitivity along the urbanization gradient.....	27
<b>REFERENCES</b> .....	30

## **RIASSUNTO**

L'uomo rappresenta al giorno d'oggi una delle maggiori minacce per la fauna selvatica. Tra gli altri effetti, la presenza umana può comportare reazioni di paura negli animali selvatici, fino a portarli ad alterare la loro ecologia per rispondere al disturbo umano. Nonostante questo, alcune specie di mammiferi selvatici hanno colonizzato con successo gli ambienti urbanizzati, abituandosi al nuovo habitat o aumentando la sensibilità nei confronti della presenza umana. In questo studio è stata analizzata, tramite l'utilizzo di fototrappole, la reazione di 10 specie di mammiferi selvatici in risposta alla presenza umana, simulata tramite diversi tipi di suono emessi artificialmente, con lo scopo di capire il modo in cui le diverse specie reagiscono al disturbo provocato dalla presenza umana e se questo cambia in relazione al livello di urbanizzazione. I risultati hanno mostrato che tutte le specie analizzate mostravano livelli molto maggiori di paura in risposta alla voce umana rispetto ai suoni di controllo (allocco e usignolo). Inoltre, è stata evidenziata una significativa differenza nei livelli di paura mostrati dalle diverse specie, con quelle ben adattate ad ambienti urbanizzati (lupo e cinghiale) che hanno mostrato i valori più alti, mentre l'istrice è risultata essere la specie meno spaventata. Contrariamente alle nostre predizioni, daino, capriolo e tasso hanno mostrato maggiori livelli di comportamenti legati alla paura in ambienti più urbanizzati, mentre la volpe ha mostrato meno paura in queste aree, rimarcando la grande varietà di possibili risposte comportamentali dei mammiferi selvatici agli ambienti urbani.

## **ABSTRACT**

In contemporary times, humans represent one of the major threats to wildlife. Among other, the human presence can elicit fear responses in wild animals, leading them to alter their ecology in response to human disturbance. Despite this, some species of wild mammals have successfully changed their behaviour for living in urbanized environments, habituating or sensitizing to human presence. This study analyzed, using camera traps, the reactions of 10 species of wild mammals to human presence, simulated through different types of artificially emitted sounds. The aim was to understand how different species respond to human disturbance and whether these responses vary across different levels of urbanization. The results indicated that all analyzed species exhibited significantly higher levels of fear in response to human voices compared to control sounds (tawny owl and nightingale). Furthermore, a significant difference in fear levels was observed among different species, with those already occupying urbanized environments (wolf and wild boar) showing the highest values, while porcupine showed the least fear. Contrary to our predictions, roe deer, fallow deer, and European badger exhibited higher levels of fearful behaviours in more urbanized environments, while only red fox displayed less fear in these areas, remarking the high diversity of possible behavioural changes of mammal populations to urban environments.

## INTRODUCTION

### **Human as super predator: known effects of human disturbance on animal behaviour**

Human activities are a major source of disturbance in wildlife communities. It is known that humans are a serious threat for many species; in fact, they can be considered as major predators, hunting and exploiting high proportions of animal populations (Darimont *et al.*, 2009). For instance, meso- and large carnivores are killed by humans 4.3 and 9.2 times more than by natural predators, respectively (Darimont *et al.*, 2015). For this reason, humans can play the role of “super predator” in the wildlife community (Darimont *et al.*, 2015). Moreover, the effects of human predators on prey communities extend beyond direct impacts, as conceptualized by the “ecology of fear” framework. Indeed, predators hunt prey species, directly affecting their population size, but they also indirectly affect the preys’ behaviour through the induced fear, influencing the use of space and foraging time and for this reason regulating the species’ density in the area and their ecology (Brown *et al.*, 1999). For this reason, it can be expected that fear of humans as “super predator” can have an important effect on the behaviour and the ecology of the wildlife community, resulting in a pervasive effect through it (Suraci *et al.*, 2019; Smith *et al.*, 2015; Smith *et al.*, 2017). For instance, recent research has shown that fear induced by humans results in a nocturnal activity rhythm shift in many wild mammals’ species, while simultaneously eliciting various changes in ecology and species interactions (Gaynor *et al.*, 2018). More specifically, disturbance caused by human presence (e. g. recreating, outdoor activity) is growing even in less urbanized area (Cordell *et al.*, 2008) heavily impacting wildlife communities (Suraci *et al.*, 2021; Doherty *et al.*, 2021; Nickel *et al.*, 2020). Therefore, studies investigating the human-induced fear are increasingly present in scientific literature, mostly relying on the observation of the response of wild animals to human voice (Suraci *et al.*, 2019; Smith *et al.*, 2017; Clinchy *et al.*, 2016; Liu *et al.*, 2023; Crawford *et al.*, 2022; Bhardwaj *et al.*, 2022; Reilly *et al.*, 2022). It is known, in fact, that the sounds produced by some predators may elicit in prey species antipredator behaviour (Blumstein *et al.*, 2000; Hauser & Wrangham, 1990; Hendrie *et al.*, 1998; Macedonia & Yount; 1991; Noë & Bshary, 1997; Swaisgood *et al.*, 1999; Zuberbühler *et al.*, 1997). Recent research has shown that human voice can lead to reduced movements and activity, together with their shift towards nighttime for large- and meso-carnivores (Suraci *et al.*, 2019). Additionally, it has been demonstrated that human voice can generate even a reduction in feeding time in pumas (*Puma concolor* (Linnaeus, 1771), causing an uncomplete consumption of carcasses and forcing them to increase their kill rate, ultimately producing an impact on the entire wildlife community (Smith *et al.*, 2017). European badgers (*Meles meles* (Linnaeus, 1758)) have also been studied using human voices; a study conducted in England (Clinchy *et al.*, 2016) demonstrated

that these mustelids were far more fearful of humans than extant (dogs, *Canis lupus familiaris* Linnaeus, 1758) or locally extinct predators (bears, *Ursus arctos* Linnaeus, 1758 and wolves, *Canis lupus* Linnaeus, 1758). The fear elicited by human voice doesn't apply to carnivores only; indeed, even large ungulates show fearful responses to human voice (Liu *et al.*, 2023; Crawford *et al.*, 2022; Bhardwaj *et al.*, 2022), and in some cases these responses can even exceed those elicited by large predators (Liu *et al.*, 2023). A study conducted in Georgia (Crawford *et al.*, 2022), showed that white-tailed deer (*Odocoileus virginianus* (Zimmerman, 1780)) were twice as likely to flee in response to human voices compared to sounds of extant (coyotes) or eradicated predators (pumas and wolves). Literature suggests that species traits (e.g., body size, diet, reproduction rate) are not strongly related to the mammals' response to human presence (Suraci *et al.*, 2021). Previous studies comparing different species focused on the effects of human disturbance on wild species' behavioural ecology metrics such as space use, movements, and activity rhythms (Smith *et al.*, 2017; Reilly *et al.*, 2022; Suraci *et al.*, 2019, Suraci *et al.*, 2021). Nonetheless, despite the fact that these ultimate effects are likely mediated by fine scale behavioural reactions (e.g., fear), little is known about the proximate effect of human presence-perception on wild animals' behaviour and its possible variation across species. Filling this knowledge gap would be needed for understanding the mechanisms underlying the behaviour-mediated human impacts on wildlife communities, providing valuable information for conservation biology.

Our first aim was to investigate whether the behavioural responses to the human disturbance differ across species. Accordingly, we presented wild mammals with human voice, using two bird calls as control sounds and camera traps to record their behavioural reactions (i.e., risk assessment and fear). Finally, we modelled the variation of the effect of the human voice on the exhibited behaviours across 10 different mammal species: wolf, red fox (*Vulpes vulpes* (Linnaeus, 1758)), wild boar (*Sus scrofa* Linnaeus, 1758), roe deer (*Capreolus capreolus* (Linnaeus, 1758)), fallow deer (*Dama dama* (Linnaeus, 1758)), red deer (*Cervus elaphus* Linnaeus, 1758), porcupine (*Hystrix (Hystrix) cristata* Linnaeus, 1758), European hare (*Lepus europaeus* Pallas, 1778), European badger and European wildcat (*Felis silvestris* Schreber, 1777).

### **Responses of mammals living in urbanized environment.**

Despite the role of super predator played by humans, different species are able to survive in urbanized environments. It is well established that the effects of urbanization on wildlife are often adverse (Dirzo *et al.*, 2014; Newbold *et al.*, 2015; Fahrig, 2003). Wildlife in urban areas is, indeed, exposed to novel environmental pressures such as high vehicular and pedestrian traffic, large-scale occurrence of impervious surfaces, chemical, acoustic, and light pollution (Grimm *et al.*, 2008).

At the same time, however, urbanized environments can increase food availability for wildlife species (Chamberlain *et al.*, 2009). Moreover, buildings and infrastructure can be used as new shelters (Lowry *et al.*, 2013) and urbanized area can be used as human shield by prey species to protect themselves from natural predators (Hebblewhite *et al.*, 2005; Berger, 2007; Muhly *et al.*, 2011). While some species cannot take advantage of these new opportunities (e.g., the European wildcat, Stahl & Artois, 1994; Nowell & Jackson, 1996, and a pure herbivore like the European hare, Hackländer *et al.*, 2002), some wild mammals can alter their ecology to live in urbanized environments. For instance, porcupines were observed in urban and suburban areas (Lovari *et al.*, 2013; Sever & Mendelsohn, 1989), consistently with the tendency of smaller and generalist species to be better suited in urbanized environments (Santini *et al.*, 2019; Suraci *et al.*, 2021). Nonetheless, even large ungulates can colonize and live in urbanized environments, as shown for deer (red deer and fallow deer, Duarte *et al.*, 2015) and wild boars (Cahill *et al.*, 2012; Podgórski *et al.*, 2013; Primi *et al.*, 2016; Stillfried *et al.*, 2017a). The latter were reported to shift their diet towards anthropogenic food (Castillo-Contreras *et al.*, 2021) and to change their behaviour according to the experienced human pressure (Podgórski *et al.*, 2013, Brogi *et al.*, 2023). Although large carnivores are very sensitive to human disturbance (Ordiz *et al.*, 2013; Oriol-Cotterill *et al.*, 2015; Suraci *et al.*, 2021; Ordeñana *et al.*, 2010; Wang *et al.*, 2015; Moll *et al.*, 2018) and many studies showed that wolves use to avoid humans and their activities (Benson *et al.*, 2015; Kaartinen *et al.*, 2015; Sazatornil *et al.*, 2016), they are also known to be able to survive in human-dominated landscape (Blanco & Cortes, 2007; Grilo *et al.*, 2019; Llaneza *et al.*, 2012; Ahmadi *et al.*, 2014; Zanni *et al.*, 2023). Moreover, recent works have demonstrated how these carnivores are able to use even human-made artifacts, such as fences, to increase their hunting efficiency (Del Frate *et al.*, 2023) or to travel along human-created linear features to maximize the likelihood to find a prey (Muhly *et al.*, 2019; Dickie *et al.*, 2017; Kittle *et al.*, 2017). Even mesocarnivores are able to live in urbanized environments, with red foxes actively colonizing urban areas (Macdonald & Newdick, 1982; Harris & Rayner, 1986; Wilkinson & Smith, 2001) and demonstrating a notable ability to survive in these environments. Red foxes in urban areas may indeed mostly rely on anthropogenic food (Baker *et al.*, 2000). A study in Zürich (Contesse *et al.*, 2004), showed that more than half of the examined fox stomachs contained anthropogenic food, with this proportion increasing from suburban areas to city center. European badgers have also been observed actively colonizing urban areas (Harris *et al.*, 2010), likely on account to their plastic diet (Pigozzi, 1991; Rosalino *et al.*, 2005; Goszczyński *et al.*, 2000); which may even include refuse and garden crops (Harris, 1984).

The response of wild animals to urban areas may include both a sensitization and a habituation to human presence. Sensitization is a process where an increased exposure to a stimulus, increases the animals' responsiveness; this helps animals

reducing the likelihood of costly or lethal encounters with humans (Blumstein, 2016). In contrast, habituation is a process where an increased exposure to a stimulus leads a decreased responsiveness. This helps mitigating the energy costs of reacting to frequent stimuli, otherwise unsustainable in urbanized environments characterized by a high frequency of encounter with humans (Rankin *et al.*, 2009; Blumstein, 2016). Nevertheless, it is worth noting that habituation may also lead to direct or incidental human-induced mortality in urbanized areas (Wynn-Grant *et al.*, 2018; Shimozuru *et al.*, 2020). The second aim of this study is thus to investigate possible variation of the behavioural response to human presence along the urbanization gradient. This issue is indeed still under scientific debate, with evidence of either habituation, sensitization, and no effect at all being reported for different species across the urbanization gradient. For instance, in California opossums (*Didelphis virginiana* Kerr, 1792) reduce their activity level in higher building density level, while bobcats (*Lynx rufus* (Schreber, 1777)) and skunks (*Mephitis mephitis* (Schreber, 1776)) don't show any significant variation of activity accountable to the experienced urbanization (Reilly *et al.*, 2022). Contrasting evidence has been collected also for European mammals, with urban wild boars showing higher human tolerance (i.e., shorter flight distance) than their rural counterparts (Stillfried *et al.* 2017b) and red deer conversely appearing more vigilant in more disturbed areas (Jayakody *et al.*, 2008). Nevertheless, most studies suggest urban populations to exhibit a reduced fear towards humans compared to rural populations (Lowry *et al.*, 2013, Sol *et al.*, 2013; Ritzel & Gallo, 2020). Finally, it is worth noting that most studies investigating this topic on a community scale were conducted in North America (Ritzel & Gallo, 2020; Reilly *et al.*, 2022), where the systematic persecution towards wildlife became substantial only from the 18<sup>th</sup> century onwards (Frank and Woodroffe, 2001; Zedrosser *et al.*, 2011). Conversely, this study was conducted in Europe, where wild animals have been persecuted by humans for millennia (Sazatornil *et al.*, 2016; Vigne, 2011; Zedrosser *et al.*, 2011). This historical difference is reported by literature as the likely cause of the observed behavioural differences in population living in the two continents (Sazatornil *et al.*, 2016; Zedrosser *et al.*, 2011). Investigating wildlife behavioural reactions to human presence in Europe may thus better inform about the long-term effect of the chronic exposure of wild animals to humans, including the possible rise of positive responses to urbanization.

To test the hypothesis of European mammal populations experiencing a higher degree of urbanization behaving more tolerant toward humans, we recorded the behavioural reactions of wild mammals to the human voice and to the control sounds in sites with different degree of urbanization. Then, separately for each species, we modelled the variation of the behavioural responses along the urbanization gradient. We predicted lower likelihoods of exhibiting risk assessment and fear toward the human voice in populations inhabiting more urbanized areas.

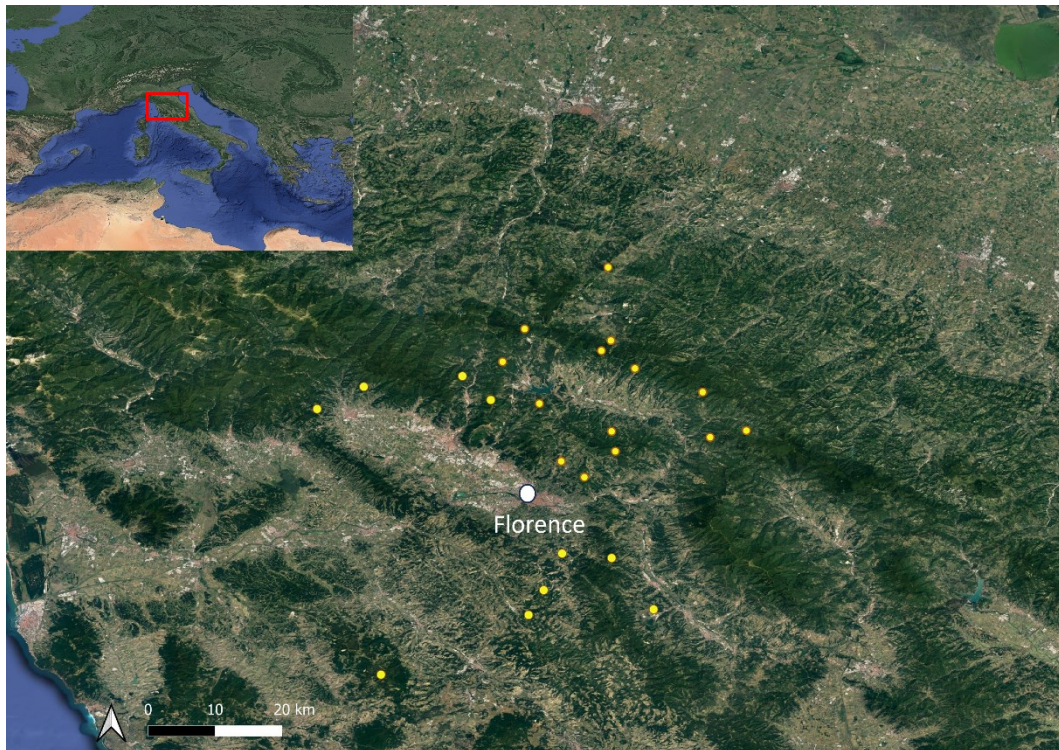


## MATERIALS AND METHODS

### Study area

The study took place in Central Italy, specifically in the Tuscany region, during the period from April to August of the years 2022 and 2023. This geographical area is characterized by a medium to high human population density (approximately 160 individuals per km<sup>2</sup>) and comprises approximately 23,000 km<sup>2</sup> (Source: IRPET).

We selected 23 sites (Fig. 1) across the provinces of Florence, Siena, Pistoia, Prato, and Arezzo with varying degrees of urbanization. The sites for placing the tests were selected based on the physiognomic characteristics of the environment. Specifically, sites were selected along semi-obligate pathways for the study species (Harmsen *et al.*, 2010), such as trails within the forest, with a preference for intersections of two different paths to maximize the likelihood of detecting animals. We also took into account the signs of presence such as feces, footprints, and ground scrapes (MacDonald, 1980), focusing on the most elusive target species (wolf).



*Figure 1.* Spatial distribution of the test sites (yellow dots) within the study area, with the position of the largest metropolitan area (Florence) being indicated by the white dot. The top-left panel shows the position of the study area (red box) in Southern Europe. Image realized with QGIS Desktop 3.32.3 version, using “Google Satellite” layer from Quick Map Service (QMS) plugin.

In the attempt to minimize the risk of detecting and testing the same individuals in different test sites, we selected sites at least 2.5 km apart (mean = 7.2 km).

According to the average species-specific home range sizes, this distance threshold was sufficient to prevent the testing of the same individuals in different sites for all species but wolves (Table 1). For the latter (whom home ranges average 82.64 km<sup>2</sup> in the study area, Mattioli *et al.*, 2018) we ensured not to test the same wolf individuals at different sites by visually identifying distinct packs through video footage (pack size, composition, and phenotypic traits).

### **Study species**

For the study we considered ten species of medium and large wild mammals present in the geographic area: red deer, roe deer, fallow deer, wild boar, porcupine, European hare, European badger, European wildcat, wolf and red fox.

There were excluded species that, although present in the area, were only occasionally recorded (e.g., *Mustela putorius* Linnaeus, 1758 and *Procyon lotor* (Linnaeus, 1758)), and those morphologically too challenging to be distinguished. It was the case of *Martes foina* (Erxleben, 1777) and *Martes martes* (Linnaeus, 1758), that we excluded because of their similarity, which made them very difficult to distinguish one from the other through infra-red light during nighttime. Finally, we excluded those species too small to reliably trigger the PIR of camera traps (e.g., micro mammals such as *Apodemus* sp. or *Rattus* sp.).

### **Sampling design**

In every test site we placed two camera traps (Browning Spec Ops Advantage BTC-8A) oriented in opposite directions. Camera traps were secured to the trees or other natural supports using a flexible steel cable locker (Master Lock Python 8417Dpro) at a height ranging from 0.5 to 3 meters.

Camera traps have been set with 24 hours of working time and with a video length of one minute after the triggering of the Passive Infrared Sensor (PIR). In the case of an excessive triggering of the PIR, caused by particular light - shadow conditions, the working period of one of the two camera traps was reduced, avoiding hours with the most intense sunlight, in order to prevent memory card saturation or battery discharge, while the second one was left with 24 hours of working time period. Camera traps were equipped with 132, 64 or 32 GB SD cards and an external battery (12V, 5Ah) that were replaced every two weeks.

For each site, one of the two camera traps was connected with a 'boombox' (Palmer *et al.*, 2022) (Boomboxes by Freaklabs and Meredith Palmer ©) programmed using Arduino software (Fig. 2). This system was directly connected to the camera trap's PIR motion sensor and played audio files over external speakers when the camera's PIR motion sensor was triggered (Palmer *et al.*, 2022).





Figure 2. Camera traps (Browning Spec Ops Advantage BTC-8A, left) with external speakers (right) used to play human voice and bird sounds during the test.

The test procedure consisted of two conditions, control and test: the control condition involved the playback of sounds of native birds in the study area (nightingale, *Luscinia megarhynchos* C. L. Brehm, 1831, and tawny owl, *Strix aluco* Linnaeus, 1758), while the test condition corresponded to the playback of human voices.

Both the test condition and the control condition were divided into two groups (A and B). Test condition A included seven different human voice tracks, while test condition B included other five different tracks with human voices. Similarly, control condition A included six tawny owl sounds and control condition B included six different nightingale sounds. All human voice and bird tracks had a duration of 5 seconds and were played at a volume of 80 decibels measured at 5 cm from the speakers. The whole set of tracks included in a group (e.g., the seven human voices of the test condition A) were uploaded in a boombox, which was attached to the camera trap. The boombox was programmed to play a randomly selected track of the group, starting from two seconds after the trigger of the pir sensor. Such setting

ensured the camera traps to start recording on video before the sound was played, preventing the possible loss of behavioural reactions of animals.

All groups of sounds were played in each site over the testing period. Control and test groups of sounds were alternated on each site and separated by two-week baseline periods (no sounds played). For instance, a possible cycle of conditions on a certain site may be: control A sounds (two weeks), no sounds (two weeks), test A sounds (two weeks), no sounds (two weeks), control B sounds (two weeks), no sounds (two weeks), test B sounds (two weeks). In the event of any issues or malfunctions, the program continued without re-evaluating the condition, causing the failure to collect data for certain conditions at specific sites.

However, the order of the group of sounds A or B was randomized for every site and the initial condition (test or control) were counterbalanced across sites, for a total of eight possible combinations. In order to limit the habituation to the spatial position of the sound source, the position of the speakers was slightly changed from first to second condition (e.g., moved to another branch of the tree), while from second to third condition the whole boombox-speaker system was moved and connected with the second camera placed in front of the first one (at about 10.20 meters of distance). From third to fourth condition, we slightly changed again the position of the speakers.

For the analysis of collected data, we considered exclusively the videos recorded by the camera connected with the boombox, which PIR actually triggered the sound play (i.e., in which the played sound was audible within the recorded video).

### Urbanization gradient assessment

To estimate the degree of urbanization experienced by the individuals being detected on the test sites, we used a Night Stable Light index (hereafter, nightlight index) as a proxy of urbanization (Sutton, 2003) from the Defensive Meteorologic Satellite Program's Operational Lynescan System (DMSP-OLS Version 4) data sets in National Geophysical Data Centre. This index is a 30 arc-second grids spanning from -65.0041661066500041 to 75.0041666666499935 latitude and from -180.0041666666500078 to 180.0041652266500023 longitude and it is expressed with a digital number from 0 (darkness) to 63 (highest brightness) (Fig. 3). For this work it has been used the latest released version (2013).

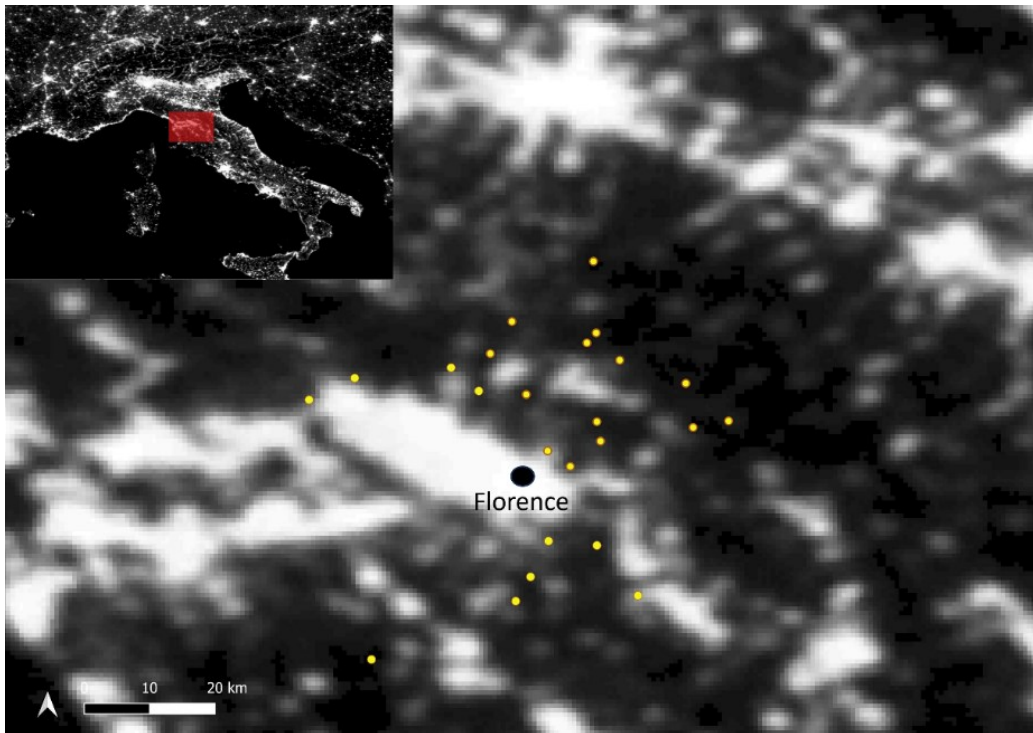


Figure 3. Nightlight index of the study area (black=low, white = high), with test sites and the position of the largest metropolitan area (Florence) being indicated by the yellow and black dots, respectively. The top-left panel shows the position of the study area (red box) in Italy. The image was drawn with QGIS Desktop 3.32.3 version, using Nightlight index, 2013 version (DMSP-OLS Version 4).

For each test site and species, the Nightlight index was averaged over a circular buffer centered on the test site itself (Fig. 4). We used species-specific buffers (Gallo *et al.*, 2022) sized for covering an area which was half of the expected home range of the different study species (Table 1). This choice allowed to minimize the inclusion of regions that were never utilized by the tested individuals while simultaneously maximizing the inclusion of areas that were actually used. Such strategy of halving the home range size was needed to account for the lack of

information pertaining to the spatial distribution of the real home ranges of the tested individuals, which might have variable size, shape, and center position.

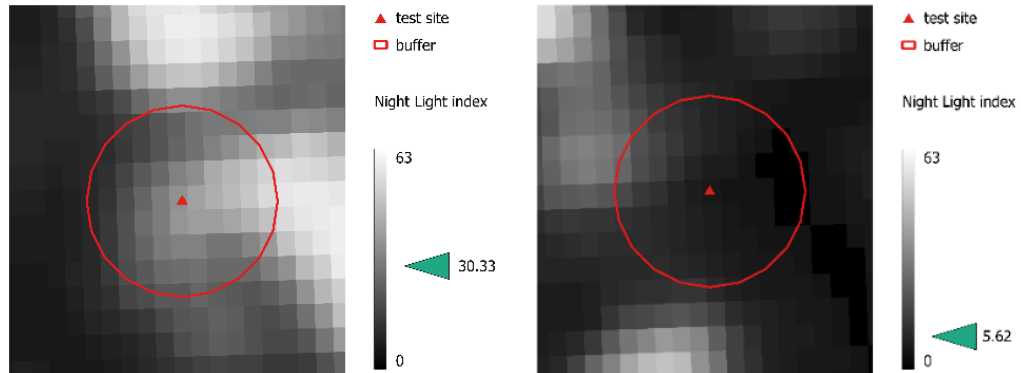


Figure 4. Example of two study sites (red triangle) with a circular buffer overlaid to the Nightlight index layer (DMSP-OLS Version 4). On left and right, examples of a medium-high and a low Nightlight indexes are reported, respectively.

**Table 1.** Average home range size of the study species, with respective references. References were selected based on publication date and study area, preferring recent studies conducted as close as possible to Central Italy. In some cases (Anile *et al.*, 2017; Mori *et al.*, 2014; Apollonio *et al.*, 2014; Davini *et al.*, 2004; Lovari *et al.*, 2017; Cavazza *et al.*, 2023) the home range size was calculated as the average between values reported for different sites, seasons, or sexes.

Species	Home range size (km <sup>2</sup> )	Reference
Red fox	1.24	Cavallini & Lovari, 1994
European badger	3.83	Remonti <i>et al.</i> , 2006
Porcupine	1.15	Mori <i>et al.</i> , 2014
European wildcat	10.06	Anile <i>et al.</i> , 2017
Wild boar	3.94	Cavazza <i>et al.</i> , 2023
Red deer	18.73	Fontana <i>et al.</i> , 2022
Fallow deer	1.62	Apollonio <i>et al.</i> , 2014 Davini <i>et al.</i> , 2004
Roe deer	0.204	Lovari <i>et al.</i> , 2017
European hare	0.23	Ferretti <i>et al.</i> , 2010
Wolf	82.64	Mattioli <i>et al.</i> , 2018

## Video and behavioural analysis

For each video we noted in an Excel file the test site, the date and time, the test condition and sound group (i.e., Control sounds A/B or Human sounds A/B) and the species observed. Additionally, we also noted the number of individuals.

To prevent the possible autocorrelation between consecutive events involving the same species in the same site, we calculated the temporal autocorrelation decay to rigorously establish objective time thresholds after which events may be considered as independent. First, we used the software R to create a dataframe with a row per minute and associated each row with the count of events observed within that minute interval. This resulted in a dataframe representing the frequency of events for each minute. Then, we used the `acf()` function to calculate the autocorrelation function (ACF) on the event frequency, measuring the correlation between observations at different time lags. Finally, we determined the first lag at which the absolute autocorrelation fell below 0.05. This time lag thus represented the point at which the likelihood of observing a new event became independent of past events. The whole process was repeated separately for each species, and we used the obtained species-specific time thresholds to merge together videos recorded within shorter lags.

Each behaviour was set to 1 if occurring in at least one of the videos belonging to the same event and 0 otherwise. All videos including one of the study species were annotated with the behaviours listed in the ethogram in Table 2 as binary variable, occurring (1) or not (0). The occurrence of the different behaviours was recorded only if they were exhibited after the sound was emitted. In the case that more than one individual were recorded in a single video, the occurrence of a specific behaviour assumed 1 if it was performed by at least one of the observed individuals and 0 otherwise.

The single behaviours were then merged into two broader behavioural responses, namely risk assessment and fear, as depicted in Table 2. "Risk assessment" included all behaviours aimed at determining whether the sound represented a real threat or not (Stankowich & Blumstein, 2005; Blumstein, 2016). Conversely, "Fear" included behaviours allowing the animal to move away from the site and/or signalling a state of strong distress, entailing a substantial energy expenditure or even interrupting vital action like foraging (Boissy, 1995; Blumstein, 2020; Brown *et al.*, 1999).

**Table 2.** Description of the coded behaviours and their subdivision into the two broader behavioural responses “risk assessment” and “fear” (see the text for more details).

Broad behavioural response	Behaviour	Description
Risk assessment	Vigilant	The animal stops moving and lifts its head above its shoulders, looking around and moving its ears scanning the surroundings.
	Look at the camera	The animal stops moving and directs its head and ears towards the camera.
Fear	Change direction	The animal changes the direction of movement after hearing the sound.
	Startle	The animal exhibits a sudden, quick, and exaggerated movement of the whole body.
	Wince	The animal exhibits a brief, rapid and slight recoil or flinching movement of the body.
	Flight	The animal runs away, moving at any speed faster than walking.

To code videos and behaviours, we used the independent software application "Wolf Tracker", which was exclusively developed for this project by Dr. Tiago Roldao. After noted the main information cited above, the software generates a Microsoft Excel file that comprises the encoded data. Inter-observer reliability was carried out with another experimenter (Dr. Martina Lazzaroni), coding a subsample of 229 videos out of 1653 (Intra-class correlation coefficient, two-way model using the irr package: Vigilant ICC = 0.808; Look at the camera ICC = 0.855; Change direction ICC = 0.804; Startle ICC = 0.921; Wince ICC = 0.676; Flight ICC = 0.795).

### Statistical analyses

The behaviours described previously were aggregated into two main behavioural categories, namely risk assessment and fear (Table 2), used as binary response variables in the subsequent models. In the case that one or more behaviours within their respective category occurred, the binary dependent variable (“fear” or “risk assessment”) assumed 1, otherwise 0. The events were then assigned to



either the day or night, comparing date and hour of the event occurrence with the times of sunrise and the sunset of the study area. These information were obtained using the `getSunlightTimes()` function from the R `suncalc` package. In order to investigate the variability of both risk assessment and fear, across i) different species and ii) populations experiencing different degrees of urbanization, a four-steps analysis was performed.

To analyse the inter-specific variability in the risk assessment towards humans (step 1a) we fitted a GLMM (Generalized Linear Mixed Model) with a binomial error structure and a logit link function (McCullagh and Nelder, 1989), using “risk assessment” as response variable. We fitted the model in R (version 4.2.2, R Core Team 2021) using the function `glmer` of the package `lme4`. We included into the model the sound (categorical predictor with three levels: tawny owl control sound, nightingale control sound, and human voice) and species (categorical predictor with 10 levels, one per tested species) as well as their interaction. We further included the species- and site-specific average night light index to control for possible effects of the experienced degree of urbanization on the likelihood of fearfull or risk assessment responses. We also included the binary predictor “diurnal” (0=nighttime, 1=daytime) to control for a possible increased fear during the day. Prior to fitting the model, we z-transformed the night light index to a mean of zero and a standard deviation of one to achieve easier interpretable estimates (Schielzeth, 2010). To account for the nested nature of data, we included the test site as random intercept effects. To avoid a model being overconfident with regard to the precision of fixed effects estimates and to keep type I error rate at the nominal level of 5% we considered all theoretically identifiable random slopes (Schielzeth & Forstmeier, 2009; Barr *et al.*, 2013). More precisely, we considered random slopes of diurnal, those of sound (the two control levels, manually dummy coded and then centred, with the human voices being the reference level), those of single species (with those of fox, porcupine, wild boar, and wolf, dummy coded and then centred that were included), and those of their interaction resulting theoretically identifiable (with that of tawny owl sound: fox that was included) within test sites. As an overall test of the fixed effects of species and its interaction with sound we conducted a full-null model comparison (Forstmeier & Schielzeth, 2011), aiming at avoiding cryptic multiple testing, whereby the null model lacked these two effects but was otherwise identical to the full model. This comparison was based on an Chi square-test (R function `anova` with the argument `test` set to “Chisq”). In case of the full-null model comparison resulting significant, we performed a further comparison between the full model with a reduced model lacking the interaction between species and sound as an overall test of the significance of their interaction. In case of the interaction being not significant, we retained the reduced model and assessed the overall significance of species as fixed term by performing a further comparison between the reduced model and the null model, the latter lacking the species but being otherwise identical to the

former. We bootstrapped model estimates using the function `bootMer` of the package `lme4`. With a maximum Variance Inflation Factor (Field, 2005) of 1.181, collinearity (determined for a linear model lacking the interaction and using the function `vif` of the package `car`; version 3.0-10, Fox & Weisberg 2011) appeared to be no issue. The model was not overdispersed (dispersion parameter: 0.913). The stability of the model estimates (i.e., `dfbeta`-values; Field, 2005) appeared to be moderate. The sample for this model comprised a total of 1380 events, in 993 of which the animals exhibited risk assessment responses.

To analyse the inter-specific variability in the fear of human voices (step 1b) we then repeated the whole process using “fear” as response variable of a further GLMM including the same set of predictors described for the previous model. We found no overdispersion issues (dispersion parameter: 0.957) and a moderate stability of estimates also for this model, and its sample of the same 1380 events included 375 events with animals exhibiting at least one of the fear behaviours.

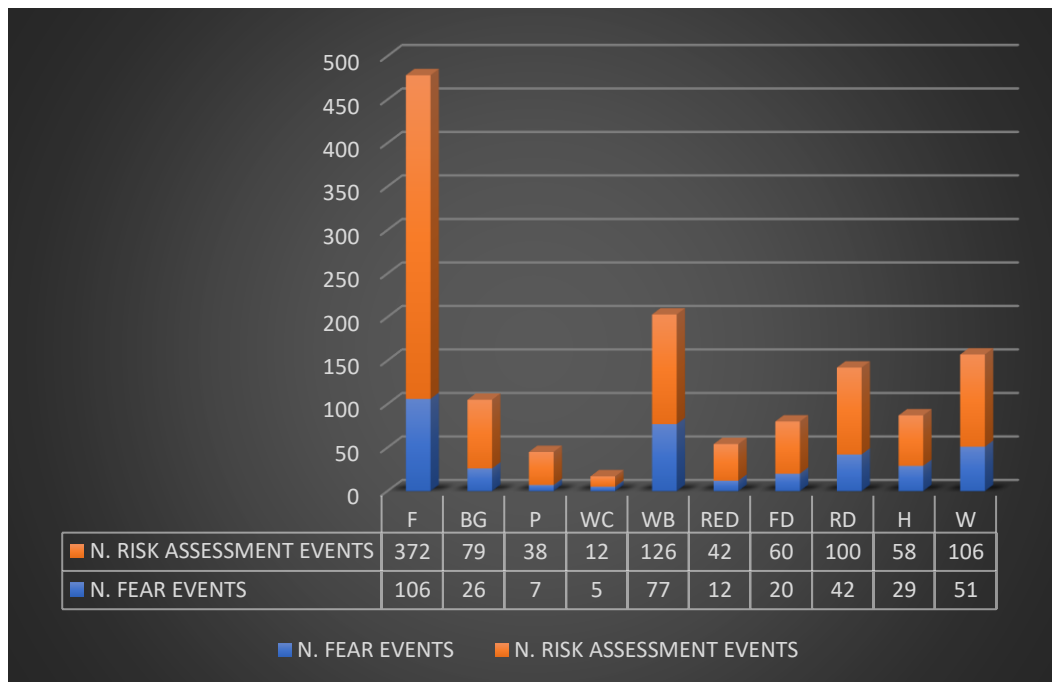
To test the effect of the experienced degree of urbanization on the likelihood of exhibiting risk assessment toward humans (step 2a) we fitted a set of species-specific GLMMs (one for each of the tested species), with a binomial error structure and a logit link function, using “risk assessment” as response variable. We included into the model the sound and the night light index as well as their interaction. We further included the binary predictor “diurnal” to control for a possible increased fear during the day, but only for those species having at least the 20% of diurnal events. Analogously to the previous models, we included the test site as random intercept effect to account for the nested nature of data. We then included the random slopes of sound and, when included in the model, that of diurnal within test sites. Since in this step we were interested about testing the effect of the night light index and its interaction with the sound, we conducted a full-null model comparison, whereby the null model lacked the night light index and the interaction term but was otherwise identical to the full model, including the presence of the sound as fixed term. In case of the full-null model comparison resulting significant, we performed a further comparison between the full model with a reduced model lacking the interaction between the night light index and sound as an overall test of the significance of their interaction. We bootstrapped model estimates using the function `bootMer` of the package `lme4`. We found no issues of collinearity nor of overdispersion, and the stability of estimates were moderate to good for all species. The dispersion parameters, the sample sizes used for these species-specific models, and the number of events with at least a risk assessment behaviour are summarized in Table 3 and Fig. 5.

We then fitted a further set of species-specific GLMMs analogous to those just described but using “fear” as response variable to analyze the effect of the experienced degree of urbanization on the fear of humans (step 2b). See Table 3

and Fig. 5 for a summary of dispersion parameters, sample size and number of fear events for each of the species-specific model.

**Table 3.** Species-specific time threshold for time autocorrelation. The table also contains the number of videos and that of independent events into which they were aggregated (see the text for more details), and the dispersion values of the species-specific models including as response variables either risk assessment or fear. “/” refers to models which could not be run on account to the small sample size.

SPECIES	TIME TRESHOLD	N. VIDEOS	N. EVENTS	RISK ASSESSMENT DISPERSION VALUES	FEAR DISPERSION VALUES
Red fox	2' 30"	593	553	0.947	0.980
European badger	2' 19"	118	110	1.004	0.559
Porcupine	2' 43"	63	54	/	/
European wildcat	2' 0"	17	15	/	/
Wild boar	4' 11"	267	178	1.059	0.918
Red deer	4' 0"	100	50	/	/
Fallow deer	3' 24"	114	72	0.595	1.052
Roe deer	2' 44"	139	127	0.783	0.930
European hare	2' 43"	91	89	1.035	1.059
Wolf	2' 25"	151	133	0.871	0.640
<i>Total</i>		1653	1381		



**Figure 5.** Number (a) of events in which risk assessment (orange) and fear (blue) were exhibited, separately for each tested species. F = red fox, BG = European badger, P = porcupine, WC = European wildcat, WB = wild boar, RED = red deer, FD = fallow deer, RD = roe deer, H = European hare, W = wolf.

## RESULTS

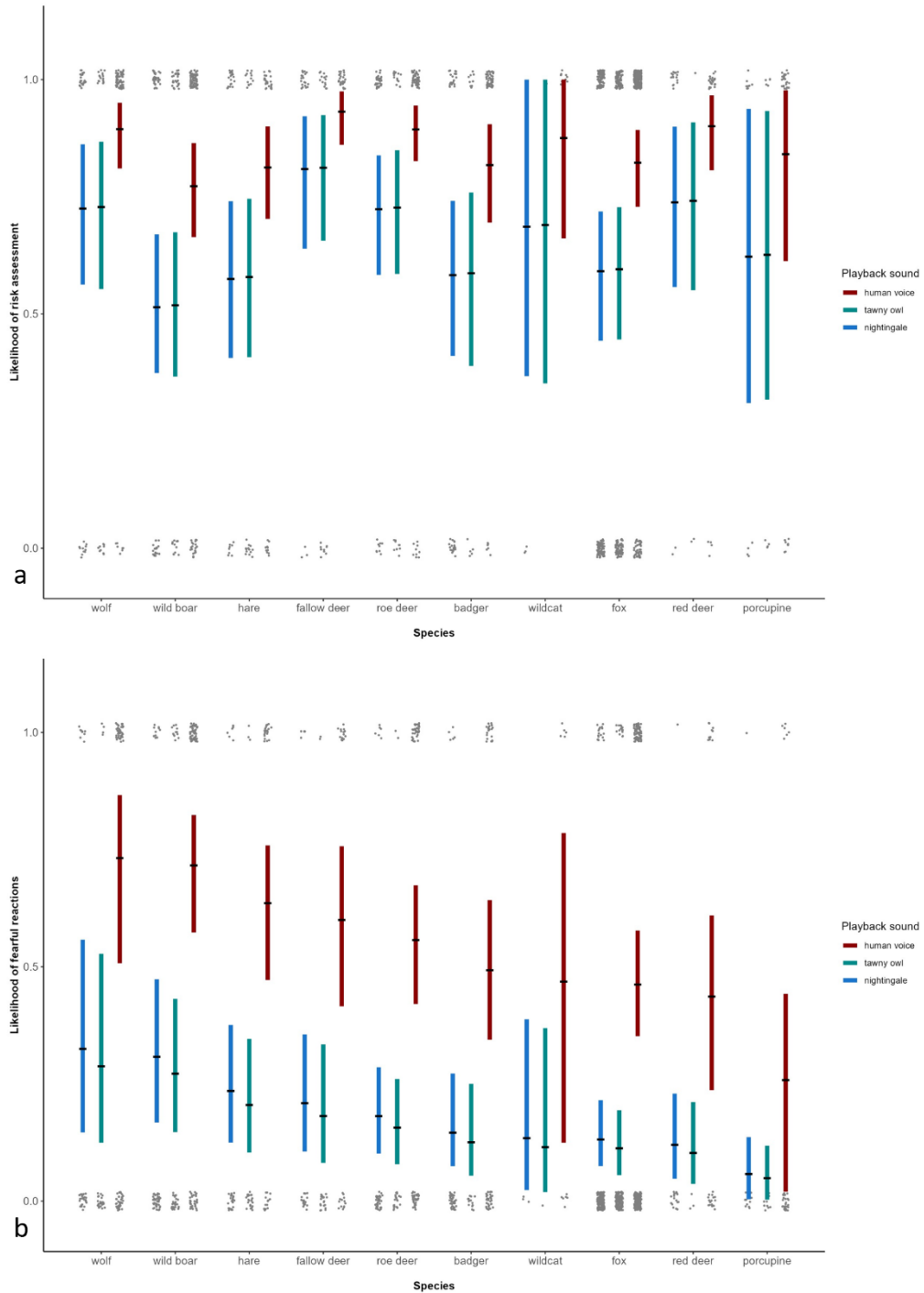
### Behavioural models

Overall, we found that species differed in their likelihood to perform risk assessment behaviour and fear behaviour. The comparison between full model and null model of step 1 resulted in significance for both risk assessment (1a) and fear (1b) ( $p$ -value =  $2.27 \times 10^{-5}$  and  $3.31 \times 10^{-7}$ , respectively). The subsequent comparisons between the full model and the reduced model, lacking the interaction between sound and species, resulted not significant for risk assessment nor for fear ( $p$ -value = 0.092 for risk assessment and 0.884 for fear) revealing a not significant variation of the effect of sound across species. Accordingly, it was retained the reduced model for both fear and risk-assessment, which revealed an overall highly significant effect of species when compared to a model lacking this predictor and being otherwise identical ( $p$ -value =  $8.47 \times 10^{-6}$  and  $1.01 \times 10^{-10}$ , for risk assessment and fear, respectively).

The species with the highest likelihood of performing risk assessment in response to human voice was fallow deer, followed by wolf, red deer, roe deer, porcupine, European wild cat, red fox, European badger and European hare, while the model predicted wild boar to have the lowest likelihood of performing risk assessment (Fig. 6a). Fearful responses were conversely most frequent for wolf and wild boar; followed by European hare, fallow deer, roe deer, European badger, European wildcat, red fox, and red deer. Porcupine was the species for which the model predicted the lowest likelihood to show fearful responses (Fig. 6b).

Moreover, all species were more likely to perform risk assessment and fear behaviour when hearing human voice than control sound. In fact, for both risk assessment and fear, the reduced model showed also significant differences between the control sounds and the reference level (i.e., human voice). In particular, the likelihood of risk assessment was significantly lower when animals heard a tawny owl sound and a nightingale sound ( $p$ -value =  $6.9 \times 10^{-8}$  and  $\beta = -1.17$ ;  $p$ -value =  $6.64 \times 10^{-7}$  and  $\beta = -1.15$ , respectively) as compared to the human voice. Analogously, fearful behaviours were far less likely to be recorded in response to tawny owl and nightingale sounds than to human voices ( $p$ -value =  $3.06 \times 10^{-10}$  and  $\beta = -1.74$ ;  $p$ -value =  $2.65 \times 10^{-11}$  and  $\beta = -1.91$ , respectively).

Finally, the “diurnal” predictor had a not significant effect on the likelihood of risk assessment ( $p$ -value = 0.408 in the reduced model), while it significantly affected the likelihood of fear ( $p$ -value =  $3.85 \times 10^{-4}$ ,  $\beta = 0.641$ ), suggesting a higher likelihood of fearful responses during daytime.



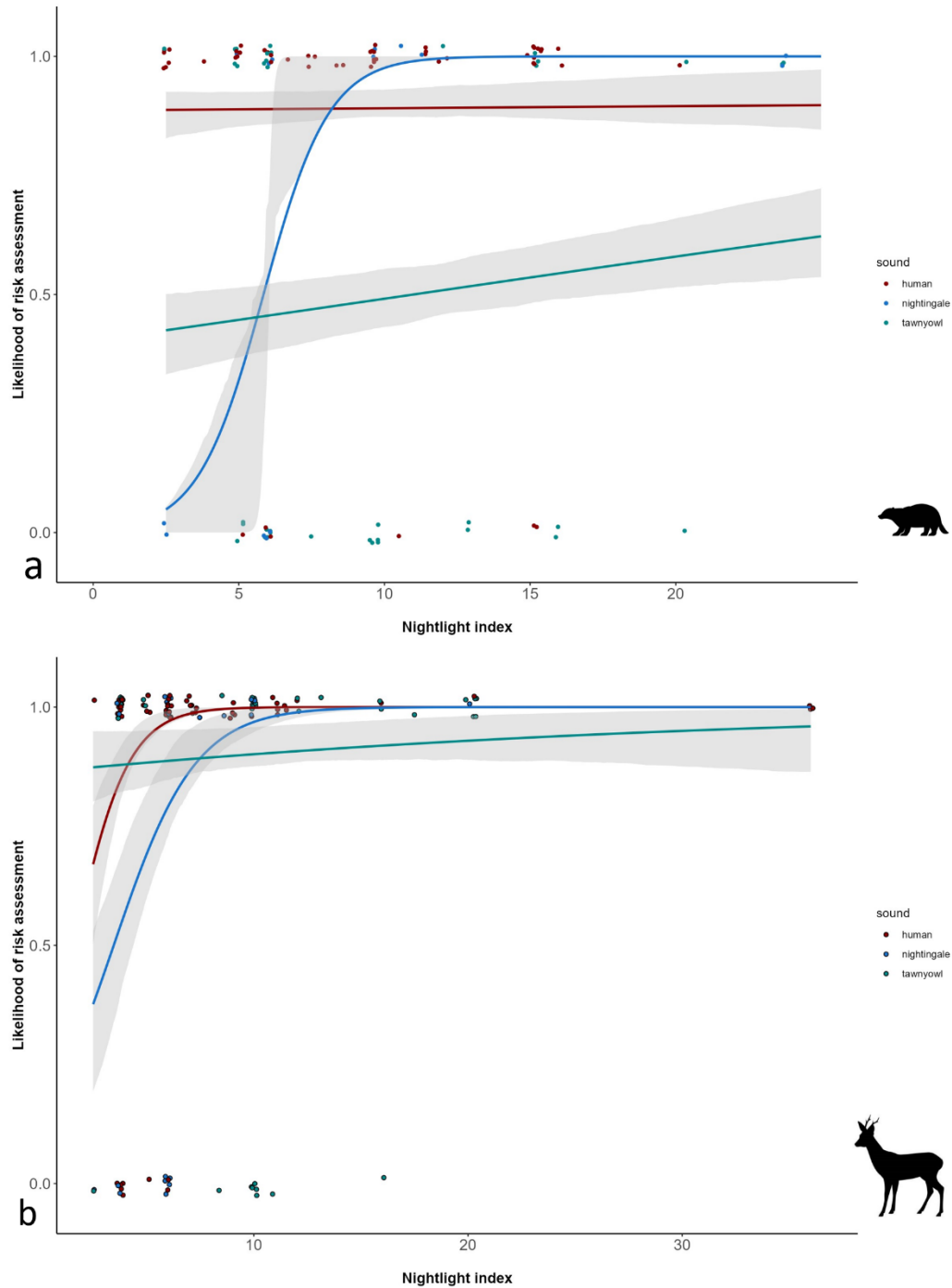
*Figure 6.* Model estimates for the variation of the likelihood of risk assessment (a) and fear (b) across different species and in response to different played sounds. The black segment represents the average likelihood estimated by models for the three sounds, while the coloured vertical bars show the 95% confidence intervals (red for human voices, green for tawny owl sounds, and blue for nightingale sound) obtained with parametric bootstrap (N = 1000 bootstraps). Grey dots represent raw observed data. Vertical and horizontal noise was manually added to raw data to reduce the overlapping of data points, allowing an easier visualization.

### Species-specific models

We could not model the likelihood of exhibiting risk assessment and fear behaviours in European wildcat, red deer, and porcupine because of convergence issues, likely accountable to the limited sample of events recorded for these species (Table 3).

The full-null species-specific model comparison of steps 2a (risk assessment) and 2b (fear) resulted not significant for wolf, wild boar, and European hare, revealing a negligible effect of urbanization on their likelihood of exhibiting risk assessment and fearful behaviours in response to the played sounds.

For the remaining four species (European badger, roe deer, fallow deer and red fox), we detected significant differences accountable to the experienced urbanization, concerning either the likelihood of risk assessment or that of fear. In particular, the full-null model comparison was significant for the risk assessment (step 2a) of European badger and roe deer ( $p$ -value = 0.021 and  $7.23 \times 10^{-4}$ , respectively). The subsequent comparison between the full model and the model lacking the interaction term resulted significant for both species ( $p$ -value = 0.029 for badger and  $p$ -value = 0.008 for roe deer), revealing a significant effect of the interaction term “sound: night light index” on the likelihood of risk assessment. European badgers inhabiting less urbanized areas (i.e., with a lower nightlight index) were most likely to exhibit risk assessment in response to the human voice than to the control sounds (Fig. 7a). At growing urbanization, the likelihood of risk assessment increased for badgers hearing both control sounds (particularly for the nightingale sounds), while it remained mostly stable in response to the human voice. In roe deer, the likelihood of exhibiting risk assessment had an overall increase with urbanization (Fig. 7b). In particular, at low levels of urbanization (nightlight index  $< 5$ ) it was comparable in response to human voice and to tawny owl sound (overlapping confidence interval) but lower in response to nightingale sound. Where the nightlight index was higher than 10, roe deer exhibited risk assessment in virtually all events: about 100% of times when the human voice or nightingale sounds were played, and about 90% of times when hearing the tawny owl.



*Figure 7.* European badger (a) and roe deer (b) likelihood of exhibiting risk assessment along the urbanization gradient (nightlight index, see the text for more details). Red line represents likelihood of risk assessment behaviours in response to human sound, while green line and blue line represent responses to control sounds of tawny owl and nightingale, respectively. Grey-shaded areas represent 50% confidence intervals, obtained with parametric bootstrap (N = 1000 bootstraps). Coloured dots represent raw observed data. Vertical and horizontal noise was manually added to raw data to reduce the overlapping of data points, allowing an easier visualization.

The full – null species-specific model comparison was significant for the likelihood of fearful behaviours (step 2b) of fallow deer and red fox (p-value = 0.015 and 0.036, respectively).

The comparison between the full model and the reduced model lacking the interaction term resulted significant for fallow deer (p-value = 0.005), revealing a significant effect of the interaction term “sound: night light index”, but not for fox (p-value = 0.13), for which the reduced model revealed a significant effect for the nightlight index itself (p-value = 0.029,  $\beta = -0.4061$ ). Fallow deer experiencing a low degree of urbanization were moderately fearful of human voices and tawny owl sounds, but apparently more fearful of nightingale control sound (Figure 8a).

Nonetheless, at growing urbanization the effect of human voices significantly diverged from that of both control sounds, with more urbanized fallow deer fearing virtually all human voices and conversely not exhibiting fearful behaviours toward control sounds anymore.

Conversely, the degree of urbanization had a significantly negative effect on the likelihood of foxes’ fearful behaviours towards any played sound (Figure 8b). This effect was particularly marked for human voices (being feared in about the 40% and 10% of events by rural and urban foxes, respectively), while the likelihood of behaving fearfully in response to the control sounds was low even for foxes inhabiting less urbanized areas.



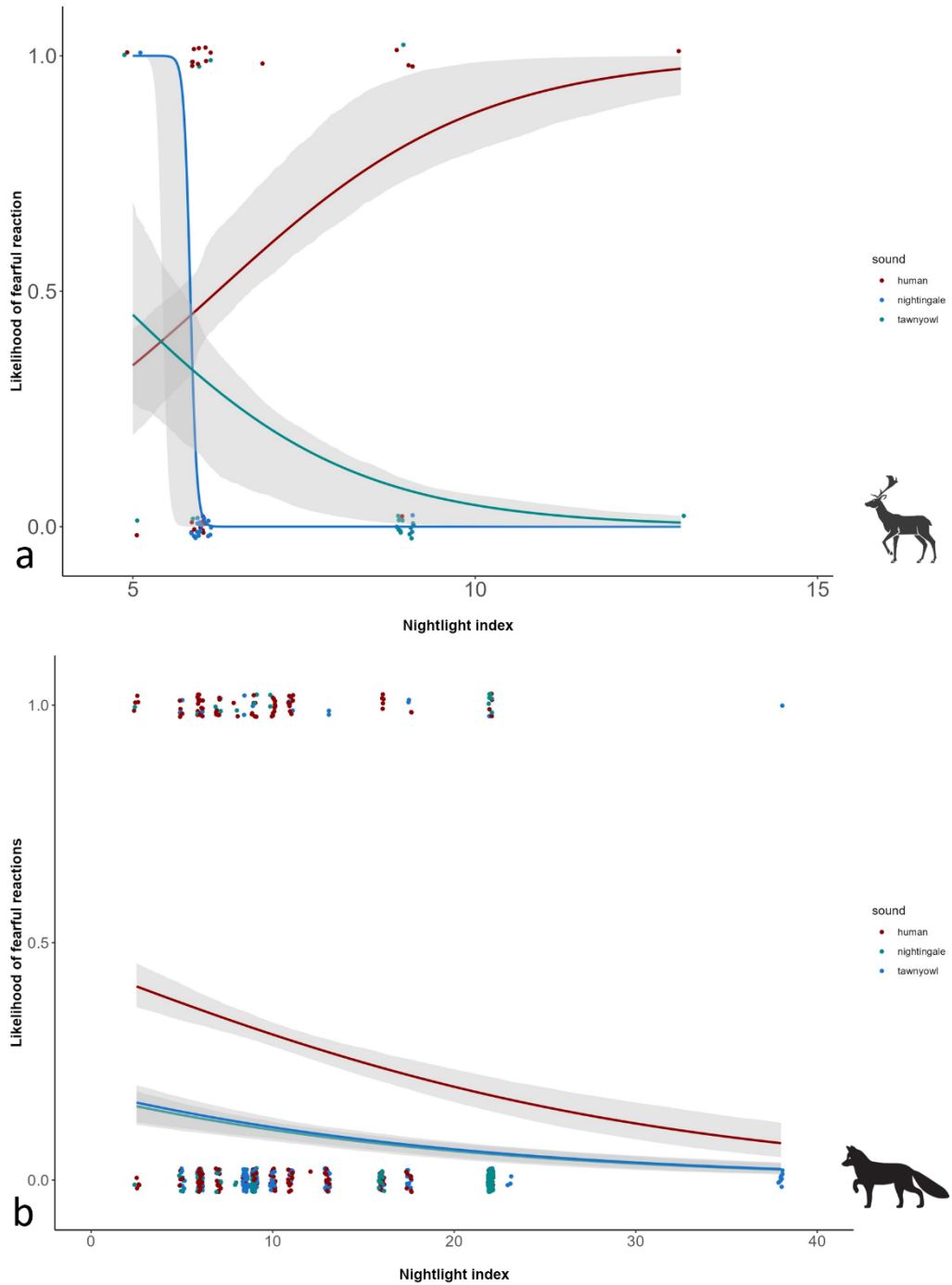


Figure 8. Fallow deer (a) and red fox (b) sensitivity in fearful reactions along the urbanization gradient. Red line represents likelihood of fearful behaviours in response to human sound, while green line and blue line represent likelihood of reactions in response to sounds of tawny owl and nightingale respectively. 50% confidence intervals were obtained with parametric bootstrap (N = 1000 bootstraps). Coloured dots represent raw observed data. Vertical and horizontal noise was manually added to raw data to reduce the overlapping of data points, allowing an easier visualization.

## DISCUSSION

### Inter-species models

The effect of the played sound on the likelihood of risk assessment and fear did not differ across species (the interaction was not significant), implying that the species more frightened by human voice were more frightened also by the two control sounds (tawny owl sound and nightingale sound). The evidence of both tawny owl and nightingale sounds actually triggering some risk assessment and fearful behaviours is likely accountable to these control sounds being played by electronic devices and thus potentially perceived as artificial by animals. Nonetheless, all species exhibited significantly higher levels of risk assessment and fear in response to human voice compared to the control sounds, suggesting that animals were still able to recognize the human voice as the most dangerous stimulus. This validated our experimental approach and highlighted the role of super-predator played by humans in wildlife communities (Clinchy *et al.*, 2016; Crawford *et al.*, 2022).

The study revealed high levels of risk assessment (Fig. 6a) for each study species. As expected, there was a difference in responsiveness among species, but the model predicted a likelihood of exhibiting this behaviour higher than 0.75 in response to human voice for every species. This agrees with previous studies that outlined how over- or under-estimate the risk of human presence may lead to significant costs (Smith *et al.*, 2021). This behavioural category indeed encompassed those behaviours that are necessary to understand whether the sound represented a real threat or not (Stankowich & Blumstein, 2005; Blumstein, 2016), in an attempt to avoid the costs entailed by fearful behaviours (Boissy, 1995; Blumstein, 2020; Brown *et al.*, 1999). Indeed, the results for the behavioural category fear, show significant differences in responsiveness among species but, in this case, the difference in the likelihood of exhibiting fearful behaviours among species were more marked (Fig. 6b). This may be attributed to the fact that this behavioural category included behaviours entailing the animal to move away from the site and/or signalling a state of strong distress, even interrupting vital action like foraging, so the energy expenditure was very high (Boissy, 1995; Blumstein, 2020; Brown *et al.*, 1999). Fearful behaviours were therefore exhibited less frequently, and only by the species that need them the most (Brown *et al.*, 1999).

The species with the highest level of fearful response to human voice was wolf. This result is in line with the role of super-predator played by humans, representing one of the main mortality causes of large carnivores (Darimont *et al.*, 2015), that tend to be heavily impacted by human presence and there were thus forced to alter their ecology in response to it (Smith *et al.*, 2017; Suraci *et al.*, 2019). Indeed, humans represent one of the main causes of wolf mortality in Italy (Musto *et al.*, 2021). Moreover, during the last centuries, wolves have been persecuted by

humans across Europe (Delibes, 1990), reaching the brink of extinction in Italy in the early 1970s with only about a hundred individuals remaining (Zimen & Boitani, 1975). The fact that the wolf exhibits the highest levels of fearful responses may, therefore, be attributed to the historical and ongoing persecution of wolves by humans. On the other hand, this is in contrast with previous study showing that wolf was positively associated with human presence (Suraci *et al.*, 2021). This could be caused by different methods of investigation; indeed, a positive correlation between the species and human presence, investigated using the detection rate of human presence and occupancy model for the target species, might reflect growing intensity in outdoor activity and recreation in undisturbed areas, offering to species with substantial space requirements no choice but to share space with people (Nickel *et al.*, 2020, Suraci *et al.*, 2021). Finally, this inconsistency in results might be caused by different study area. Previous studies were indeed conducted in North America, while we investigated mammals' reactions in Europe, where wild animals have been persecuted by humans for millennia (Sazatornil *et al.*, 2016; Vigne, 2011; Zedrosser *et al.*, 2011) and may, therefore, have developed a stronger fear towards human presence. In comparison to wolves, wild boar and hare exhibit levels of fearful responses that are comparable but slightly lower. This may be explained by the hunting pressure to which these species are subjected to by humans, that can therefore influence their behaviour. Specifically, similarly to wolves, humans appear to be the primary cause of mortality for wild boars in Italy (Merli *et al.*, 2017). This may explain the reason why wild boars are among the species with the highest likelihood of exhibiting fear-related behaviours in response to human presence, second only to wolves.

Deer species showed lower levels of fear to human voice compared to those of wolf, wild boar and hare but the likelihood to perform fearful responses was still above the average for fallow deer and roe deer, that are both heavily hunted species. This aligns with previous studies that showed how ungulates were frightened by human presence (Liu *et al.*, 2023; Crawford *et al.*, 2022; Bhardwaj *et al.*, 2022). Particularly, in Italy roe deer are frightened by humans to the extent of altering their behaviour, even when humans do not pose a direct threat (Grignolio *et al.*, 2011). In this context, the lower fear levels performed by red deer were surprising but may be partially explained by the small sample of sounds we were able to perform on this species (Table 3). European badger, wildcat and red fox showed lower fearful response to human presence with red fox showing the lowest level of fear among the tested carnivores, consistently with Suraci *et al.*, 2021 that outlined that red fox is positively associated with human presence and was the only species to be positively associated even at medium-high levels of human presence. European wildcat showed comparable levels of fearful response with red fox and European badger. However, the notable wide confidence interval obtained for this species require cautions when interpreting this result, suggesting that

more data are needed to better understand the behavioural response of European wildcats to human voice. Porcupine was the species with lowest level of fearful responses to human voice. The fact that porcupine and European badger were both among the species showing the lowest levels of fearful responses may be explained by the fact that in Italy, these mammals are non-huntable species. Moreover, these species are strictly nocturnal (Luzi *et al.*, 2021; Mori *et al.*, 2020), so their strategy for avoiding humans might involve temporarily avoiding them instead of exhibiting fearful behaviours, such as fleeing, when encountering humans. Indeed, the heightened likelihood of fearful behaviours observed during daytime for all species may suggest a higher sensitivity of mammals to disturbance when there is a higher likelihood of meeting people, consistently with the human-induced activity shifts to nocturnal hours observed across mammals (Gaynor *et al.*, 2018).

In accordance with Suraci *et al.*, 2021, this study has demonstrated that there is no relationship between species traits (e.g., body size, diet and reproduction rate) and fear towards human presence. However, our results suggest a connection between the fear of human presence and the historical relationship between humans and species, with those more persecuted (i.e., wolf, wild boar) generally exhibiting higher levels of fear. Moreover, the evidence of wolf and wild boar being the most frightened by humans is in apparent contrast with the successful domestication of their ancestors, since a higher tolerance of the human proximity might have been expected to facilitate the domestication. Since both species are increasingly present in human-dominated landscapes (Zanni *et al.*, 2023, Castillo-Contreras *et al.*, 2021), this contrasting evidence also calls into doubt possible links between a species' average boldness toward humans and its potential to successfully occupy urban areas.

### **Sensitivity along the urbanization gradient**

In contrast with our hypothesis, some study species (wild boar, wolf, and European hare) did not show any change in the sensitivity along the urbanization gradient neither for risk assessment nor for fear. This could be attributed to the fact that the maximum level of urbanization reached by the study sites was approximately 39 in a range of 0-63. This leaves uncertainty about whether species that have not shown any change in sensitivity up to this level of urbanization may conversely do so in even more urbanized areas. However, it can be stated that among this range of urbanization gradient, no change in sensitivity was showed for wild boar, wolf and European hare. This is in contrast with previous studies that outlined how wild boar in more urbanized areas were more tolerant towards human presence (Stillfried *et al.*, 2017b). Moreover, these results showed that even in species already occupying urban environments such as wolf (Blanco & Cortes, 2007; Grilo *et al.*, 2019; Llana *et al.*, 2012; Ahmadi *et al.*, 2014) and wild boar (Cahill *et al.*,

2012; Podgórski *et al.*, 2013; Primi *et al.*, 2016; Stillfried *et al.*, 2017a), urban populations may retain fearful behaviours as well as their rural counterpart, similar to what we found for species that are negatively impacted by human-induced landscape transformation, such as European hare (Edwards *et al.*, 2000; Smith *et al.*, 2005).

On the other hand, European badger, roe deer, fallow deer, and red fox showed a change in sensitivity to the sound along the urbanization gradient. However, these results must be considered cautiously for European badger and fallow deer, due to the sample size and the suboptimal distribution of test sites along the urbanization gradient, skewed toward low to medium values of nightlight index.

Our results showed that, with increasing urbanization, European badger and roe deer exhibited an elevated level of risk assessment in response to all types of sounds, except for those that already had values close to the maximum (Fig. 7). This could be caused by the fact that urban European badgers and urban roe deer could have exercised greater caution due to a higher risk of mortality in more urbanized environments (Wynn-Grant *et al.*, 2018; Shimosuru *et al.*, 2020), inducing them to overreact even to non-lethal stimuli (Smith *et al.*, 2021).

Contrary to our prediction, fallow deer showed higher fearful response to human voice in more urbanized areas (Fig. 8a). This result, combined with the increased levels of risk assessment in urban roe deer in response to human voice, may suggest that deer (e.g. roe deer and fallow deer) could be more sensitive to human disturbance in urbanized areas, due to the increased human presence in these environments (Grimm *et al.*, 2008) showing therefore sensitization instead of habituation (Blumstein, 2016); this is in consistent with a previous study showing that deer in more disturbed areas were more vigilant than individuals living in less disturbed environments (Jayakody *et al.*, 2008). This might be caused by the fact that these populations were more conscious of the risk associated with human presence in more urbanized areas. A heightened sensitivity to human presence may indeed help wild animals to reduce the likelihood of a dangerous encounter with humans (Blumstein, 2016), that represents a super-predator for ungulates (Darimont *et al.*, 2015).

On the contrary, in line with our prediction, fox showed a reduced sensitivity in response to the sounds in more urbanized area along the urbanization gradient (Fig. 8b) demonstrating habituation to human presence in urbanized areas. The higher boldness of “urban foxes” likely enabled them to prevent costly overreactions to not dangerous stimuli (Rankin *et al.*, 2009; Blumstein, 2016) leveraging the advantages offered by urbanized environments, such as increased food resources (Chamberlain *et al.*, 2009). Indeed, foxes frequently use anthropogenic food (Baker *et al.*, 2000; Contesse *et al.*, 2004) and actively colonize urban areas (Macdonald & Newdick, 1982; Harris & Rayner, 1986; Wilkinson & Smith, 2001, Bateman & Fleming, 2012), demonstrating great proficiency in

inhabiting these environments. Therefore, the result obtained for foxes is in line with previous work that outlined how animals inhabiting urbanized areas exhibit reduced fear towards humans (Sol *et al.*, 2013; Ritzel & Gallo, 2020).

Our results shed light on the great complexity of the possible behavioural response that different species and populations may develop to coexist with humans, focusing on the proximate effects of the human disturbance on their behaviour. We detected very different attitudes towards human voices across mammal species, surprisingly observing the highest fear levels in species such as wolf and wild boar which are increasingly occupying urban areas. We also showed that urban populations of mammals may exhibit unpredictable changes in sensitivity toward human presence in comparison with their rural counterparts, including habituation, sensitization, or no differences at all (Blumstein, 2016). With a human presence globally increasing, deepening our comprehension of the behavioural mechanisms underlying animal responses to humans is of utmost importance to enhance wildlife conservation strategies and promote coexistence with humans.

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