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Nightlife challenges: how urban intensity, noise and artificial light can shape the distribution of a nocturnal predator

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1. INTRODUCTION

Urbanisation, together with intensive agricultural practices, is the most severe human-induced environmental change of the 21st century. It is generally the process by which human settlements grow and expand, with higher percentages of people coming to live in the city, often moving away from rural areas (Gaston 2010). As we move forward, the global population will keep growing, with towns and cities constantly expanding in parallel to the demographic increase. At present, almost 55 % of the world's 7.7 billion population lives in urbanised areas (United Nations 2019a, b). According to the most recent UN projections, the overall growth of the world's population combined with the urban land-cover increase could bring the global population to 8.5 billion by 2030 and 9.7 billion by 2050 (with c. 90 % of the increase condensed in Asia and Africa), if the growth pace will not slow down (United Nations 2019b). These increments in terms of people and urban areas present complex challenges for the cities of the future.

As a global phenomenon, urbanisation is one of the most critical alterations for natural ecosystems, being a significant threat to their functioning and biodiversity (Foley *et al*. 2005, McKinney 2008, Aronson *et al*. 2014). The main impact of urban development is associated with habitats loss, fragmentation and degradation (Mcdonald *et al*. 2008, Sushinsky *et al.* 2013), which determines the most direct and drastic decline of biodiversity due to the physical removal of habitats in order to create space destinated to buildings and artificial infrastructures. The increment of urban land-use often leads to other sources of disturbance for the wildlife that survives in urban areas, like an increase in air pollution (Herrera-Dueñas *et al.* 2014), anthropogenic noise intensity (Proppe *et al.* 2013, Fröhlich & Ciach 2019), roadkills (Coffin 2007, Grilo *et al*. 2020), the impact of artificial light at night (Molenaar & Sanders 2006, Van Doren *et al*. 2017) and replacement of lost native species with exotic ones, leading to a biological homogenization that alters and reduce the biological uniqueness of local ecosystems (Blair 2001, Gaertner *et al.* 2017). These effects contribute to debilitating ecological processes across urbanized landscapes. Therefore, the need to reconcile urban development with biodiversity conservation is more essential than ever. The improvement of strategies aimed at finding a trade-off between the increase of built-up areas and the need to preserve nature in cities is important to enhance the quality of life. Indeed, over the last years, it was recognized as a goal by the United Nations, in the perspective of a sustainable future (United Nations 2016).

This has led to the question about how we should manage urban development in a region, finding its best spatial arrangement maximising native biodiversity within (Soga *et al.* 2014). In a nutshell, two strategies have been identified. One implies a separation between urban and natural areas, dedicating some lands to intensive urban uses, with some spared for biodiversity only (Lin & Fuller 2013, Soga *et al.* 2014). The other emphasises the sharing of land between built-up areas and nature, mixing low-density urban areas with green spaces (Lin & Fuller 2013, Soga *et al.* 2014). These alternatives derive from a framework known as land-sparing and land-sharing (hereafter LSAS), conceptualised to sustain biodiversity in human-modified landscapes (Green *et al.* 2005, Lin & Fuller 2013). Though, it was originally born not for urbanised settings, but in relation to agricultural systems, with the purpose to identify a trade-off between food production and biodiversity conservation (Green *et al.* 2005).

Hereafter, (i) the development of the LSAS framework will be briefly reviewed, highlighting the passage and connection between agricultural and urban systems, and (ii) the case study object of this dissertation will be presented.

1.1. Land-sparing and land-sharing: from agricultural to urban systems

The ideas of land-sparing and land-sharing developed in the early 2000s, when a lively discussion started about how to best ensure food supply reducing the impact of agricultural production on biodiversity. In other words, the question was in terms of what strategies could be developed to meet the global increasing demand for food at the least cost to native biodiversity (Green *et al*. 2005, Phalan *et al*. 2011). Today, agricultural fields occupy at least c. 40 % of the terrestrial land around the world (Foley *et al.* 2011). Over the last decades, they expanded to increase crop productivity per unit of land, causing conflicts with nature conservation goals. The intensification of agricultural systems can alter the environment if not managed efficiently, leading to biodiversity decline and ecosystem services alteration (e.g. excessive loss of natural habitats and species richness, pollination and pest control) (Green *et al*. 2005, Stott *et al*. 2015). In this perspective, the LSAS framework has been presented as a possible solution. On one hand, land-sparing idealises a net separation between intensive agricultural lands and natural areas across a region, i.e. agricultural lands are designated only for production and they are used intensively (high-yield farming), but with some parts being totally spared for biodiversity conservation only (Green *et al*. 2005, Phalan *et al*. 2011). Since farmland is high-yield, in a given region fewer units of land are needed to maximise productivity and achieve a given level of food output. This allows more non-farmed units to be spared for nature conservation, having high value for wildlife. For example, such a strategy can be fulfilled with the creation of natural parks and reserves, delimitated in the territory and legally protected, aimed at preserving biodiversity from human pressures (Michael *et al*. 2016). On the other hand, land-sharing implies integrating natural areas in agricultural lands across a region, i.e. agricultural lands are not only designated for food production, but they share some natural spaces destined for wildlife conservation. In this case, in a given region, farmland acquires a higher wildlife value, but, compared to land-sparing, to achieve the same level of food output more units of farmland are needed and fewer are available only for biodiversity. This approach is also called 'wildlife-friendly farming' (Green *et al*. 2005, Phalan *et al*. 2011). This strategy found application in the agri-environmental schemes of the European Union and Australia, aimed at making farmland more sustainable, reducing the negative effects of intensive agriculture on wildlife and ecosystem services (Michael *et al*. 2016, Renwick & Schellhorn 2016). However, the LSAS paradigm represents the extreme endpoints of a continuum. It means that this is not a static dichotomy, but intermediate options are also possible. Sometimes, mixed strategies combining both high-yield and low-yield farming with natural habitats may be better alternatives for wildlife conservation rather than choosing either land-sparing or land-sharing (Finch *et al*. 2019). It could be advantageous having an area spared for conservation, surrounded by some low-yield farmland (which may act as a transition zone) alongside a smaller high-yield agricultural land (Fraanje 2018).

Nevertheless, an increase in food demand is only one side of the coin. Another consequence of the demographic increase is the expansion of towns and cities, as an increasing urban population needs more space to live and settle. Achieving this with the minimal impact on local biodiversity and ecosystem services is challenging and the LSAS framework suits well to this situation (Lin & Fuller 2013). Similar to agricultural intensification, urbanisation causes the reduction of natural habitats and the alteration of ecological integrity in a given landscape (McKinney 2002, Nelson *et al.* 2009), posing the same problems in terms of biodiversity conservation. In urban systems, a land-sparing scenario involves compact cities in the form of high-density built-up areas, with few large green areas in which biodiversity is condensed, often represented by large parks and nature reserves or smaller ones with elements of contiguity (Soga *et al.* 2014, Stott *et al*. 2015). This urban design can be found in big European and Japanese cities (Stott *et al*. 2015) (**Figure 1**). Under a land-sharing scenario, cities are in the form of low-density built-up areas interspersed with green spaces such as hedgerows, tree rows, large household gardens and parks (Stott *et al.* 2015). In this case, biodiversity is more distributed across the entire urban area, but in a series of many smaller and fragmented green spaces (Soga *et al*. 2014). This scheme can be found in the suburbs and districts of some Australian, European and American cities (Stott *et al*. 2015) (**Figure 2**). With growing recognition of the importance of biodiversity for human health in cities (Brown & Grant 2005, Sandifer *et al*. 2015), understanding how these different land management approaches affect urban biodiversity in relation to urban intensity is of key importance. The LSAS framework can therefore provide valid insights to inform environmentally-friendly planning for creating and renewing cities.

Figure 1. Example of land-sparing approach applied in a district of Tokyo (Japan). Photo adapted from appliedecologistsblog.com and provided by Masa Soga.

Figure 2. Example of land-sharing approach applied in a district of Ratingen (Germany). Photo adapted from Google Images.

LSAS studies generally illustrate curves that help to visualise whether species would be most benefited under land-sparing or land-sharing, along a gradient of urban intensity. First of all, species are usually labelled as ‘winners’ and ‘losers’. The former are described by an increasing curve, as an increment in urban cover increases species presence or density (Stott *et al*. 2015). The latter are described by a decreasing curve, as an increment in urban cover results in a decline of species presence or density (Stott *et al*. 2015) (**Figure 3**). Whether then species prefer land-sparing or land-sharing can be expressed by their degree of tolerance along the gradient. Land-sparing is better when species are totally maximised at low (losers) and high (winners) levels of urban intensity, while land-sharing is better when they manifest a consistent decrease (losers) and increase (winners) only at high levels of urban intensity, showing a more tolerant relationship along the gradient as the natural habitat changes (Stott *et al*. 2015) (**Figure 3**). These concepts are equally applicable to agricultural systems, for which the gradient is typically represented by the yield (Green *et al*. 2005).

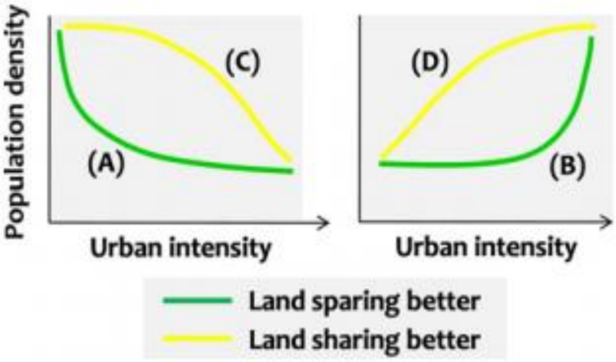

Figure 3. Examples of curves that show the relationship between urban intensity and species’ population density. Curve (A) and (C) indicate a ‘loser’ species, while (B) and (D) a ‘winner’ species. Land-sparing is better when species density decreases strongly at low levels of urban intensity (green curve A) and when increases at high levels of urban intensity (green curve B). Land-sharing is better when species density decreases at high urban intensity levels (yellow curve C) and when increases at low levels of urban intensity (yellow curve D). Picture adapted from Soga *et al.* 2014.

Most empirical LSAS studies used birds as a measure of biodiversity (Hulme *et al.* 2013, Geschke *et al*. 2018, Finch *et al.* 2019, Ibáñez-Álamo *et al.* 2020). Fewer studies focussed on other taxa; some examples concerned plants (Collas *et al*. 2017), reptiles (Rotem & Ziv 2016), ground beetles and butterflies (Soga *et al*. 2014). Bird species have been largely used as they are excellent environmental indicators, able to indicate the health status of ecosystems. Their distribution and population trends often reflect those of other species (Şekercioğlu 2006). Widespread around the world, they can be found in almost every habitat, representing key components of ecosystems; they are mobile, sensitive and responsive to habitat changes (Gregory *et al*. 2003, Şekercioğlu 2006). Alterations in bird populations and distribution can provide useful indications of environmental issues, as they usually occupy high trophic levels in food webs (Gregory *et al.* 2003, Şekercioğlu 2006).

1.2. Owls in urban areas: how can they thrive?

While these studies primarily involved diurnal birds, the response of nocturnal species has not been investigated well. This is probably due to their nocturnal and cryptic habits, accompanied by their general low detectability (Isaac *et al*. 2013), which could make surveys more challenging. Moreover, surveys during night hours sometimes could not be easy for access restrictions to some areas, especially in urban settings.

Owls (Strigiformes) are likely the most common group of nocturnal birds (Mikkola 2019). Being exceptional predators often at the at the highest trophic level of their food web, they have a significant influence on terrestrial ecosystems quality and equilibrium (Isaac *et al*. 2013). They primarily help to manage other animal species (often small mammals) by controlling their population sizes within an ecosystem (Paz 2013, Saufi *et al*. 2020). Therefore, some owls can be a great benefit to places where rodent populations are high. Dense urban areas usually suffer from an abundance of rats and mice spreading diseases, and rural communities have their crops consumed, soil eroded by burrowing voles and field mice with yield reduced by their grazing effect (Brown *et al*. 2007). Without their natural predators, such as owls, rodent pest populations could explode, reaching excessive numbers. Owls have been proved to be good biological control agents as they can limit the amount of these pests, increasing environmental quality in urban and rural areas (Labuschagne *et al*. 2016, Saufi *et al*. 2020). Besides, given their trophic role, they have high bioaccumulation capabilities (Dal Pizzol *et al*. 2020). Owls can be used to assess environmental pollution, checking the levels of contaminants present in the environment. Their feathers and pellets can indeed be employed to detect and quantify chemical compounds (Ansara-Ross *et al*. 2013, Dal Pizzol *et al*. 2020).

Therefore, a stronger presence of owls in urban landscapes may favour the natural control of rodents (e.g. in parks, green spaces and near water bodies), replacing the large use of traps and rodenticides. It may also add naturalistic value in human-modified environments, as owls are typically unusual to people sight. They generally rest in daylight hidden in tree foliage and they hunt during the night (Mikkola 2019). In general, the ability of owls to deal with urban environments has been shown to depend on the availability of space and habitats for nesting and foraging to survive (Fischer *et al.* 2015, Poppleton 2016). Understanding what spatial arrangement suits well to owls in these contexts can provide useful inputs to achieve this goal. Though, to have a more exhaustive overview, relevant factors occurring in urban areas that might affect owls should be considered.

Being predators that largely rely on hearing and moving at night, their presence in urban settings could also be influenced by anthropogenic noise and artificial light at night (ALAN), two common pollutants that accompanied the urban development over the years (Hölker *et al*. 2010, Gaston *et al*. 2013, Manzanares Mena & Macías Garcia 2018). Since most owls use hearing to locate preys, high levels of noise (e.g. road traffic) can reduce their hunting ability, with negative repercussions on their fitness and potential disappearance from such areas (Delaney *et al*. 1999, Fröhlich & Ciach 2018). Excessive noise may also interfere with territory establishment and defence, discouraging owls to colonize places in that condition. This is due to higher energy costs because a more consistent and frequent vocal activity would be required as calls would be hampered by high noise levels (Nemeth *et al*. 2013). On the other hand, natural light (i.e. sunlight) is crucial for birds, as it provides a direct stimulus to regulate circadian rhythms, which in turn control their physiological and behavioural processes (Dominoni 2015). Since light is so important, excessive artificial light at night can disrupt this natural regulation and affect such processes, leading to alterations in ecological functions like predation, singing and migration (Da Silva & Kempenaers 2017, Van Doren *et al*. 2017, Dominoni & Nelson 2018). Thanks to their anatomical and physiological eye adaptations, owls have evolved to hunt efficiently in nearly total darkness, while they generally hide during the daylight (Mikkola 2019). Therefore, ALAN might interfere with this natural rhythm and weaken their visual sensitivity, consequently reducing their hunting success. Brighter conditions could make them lose a great advantage over preys (especially small mammals), as they might notice the predator in great advance or be generally more eased to escape.

Assessing what spatial allocation should be better to help owls thriving in urban landscapes and whether anthropogenic noise and ALAN can affect their presence are the key questions of this research, and the Tawny Owl *Strix aluco* has been taken as model species. Widely distributed throughout most of Europe, the Tawny Owl is one of the most common owls of the continent (Mikkola 2019). Mainly a woodland species, it can be found in urban contexts, on condition that it can find suitable habitat requirements to breed, such as nest sites (Solonen & Ursin 2008, Mikkola 2019). These reasons make this owl a good model species. If well managed and friendly-environmentally designed, urban areas might represent important ecosystems, in which the species could establish, without abandoning them in a second moment. Thanks to its wide distribution, the species presence could be improved in many urban settings across Europe.

From this perspective, the Tawny Owl was surveyed along an urban gradient to evaluate:

(i) How it responds to urban intensification, i.e. whether land-sparing or land-sharing will most benefit the species in urban landscapes

(ii) Whether anthropogenic noise and ALAN can affect its presence probability

2. MATERIALS AND METHODS

2.1. Study species

The (Eurasian) Tawny Owl (*Strix aluco* Linnaeus, 1758) is a medium-sized owl that primarily inhabits broad-leaved, deciduous and mixed woodland habitats, often close to rivers and clearings; it may also be found in urban parks, gardens and open tracts of farmland (Mikkola 2019). The Tawny Owl is easy to recognise for some morphological peculiarities: it is a round-headed owl with a complete facial disc, large dark eyes and without ear tufts (Mastrorilli 2018, Mikkola 2019) (**Figure 4**). It may be observed in three different colour morphs (brown, grey and rufous) with also intermediates (Mikkola 2019), and they depend on genetic traits (feather colour is hereditary) and climate (Karell *et al.* 2011).

Adult males and females are very similar in appearance, but they differ in size with females heavier than males (M 315-550 g, F 410-650 g; Mastrorilli 2018, Mikkola 2019). In the field, sexes can be easily distinguished by their calls. Male territorial hoot is a drawn-out '*hoòo*', followed by a brief pause, before a softer '*hu*' and then a by a final tremulous '*huhuhuhooo*' (Mikkola 2019).

Figure 4. Tawny Owl sitting on a tree branch. Photo adapted from BTO (British Trust of Ornithology) website.

Females instead are characterized by a loud '*ke-wick*' contact call (Southern 1970, Mikkola 2019). Once established, Tawny Owls pairs remain on the breeding territories throughout the year and are highly territorial.

A resident couple will often vocally duet to defend its territory, with the male hooting and the female dropping her contact call into the pauses between bouts of hooting. This defensive behaviour may also be reinforced by visual displays (Southern 1970). Territorial activity increases in autumn, when courtship begins and young owls look for mates and seek to establish their own territories, while adults defend theirs in readiness for the spring breeding season (Southern 1970, Zuberogoitia & Martìnez 2000). The species form monogamous pairs and requires suitable tree cavities to breed. In their absence, other natural sites including crow nests, holes in buildings and nest boxes can be used (Cramp 1985, Mikkola 2019). First eggs are normally laid at the end of winter, between February and March, and the hatching is asynchronous. Tawny Owls can scarcely be seen in daylight, when they roost in dense foliage, tree trunk or even sometimes in old buildings and sheds (Cramp 1985, Mikkola 2019). Tawny Owls are sedentary, with immature individuals dispersing only a few kilometres away (Cramp 1985). Tawny Owl feeds predominantly on a great variety of small mammals (rodents such as field mice and voles) but its diet can also include birds, amphibians, reptiles and fishes; in flight this owl can even seize bats and insects (Zawadzka & Zawadzki 2007, Grzędzicka *et al*. 2013, Mikkola 2019). It mainly hunts using perches, from which they guard the territory looking for preys (Mastrorilli 2018, Mikkola 2019).

2.2. Study area

The study was carried out in the urban and suburban area of Turin, Piedmont (45°04’13.2’’N, 7°41’12.7’’E, northwest Italy). Turin is the capital city and the most populated of the Piedmont Region, with 851240 residents (resident population in 2020, according to ISTAT). However, the Turin metropolitan area (an urban agglomeration including the municipality of Turin as well as other 53 municipalities due to their urban proximity) has a population of almost 2 million people. The city is located along the Po river and it is surrounded by the Alps on the northern and western side and by a hill on the eastern side. The climate is moderately continental with cold and dry winters, while summers are humid and hot.

In order to sample the Tawny Owl, playback surveys were conducted along an urban gradient. Semi-natural areas (i.e. areas with urban cover equal to zero) were represented by some protected areas of the Regional Natural Park ‘Aree protette del Po Piemontese’, particularly the ‘Parco Naturale della Collina di Superga’, 'Riserva Naturale del Meisino e dell’Isolone di Bertolla’ and ‘Riserva Narturale Arrivore e Colletta’. A minor part of urbanised areas was represented by these reserves, while the majority was represented by areas with different levels of urban cover across the Turin hills (**Figure 5**). The Superga Park is a large broad-leaved woodland area mainly dominated by oaks-hornbeams (*Quercus* and *Carpinus* species) and chestnut trees (*Castanea sativa*), with the presence of some conifer and black locust (*Robinia pseudoacacia*) formations. Contrary, the other two natural reserves are mostly defined by riparian formations of poplar and willow trees (*Populus nigra* and

Salix alba), given the proximity to the river. The hills are characterized by the same vegetation formations as those of the Superga Park, but with a greater prevalence of black locusts and exotic conifers, that replaced the oaks over the years.

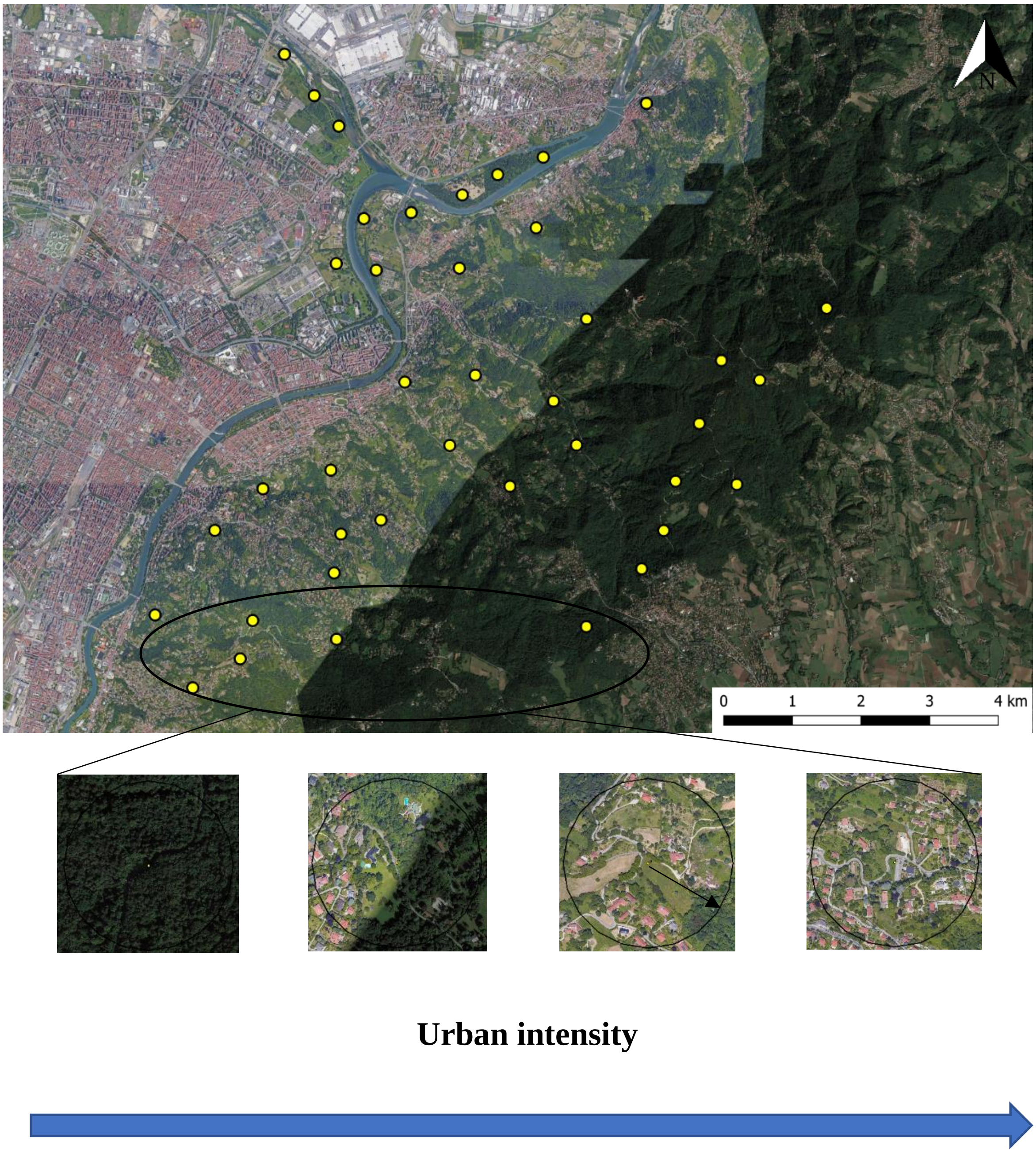

Figure 5. Study area in the urban matrix of Turin with sample points (n = 40). To give an example of the variation in urban intensity (buildings and roads network), four sample points within the ellipse on the main panel are presented in detail in the four panels below. The black arrow indicates the 200 m detectability radius, set as a threshold for playback and the analysis, on the basis of a field test conducted prior to the survey. Satellite image adapted from Google Earth.

2.3. Study design and field survey

To evaluate Tawny Owl response to urbanisation, 40 sample points placed in the urban matrix of Turin (**Figure 5**) were surveyed using the playback technique, commonly employed to survey elusive birds, as it improves their detection probability (Hardy & Morrison 2000, Navarro *et al*. 2005, Worthington-Hill & Conway 2017). This method consists of broadcasting conspecific recorded calls in order to elicit their vocal reply (Johnson *et al.* 1981, Worthington-Hill & Conway 2017). This is effective and particularly useful for those species, like owls, that exhibit territorial behaviour because they will be more inclined to respond to defend their territories (Haug & Didiuk 1993, Pilla *et al*. 2018).

Sample points were randomly selected using Quantum GIS Software (v. 3.4.5, QGIS 2020). First, the study area was divided into a grid of 1 km x 1 km squared plots and 40 of them were selected at random. In the next step, from a multitude of points, one was selected randomly in each of these plots. Selected points were then appropriately relocated close to their "a priori" spatial designation when they were in inaccessible places (e.g. in private streets, in front of houses and in the middle of the wood). When possible, sample points were relocated along the roads, in order to define transects aimed at optimising the movements in the field. This operation was also conducted using QGIS.

Sample points were surveyed twice within the courtship season (i.e. two visits for each point), from the 21st of September to the 10th of November 2020. At least two weeks passed between consecutive visits at the same point. In addition to the breeding season, autumn is the best period to survey the Tawny Owl, as it has a peak in vocal activity for seeking mates and defends territories (Southern 1970, Zuberogoitia & Martìnez 2000).

Playback was delivered using a handheld Bluetooth wireless speaker (Tronsmart Element, T6 Mini) positioned at chest height (Pilla *et al.* 2018), c. 1.6 m above the ground. The device was designed to spread sound at 360° to ensure that vocalisations were broadcast in all directions. The call sequence consisted of territorial vocalisations of two different Tawny Owls couples (both male and female calls), downloaded from the Xeno-canto website (www.xeno-canto.org), which were then uploaded to a smartphone and broadcast with the speaker via Bluetooth. Recordings of multiple pairs were used (i) to simulate a greater species density in order to increase the probability of a reply, as owls will be more inclined to respond to defend their territories against many competitors nearby, and (ii) to avoid that the same recording led to addiction. A fixed broadcast volume was set at a level equivalent to the sound pressure level of natural vocalizations. A sound level meter (SLM Meterk MK 09) was used to adjust the volume to match the species natural levels, so 82 ± 3 dB (Vrezec & Bertoncelj 2018). Such values were obtained positioning the SLM at a distance of 1 m. At each sample point, the playback session lasted 13 minutes and it was structured as follows:

- 2’ of passive listening
- 2’ of playback (1st couple broadcast)
- 2’ of passive listening
- 2’ of playback (2nd couple broadcast)
- 5’ of passive listening

Playback was stopped as soon as an owl responded.

Surveys were performed in good weather conditions, i.e. not on rainy or windy days, as these factors have been proved to significantly reduce owls’ response and the ability of surveyor to hear them (Braga *et al.* 2009, Johnson *et al.* 2009, Zuberogoitia *et al.* 2019). Moreover, they were carried out five minutes after sunset and lasted generally one hour and a half, depending on the time spent moving in the field between sample points and on how many were surveyed on the same night (1 to 3 points/night).

2.4. Playback field trial prior to the survey

A field test prior to this study was conducted to decide which detectability radius consider for the playback survey and the following inference in the analysis. This experiment was conducted in farmland and woodlands areas (to evaluate both open and closed habitats) within an agricultural landscape for five nocturnal birds, including the Tawny Owl. By broadcasting their calls from different random locations, the effect of distance on surveyor detection capability was evaluated and compared in both habitats, and also between seasons only in woodland. The full results are presented in Appendix B, but a summary is given here.

In each habitat, one transect was established with ten points, spaced 200 m apart, and each point was visited eight times (i.e. eight repetitions). At each repetition, one researcher (the ‘broadcaster’) moved in a random location around one single surveyor (the ‘observer’) and broadcast species calls. The surveyor stayed fixed at each point, noting the time and species when a call was detected and he also estimated playback distances (assigning calls to distance classes of between 0-100 m, 100-200 m, 200-300 m, 300-400 m, 400-500 m and >500 m). At each repetition, the surveyor did not know the location of the broadcaster. A handheld GPS (Garmin eTrex 10) was used to identify survey points and to note the location of each playback made by the broadcaster. One survey was conducted in farmland and one in woodland in winter (between the end of February and the beginning of March 2020); then a third survey was repeated only in woodland in summer (mid-July 2020) to test for a seasonal effect in this habitat. Surveys were performed in good weather conditions (i.e. not on rainy or windy days) and in daylight, partly due to access restrictions, but also to minimise the potential confounding effects of real (rather than recorded) vocalizations. Playback was delivered using a handheld Bluetooth wireless speaker positioned at chest height, c. 1.6 m above the ground. The device was designed to spread sound at 360° to ensure that vocalisations were broadcast in all directions. After all species calls were broadcast, the broadcaster moved to another random location unknown to the surveyor and repeated it. This procedure was carried out eight times for each point (i.e. eight repetitions made in eight random locations for each of the ten points). The start and end of each repetition were notified to the surveyor by text message. Once all the repetitions for a point were completed, the surveyor moved to the next point along the transect. Broadcast calls were adjusted with a sound level meter at a volume equivalent to the sound pressure level of natural vocalizations, to match realistic conditions.

To evaluate the effect of distance on detection probability, binomial generalized linear mixed models (GLMMs) were fitted to the ability to hear playback calls (1 = calls heard, 0 = calls not heard) specified as the response variable. Distances, habitat and species were specified as fixed effects, while survey point identity was specified as a random effect in order to account for repeated observations from the same point. To test for a seasonal effect in woodland, season variable was included, also specifying an interaction term with distance. Garmin BaseCamp software was used to download location data from the GPS and to calculate real distances between the surveyor and broadcaster.

In the light of the results, 1200 broadcasts were carried out in total: 400 in farmland (first survey) and 400 in woodland (second survey) in winter, and 400 in woodland in summer (third survey). Almost 78 % of the broadcast calls were detected. The ability to hear playback calls declined with distance in both habitats ($p < 0.001$) and detection probabilities were higher in woodland than farmland ($p < 0.001$). In woodland, the probability of hearing calls was significantly higher in winter ($p < 0.05$), likely due to the fact that in summer trees foliage hampers sound diffusion, and therefore the ability to hear bird calls. Though, the effect of distance on the ability to hear playback calls did not change between seasons (p > 0.05), i.e. no difference in slope between winter and summer was found. As for the Tawny Owl, the probability of hearing its calls was generally high at a distance of 200 m (96 % in woodland and 80 % in farmland) (**Figure 6**), while it dropped at 300 m by almost 30 % in woodland and 55 % in farmland. Within woodland, detection probabilities dropped by almost 20 % at 200 m and 35 % at 300 in summer (**Figure 6**).

Thus, a 200 m detectability radius was identified and set as maximum threshold for the Tawny Owl field survey, as most of the detected calls registered during the experiment were within this distance.

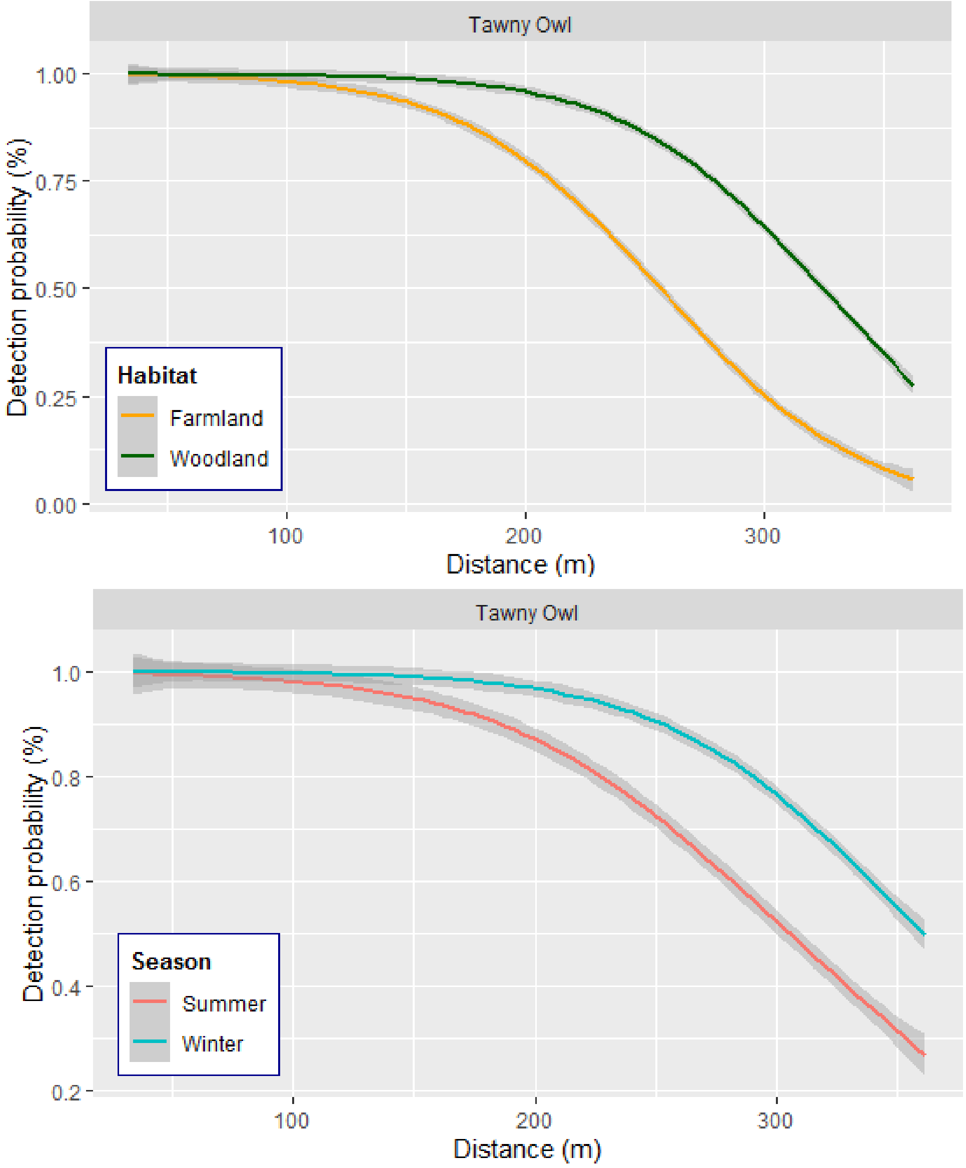

Figure 6. Binomial GLMMs showing the predicted probabilities of hearing playback calls in farmland (n = 400) and woodland (n = 400) in relation to distance (above), and the predicted probabilities of hearing playback calls in woodland in relation to distance and season (n = 400 in winter and n = 400 in summer) (below). Both models are referred to the Tawny Owl.

Therefore, the results of the experiment suggest that any inference from playback could only be reliably related to this radial distance around the surveyor, i.e. inferences about the owl should be limited to 200 m because most of the detected calls will be within that distance.

Moreover, this distance should be reliable given that the average size of an urban Tawny Owl territory is estimated to be around 20 ha (which corresponds to a c. 250 m radius) (Galeotti 1994). Therefore, inferences made in an area with a radius of 200 m, should be quite representative of Tawny Owls territories. Within the study area, there was a distance of at least 500 m between sample points, able to avoid potential territory overlapping.

2.5. Anthropic variables

Different predictor variables related to the effects of urbanisation were considered in this study: urban cover, housing cover, anthropogenic noise and light pollution in terms of SQM (Sky Quality Meter) and radiance values.

Urban cover was expressed by both buildings and roads network. It was calculated using QGIS software, employing the most recent Regional land-use map available ('Mappatura del Consumo di suolo in Piemonte 2017'), downloaded from the official database for GIS services of ARPA Piemonte (Geoportale ARPA Piemonte, www. webgis.arpa.piemonte.it). The following procedure was used to calculate urban cover area within each sample point:

- Being a WMTS (Web Map Tile Service), the land-use map was converted in a vectorial format and overlayed to a satellite image showing the study area.

- A circular buffer zone with a 200 m radius (detectability radius) was set around all sample points, in order to consider only the land-use within this distance.

- Each point (with its buffer) was singularly selected, exported and saved. Then, they all were clipped individually with the vectorial land-use map, so that urban land-use could be calculated in each point separately.

- In each point, urban land-use was selected and the area calculated in m^2 using the field calculator in the layer's attributes table. When necessary, selected urban land-use was corrected manually, by (i) adding polygons that covered buildings that were not included in the land-use map, and (ii) removing parts that were not strictly urbanised.

- The area was then converted in percentage, dividing it by the total area of the 200 m radius-buffer zone and multiplied by 100.

Housing cover, inclusive of only buildings, was obtained creating specific polygons over them, keeping the satellite image in the background. The area was calculated in the same way as for urban cover.

Anthropogenic noise, represented by traffic noise, was measured in the field using a sound level meter (SLM Meterk MK 09). At each sample point and visit, during the first two minutes of playback passive listening, the device was kept at 1 m above the ground and dB values were registered. Then, they were reported in a specific sheet and the average value for each point was calculated.

SQM (Sky Quality Meter) is a device that measures the brightness of the night sky in mag/arcsec^2 (magnitudes per square arcsecond). In other terms, it provides an indication of sky quality, i.e. how dark the night sky is. Therefore, since night sky brightness is one indicator of light pollution (Falchi *et al.* 2016), SQM provides useful information, allowing to see whether artificial light at night is making an adverse impact on the darkness of the night sky. SQM data used in this study derives from the World Atlas of artificial sky luminance, created in 2015 to quantify light pollution on a global scale, providing a helpful tool for various disciplines interested in this topic, such as ecology and environmental protection (Falchi *et al.* 2016). The Atlas was computed with light pollution propagation software using different satellite data and a new database of SQM measurements (Falchi *et al.* 2016). The former includes radiance data obtained from VIIRS (Visible Infrared Imaging Radiometer Suite) Day/Night Band (DNB), updated until 2020, which in this study was used as another parameter to evaluate light pollution.

Radiance can be considered as the amount of light emitted or reflected by artificial infrastructures that alters sky quality. One feature of DNB data is indeed the detection of electric lighting on the world's surface (Falchi *et al.* 2016, Elvidge *et al.* 2017).

Both SQM and radiance data were available from open-source maps, illustrating two different informative layers: World Atlas, which showed a sky brightness map and VIIRS, which showed a radiance map (www.lightpollutionmap.info). By inserting sample point coordinates on these maps, SQM and radiance values were identified.

2.6. Data analysis

First, Kruskal-Wallis test was used to evaluate whether there were differences in Tawny Owl detections between the months in which the survey was conducted and the time of the night (twilight and night) (McKight & Najab 2010). A significant test result (as measured by the chi-squared statistic) indicates that there are differences between the levels of the variable, i.e. differences between months and time of night.

Then, to evaluate the effect of urban intensity and anthropogenic factors on Tawny Owl presence, a mixed modelling approach was used, fitting binomial generalized linear mixed models (GLMM) to the probability of presence in the urban environment (1 = presence; 0 = absence) as the response variable. Survey point identity was specified as a random effect in order to account for repeated observations from the same point**.** Urban cover, housing cover, anthropogenic noise, SQM and radiance values were specified as fixed effects. The first model analysed the response of the species along a gradient of urban intensity, expressed by urban cover. Then, one model for each anthropogenic factor was also fitted to evaluate their effect on the species probability of presence. These univariate models were then compared using AIC (Akaike's Information Criterion) for model selection, i.e. to identify which model was most likely to be the best to fit the data, and thus to identify the most relevant covariate affecting the response variable (Burnham & Anderson 2002). Given the small sample size (n/K ratio < 40), an AIC corrected for small sample sizes (AICc) was used. Lower AICc indicated which models were better and a ΔAICc < 2 meant that the models had the same likelihood of being the best, i.e. they can be considered equivalent. Finally, a combined model with all covariates was also fitted to the probability of presence to verify the results from AIC, i.e. if the anthropic variables of the best univariate model(s) had a main role and effect in a full general model. All GLMMs were validated using the Hosmer-Lemeshow goodness of fit test (Hosmer & Lemeshow 2000), where a significant test result (as measured by the chi-squared statistic) indicates poor model fit.

Before modelling, some steps were made to ensure the quality of the analysis. Predictor variables were scaled, as they were measured in different measurement units. In this way, their parameter estimates were standardized sizes and were on a comparable scale. Then, VIF (Variance Inflation Factor) was used to check for potential correlation between predictor variables, and a value that exceeds 5 or 10 indicates problems of collinearity (James *et al.* 2014). Since urban and housing cover were highly correlated (both VIF > 11), the latter was discarded, as it was less comprehensive in terms of urban intensity. Possible non-linear effects for predictor variables were checked adding a quadratic term in the models. A significant non-linear effect ($p < 0.05$) was found only for the SQM variable. Spatial autocorrelation of the binary dependent variable was also checked using Moran's test (Rangel *et al*. 2010), which showed no spatial autocorrelation (Moran's $I = 0.09$, $p > 0.05$).

Statistical analyses were carried out using R software (v. 3.6.3, R Core Team 2020). GLMMs were fitted in the lme4 package (Bates *et al*. 2015) and their results visualised with ggplot2 (Wickham 2016).

3. RESULTS

Tawny Owls were detected 39 times (48.8 %) in total (n = 80, i.e. 40 sample points visited twice). The number of detections was essentially the same between the two visits: 19 during the first and 20 during the second. Throughout the whole survey, 56 Tawny Owls responded to playback. Among these, 32 were males, 22 females and 2 individuals did not reply vocally, so their sex was unknown, yet the birds were seen because they flew over. In addition, within these detected birds, there were 13 couples, i.e. males and females replied together to the playback stimulus. Tawny Owls detections were not influenced by the month in which the survey was carried out ($\chi^2 = 1.7$, $df = 2$, $p > 0.05$) nor by the time of the night, i.e. no differences between twilight and night were found ($\chi^2 = 0.9$, $df = 1$, $p > 0.05$). Therefore, field survey was not influenced by these two factors and they were not considered further.

3.1. Tawny Owl response to urban intensity

Tawny Owl showed an unfavourable response to urban intensity. The probability of presence declined significantly along the urban gradient (ranged from 0 to 53.9 %) in the urbanised matrix of Turin (slope = -1.01 ± 0.44, z = -2.31, $p < 0.05$) (**Table A1**, Appendix A). Though, as the urban cover started to intensify, predicted probabilities did not drop sharply, but they decreased approximately with a linear trend, showing a certain degree of tolerance (**Figure 7**). At 10 % of urban cover the probability of presence was still over 50 % (estimated probability = 0.57). When urban cover increased to 14 %, the probability declined to 50 %. The Hosmer-Lemeshow test showed a good model fit ($\chi^2 = 12.9$, $df = 8$, $p > 0.05$).

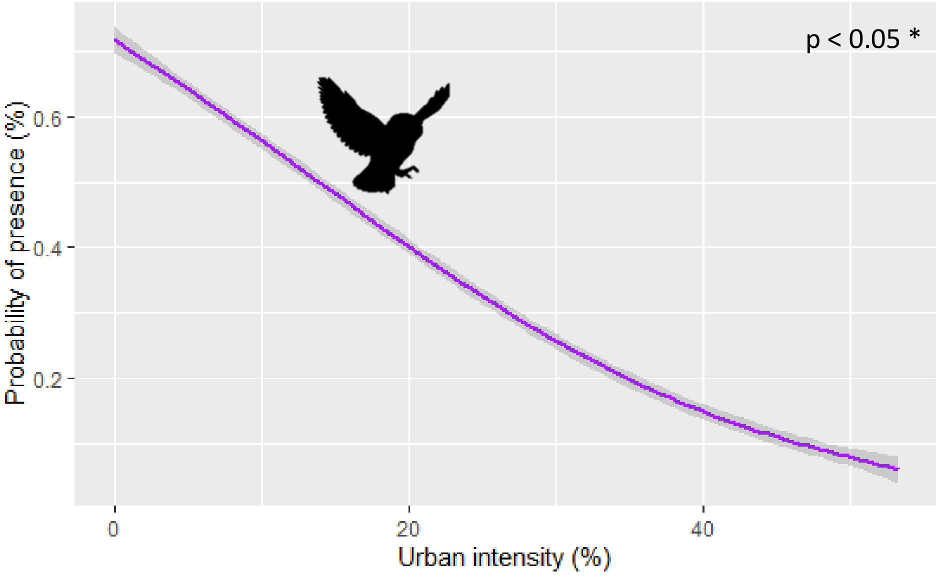

Figure 7. Binomial GLMM showing Tawny Owl predicted probability of presence in relation to urban intensity (n = 80). The gradient is represented by urban cover, which included both buildings and roads network.

3.2. Effect of anthropogenic noise and light pollution

Both noise and light pollution affected the species within the landscape. Tawny Owl was indeed scarcely present in noisier locations (slope = - 0.98 ± 0.48, z = - 2.04, $p < 0.05$) (**Table A2**, Appendix A). Within the study area, anthropogenic noise ranged between 36.7 and 56.9 dB, with a mean of 46.8 ± 5.3 dB. Overall, predicted presence probabilities were high until 46.5 dB, where the estimated probability was 50 % (**Figure 8**). Therefore, in order to ensure good chances (presence probability ≥ 50 %) for Tawny Owls to be hosted in urban settings, noise levels should not be higher than 46.5 dB. The Hosmer-Lemeshow test showed a good model fit ($\chi^2 = 15.3$, *df* = 8, $p > 0.05$).

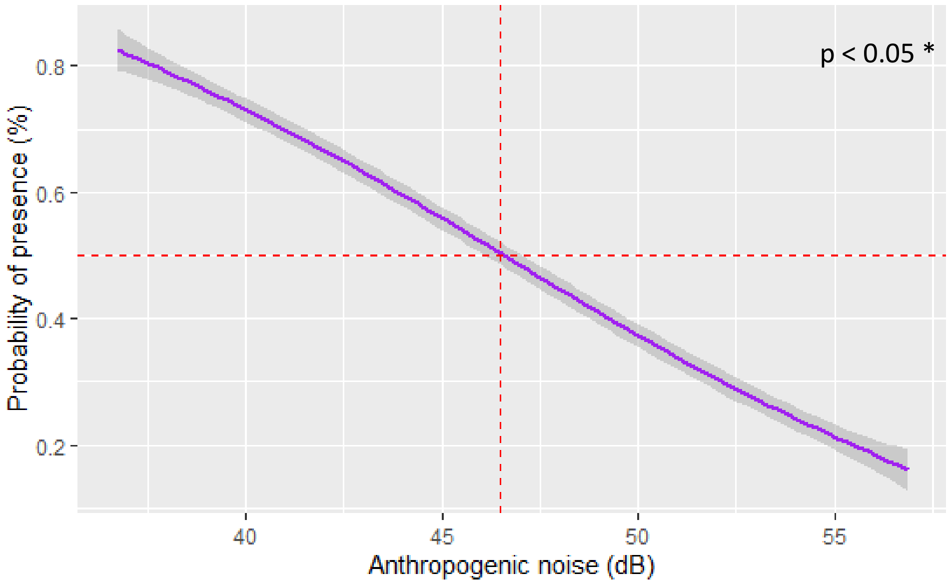

Figure 8. Binomial GLMM showing predicted presence probabilities in relation to anthropogenic noise (n = 80). The red dashed lines intersect the curve at the point in which the probability is 50 % at 46.5 dB.

Tawny Owl was also affected by light pollution. Based on the Word Atlas SQM values, the species was more likely to be found in places where the night sky was darker (higher SQM readings), i.e. less impacted by artificial light at night (slope = 1.01 ± 0.44, z = 2.28, $p < 0.05$) (**Table A3**, Appendix A). Within the study area, SQM measurements ranged between 18.29 and 19.48 mag/arcsec^2, with a mean of 18.8 ± 0.4 mag/arcsec^2 (**Figure 9b**). Overall, predicted presence probabilities were high starting from 19.08 mag/arcsec^2, where the estimated probability was 50 % (**Figure 9a**). Around 18.3 mag/arcsec^2, the species showed a moderate presence, probably explained by the presence of suitable requirements for its survival (e.g. nest sites) that could have mitigated the negative effect of artificial light. Nevertheless, the trend shows a strong preference for darker conditions, for which predicted probabilities are much higher. To ensure good chances (presence probability ≥ 50 %) for Tawny Owls to be hosted in urban settings, the sky should be quite dark, around 19.1 mag/arcsec^2 according to the readings deriving from SQM devices. The Hosmer-Lemeshow test showed a good model fit ($\chi^2 = 12.9$, $df = 8$, $p > 0.05$).

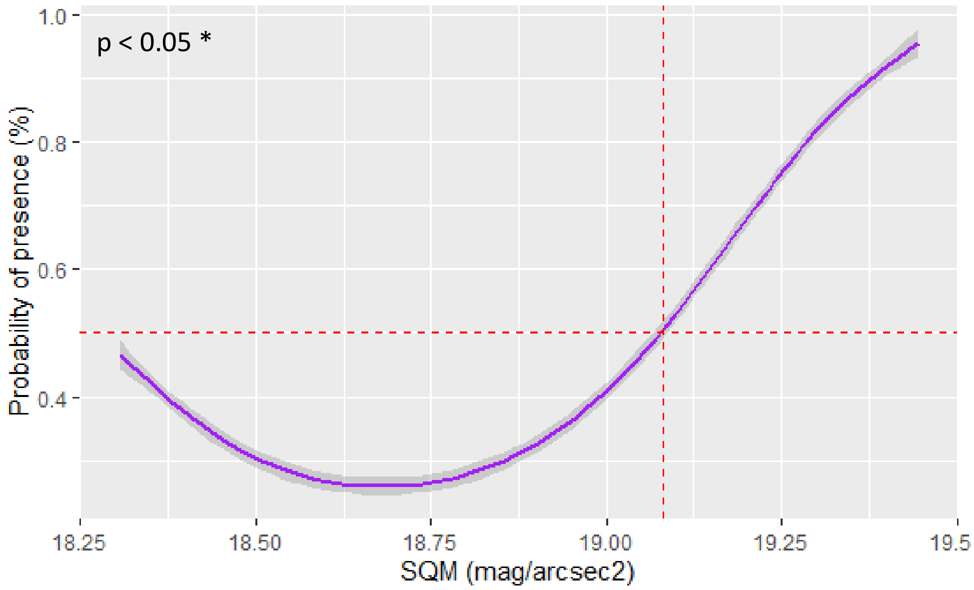

Figure 9a. Binomial GLMM showing predicted presence probabilities in relation to SQM measurements (n = 80). The red dashed lines intersect the curve at the point in which the probability is 50 % at 19.08 mag/arcsec^2.

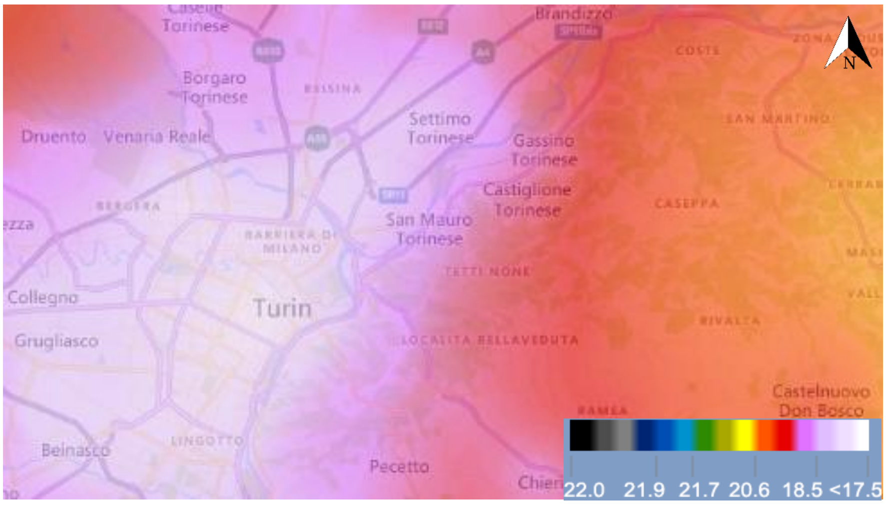

Figure 9b. Study area represented with SQM values theme. The legend on the right corner shows the scale of colours associated to SQM values. Brighter colours indicate lower levels of sky darkness (i.e. sky quality), therefore areas more impacted by artificial light. Moving out from the city towards the hill, the sky gets darker favouring Tawny Owl presence. Photo and legend adapted from www.illuminationmap.info (Credits: World Atlas 2015 - Falchi *et al*. 2016: Supplement to The New World Atlas of Artificial Night Sky Brightness. GFZ Data Services).

Radiance, the second parameter used to evaluate light pollution, also manifested an impact on the species, in agreement with SQM results. The effect of radiance on Tawny Owl probability of presence was highly significant (slope = - 1.16 ± 0.44, z = - 2.67, $p < 0.01$) (**Table A4**, Appendix A) and measurements ranged between 2.02 and 46.47 $W \cdot sr^{-1} \cdot m^{-2}$, with a mean of 16 ± 11.8 $W \cdot sr^{-1} \cdot m^{-2}$ (**Figure 10b**). Overall, predicted presence probabilities were high until 14.9 $W \cdot sr^{-1} \cdot m^{-2}$, where the estimated probability was 50 % (**Figure 10a**). Therefore, Tawny Owls will be likely more present (presence probability ≥ 50 %) in urban settings without excessive artificial light, possibly limited to 15 $W \cdot sr^{-1} \cdot m^{-2}$. The Hosmer-Lemeshow test showed a good model fit ($\chi^2 = 12.4$, *df* = 8, $p > 0.05$).

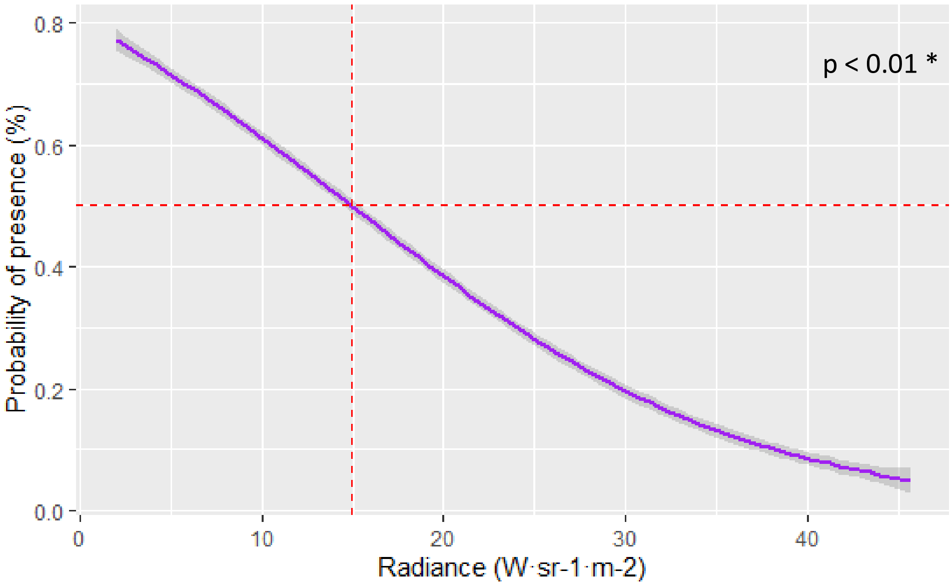

Figure 10a. Binomial GLMM showing predicted presence probabilities in relation to radiance measurements (n = 80). The red dashed lines intersect the curve at the point in which the probability is 50 % at 14.9 $W \cdot sr^{-1} \cdot m^{-2}$.

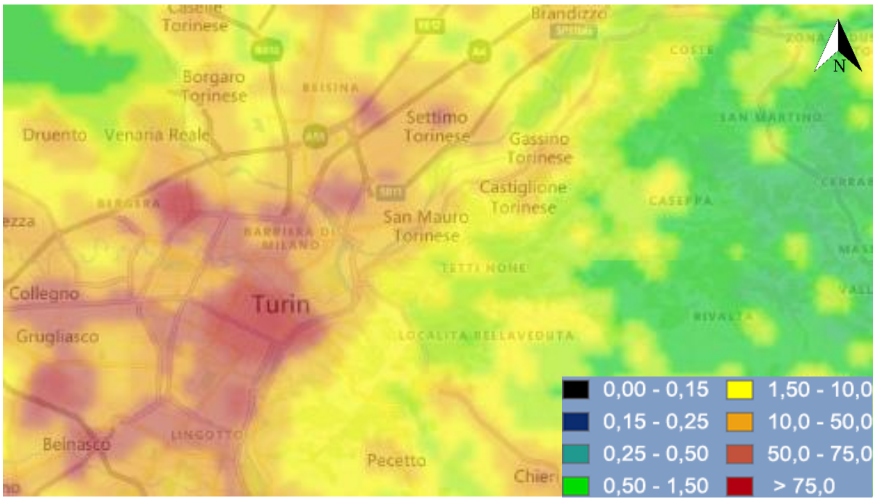

Figure 10b. Study area represented with radiance values theme. The legend on the right corner shows the scale of colours associated to radiance values. Heater colours indicate higher levels of radiance, therefore areas more impacted by artificial light. Moving out from the city towards the hill, they decrease favouring Tawny Owl presence. Photo and legend adapted from www.illuminationmap.info (Credits: Jurij Stare, VIIRS - Earth Observation Group, NOAA National Geophysical Data Center).

Comparing the univariate models with AICc, those with SQM and radiance provided the best models (ΔAICc < 2) (**Table 1**), suggesting that light pollution is likely to have a greater influence in determining Tawny Owl occurrence. Indeed, the final combined model (which had the lowest AICc) confirmed this hypothesis, as the only significant effects were associated to SQM (slope = 1.22 ± 0.52, z = 2.37, $p < 0.05$) (**Table A5**, Appendix A) and radiance (slope = - 1.54 ± 0.77, z = - 1.99, $p < 0.05$) (**Table A5**, Appendix A).

Model	**AICc**	**ΔAICc**
Combined model	100.57	0.00
SQM model	100.83	0.27
Radiance model	102.34	1.77
Urban model	105.84	5.28
Noise model	106.92	6.35

Table 1. Models with their associated AICc score. They are ranked from the lowest AICc to the highest, as a lower score indicates a better model, which here is represented by the combined model. However, models with ΔAICc < 2 can be considered equivalent.

Therefore, in an overview where all urban covariates are considered together, light pollution emerged as the most relevant factor. The Hosmer-Lemeshow test showed a good model fit ($\chi^2 = 9.6$, $df = 8$, $p > 0.05$). Nonetheless, maintaining again the presence of the species at 50 % as threshold, predicted probabilities did not differ substantially from univariate models, especially for SQM, for which the probability of presence was 50 % at 19.14 mag/arcsec^2 (while previously was 50 % at 19.08 mag/arcsec^2). As for radiance, the probability was 50 % at 13.4 W·sr^{-1}·m^{-2} (**Figure 11**).

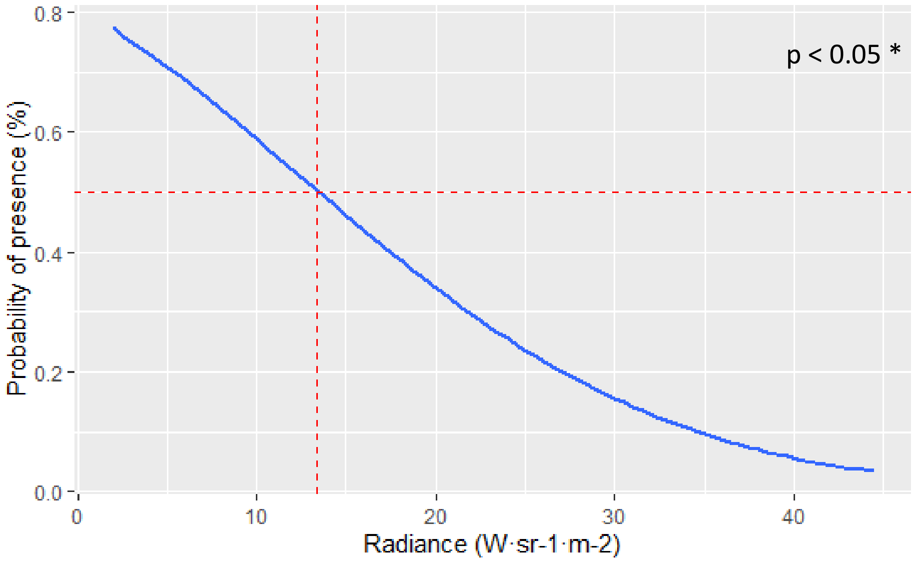

Figure 11. Binomial GLMM (combined model) showing predicted presence probabilities in relation to radiance measurements (n = 80). The red dashed lines intersect the curve at the point in which the probability is 50 % at 13.4 W·sr^{-1}·m^{-2}, a radiance value slightly smaller compared to the univariate model (50 % at 14.9 W·sr^{-1}·m^{-2}).

4. DISCUSSION

Overall, the results of this study showed a negative effect of urbanisation, highlighting how typical factors associated with urban development can influence the occurrence of nocturnal wildlife. The Tawny Owl is known for being able to live in urban settings, but as long as suitable nest sites for breeding can be found and prey is available, including wintering birds which usually are an important component in the diet of owls inhabiting urban areas (Solonen & Ursin 2008, Grzędzicka *et al*. 2013). Nevertheless, the Tawny Owl remains a species strictly associated with wooded areas, highly important for its survival in human-modified environments (Ranazzi *et al*. 2000, Fröhlich & Ciach 2018). Fröhlich & Ciach 2018 showed that the distribution of this species is positively correlated with the availability and size of woodland habitats in urban environments. The reduction of both implied indeed a decline in species occurrence. Urbanisation, most of the times, involves an excessive contraction or removal of greenspaces such as wood patches, sacrificed for new built-up areas. Hence, what trade-off between natural habitat and urban land-use could let this owl thrive within urbanised landscapes? Along the gradient of urban intensity, the Tawny Owl behaved like a ‘loser’ species, as the probability of presence started to decline as soon as urban cover started to intensify. Nonetheless, the decline was not sharp (which occurs for typical land-sparing species), but almost linear, with a probability of presence ≥ 50 % until 14 % of urban cover. For this reason, the Tawny Owl can be associated with ‘urban adapters’, species capable to tolerate moderate levels of urban intensity but decline at higher levels. Differently, an ‘urban avoider’ is defined as a sensitive species that rapidly declines when urban cover increases, while an ‘urban exploiter’ benefits from urbanisation and increases its presence or population as urban cover grows (Gagné & Fahrig 2010, Geschke *et al.* 2018). Therefore, results indicate that the Tawny Owl may be able to adapt and find benefits in urban areas, but essentially in low-density contexts (e.g. low-density suburbs). Contrary to exploiters, its presence did not increase with urban intensity nor it dropped drastically as it would happen for avoiders.

Being a near-linear relationship, the curve (**Figure 7**) suggests a middle ground between land-sparing and land-sharing, if compared to **Figure 3**. However, results from model comparison and the combined model showed that in an overview, urban cover was not relevant as much as noise and light pollution. This indicates that the Tawny Owl is likely to tolerate a reasonable level of urban intensity as long as noise and light conditions are favourable, i.e. when such conditions are considerably quiet and dark (see next paragraphs).

They have a greater role in determining Tawny Owl distribution, which would be explained only partially if urban cover was considered alone and noise and light were neglected. Hence, if these conditions are met, the spatial arrangement that is likely to most benefit this avian predator in urban environments is a land-sharing scenario. Though, in most cases, land-sparing has been generally demonstrated to be a better solution to ensure biodiversity conservation and also to guarantee higher ecosystem services (Sushinsky *et al*. 2013, Stott *et al*. 2015, Villaseñor *et al*. 2017). This is explained by the fact that several species are 'urban avoider', unable to adapt and survive even at low levels of urban intensity (Gagné & Fahrig 2010, Geschke *et al.* 2018). These species are often specialistic, endemic and more threatened than those associated with land-sharing, which are instead more common. For this reason, land-sparing is typically recognised as the best choice for biodiversity conservation, as it can sustain a more valued wildlife.

In the same line, Soga *et al*. 2014 showed that in the city of Tokyo land-sparing was mainly better, allowing higher population sizes of insects (butterflies and ground beetles) in high-level urban areas. Though, at lower levels of intensity, they found that butterflies were more favoured by land-sharing. Besides, in a more recent study, Ibáñez-Álamo *et al*. 2020 evaluated the LSAS framework in nine European cities to see which approach was associated with a higher diversity of birds. They found that land-sharing urban areas were significantly associated with higher species richness of birds during winter, but not during the breeding season, suggesting the importance of integrating a temporal component when analysing urban biodiversity. Furthermore, another point of view in favour of land-sharing can be provided by predator's (such as owls) territory requirements. With land-sparing urban greenspaces are condensed in large but few areas. This could potentially limit their occurrence, as only few individuals would be able to establish a territory. By contrast, if greenspaces were more interspersed across the landscape, predators could be eased to establish territories without overlapping conflicts (i.e. less competition for the same nest sites). In this case, Tawny Owls could be well spread across a given urban region, performing biological control on rodent populations and other preys over a more extended area.

Any debate about how to best manage a city in terms of comparting green and urban areas, should also take into account people's view on this matter, as they are an integrative living part of urban ecosystems. Do they prefer living in a city featured by land-sparing or land-sharing? Soga *et al*. 2015 investigated the relationship between different urban forms and human recreational use of greenspaces. Within the city of Tokyo, they selected five pairs of LSAS areas and analysed the use made by residents through a questionnaire survey. They found that the majority preferred land-sharing rather than land-sparing. The degree of satisfaction for greenspaces and their recreational use were both higher in land-sharing regions. Given that urban nature and biodiversity provide positive interactions and benefits for human health and well-being (Brown & Grant 2005, Soga & Gaston 2020), planning decisions should be pondered well. All these findings and standpoints in support of land-sharing have not been addressed to discredit land-sparing, but to highlight that biodiversity-friendly cities could be developed based on both land-approaches. The design of urban areas falls frequently into one of the two canonical schemes (Lin & Fuller 2013), but, after all, they just emphasise the endpoints of a continuum (Finch *et al*. 2019). This means that mixed strategies, where elements from both sparing and sharing are combined, can be possible. Implementing greenspaces of various forms may be valuable and rewarding to meet the needs of both:

(i) urban adapter and avoider species
(ii) biodiversity conservation goals and social desires or necessities

In this way, a variegated presence of greenspaces can host species that tolerate urbanisation at different levels. However, more studies will be necessary to evaluate what mixed strategy will be better to benefit both types of species, without having unbalanced situations on one side or the other. As for the second point, additional investigations on the human-nature relationship would be useful to plan biodiversity-friendly cities, whose development may vary based on different people's cultures and traditions. This component has great relevance for creating or renewing sustainable cities, aimed at reducing the conflict between humans and biodiversity.

4.1. Anthropogenic noise

What emerged from this study is that not only urban intensity can shape Tawny Owl distribution, but also noise and ALAN had a significant role. As expected, noisier locations in the study area were avoided by the species. When anthropogenic noise was greater than c. 47 dB the probability of presence dropped below 50 %. The dominant noise source was represented by road traffic, but noise from buildings also occurred. This finding agrees with previous studies that evaluated the effect of noise intensity on owls in urban areas. Indeed, Fröhlich & Ciach 2018 found a negative relationship between Tawny Owl occurrence and noise intensity in the city of Krakow (Poland). Moreover, the same authors showed that noise intensity can also alter the structure of owls' community, reducing their species richness in urban landscapes (Fröhlich & Ciach 2019). The negative impact of this factor can be explained by owls' predatory behaviour, which relies on their remarkable hearing ability, therefore susceptible in noisy environments (Mason *et al*. 2016). Adaptations in their ear structure allow them to discriminate variations in the location of sound and to identify the sources accurately (Mikkola 2019). For this reason, most owls rely on their aural abilities for hunting, extremely useful when preys move unseen in the environment (Mikkola 2019). Secondly, excessive loud places can be stressful for owls in terms of greater energy costs associated with their vocal activity. High levels of noise coming from roads and buildings could hamper intra-specific communications. For example, this would lead to more intense and frequent efforts to defend territories and find mates. Given such disadvantages, owls have difficulties thriving in these environments and therefore abandon them, lowering their occurrence in urban landscapes.

4.2. Artificial light at night

The effect of ALAN was also proved to be negative. Tawny Owl presence was indeed significantly higher in darker conditions. Results showed that both SQM and radiance measurements have been valuable parameters to evaluate the impact of light pollution. However, a difference was identified in the nature of the effect. As for SQM, a non-linear effect was found, showing a slight success in occurrence even at low levels of sky quality. This can be explained by the possibility to persist in brighter conditions as long as other key requirements are available to compensate for the lack of darkness (e.g. suitable nest sites, prey abundance). This supports the idea of the Tawny Owl as an 'urban adapter'. Nonetheless, species presence started to increase strongly (probability ≥ 50 %) when SQM values were beyond c. 19.1 mag/arcsec^2, considering both the univariate and the combined model. According to the Bortle scale, a nine-level numeric scale used by astronomers to measure the night sky's brightness of a particular location (class 1 = 'excellent dark-sky site'; class 9 = 'inner-city sky'), SQM values approximately between 19.1 and 20.4 mag/arcsec^2 identify a 'suburban sky' (class 5). This is the sky type under which the probability of presence was ≥ 50 %. By definition, it is a sky where light sources are still evident in most if not all directions and the Milky Way is faint or invisible near the horizon and washed out overhead. As for radiance, the pattern was different because the effect of radiance on Tawny Owl probability of presence was a more linear decreasing relationship.

Though, results indicated the same outcome, showing a decline in presence probability as artificial light increased (probability < 50 % at radiance levels starting around 13-15 $W \cdot sr^{-1} \cdot m^{-2}$, considering both the univariate and the combined model. Therefore, these findings suggest that the Tawny Owl tends to avoid as much as possible places featured by ‘artificial skyglow’, the most evident effect of light pollution, i.e. when ALAN is spread in the atmosphere increasing the night sky’s luminance (Falchi *et al*. 2016). Moreover, results from model selection showed that the models with light pollution covariates were the best to fit the data. This highlights the great relevance of ALAN in shaping Tawny Owl distribution and the importance of integrating such a component in urban greenspaces design and studying nocturnal wildlife in urbanised environments. This hypothesis was also confirmed in the final combined model inclusive of all covariates, as light pollution was the only factor for which the effect was significant ($p < 0.05$), both in terms of sky quality and radiance. So, high-lit green areas will be more likely avoided or abandoned by the Tawny Owl.

At present, limited research has focussed on the potential impact of ALAN on nocturnal wildlife, and strictly on night predators. Recent studies highlighted contrasting results. Marín-Gómez *et al*. 2020 found a negative relationship between ALAN (and noise) and the presence of the Mottled Owl *Ciccaba virgata* in the city of Xalapa (Mexico). By contrast, Rodríguez *et al*. 2020, showed that ALAN turned out to be a helpful driver for the Burrowing Owl *Athene cunicularia* to colonize urban environments. This study was conducted in a suburban area in La Pampa (Argentina) and the authors showed that the species spent a lot of time close to streetlights at night because a great quantity of invertebrates was attracted by such sources of light. This allowed the owl to take advantage of ALAN, which eased its hunting success, given that its diet is mainly based on invertebrates (Mikkola 2019, Rodríguez *et al*. 2020). Therefore, it was proved that ALAN was able to change invertebrate availability and benefit the Burrowing Owl, shifting its space use mostly near to streetlights as they increased its foraging efficiency. Here, one key point emerging from these studies that could explain the contrasting response to ALAN is owls’ diet. Unlike the latter species, the Tawny Owl (and the Mottled Owl) feeds mainly on small mammals that, contrary to insects and other invertebrates, do not have the same behaviour and are not attracted to light. Thus, the advantage demonstrated for the Burrowing Owl is likely to be limited to those species that primarily feed on invertebrates. Hence, owls’ trophic condition could play an important role in determining the response to artificial light at night.

In addition, another reason that can justify Tawny Owl's preference for darker conditions is associated to their eye anatomical adaptations. Generally, all owls have adaptations that allow them to hunt at night, but strictly nocturnal species (c. 69 % according to Mikkola 2019), like the Tawny Owl, have more light-sensitive rods in the retina (c. 56000 per mm^2 in the Tawny Owl) (Mikkola 2019). This high sensitivity to light can make them blinded to strong sunlight and that is why they are rarely seen in daylight (Mikkola 2019). The number of light-sensitive elements in the retina, mostly rods, is very high and increases both visual acuity at low light levels and sensitivity to light. Nevertheless, this cannot be generalized to all owls, because species like the Burrowing Owl mentioned before are less sensitive and so can hunt during the day (Mikkola 2019). This should confirm the possibility for such owl to tolerate streetlights.

4.3. Conclusions and recommendations

The Tawny Owl is an apex predator in urban ecosystems whose presence influences other species. A decline in owl's occurrence can have negative cascading effects on its preys, leading to an increase in their populations. This study enriches the body of evidence that shows the negative effects of urbanization on owls' distribution and underpins the importance of integrating suitable actions to encourage its presence across urban landscapes, preventing excessive disturbance by noise and artificial light at night. In particular, ALAN has been demonstrated to be a driver of high relevance in shaping Tawny Owl distribution. The following practical measures are suggested to enhance its presence in these human-modified environments.

1) The presence of Tawny Owls in urban environments could be improved by maintaining a good proportion of natural and native vegetation, preferably in the forms of well-wooded urban parks and public/private gardens. Including and preserving old trees would be a valuable action, as they can often provide natural holes and cavities suitable for nesting. When the presence of natural nest sites is missing, the installation of suitable nest-boxes can help the species to breed in urban areas. The provision of nest-boxes is often a productive habitat-management option and has been proved to be capable of increasing the numbers of many owl species, including the Tawny Owl (Karell *et al*. 2009, Mikkola 2019).

2) To minimise excessive traffic noise, a relevant measure could be concentrating most greenspaces in locations within the urban landscape where traffic is generally less intense. A wooded patch surrounded by multiple main roads would not be an appropriate option. However, trees established along main roads can act as an acoustic barrier, being effective in reducing noise levels. Besides, tree rows provide aesthetic advantages and improve air quality.

3) Finally, to minimise the negative effects of artificial light at night opportune measures are needed. Valuable options, mostly recommended by Gaston *et al*. 2012, that may be adopted by planners to mitigate the adverse ecological effects of light pollution in urban environments are:

(i) Preventing target areas from being artificially lit;
(ii) Reducing the duration of lighting at night;
(iii) Directing the light downwards to the ground;
(iv) Shielding light sources to avoid glare and light scattering upwards and in unintended areas nearby;
(v) Dimming light intensity and changing its spectral composition with proper filters or other light sources

Increasing and keeping woodland areas unlit across urbanised landscapes would be the best action to attract owls for breeding and reduce the ecological effects of artificial light at night. Otherwise, if this was not possible, reducing the duration of night lighting turning off the streetlights within urban parks and gardens (and elsewhere) would be also beneficial. Basically, using streetlights only where and when necessary would be advantageous overall, as they represent one of the greatest contributors to light pollution. Nevertheless, when removing or limiting the number of lights from buildings and streets is not feasible for socio-economic reasons, making them more sustainable is a good alternative. Downlighting and shielding light sources can reduce artificial skyglow and thus improve the night sky's quality. Changing light intensity and spectral composition can limit potential damages to biological functions. ALAN light spectrum is different from those of sunlight or moonlight, and it depends on the kind of lighting device that is being employed. Artificial lights vary widely in brightness and colour composition. Today, whiter lighting sources with a strong component in the blue portion of the spectrum are largely used because they are more energy-efficient and long-lasting, but they are also responsible for disrupting biological processes in both humans and other organisms (e.g. vision, circadian rhythms, sleep) (Gaston *et al*. 2015). Over the last century, street and residential lighting largely shifted from traditional incandescent bulbs to modern LEDs, which generally emit a higher proportion of blue wavelengths (Hatori *et al*. 2017). Making light warmer or filtering it to avoid critical regions of the spectrum can be productive (Gaston *et al*. 2012). This suite of mitigations has the potential to make urban nightscapes more sustainable and to benefit not only the Tawny Owl, but also wildlife in general, including an improvement in people's health. Moreover, these measures can have in turn advantages for the human society itself in terms of energy consumption and costs, landscape aesthetics and carbon emissions.

In a nutshell, the presence of this avian nocturnal predator is important to regulate the trophic equilibrium of the nest-web and contributes to increasing the quality of urban landscapes. Being able to adapt to urbanised settings, its presence can be reinforced or restored through a spatial arrangement where suitable wooded greenspaces are interspersed with built-up areas. This framework may be rather successful if adequate measures are addressed to prevent high levels of anthropogenic noise and artificial light at night, which in turn can also benefit other species and human health, making cities and urban areas more sustainable and biodiversity-friendly.

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APPENDICES

APPENDIX A: Model parameter estimates - Tawny Owl survey

Table A1. Tawny Owl presence probability in relation to urban intensity.

Variable	Estimate	Standard error	Z value	P value
Intercept	- 0.116	0.328	- 0.352	0.725
(S) Urban cover	- 1.006	0.435	- 2.311	0.021

Model output showing fixed effects. Model formula: *Owl presence ~ SUrban cover + (1|Point)*, where *Owl presence* stands for the '1 = presence; 0 = absence' and *Urban cover* was scaled (*S*). The random effect is expressed by survey points *'(1|Point)'*.

Table A2. Effect of anthropogenic noise on Tawny Owl presence probability.

Variable	Estimate	Standard error	Z value	P value
Intercept	- 0.059	0.382	- 0.154	0.878
(S) Noise	- 0.979	0.480	- 2.041	0.041

Model output showing fixed effects. Model formula: *Owl presence ~SNoise + (1|Point)*, where *Owl presence* stands for the '1 = presence; 0 = absence' and *Noise* was scaled (*S*). The random effect is expressed by survey points *'(1|Point)'*.

Table A3. Effect of SQM values on Tawny Owl presence probability.

Variable	Estimate	Standard error	Z value	P value
Intercept	- 0.936	0.501	- 1.869	0.062
(S) SQM	0.832	0.386	2.156	0.031
I(SSQM^2)	1.008	0.443	2.277	0.023

Model output showing fixed effects. Model formula: *Owl presence ~SSQM + I(SSQM^2) + (1|Point)*, where *Owl presence* stands for the '1 = presence; 0 = absence' and *SQM* was scaled (*S*). *I(SSQM^2)* is the quadratic term that indicates a non-linear effect. The random effect is expressed by survey points *'(1|Point)'*.

Table A4. Effect of radiance on Tawny Owl presence probability.

Variable	**Estimate**	**Standard error**	**Z value**	**P value**
Intercept	- 0.111	0.317	- 0.349	0.727
(S) Radiance	- 1.164	0.436	- 2.671	0.008

Model output showing fixed effects. Model formula: *Owl presence ~SRadiance + (1|Point)*, where *Owl presence* stands for the '1 = presence; 0 = absence' and *Radiance* was scaled (*S*). The random effect is expressed by survey points *'(1|Point)'*.

Table A5. Combined model.

Variable	**Estimate**	**Standard error**	**Z value**	**P value**
Intercept	- 1.223	0.569	- 2.147	0.032
(S) Urban cover	- 0.224	0.403	- 0.555	0.579
(S) Noise	- 0.313	0.356	- 0.879	0.379
(S) SQM	- 0.580	0.676	- 0.858	0.391
I(SSQM^2)	1.223	0.517	2.369	0.018
(S) Radiance	- 1.542	0.774	- 1.992	0.046

Model output showing fixed effects. Model formula: *Owl presence ~SUrban + SNoise + SSQM + I(SSQM^2) + SRadiance + (1|Point)*, where *Owl presence* stands for the '1 = presence; 0 = absence' and all covariates were scaled (*S*). *I(SSQM^2)* is the quadratic term that indicates a non-linear effect. The random effect is expressed by survey points *'(1|Point)'*.

APPENDIX B: Field evaluation for playback surveys: species-specific detection probabilities and distance estimation errors in a nocturnal bird community (manuscript accepted in *Bird Study*)

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Short title: Playback field evaluation

Keywords: binomial GLMM, broadcast experiment, call detection, bird monitoring, elusive birds, owls

ABSTRACT

Capsule: During playback experiments, the distance from the surveyor to the call influences the chances of detection across nocturnal species in farmland and woodland habitats.

Aim: To evaluate how distance affects surveyor detection capability, expressed as the probability of hearing broadcast calls and of estimating their distances correctly, in a nocturnal bird community.

Methods: We conducted a playback field experiment in farmland and woodland areas within an agricultural landscape in winter and summer 2020. Vocalisations of five species (Little Owl *Athene noctua*, Tawny Owl *Strix aluco*, Long-eared Owl *Asio otus*, Common Nightingale *Luscinia megarhynchos*, Water Rail *Rallus acquaticus*) were broadcast at various distances to a surveyor, who attempted to detect them and, if successful, to classify them into predefined distance zones. Binomial GLMMs were used to estimate detection probability as a function of distance, and the effects of habitat and season on this relationship.

Results: The distance of the broadcast call from the surveyor had a significant effect on detection probability in both habitats. In woodland, the probability of hearing calls was significantly higher in winter, while estimating distances correctly was generally higher in summer. An increase in field experience improved our detection capability, mainly in terms of distance estimation, whose errors were mostly overestimations.

Conclusions: The probability of hearing calls and distance estimation accuracy varied between species. Most Little and Tawny Owl calls were detected within a 200 m radius of the surveyor, while this was 100 m for the other species. For a multi-species community-level study, playback surveys are thus likely to be most representative of a 200 m radius surrounding the surveyor where the probability of detection is highest, while estimates of distance from the observer are likely to be inaccurate in most cases. Field evaluations such as this should be implemented prior to actual playback surveys.

INTRODUCTION

Playback is commonly used to survey birds as it represents an efficient method to census elusive species by improving their detection probability (Hardy & Morrison 2000, Navarro *et al.* 2005, Stermin *et al.* 2017). This technique consists of broadcasting generally conspecific recorded calls in order to elicit their vocal reply (Johnson *et al.* 1981, Worthington-Hill & Conway 2017). This is particularly useful for those species that exhibit territorial behaviour because they will be more inclined to respond in order to defend their territories (Haug & Didiuk 1993, Pilla *et al.* 2018). Relying only on spontaneous vocalisations can be insufficient because they may limit census performance (Crowe & Longshore 2013). It is known that factors such as habitat, seasonality, time of day and weather can influence response rates during playback surveys (Hardy & Morrison 2000, Currie *et al.* 2002, Polak 2005, Braga *et al.* 2009, Johnson *et al.* 2009). In addition, more technical parameters such as sound amplitude level and surveyor detection ability or experience (Crowe & Longshore 2013, Zuberogoitia *et al.* 2020) are also fundamental as they enable a detectability radius to be defined, which is a threshold distance expressing at what scale bird distributions can be better estimated, i.e. a distance around playback points within which a surveyor has higher probabilities to detect birds. Usually, only responses detected at a distance within the radius are included in the analysis, since it provides some level of security, so that results include most individuals actually occupying a given area (Centili 2001, Johnson *et al.* 2009, Bolboacă *et al.* 2015). Therefore, the detectability radius has a key role in minimizing biases. During aural surveys, distance estimation is clearly more difficult than for visual detections and making errors in estimation can consequently bias the results (Marques 2004).

Field evaluations prior to actual playback surveys therefore represent a useful step to adjust the method by setting a fixed distance (and so a radius) calibrated on the surveyor's detection capability in the field (Esclarski & Cintra 2014), where radial distance is a function of the surveyor's ability to estimate bird-surveyor distance and to hear broadcast calls. Experimental trials of this kind can help researchers to conduct playback surveys as accurately as possible. From this perspective, we carried out a field experiment aimed to evaluate the effect of distance on detectability in different habitats within an agricultural landscape, by addressing the following questions:

(i) Does distance influence the surveyor's ability to hear playback calls and to estimate their distances correctly in farmland and woodland?

(ii) Does the effect of distance in woodland have the same effect on detection probability in summer and winter?

In this way, we aimed to understand at what scale nocturnal species detection and distribution can be estimated in this landscape. As target species, we used territorial playback songs/calls of Common Nightingale *Luscinia megarhynchos*, Little Owl *Athene noctua*, Tawny Owl *Strix aluco*, Long-eared Owl *Asio otus* and Water Rail *Rallus acquaticus*. Within our study region, these species form a common bird community with similar elusive habits. These birds are territorial, hard to see, and more active at night. For these reasons, they are frequently censused through playback, especially from dusk and at night (Zuberogoitia & Campos 1998, Schmidt *et al*. 2006, Brambilla & Jenkins 2009, Seoane & Galvàn 2010, Stermin *et al*. 2017). Through our experiment, we attempted to provide a valid insight into the playback method in surveying our target species effectively.

METHODS

Study area

The study was carried out in the Piedmont Region, northern Italy. We conducted playback surveys in an agricultural landscape dominated by arable crops and interspersed with small woods, within the Natural Park 'Parco del Po Vercellese-Alessandrino', in the southern part of Vercelli Province. The first site consisted of a typical intensive agricultural landscape close to a wetland area (named ‘Riserva Naturale Speciale e Zona di Salvaguardia della Palude di San Genuario’, 8°10'54"E, 45°13'7"N) dominated by rice fields, the most important cultivation of the area. The second site was an oak-hornbeam (*Quercus* and *Carpinus* species) woodland area (named ‘Parco Naturale del Bosco delle Sorti della Partecipanza’, 8°16'1"E, 45°13'50"N). Both sites are SCIs (Sites of Community Importance) and ZSPs (Zones of Special Protection under the Birds Directive).

Field survey protocol

We designed the playback field experiment as follows: in each habitat we established one transect with ten points, spaced 200 m apart, and each point was visited eight times (i.e. eight repetitions). At each repetition, one researcher (the ‘broadcaster’) moved to a random location around one single surveyor (the ‘observer’) and broadcast the whole call sequence (noting the time of broadcast) of all five species. The surveyor stayed fixed at each point and (i) noted the time and species when a call was detected and (ii) estimated playback distances (assigning calls to distance classes of between 0 - 100 m, 100 - 200 m, 200 - 300 m, 300 - 400 m, 400 - 500 m and > 500 m). At each repetition, the surveyor did not know the location of the broadcaster. We used a handheld GPS (Garmin eTrex 10) to identify survey points and to note the location of each playback made by the broadcaster. We conducted one survey in farmland and one in woodland in winter (between the end of February and the beginning of March 2020); then we repeated a third survey only in woodland in summer (mid-July 2020) to test for a seasonal effect in this habitat. We performed all surveys in good weather conditions (i.e. not on rainy or windy days). Although the target species were nocturnal (Long-eared Owl, Tawny Owl), crepuscular, or more vocally active at night (Water Rail, Little Owl, Nightingale), we carried out the surveys in daylight, partly due to access restrictions, but also to minimise the potential confounding effects of real (rather than broadcast) vocalizations.

We delivered playback using a handheld Bluetooth wireless speaker (Tronsmart Element, T6 Mini) positioned at chest height (Pilla *et al.* 2018), c. 1.6 m above the ground. The device was designed to spread sound at 360° to ensure that vocalisations were broadcast in all directions. The call sequence consisted of territorial vocalisations of the five species, downloaded from the Xeno-canto website (www.xeno-canto.org), which were then uploaded to a smartphone and broadcast with the speaker via Bluetooth. We always maintained the following order for the sequence: Common Nightingale > Water Rail > Little Owl > Long-eared Owl > Tawny Owl. For each species, broadcast calls lasted 30 seconds, without intervals between them. After the whole sequence had been completed, the broadcaster moved to another random location unknown to the surveyor and repeated it. This procedure was carried out eight times for each point (i.e. eight repetitions made in eight random locations for each of the ten points). The start and end of each repetition was notified to the surveyor by text message. Once all the repetitions for a point were completed, the surveyor moved to the next point along the transect.

We adjusted a fixed volume for all broadcasts at a level equivalent to the sound pressure level of natural vocalizations. We used a sound level meter (SLM Meterk MK 09) to set the volume in order to match natural levels: 81 ± 1 dB for Common Nightingale (Kiefer *et al.* 2011); 82 ± 1 dB for Little Owl (Jacobsen *et al.* 2013, Clewley *et al.* 2016); and, 83 ± 1 dB for Tawny Owl (Vrezec & Bertoncelj 2018). We were unable to find information on Water Rail and Long-eared Owl vocalizations, so we respectively set 80 ± 1 dB and 73 ± 1 dB, i.e. relatively low values matching our personal observations of these species relative to the others listed above. We obtained all dB values by positioning the SLM at a distance of 1 m.

Data analysis

We used Garmin BaseCamp software to download location data from the GPS and to calculate real distances between the surveyor and broadcaster. To evaluate the effect of distance on detection probability, we used a mixed modelling approach, fitting binomial generalized linear mixed models (GLMM) to explain the probability of hearing playback calls (binomial response: 1 = calls heard; 0 = calls not heard) and the probability of estimating distances of those calls that were detected correctly (binomial response: 1 = distances estimated in the correct class; 0 = distances not estimated in the correct class). Survey point identity was specified as a random effect in order to account for repeated observations from the same point, and real distances, habitat and species were specified as fixed effects. To test for a seasonal effect in woodland, we used the same approach and included season (winter or summer) and the interaction term between Real distance and season. Before modelling, the 'Real distance' variable was scaled. Models were validated using the Hosmer-Lemeshow goodness of fit test (Hosmer & Lemeshow 2000), where a significant test result (as measured by the chi-squared statistic) indicates poor model fit. When this occurred, we used Cook's distance approach (Cook 1979) to identify and remove potential outliers.

Since we always maintained the same order of species to broadcast calls, there was potential temporal autocorrelation in the probability of detecting a call between species, for both distance estimation and the resulting classification into distance classes, since the observer would have known that the whole broadcast came from the same location (i.e. at the same distance). In other words, after hearing the first call, the surveyor could have been more likely to detect subsequent calls in the sequence, as they would have known what came next. For this reason, GLMMs fitted to the ability to hear playback calls could potentially be affected by non-independence. Therefore, to verify their consistency, we also ran models based on generalized estimating equations (GEEs) that accounted for the potential non-independence by fitting broadcast call order as a temporal correlation structure and defining each broadcast of the five species within a playback repetition as a group that combined point identity and repetition number.

Statistical analyses were carried out using R software (v. 3.6.3; R Core Team 2020). GLMMs were fitted in the lme4 package (Bates *et al*. 2015) and their results visualised with ggplot2 (Wickham 2016). GEE models were fitted in the geepack package (Halekoh *et al*. 2006).

RESULTS

We carried out 1200 broadcasts in total: 400 in farmland (first survey) and 400 in woodland (second survey) in winter, and 400 in woodland in summer (third survey). Real distances ranged between 34.6 and 365.5 m and the number of broadcast calls, correct distance estimates and calls detected varied among distance classes. Estimating playback distances correctly (c. 28 % of broadcasts were estimated in the correct distance band) was more difficult than being able to hear broadcast calls (c. 78 % of calls were detected; **Table 1**).

Effect of distance on detectability in both habitats in winter

The ability to hear playback calls across all species declined significantly with distance (slope = -1.64 ± 0.17, z = -9.69, $p < 0.001$; **Table S1a**, Appendix). Predicted probabilities of hearing calls were often high at 200 m, especially in woodland, and the easiest species to hear was Little Owl (estimated probability = 0.97), followed by Tawny Owl (0.96), Common Nightingale (0.82), Water Rail (0.81) and Long-eared Owl (0.67; **Figure 1**). At a distance of 300 m, probabilities dropped, particularly for Long-eared Owl, Water Rail and Common

Nightingale (respectively 0.14, 0.26 and 0.28 in woodland). Detection probabilities were always significantly higher in woodland than farmland ($p < 0.001$). The Hosmer-Lemeshow test showed a good model fit ($\chi^2 = 8.09$, *df* = 8, $p > 0.05$). The GEE model supported the GLMM in that hearing playback calls declined with distance very similarly (slope = -1.61 ± 0.15, w = 110.96, $p < 0.001$; **Table S1b**, Appendix). The lack of any qualitative difference between the GLMM and GEE results thus suggests that potential temporal autocorrelation between the calls in a given sequence did not affect the conclusions regarding the estimates of probability of hearing calls in relation to distance.

The ability to estimate playback distances correctly for calls that were detected declined significantly with distance (slope = -1.39 ± 0.16, z = -8.56, $p < 0.001$; **Table S1c**, Appendix). Predicted probabilities of assigning distances to the correct distance band were low: all < 18 % at 200 m and < 3% at 300 m (**Figure 2**). In woodland at 200 m, the best estimates were associated with Common Nightingale (0.17) and the lowest with Long-eared Owl (0.04). Probabilities were significantly higher in woodland than farmland ($p < 0.01$). The Hosmer-Lemeshow test showed a good model fit ($\chi^2 = 9.40$, *df* = 8, $p > 0.05$).

For detected calls, in the first and second survey, distances estimated wrongly were all overestimation errors, i.e. the surveyor always placed estimates in a distance class further than the correct one. In total, 248 overestimations were made in the first survey and 215 in the second (**Table S2**, Appendix). The number of misclassifications declined in consecutive surveys for each species except for the Long-eared Owl (**Table S3**, Appendix).

Seasonal variation in woodland

The effect of distance on the ability to hear playback calls was significant (slope = -1.42 ± 0.19 , z = -7.67, $p < 0.001$; **Table S1d**, Appendix), but did not change between the second and third survey, i.e. there was no difference in slope between winter and summer (parameter estimate = -0.16 ± 0.32, z = -0.5, $p > 0.05$). However, season was significant ($p < 0.001$) and predicted probabilities were higher in winter (**Figure 3**). Little Owl and Tawny Owl were the easiest species to detect, and Long-eared Owl the hardest (respectively 0.97, 0.97 and 0.74 at 200 m in winter). At 200 m, probabilities were generally high, but at 300 m they were always less than 52 % in summer and 72% in winter. The Hosmer-Lemeshow test did not show a good model fit ($\chi^2 = 26.0$, *df* = 8, $p < 0.05$). We investigated this poor model fit by looking for possible outliers that mostly negatively influenced the model and we dropped the number of observations (n = 6) which revealed the highest Cook’s distance values. This was the minimum number of observations that enabled an improvement in model fit (χ^2 =

11.0, *df* = 8, $p > 0.05$). No qualitative differences were found in the model results (**Table S1e**, Appendix).

Again, the GEE model did not show differences compared to the GLMM, neither in terms of the distance effect on the ability to hear calls (slope = -1.04 ± 0.24 , w = 19.19, $p < 0.001$; **Table S1f**, Appendix) nor in terms of difference in slope between seasons (parameter estimate = -0.45 ± 0.30, w = 2.20, $p > 0.05$).

Overall, playback distances were estimated increasingly erroneously in more distant zones (slope = -0.76 ± 0.12, z = -6.14, $p < 0.001$; **Table S1g**, Appendix) and there was a significant seasonal variation (parameter estimate = -0.58 ± 0.23, z = -2.56, $p < 0.05$). Predicted probabilities were generally higher in summer than in winter (**Figure 4**), and higher at 200 m than 300 m for all species. Higher probabilities were associated with Little Owl and Common Nightingale (both 0.32 at 200 m and 0.14 at 300 m in summer), while the Long-eared Owl remained the most difficult species to estimate (0.20 at 200 m and 0.08 at 300 m in summer). The Hosmer-Lemeshow test did not show a good model fit ($\chi^2 = 29.0$, *df* = 8, $p < 0.05$). So, as before, we dropped the minimum number of observations (n = 20) with the highest Cook's distance values which enabled to improve the model fit ($\chi^2 = 14.0$, *df* = 8, $p > 0.05$). No qualitative differences were found in the model results, except for an increase in the significance of seasonal variation (parameter estimate = -0.89 ± 0.28, z = -3.16, $p < 0.01$; **Table S1h**, Appendix).

In the third survey, overestimations decreased (from 100 % in both the first and second survey to 64 % in the third), but there were also some underestimations (36 %) which occurred between 0-100 m and 100-200 m. However, the surveyor made in total fewer wrong estimates (n = 139). In fact, no erroneous estimates were made in the two furthermost classes (**Table S2**, Appendix). In relation to species, errors decreased overall (**Table S3**, Appendix).

DISCUSSION

Through this field evaluation, we investigated the effect of distance on surveyor detection capability, expressed in terms of being able to hear playback calls and estimating distances to the calls correctly. Other studies have attempted to evaluate the response distance of elusive birds and the distance from the surveyor (Proudfoot *et al.* 2002, Flesch & Steidl 2007, Bartolommei *et al.* 2012), because its measurement helps to improve detection and determine bird densities. Monitoring nocturnal birds, Puglisi & Bartolommei (2012) estimated the distance of detected birds from the surveyor, selecting four distance classes (<

50, 50 - 100, 100 - 300 and > 300 m). They always detected Long-eared Owl at distances less than 100 m, whereas Little Owl and Tawny Owl were detected across all classes. Such classes were considered by Bartolommei *et al*. (2012), who adopted a 300 m radius in their methods to investigate the presence and distribution of Little Owl and Tawny Owl according to land-use categories in an agricultural landscape of Central Italy. Instead, unlike Bartolommei *et al*. (2012), in our experiment we specifically fitted models to evaluate separately the probability to detect calls and to estimate distances correctly in relation to distance, testing also a seasonal effect.

Some playback field experiments have already been conducted in forested habitats to evaluate distance estimates and their error structure for various songbirds, using known distances. Alldredge *et al*. (2007) used playback songs of several birds (Acadian Flycatcher *Empidonax virescens*, Black-and-white Warbler *Mniotilta varia*, Black-throated green Warbler *Dendroica virens*, Red-breasted Nuthatch *Sitta canadensis*, and Wood Thrush *Hylocichla mustelina*) and found that surveyors had difficulties to identify what was the distance to the bird song at distances beyond 65 m. They also pointed out that, after training, surveyors reduced distance estimation errors. In our approach, we instead used unknown distances, chosen randomly by the broadcaster, and the surveyor was unaware of their location. This had the objective of simulating real situations in the field, when surveyors have to census species that can be anywhere. Moreover, in our study, we considered detection both in terms of the ability to estimate distances and the ability to hear broadcast calls.

The effect of distance on surveyor detection capability

Our results showed that detectability varied due to both species and distance. The decrease in detectability was especially marked in those species whose calls are low in acoustic intensity. In particular, this was the case for the Long-eared Owl, the hardest species to hear and to estimate distance. This was consistent with our expectations as its territorial call is not very loud. On the contrary, Little Owl and Tawny Owl were the easiest species to detect, thanks to their shrill and more acute vocalisations. Water Rail and Common Nightingale were challenging to detect, but not as difficult as Long-eared Owl, although during the summer survey, Common Nightingale showed estimates as high as those for Little Owl, and Water Rail as high as those for Tawny Owl. Detecting playback calls was less difficult than estimating their distances correctly, but we noted an improvement in both (respectively a c. 20 % and 28 % increase) between the first and the second survey. In woodland, detectability was higher overall. This is a surprising result as we did not expect such a striking difference compared to farmland. Nevertheless, the latter habitat, being an open environment, could have been more influenced by potential background noise (e.g. from roads nearby), which may explain this divergence. Though, we suggest caution in interpreting this difference and more field trials would be useful to better assess this aspect.

The ability to hear playback calls in woodland did not improve during the third survey in summer. The probability of hearing broadcast calls was significantly lower in summer than winter ($p < 0.001$). This can be explained by the likely blocking effect of the dense vegetative structure characterizing woodland in this season. Moreover, in summer this habitat is more disturbed in terms of background sounds: Throughout the summer survey, there was a continuous noise, represented especially by the singing of grasshoppers and Common Blackbirds *Turdus merula*. Together with the thick foliage, sound diffusion was hampered. Therefore, in summer woodland can act as a natural “acoustic barrier”, limiting the surveyor’s ability to hear bird calls (**Figure 5**). Conversely, in winter, there was less acoustic disturbance.

Despite the dense vegetation and background noise, the effect of distance on the ability to estimate playback distances improved significantly in summer, during the last survey. This fact is likely due to an increase in our field experience. After the first survey, we were able to better calibrate estimates and reduce errors, in particular in terms of overestimated distances. For detected calls, distance estimate errors decreased by 8.3 % between the first and second survey and by 19 % between the second and the third. Surveyor experience has already been demonstrated to be a relevant factor affecting bird detection probabilities (Booms *et al*. 2010, Jiguet & Williamson 2010, Johnston *et al*. 2018), including nocturnal species (Zuberogoitia *et al*. 2020). A radial distance of about 200 m, at which playback could be heard, has previously been adopted to census Tawny Owls (Appleby *et al*. 1999). In another case, a distance of 300 m was used for Tawny Owl and Little Owl (Bartolommei *et al*. 2012) as it proved to be the best estimated distance for both species. Detection radius is not a constant value and it varies across studies, because it changes according to target species, habitat and surveyor detection capability (Centili 2001, Esclarski & Cintra 2014, Menq & Anjos 2015, Zuberogoitia *et al*. 2020). Therefore, given these sources of variation, tests like ours should be made before playback surveys.

Based on our results, at 300 m we found that the detection capability was quite weak overall, mainly in terms of the ability to estimate distances correctly. Therefore, we suggest that a 200 m detectability radius should be set as maximum threshold. In our study any inference from playback can only be reliably related to this radial distance around the surveyor, i.e. inferences about our target species should be limited to 200 m because most of the detected calls will be within that distance. For Common Nightingale, Water Rail and Long-eared Owl, which were generally more difficult to detect than Little Owl and Tawny Owl, a radius of 100 m could certainly be a good option. However, for a multi-species community level study, a common cut-off can ease the comparison of results at the same scale among all species. In this case, a 200 m limit would be a reasonable alternative. Distance estimates were, however, generally poor, and for most species the probability of accurately estimating distance was greater than 0.50 only at distances of 100 m or less. Distance sampling methodology is an appropriate tool to estimate density when distances to species are known, but it assumes distances to be estimated without errors (Buckland *et al.* 1993), which was not the case in our study. Indeed, errors occur even with wide distance classes and experienced observers (Neubauer & Sikora 2020). We should stress that density estimation was not the purpose of our study. Instead, our goal was an attempt to understand at what scale detection and distribution could be estimated for our target species, which is likely a 200 m radius. At greater distances, detection probabilities became very low.

Based on different study objectives, researchers could carry out field experiments like this for their species of interest, identifying a suitable detectability radius through the evaluation of the two detectability components analysed prior to the actual surveys of the species. We recommend that our methods should be generally considered with more caution for Long-eared Owl, Common Nightingale and Water Rail. We particularly acknowledge that in our study, the component related to distance estimation could not be carried out accurately for these three species without training.

Field experiment timing and potential bias

As we described in methods, we maintained the same order of species calls during the experiment, potentially leading to a non-independence bias among subsequent calls of different species. However, our results showed that this methodological choice unlikely affected GLMM outcomes. Estimates relative to the effect of distance on detectability did not differ substantially between GLMM and GEE approaches, and the significance levels of variables did not change. This suggests consistency between the two modelling approaches, hence we are confident that this kind of bias did not affect the validity of our analysis regarding the surveyor’s ability to hear broadcast calls.

Although the focus of this study was on crepuscular and nocturnal species, the playback experiment was carried out during daytime. This was partly due to access restrictions in some parts of the study area (particularly in rice fields), but also in order to avoid confounding real vocal responses from the study species. Similarly, the experiments started in late winter, when some of our target species are not vocally active or had not yet returned from their wintering areas (in particular Little Owl, Water Rail and Common Nightingale). In order to make use of these results to inform methods for playback surveys of the target species, the underlying assumption that the performance of the surveyor is not affected by time of day and season needs to be addressed. In terms of the former, we would expect that background noise is likely to be higher in the daytime, both from natural and anthropogenic sources, hence we can consider our estimates to be appropriately conservative (i.e. we expect that performance would be higher at night). In terms of the latter, we did find evidence of seasonal effects in woodland, although these were inconsistent between probability of detection (which was marginally greater in winter) and probability of correct distance estimation (which increased in summer). However, the latter results did not change our overall conclusions regarding methodological recommendations, i.e. that playback surveys are likely to be most representative of a 200 m radius surrounding the surveyor where the probability of detection is highest, while estimates of distance from the observer are likely to be inaccurate in most cases.

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APPENDIX

Table S1: parameter estimates from the binomial GLMM/GEE explaining the ability to hear playback calls and estimate distances correctly

Table S1a. Ability to hear playback calls in farmland and woodland in relation to distance.

Variable	Estimate	Standard error	Z value	P value
Intercept	1.399	0.398	3.511	0.0004
SReal distance	-1.636	0.169	-9.696	< 2e-16
Habitat (Woodland)	1.859	0.513	3.627	0.0003
Species (Little Owl)	2.089	0.458	4.562	5.1e-06
Species (Long-eared Owl)	-0.897	0.351	-2.561	0.010
Species (Tawny Owl)	1.720	0.430	4.001	6.3e-05
Species (Water Rail)	-0.065	0.358	-0.181	0.856

Model outcome showing fixed effects. The reference level (Intercept) is represented by ‘Farmland’ for Habitat and ‘Common Nightingale’ for Species. Random effect variance: 0.8 ± 0.9.

Table S1b. Ability to hear playback calls in farmland and woodland in relation to distance (GEE model).

Variable	Estimate	Standard error	w value	P value
Intercept	1.297	0.272	22.679	1.9e-06
SReal distance	-1.613	0.153	110.959	< 2e-16
Habitat (Woodland)	1.466	0.316	21.463	3.6e-06
Species (Little Owl)	1.896	0.416	20.730	5.3e-06
Species (Long-eared Owl)	-0.784	0.296	7.032	0.008
Species (Tawny Owl)	1.576	0.410	14.763	0.0001
Species (Water Rail)	-0.053	0.261	0.040	0.841

Model outcome showing fixed effects. The reference level (Intercept) is represented by ‘Farmland’ for Habitat and ‘Common Nightingale’ for Species. Model alpha parameter: 1.2 ± 0.1.

Table S1c. Ability to estimate playback distances correctly in farmland and woodland in relation to distance.

Variable	Estimate	Standard error	Z value	P value
Intercept	-2.516	0.482	-5.220	1.7e-07
SReal distance	-1.393	0.163	-8.560	< 2e-16
Habitat (Woodland)	1.888	0.585	3.230	0.001
Species (Little Owl)	-0.290	0.309	-0.940	0.348
Species (Long-eared Owl)	-1.593	0.355	-4.490	7.0e-06
Species (Tawny Owl)	-0.441	0.312	-1.410	0.157
Species (Water Rail)	-0.241	0.308	-0.780	0.435

Model outcome showing fixed effects. The reference level (Intercept) is represented by 'Farmland' for Habitat and 'Common Nightingale' for Species. Random effect variance: 1.3 ± 1.2.

Table S1d. Ability to hear playback calls in woodland in relation to distance and season.

Variable	Estimate	Standard error	Z value	P value
Intercept	0.916	0.419	2.190	0.029
SReal distance	-1.419	0.185	-7.670	1.8e-14
Season (Winter)	1.601	0.299	5.350	8.8e-08
Species (Little Owl)	2.335	0.452	5.160	2.5e-07
Species (Long-eared Owl)	-0.105	0.323	-0.320	0.746
Species (Tawny Owl)	2.335	0.452	5.160	2.5e-07
Species (Water Rail)	0.107	0.327	0.330	0.742
SReal distance:Season (Winter)	-0.161	0.322	-0.500	0.617

Model outcome showing fixed effects. The reference level (Intercept) is represented by 'Summer' for Season and 'Common Nightingale' for Species. Random effect variance: 1.1 ± 1.

Table S1e. Ability to hear playback calls in woodland in relation to distance and season (without outliers).

Variable	Estimate	Standard error	Z value	P value
Intercept	0.975	0.543	1.790	0.073
SReal distance	-1.646	0.208	-7.930	2.2e-15
Season (Winter)	1.953	0.339	5.740	9.2e-09
Species (Little Owl)	2.563	0.479	5.350	8.7e-08
Species (Long-eared Owl)	-0.003	0.343	-0.010	0.994
Species (Tawny Owl)	2.715	0.494	5.490	4.0e-08
Species (Water Rail)	0.179	0.347	0.520	0.605
SReal distance:Season (Winter)	-0.139	0.369	-0.380	0.707

Model outcome obtained removing the outliers. The reference level (Intercept) is represented by ‘Summer’ for Season and ‘Common Nightingale’ for Species. Random effect variance: 2.2 ± 1.5.

Table S1f. Ability to hear playback calls in woodland in relation to distance and season (GEE model).

Variable	Estimate	Standard error	w value	P value
Intercept	0.760	0.255	8.870	0.003
SReal distance	-1.038	0.237	19.190	1.2e-05
Season (Winter)	1.364	0.320	18.180	2.0e-05
Species (Little Owl)	1.987	0.391	25.860	3.7e-07
Species (Long-eared Owl)	-0.091	0.255	0.130	0.722
Species (Tawny Owl)	1.981	0.395	25.200	5.2e-07
Species (Water Rail)	0.083	0.226	0.130	0.715
SReal distance:Season (Winter)	-0.448	0.302	2.200	0.138

Model outcome obtained removing the outliers. The reference level (Intercept) is represented by ‘Summer’ for Season and ‘Common Nightingale’ for Species. Model alpha parameter: 0.3 ± 0.2.

Table S1g. Ability to estimate playback distances correctly in woodland in relation to distance and season.

Variable	Estimate	Standard error	Z value	P value
Intercept	-0.239	0.269	-0.890	0.374
SReal distance	-0.756	0.123	-6.140	8.4e-10
Season (Winter)	-0.619	0.188	-3.300	0.0009
Species (Little Owl)	-0.032	0.253	-0.130	0.899
Species (Long-eared Owl)	-0.676	0.262	-2.580	0.009
Species (Tawny Owl)	-0.162	0.254	-0.640	0.525
Species (Water Rail)	-0.162	0.254	-0.640	0.525
SReal distance:Season (Winter)	-0.582	0.227	-2.560	0.010

Model outcome showing fixed effects. The reference level (Intercept) is represented by ‘Summer’ for Season and ‘Common Nightingale’ for Species. Random effect variance: 0.3 ± 0.6.

Table S1h. Ability to estimate playback distances correctly in woodland in relation to distance and season (without outliers).

Variable	Estimate	Standard error	Z value	P value
Intercept	-0.344	0.292	-1.180	0.238
SReal distance	-1.010	0.141	-7.150	8.5e-13
Season (Winter)	-0.875	0.223	-3.920	8.9e-05
Species (Little Owl)	-0.036	0.269	-0.130	0.893
Species (Long-eared Owl)	-0.923	0.285	-3.240	0.001
Species (Tawny Owl)	-0.183	0.270	-0.680	0.499
Species (Water Rail)	-0.216	0.271	-0.800	0.426
SReal distance:Season (Winter)	-0.888	0.281	-3.160	0.0016

Model outcome obtained removing the outliers. The reference level (Intercept) is represented by ‘Summer’ for Season and ‘Common Nightingale’ for Species. Random effect variance: 0.4 ± 0.6.

Tables S2-S3: errors in distance estimation

Table S2. Errors in distance estimation made by the surveyor across surveys. The total number of broadcast calls is 400 in each survey.

Distance class (m)	Survey	Number of detected broadcasts	Number of wrong estimates	Percentage of wrong estimates (%)	Number of OE	Percentage of OE (%)	Number of UE	Percentage of UE (%)
0-100	First	288	0	0	0	0	0	0
100-200			36	14.5	36	14.5	0	0
200-300			61	24.6	61	24.6	0	0
300-400			67	27.0	67	27.0	0	0
400-500			46	18.6	46	18.6	0	0
>500			38	15.3	38	15.3	0	0
Total			248	100	248	100	0	0
0-100	Second	366	0	0	0	0	0	0
100-200			46	21.4	46	21.4	0	0
200-300			107	49.8	107	49.8	0	0
300-400			48	22.3	48	22.3	0	0
400-500			10	4.7	10	4.7	0	0
>500			4	1.9	4	1.9	0	0
Total			215	100	215	100	0	0
0-100	Third	289	33	23.7	0	0	33	66.0
100-200			44	31.7	27	30.3	17	34.0
200-300			39	28.1	39	43.8	0	0
300-400			23	16.6	23	25.8	0	0
400-500			0	0	0	0	0	0
>500			0	0	0	0	0	0
Total			139	100	89	100	50	100

Number and percentages of wrong distance estimates (for the calls that have been detected) per distance class made by the surveyor. Overestimates (OE) consist in estimates made in a class further than the correct one (i.e. further from the surveyor position), while underestimates (UE) consist in estimates made in a class prior than the correct one (i.e. closer to the surveyor position). Distances estimated wrongly declined across surveys, with underestimates placed only in the first two distance classes of the last survey. The first column indicates all the possible distance classes planned for the experiment, in which the surveyor could assign playback calls. Unlike **Table 1**, which provides real distance classes (i.e. those where the broadcaster actually stationed at), here there are also ‘400 - 500 m’ and ‘> 500 m’ because the surveyor, being unaware of the broadcaster’s position, could assign calls in these two classes too.

Table S3. Errors in distance estimation made by the surveyor across the surveys in relation to species. The total number of broadcast calls is 400 in each survey.

Species	**Survey**	**Number of detected broadcasts**	**Number of wrong estimates**	**Percentage of wrong estimates (%)**	**Number of OE**	**Percentage of OE (%)**	**Number of UE**	**Percentage of UE (%)**
Common Nightingale	First	288	44	17.7	44	17.7	0	0
Water Rail			44	17.7	44	17.7	0	0
Little Owl			62	25.0	62	25.0	0	0
Long-eared Owl			39	15.7	39	15.7	0	0
Tawny Owl			59	23.8	59	23.8	0	0
Total			248	100	248	100	0	0
Common Nightingale	Second	366	33	15.4	33	15.4	0	0
Water Rail			37	17.2	37	17.2	0	0
Little Owl			45	20.9	45	20.9	0	0
Long-eared Owl			51	23.7	51	23.7	0	0
Tawny Owl			49	22.8	49	22.8	0	0
Total			215	100	215	100	0	0
Common Nightingale	Third	289	19	13.7	10	11.2	9	18.0
Water Rail			23	16.5	13	14.6	10	20.0
Little Owl			39	28.1	28	31.5	11	22.0
Long-eared Owl			19	13.7	10	11.2	9	18.0
Tawny Owl			39	28.1	28	31.5	11	22.0
Total			139	100	89	100	50	100

Number and percentages of wrong distance estimates (for the calls that have been detected) per distance class made by the surveyor. The table reflects **Table S2**, but here over- (OE) and underestimates (UE) are referred to species. Generally, most distances estimated wrongly are associated with owls.

TABLES

Table 1. Summary of the values obtained during the field experiment.

Distance class (m)	Number of broadcast calls	Percentage of broadcast calls (%)	Number of correct distance estimates	Percentage of correct distance estimates (%)	Number of calls detected	Percentage of calls detected (%)
0-100	315	26.3	148	46.9	312	99.1
100-200	615	51.3	148	24.1	490	79.7
200-300	240	20.0	36	25.7	132	55.0
300-400	30	2.5	5	16.7	9	30.0
Total	1200	100	337	28.1	943	78.6

Number and percentage of broadcast calls, correct distance estimates and calls detected according to distance classes.

LEGENDS TO FIGURES

Figure 1: Binomial GLMM showing the predicted probabilities of hearing playback calls in farmland (n = 400) and woodland (n = 400) in relation to distance.

Figure 2: Binomial GLMM showing the predicted probabilities of estimating distances correctly in farmland (n = 400) and woodland (n = 400) in relation to distance.

Figure 3: Binomial GLMM showing the predicted probabilities of hearing playback calls in woodland in relation to distance and season (n = 400 in winter and n = 400 in summer).

Figure 4: Binomial GLMM showing the predicted probabilities of estimating distances correctly in woodland in relation to distance and season (n = 400 in winter and n = 400 in summer).

Figure 5: Pictures taken in woodland at the same point in winter and summer to show the difference in terms of vegetation structure, which can act as a natural "acoustic barrier".

FIGURES

Figure 1

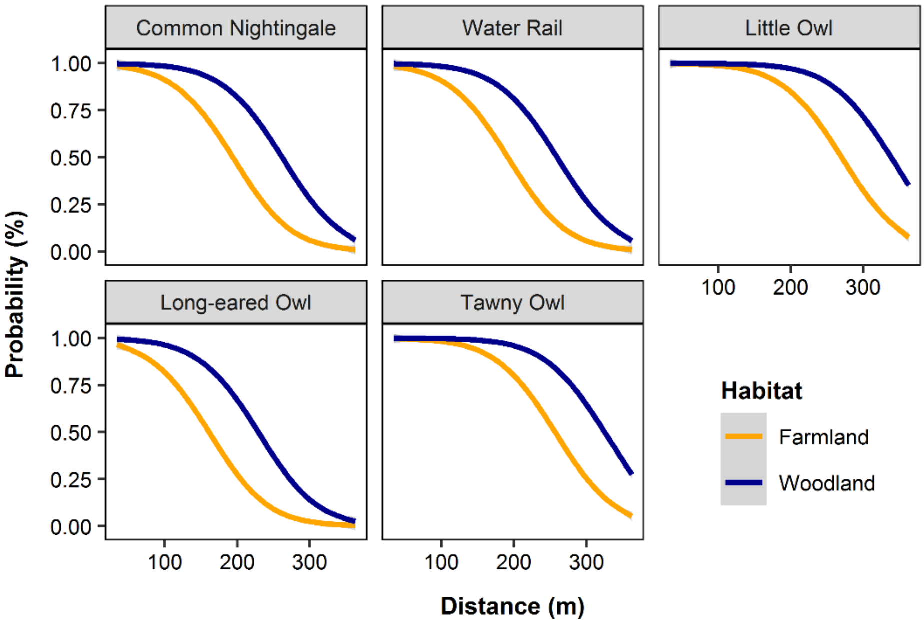

Figure 2

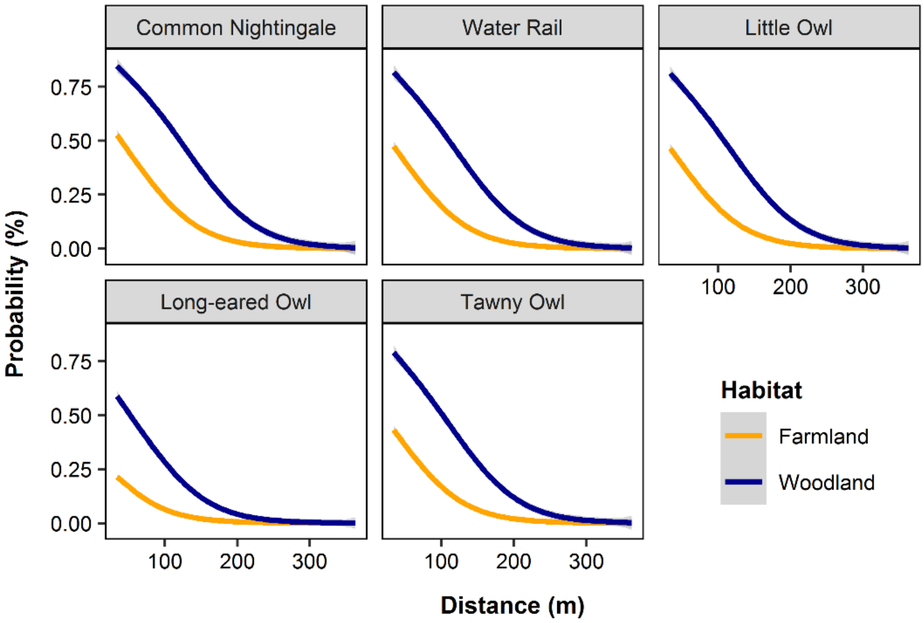

Figure 3

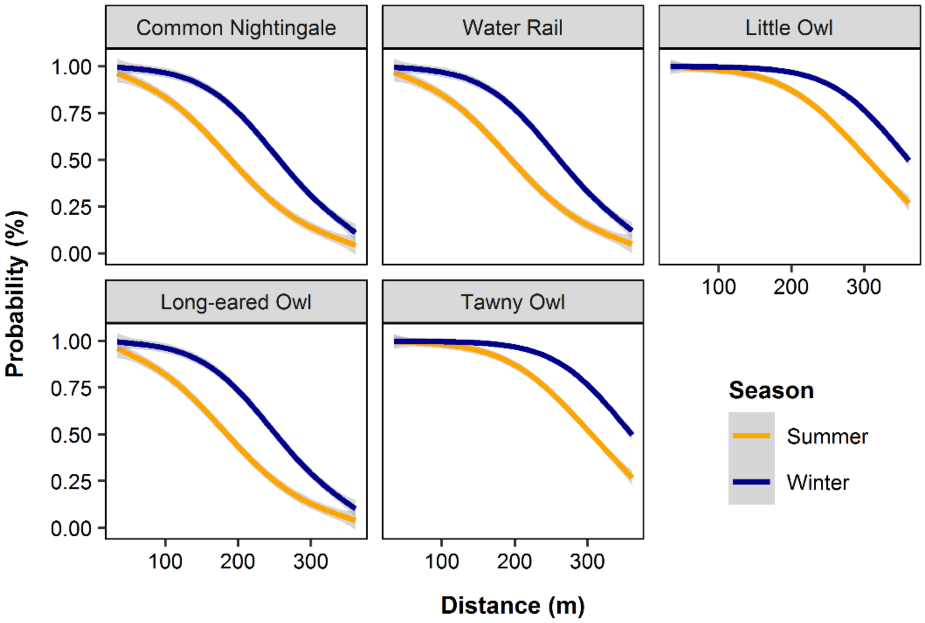

Figure 4

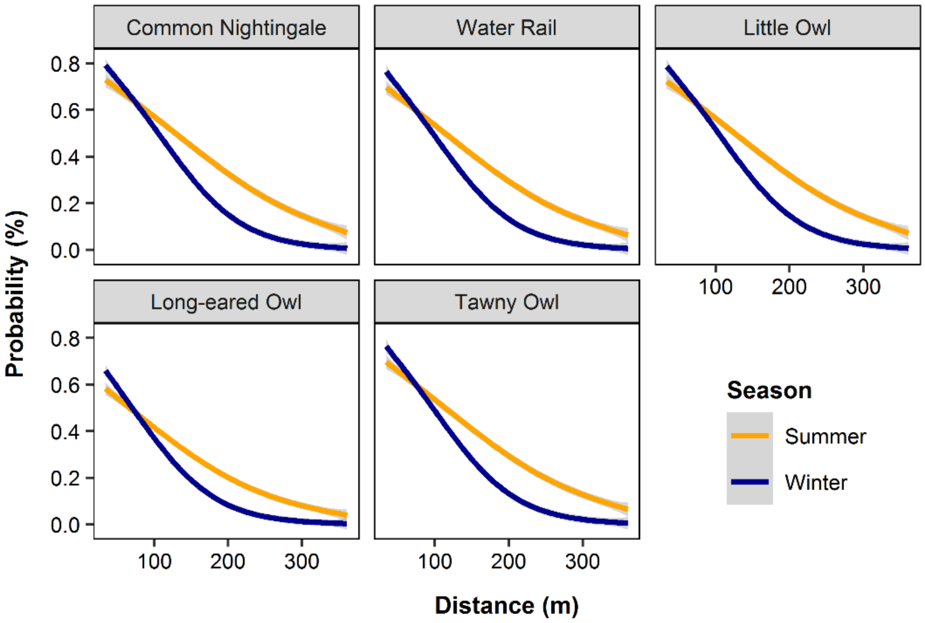

Figure 5

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