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Presence of humans and domestic cats affects bat behaviour in an urban nursery of greater horseshoe bats (*Rhinolophus ferrumequinum*)

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ABSTRACT

Proximity to humans is a primary stressor for wildlife, especially in urban habitats where frequent disturbance may occur. Several bat species often roost in buildings but while the effects of disturbance inside the roost are well documented, little is known about those occurring in the proximity of roosts. We tested the effects of anthropogenic stressors on bats by monitoring reactions to disturbance in a colony of greater horseshoe bats (*Rhinolophus ferrumequinum*). We assessed disturbance by recording and quantifying the presence of people, domestic cats and noise sources near the roost. Disturbance outside the roost caused the disruption of roosting clusters; when cats entered the roost, bats decreased indoor flight activity. Emergence timing was delayed when people were close to the roost exit, and the delay increased along with the number of people. The occurrence of a cat increased the degree of group clustering during emergence. Cats entered the roost especially when young bats were present, and bat remains occurred in 30% of the cat scats we examined. We show that the occurence of human activities near roosts and free-ranging domestic cats are important albeit overlooked sources of disturbance.

1. Introduction

Proximity to humans is a primary stressor for wildlife. While large-scale effects of deterministic human impacts on wildlife, such as habitat loss and fragmentation, are very well documented (e.g. Fahrig, 1997; Fischer and Lindenmayer, 2007), the small-scale adverse effects of human disturbance are less studied (Bennet et al., 2009). The absence of many wildlife species from human-dominated landscapes may in fact not only be due to scarcity of key resources such as food or suitable habitat, but also to stressors such as vehicular traffic, artificial illumination, and presence of people and domestic animals (Lowry et al., 2013).

Urban habitats pose novel physiological, ecological and behavioural challenges that exclude many species (Croci et al., 2008), while others may persist or even thrive in human-dominated environments (Lowry et al., 2013), since the latter act as filters to mammalian communities (Santini et al., 2019). Persisting species, called synurbic, are often deemed tolerant to human disturbance, but in fact this might still affect negatively their life activities, and ultimately their fitness. Cities and other urban settlements are expanding worldwide, replacing natural landscapes, and will represent a globally dominant environment in the near future (Seto et al., 2010). The fact that many species providing valuable ecosystem services or that are at risk in other habitat types may tolerate urbanization and settle in urban habitats makes such environments still valuable for conservation (Luna et al., 2018). Even synurbic species, however, may be subject to subtle, sub-lethal effects induced by the presence of humans or domestic animals, which might have key implications for activities such as foraging or reproduction (Beckerman et al., 2007) and contribute to shape “landscapes of fear” (Laundré et al., 2010). Detecting and managing potential wildlife stressors in urban environments is therefore a priority of 21st century biodiversity preservation.

Urban wildlife can go unnoticed, or may be perceived as a nuisance by people, which often leads to conflicts with humans (Manfredo and Dayer, 2004). Yet, the presence of wildlife in urban areas may be desirable (López-Baucells et al., 2017) when it provides ecosystem services, from suppression of insects harmful to human health to the economic benefits of attracting wildlife enthusiasts – i.e., eco-tourists (Christiansen et al., 2013; Moore et al., 2016). Even apparently benign interactions with people, however, may alter animal behaviour (Blanc et al., 2006), and lead to management problems, so the dynamics of human-wildlife interactions in urban areas warrant special attention.

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Many bat species cannot cope with urban landscapes, while others can, often roosting in buildings or foraging near street lamps (e.g. Russo and Ancillotto, 2015). Buildings, in particular, have a great value as bat roosts (Kunz, 1982), when they replicate the structural and functional properties found in natural roosts. In fact, they are largely available in urbanized areas, and may even provide microclimatic advantages over natural roosts, especially in terms of thermal stability (Lausen and Barclay, 2006).

Bats make an especially interesting case of human-wildlife interaction for several reasons. While colonies in buildings may lead to conflict with people (Stone et al., 2015a,b), insectivory by bats is often welcome as bats suppress arthropods harmful to public health that thrive in cities such as mosquitos and midges (Russo et al., 2018). Many bat species are at risk, so their protection is a well-recognized social and environmental issue also in urban environments (Russo and Ancillotto, 2015), where roost protection has paramount conservation importance. Bats typically show negative responses to human presence inside their roosts (Speakman, 1991; Cardiff et al., 2012; Tanalgo et al., 2016; Hayman et al., 2017), but almost nothing is known for the effects of human disturbance in their surroundings (but see Shirley et al., 2001).

Urban bats are also exposed to predation by invasive species (Welch and Leppanen, 2017) and domestic cats, which may locally induce high bat mortality (Ancillotto et al., 2013; Scrimgeour et al., 2012; Vlaschenko et al., 2019). Besides killing their prey, predators may induce non-lethal yet highly harmful effects on it (Beckerman et al., 2007), but whether this also holds true for bats is unknown.

In this study, we test the behavioural responses to disturbance by humans and domestic cats on a reproductive colony of greater horseshoe bats (*Rhinolophus ferrumequinum*) roosting in a building within a village of central Italy. Albeit being classified as Least Concern in the IUCN global redlist (Piraccini, 2016), *R. ferrumequinum* is a species of conservation importance in Europe due to its decreasing trend, and is listed as Vulnerable in the Italian IUCN Red List (http://www.iucn.it/scheda.php?id=-887237732). While underground sites are preferred during hibernation, maternity colonies are typically found in buildings (Dietz et al., 2009).

Here we hypothesize that anthropogenic disturbance will alter colony behaviour during daytime roosting and emergence. Specifically, we predict that disturbance occurring outside the roost during the day will induce alarm reactions such as escape behaviour, while disturbance during emergence will alter behavioural patterns, as bats perceive predation risk on emergence and hence show anti-predatory responses such as changes in timing and emergence clustering (Kalcounis and Brigham, 1994).

Predation by domestic cats may take a heavy toll on bat colonies in buildings (Ancillotto et al., 2013; Scrimgeour et al., 2012). Although there is clear evidence that cats may represent a serious threat to bats (e.g. by predation report and rescue centres: Ancillotto et al., 2013), effects on colonies and individual behaviour is poorly known; thus, we also monitored activity of domestic cats inside and nearby our study site, and hypothesize that cats may spread fear among bats, inducing risk-avoidance behaviours, e.g. when the predator makes incursions inside the roost or stalks bats during emergence, that may imply a reduction in bat individual fitness. We also investigated whether cats entering the roost actually fed on bats to establish whether bat reactions were linked to real, or only perceived, predation risk.

2. Materials and methods

2.1. Study site and video recording

The bat colony under investigation was located in an unused building in the historical centre of Barrea (L'Aquila), a village hosting a resident population of ca. 700 inhabitants in Abruzzo, Lazio and Molise National Park (central Italy). Bats hung to the ceiling of a 5 × 3 x 4 m room located at the first floor of the building, from which they emerged in the evening through an open window. The spaces around the building host several events in summer both in daytime and early evening. Since 2016, tourists are brought to watch emerging bats, an important activity that has attracted much attention on the colony, raising public awareness on the importance of promoting bat conservation.

In winter 2016, when bats were not yet present at the site, a daylight CCTV camera (IP AXIS Communication Bullet, 2.8 12 mm lens) was installed in the roost, framing the entire ceiling of the room to which bats hang. In daytime, ambient light was sufficient to obtain a clear view of the roost through the VC system. Real-time monitoring was allowed through a Wi-Fi connection, and recordings were made continuously over the 24 h through a video recorder. We used the NVR 3 Enterprise software (ACTi Corporation, Taiwan) to save 30-min avi video files to an external hard disk for later analyses. In 2017, the colony was made of 210 adult *R. ferrumequinum*, plus a few *Myotis emarginatus*. In that year, when we made our observations, bats occupied the roost on May 20th and left on September 2nd, with 111 pups being born in May–June and becoming able to fly at the end of July.

2.2. Disturbance assessment

One of us (GV) assessed disturbance by recording human presence and activities while walking a ca. 150 m path along the outer walls of the roost building every 30 min from dawn to dusk, noting the presence and number of people and/or domestic cats (assumed to act as potential predators), as well as the occurrence and nature of noise sources such as cars, people or active machinery. To avoid disturbing the bats during data collection, the observer sat down quietly and remained still and silent; video-monitoring confirmed that bats never reacted to the presence of the observer. We also recorded the number of people and cats that stayed outside the roost during dusk emergence (e.g. during bat watching sessions organized for tourists) since 30 min. before emergence until 15 min. after the last bat had left the roost. During bat watching events, people were asked to keep silent and stay at least 10 m away from the route followed by emerging bats; cats were recorded when they were 10 m or less from the roost exit or the emerging bats.

Since in previous years we had noticed the occasional access of domestic cats inside the roost, we also assessed their presence through a camera-trap (Acorn 5310A, Acorn Ltd) located at the ground level in the room where bats roosted; the camera was set to record 25 s video recordings, and was active on a 24-hrs basis over the entire study period. The camera was kept operating from July 3rd until September 11th.

Every 10 days, after bats had emerged at dusk, we entered the roost and collected any cat scat found therein. We stored scats in ethanol for later prey item identification (Klare et al., 2011).

2.3. Diurnal behaviour of bats

Based on preliminary observations of video recordings we adopted a modified version of the ethogram described by Cardiff et al. (2012), selecting two easily recognized behaviours that may be altered by disturbance: a) numbers of individuals roosting solitarily, i.e. not clustering with other colony mates, and b) numbers of indoor flight events. We concentrated on these events because they were easy to record (unlike, for instance, the number of bats in a cluster, which was often difficult to establish precisely from videos), were both descriptors of cluster disruption following disturbance events, and had potential effects on energy expenditure (flight is a costly activity, and clustering reduces the energetic expense of thermoregulation).

We assessed disturbance by selecting 10-min intervals following a disturbance event that had taken place outside or inside the roost; the corresponding video recordings were then processed with the software Solomon Coder ver. beta 14.03.10 (Péter, 2011; available at http://solomoncoder.com), and the selected behaviours recorded along the

Table 1
Generalized linear mixed models describing the effects of disturbance on diurnal behaviour in a *Rhinolophus ferrumequinum* maternity colony roosting in a building in a village of Italian central Apennines. Disturbance is meant as the presence of humans or noise by machinery in the immediate surrounding of the roost, while "cat visit" refers to a domestic cat entering the roost. * = p < 0.05; *** = p < 0.001; n.s. = not significant.

Model		R^2	Estimate ± Standard Error	T	P
Numbers of indoor flights	˜ Disturbance	0.10	−0.035 ± 0.030	−1.062	n.s.
	˜ Cat Visit	0.46	−0.225 ± 0.065	−3.474	***
Numbers of bats roosting solitarily	˜ Disturbance	0.38	1.746 ± 0.483	3.613	***
	˜ Cat Visit	0.14	1.099 ± 0.872	1.043	n.s.

entire duration of the interval. We applied the same procedure to analyse an equal number of randomly selected 10-min control recordings made within the same recording day: each of these was paired to a corresponding disturbance interval using a progressive number.

2.4. Emergence behaviour

One of us (GV) watched bat emergence every day from a place that was out of the flight path bats followed to avoid affecting emergence behaviour, visually counting bats with the aid of a bat detector (Echo Meter M3+, Wildlife Acoustics) and a tally counter. We then analysed emergence patterns assessing four behavioural descriptors (Duvergé et al., 2000): a) emergence time of the first bat (*start*, in min after sunset), b) emergence time of the median bat (*time*, in min after sunset), c) duration (time elapsed between the first and last bat exiting the roost; in min), and d) degree of emergence clustering, i.e. a measure of the tendency bats show to emerge as distinct groups, after Speakman et al. (1992). In most cases we could easily contrast bats against the light sky background, but observation conditions varied across evenings, so we used for analysis only the descriptors that could be clearly recorded on a given evening.

2.5. Analysis of cat scats

We examined the contents of cat scats to search for bat bones or fur, and quantified bat consumption as the percentage of scats including any bat remains; when possible, bone fragments and fur were identified to species following published keys (Teerink, 2004; Dietz et al., 2009; Lanza et al., 2012) and personal reference materials.

2.6. Statistical analyses

We used generalized linear mixed models (GLMMs) with a Poisson error distribution and a log-link function: we built models using each behavioural indicator separately as the response variable, disturbance presence or absence as the categorical explaining variable, and recording day as a random effect. We ran this analysis separately for disturbances occurring outside and inside the roost respectively.

We also searched for temporal matches between the access of domestic cats and colony presence and reproductive condition by running a binomial model using the cat visit on a given day as the response variable, and a categorical variable indicating whether non-volant young were absent (0) or present (1), or volant juveniles were present (2). In all tests, we set significance at $p < 0.05$.

We tested the effects of disturbance on emergence behaviour by using generalized linear models (GLMs) with normal error distribution: first we built a full model for each of the four emergence descriptors used as response variables, including the presence/absence of cat at emergence as a fixed factor, and Julian day, the number of emerging bats, and the number of people watching bat emergence as covariates. For each response we selected the best fitting model by following a backward stepwise model selection procedure, ranking potential models according to AICc values and using the function stepAIC provided in the MASS package (Ripley et al., 2013) in R 3.3.2 (R core Team, 2018). We considered valid only models with $\Delta AICc < 2$ (Burnham and Anderson, 2003).

3. Results

3.1. Effects of disturbance on bat behaviour

We recorded 25 daytime disturbance events occurring outside the roost, i.e. noisy people gathering in the vicinity of the roost (n = 11), active machinery (e.g. lawnmowers; n = 9), and high-volume music (n = 5), occurring on average every 4–5 days. We also recorded colony emergence on 87 evenings, in 15 of which > one person (range 2–18) watched bat emergence.

In agreement with our hypothesis, bats showed significant behavioural responses to the occurrence of human activities outside the roost: when disturbance took place outside the roost in daytime, we counted higher numbers of bats roosting alone than in paired control recordings ($p < 0.001$; Table 1). Bats reacted to disturbance such as activation of machinery near the roost by taking off and hanging to a different spot on the ceiling, disrupting clusters and staying alert afterwards (Fig. 1; Video S1).

As we expected, colony emergence was also influenced by the presence of people in proximity to roost entrance, yet different factors showed diverse effects on bats, and only one potential model per behaviour was valid according to model selection (Table 2). Emergence (n = 60) was only influenced by the number of individuals present in the colony, lasting longer when more bats emerged ($p < 0.001$). The time of emergence of the first bat changed only according to sunset

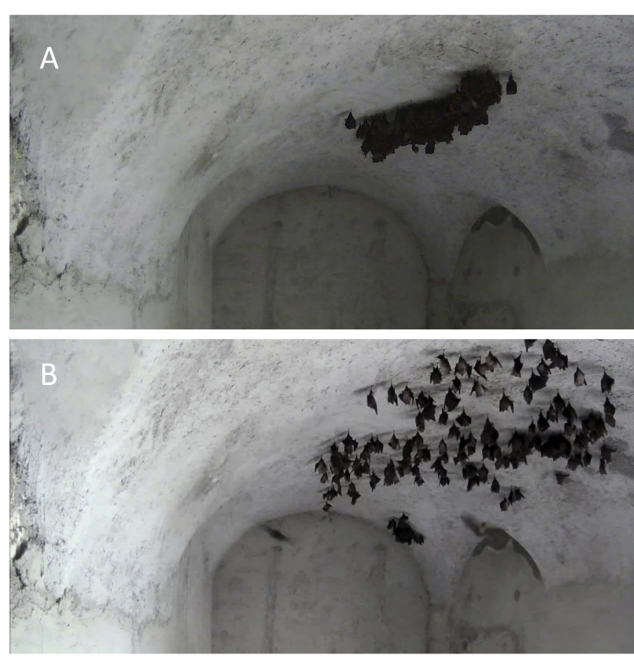

Fig. 1. Roosting behaviour of the colony of *Rhinolophus ferrumequinum* under control conditions (A) and after a disturbance event occurring outside the roost, which typically disrupted bat clusters (B).

Table 2
Generalized linear models minimum adequate models describing the effects of day, numbers of bats and disturbance on four descriptors of emergence behaviour in a *Rhinolophus ferrumequinum* maternity colony roosting inside a building in a village of Italian central Apennines. Duration = time elapsed between the first and the last emergence of individual bats; Start = time of emergence of the first bat expressed in min after sunset; Median time = time of emergence of the median bat expressed in min after sunset; Clustering = degree of colony clustering during emergence. *** = p < 0.001; * = p < 0.05.

Model	R^2	Estimate ± Standard Error	T	P
Duration ~ N bats	0.44	0.083 ± 0.017	4.775	***
Start ~ Julian day	0.38	0.254 ± 0.040	6.299	***
Median time ~ N people	0.28	0.509 ± 0.012	0.981	*
Clustering ~ Cat presence	0.61	16.773 ± 2.478	6.767	***

time, delaying from early to late summer ($p < 0.001$), while the median bat delayed emergence in response to greater numbers of people close to the roost exit during emergence ($p < 0.05$).

3.2. Effect of cats on bats

The camera trap recorded 91 videos from which we ascertained that cats had entered the roost at least 20 times (as documented by 30 video recordings and direct observations). Cats entered the roost only on days when bats were present, and the presence of a cat in the roost was more likely when flying juveniles were present (Fig. 2; binomial test $p < 0.01$). Most (85%) cat visits occurred during three weeks corresponding to the time when flying juveniles were present in the roost, when one or two cat inspections took place every one or two days.

Fur colour allowed us to established that two cats entered the roost (Fig. 3), yet most visits (90.0%) were from the same individual (a non-neutered adult male): the latter was also observed attempting to seize bats flying indoor at night (from camera trap) and outdoor during emergence (directly observed by authors), yet we witnessed no predation. The remaining video recordings pictured other animals occasionally visiting the roost, i.e. lizards (*Podarcis* spp.; n = 2) and a stone marten (*Martes foina*; n = 6), or bats flying inside at night (n = 23); 33 more recordings were apparently triggered for no evident reason. No interaction was observed between bats and such other visitors. Cats visited the roost more often ca. 1 h before bats' emergence (n = 10) or during the day (n = 6) than at night (n = 4), with visits lasting between 1 and 35 min. When a cat accessed the roost, bats flew indoor less frequently than in control recordings ($p < 0.001$; Table 1).

The presence of a cat near the roost exit during bat emergence also influenced the degree of emergence clustering ($p < 0.001$; Table 2), which significantly increased when the cat was present.

Over the study period, we collected 33 cat scats, 9 of which contained *R. ferrumequinum* fur (n = 9) and jaw fragments (n = 5). By examining size and tooth eruption patterns of jaw remains, we established that preyed bats were both juveniles (= 3) and adults (n = 2). Other prey remains comprised wood mice (*Apodemus* sp.; n = 18), birds (n = 8), and shrews (*Sorex* spp.; n = 5).

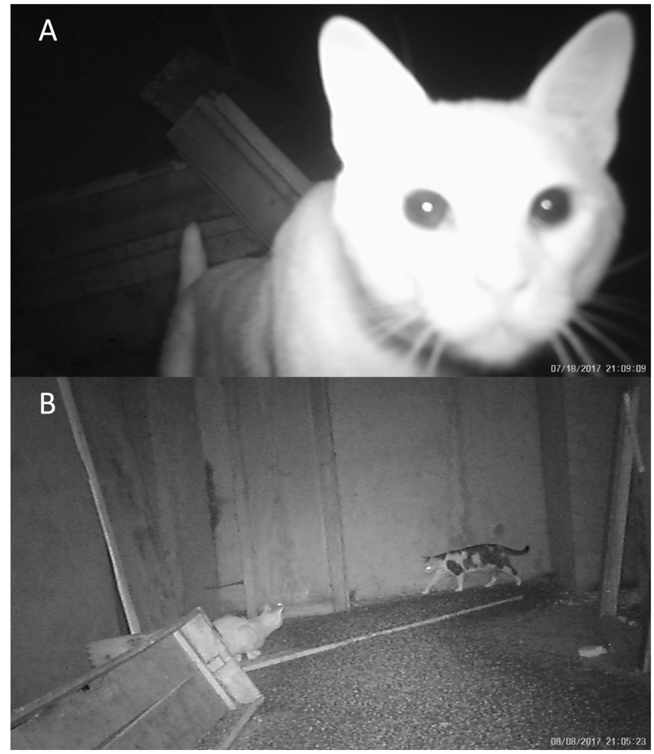

Fig. 3. Frames extracted from videos shot by a camera trap set inside the maternity roost of *Rhinolophus ferrumequinum* monitored in central Italy; A: cat inspecting the camera trap; B: two cats visiting the roost.

4. Discussion

In this study, bats in a maternity roost showed reactions to human disturbance or domestic cats both in daytime and during emergence behaviour.

As we predicted, disturbance events occurring outside the roost induced the disruption of bat clusters in the roost and the consequent increase in the number of bats roosting solitarily. It may be assumed that such events bring about adverse reaction, especially if they take place frequently, e.g. once or more times a day (which was not the case

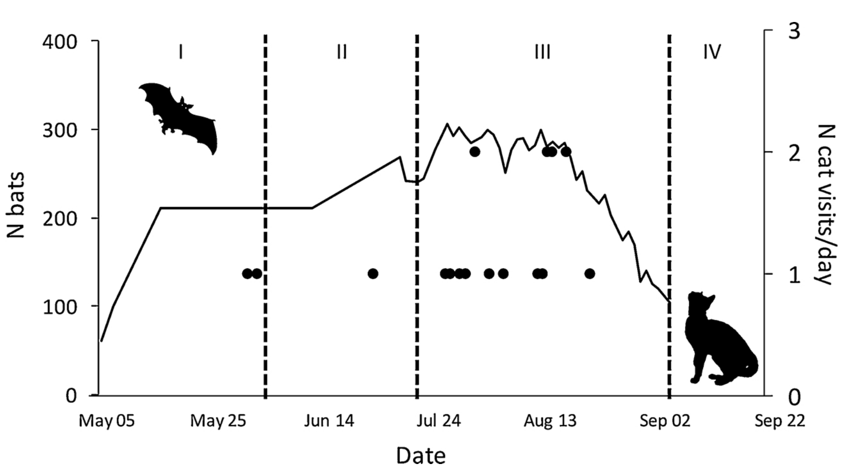

Fig. 2. Variation in colony size (continuous line) and numbers of cat visits (filled circles) in a maternity roost of *Rhinolophus ferrumequinum* roosting in a building in central Italy. Different phases of the reproductive cycle are separated by dashed lines: I = pre-parturition; II = non-flying juveniles present; III = flying juveniles present; IV: no bats present.

of the colony we investigated), since they interrupt social thermoregulation and interactions such as allogrooming and parental care (Kunz and Hood, 2000). This reaction is probably an escape response to a sudden alarm that spreads across the cluster when the source of disturbance is not identified by the bats. The disruption of clusters, leading bats to roost solitarily, may lead to a ca. 60% increase in energy expenditure (Roverud and Chappell, 1991). Adverse effects of cluster disruption may also concern social interactions, such as performing social bonding (Ancillotto et al., 2012), information transfer (Kerth and Reckardt, 2003) and roost switching (Maltagliati et al., 2013; Russo et al., 2017). In the long term, repeated disturbance may thus disrupt social relationships among colony members (Maldonado-Chaparro et al., 2018) by decreasing reciprocal tolerance and familiarity among colony members, such as allogrooming (Ancillotto et al., 2014), social thermoregulation (Pretzlaff et al., 2010), and coordinated foraging (Wilkinson and Boughman, 1998).

As we predicted, human presence in proximity of the roost altered the behaviour of bats leaving the roost, which delayed emergence. Emergence time in insectivorous bats constitutes a trade-off between the risk of falling prey to visual aerial predators (Mikula et al., 2016) and the advantage of getting access to the abundant insect food available at dusk (Jones and Rydell, 1994; Russo et al., 2007). Interspecific differences in emergence time in bats are in fact strongly influenced by flight speed and diet (Jones and Rydell, 1994): species that exhibit a slow flight tend to leave the roost later than those that fly faster to compensate for their lower ability to escape predators (e.g. Jones and Rydell, 1994; Rydell et al., 1996).

Optimising the timing of emergence is therefore important for individual fitness, particularly for females during energy-demanding phases such as pregnancy and lactation (Duvergé et al., 2000). The responses to human presence we noticed should therefore be taken into account when watching bats on emergence to assess colony size or carry out eco-touristic activities (Mann et al., 2002; Cardiff et al., 2012), so that observers should be located as far as possible from the path emerging bats follow and minimize disturbance.

In our study, domestic cats stood out as one of the major sources of concern for the preservation of the bat nursery we investigated. Timing of cat accesses to the roost, scat analysis and behavioural responses of roosting and emerging bats to cat presence support our predictions that cats may exert both direct and indirect effects on bats through predation and sub-lethal stress induced by the predator's presence. Although we cannot rule out that cats acted as scavengers rather than predators, this is unlikely since predation attempts were repeatedly observed at the site (pers. obs.).

Based on our data, cats might not be able to take a direct heavy toll on the colony in question, yet they sometimes specialize into preying upon roosting bat, with especially serious consequences (e.g. Ancillotto et al., 2012; Scrimgeour et al., 2012). In fact, cats are the most frequently observed invasive species preying upon bats (Welch and Leppanen, 2017), and are globally listed by IUCN among the 100 worst invasive species (Lowe et al., 2001). Moreover, predators can affect adversely their prey population density even if they consume few prey items because intimidation may have a major effect and actually be a main aspect of trophic interactions (Preisser et al., 2005). In social groups such as those of bats, even the killing of few subjects may disrupt social dynamics, so it should never be neglected (McComb et al., 2001; Rossiter et al., 2002; Wooddell et al., 2016). Besides, bats also reacted to cats showing anti-predatory behaviour, such as decreasing indoor flight activity when the cat was in the roost and increasing clustering on emergence to dilute predation risk (Speakman et al., 1992; Irwin and Speakman, 2003). We propose that these effects too may be adverse, e.g. by disrupting flight training and social bonding in juveniles or, in the case of changes in emergence patterning, by altering social foraging. More generally, repeated exposure to predators may induce 'sustained psychological stress' in their potential prey that is similar to chronic stress in humans and may have detrimental fitness effects in the long run (Clinchy et al., 2013). Protracted stress might induce bats to leave the roost in the middle of the reproductive season and move somewhere else, with clear adverse energetic consequences.

Our work emphasizes the importance of behavioural assessment in evaluating the effects of biotic environmental stressors on bats, which may also provide insights into the impact of urbanization on these mammals. Further studies may also be conducted to assess how landscape configuration and different urban scenarios may influence bat reactions in roosts, as well as to test effects on other fitness indicators such as reproductive success (Ancillotto et al., 2016) and stress physiology. Information such as that we provide may inform management of bat colonies in urban environment and help devise the best strategies to ensure bat conservation in urban habitat in the long-term (Stone et al., 2015a,b; Kingston, 2016; Zeale et al., 2016). Our results point at the importance of minimizing human presence near bat colonies and the urgent need for domestic cats to be excluded from sites hosting bat colonies.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.beproc.2019.04.003.

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