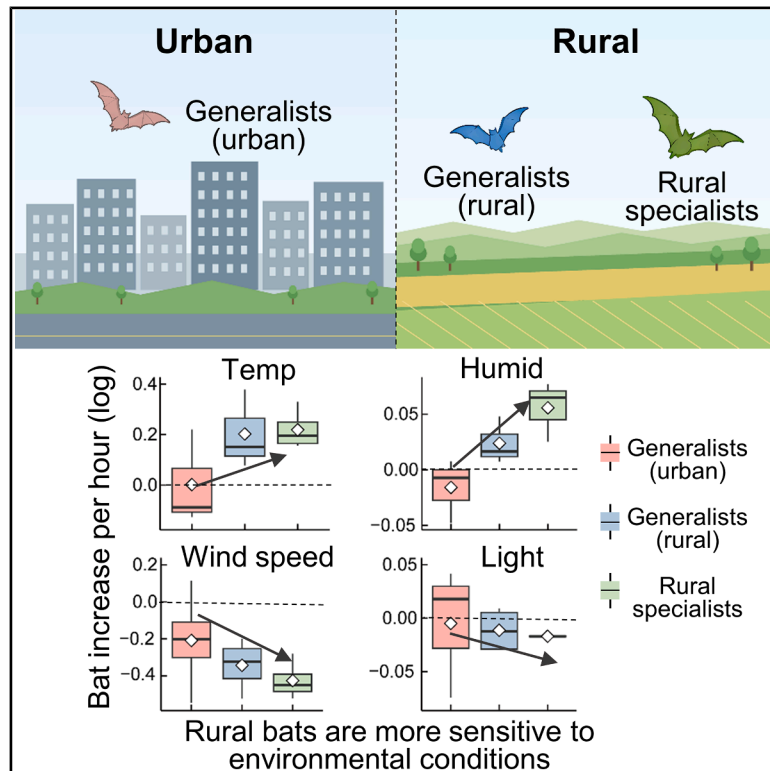


Urban habitats offer buffered environmental conditions for city-dwelling bats

Graphical abstract



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In brief

Biological sciences; Zoology;
Evolutionary ecology

Highlights

- We recorded 95,473 bat encounters from 11 species across 1,151 site-nights
- Urban habitats buffer environmental variability
- Urban bats were active across a broader range of environmental conditions
- Rural specialists avoided cities and were active in a narrower range of conditions



Article

Urban habitats offer buffered environmental conditions for city-dwelling bats

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SUMMARY

Urbanization reshapes local climates, potentially altering how animals respond to environmental variation. We used continuous acoustic monitoring at 12 urban and 15 rural sites across a steep aridity gradient in Israel, recording bats for 2.5 months from midsummer to autumn. Across 1,151 site-nights, we detected 95,473 encounters from 11 species. Rural bat activity was strongly associated with temperature, humidity, wind speed, and illumination, whereas urban activity was less sensitive to these environmental factors and to building height and density. Rural specialists avoided cities and were active within relatively narrow environmental ranges, while generalists occurred in both habitats and used broader activity conditions in cities. Urban bat activity also remained comparatively stable as rural activity declined seasonally. These findings show that cities may buffer environmental variability, allowing bats to forage across broader weather and potentially remain active later in the year.

INTRODUCTION

Accelerated urbanization has brought about vast environmental changes, from habitat fragmentations to pollution of food resources and changes in local weather conditions.^{1,2} We are only now beginning to understand the effects of these rapid human-induced environmental changes on animal behavior and ecology.^{3–6} In most reported cases, biodiversity has been found to decrease with intensification and expansion of urbanization, including in bats, which we focus on here.^{7–15}

Urban ecosystems are highly dynamic and are generally characterized by novel structures and microhabitats producing noise and light pollution, as well as heat compared with non-urban environments,¹ driving city-dwelling animals to modify their activity patterns in order to exploit them.^{16,17} Several studies have found that urban populations of various avian and mammalian species are bolder and more territorially aggressive than their rural counterparts.^{18–20} Some species alter their behavior to contend with human disturbance, such as advancing their dawn singing or avoiding more developed areas of the city.^{21–23} In bats, several examples of foraging plasticity in urban environments have been reported, including fruit bats adjusting their foraging strategies to diversify their diet in urban habitats,²⁴ and evidence suggesting that human-provided food resources in urban environments can alter optimal foraging decisions and residency patterns.^{25,26}

In parallel to urbanization, weather conditions play an important role in shaping the activity patterns of most animals.^{27,28} For example, damselflies are more likely to operate in windless environments,²⁹ some birds reduce their activity during wind and rain,³⁰ and bats emerge from their roosts later under higher ambient temperatures in both very dry and very wet years.³¹ Interestingly, the impact of weather on animal activity could be modulated by urbanization, which mostly buffers climatic effects, maintaining more stable weather conditions.^{32–34} City lights might also obscure natural light sources such as the moon, masking this signal for the emergence timing of nocturnal animals.³⁵

In this study, we set out to examine how the interaction of urbanization and environmental conditions (i.e., weather and illumination) affects bat activity, using comprehensive passive acoustic monitoring to explore the large-scale spatiotemporal habitat use of insectivorous bats. Most previous studies on urban-induced behavioral changes were based on limited temporal or spatial scales or have focused on a single species.^{19,36–39} A few studies have focused on the effects of weather on bat activity in cities but did not compare the behavior with that of bats inhabiting rural sites.^{38,39} We, thus, aimed to address this knowledge gap. An automated remote monitoring system, such as that enabled by passive acoustic monitoring,⁴⁰ is highly suitable for this purpose, especially for species that constantly emit sound, such as echolocating bats. We took advantage of the extremely steep climate gradient and the high bat species richness in Israel and monitored



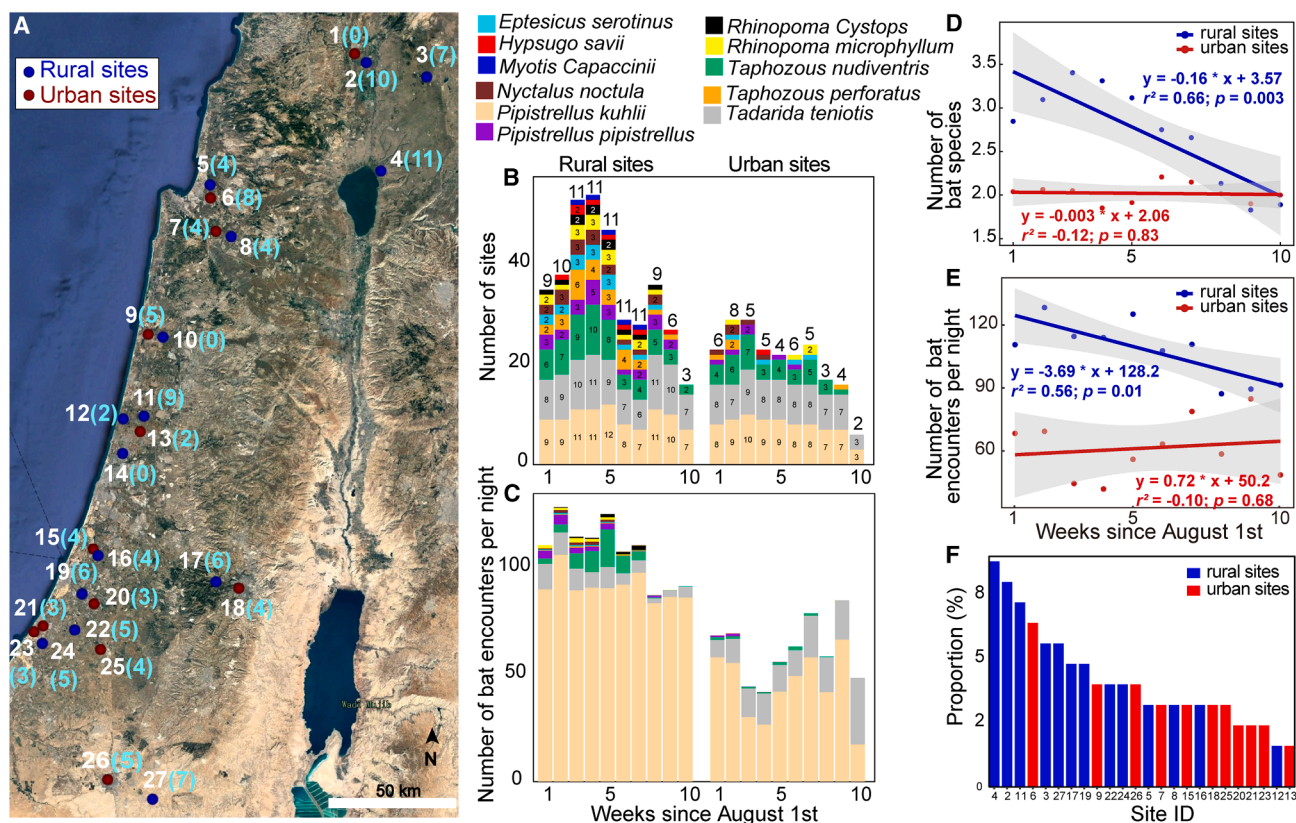


Figure 1. Survey sites, detected bat species, and bat occurrences

(A) The 27 monitoring sites, with blue dots representing rural sites and red dots representing urban sites. The number in brackets following each site ID depicts the number of detected species at the site.

(B) The weekly number of sites at which each species was detected, with rural sites on the left and urban sites on the right. Species are organized according to commonality. The number above the bars depicts the number of species detected across all sites for each week, while the numbers inside the bars depict the number of sites at which each species was detected. For clarity, values of 1 inside the bars were omitted.

(C) Average number of daily occurrences of each bat species per week summed for all sites (rural on the left and urban on the right).

(D) Temporal trends in the number of bat species at rural and urban sites from early August onward. Blue and red lines indicate linear regressions for rural and urban sites, respectively, with shaded areas representing 95% confidence intervals.

(E) Temporal trends in nightly bat encounters at rural and urban sites from early August onward. Blue and red lines indicate linear regressions for rural and urban sites, respectively, with shaded areas representing 95% confidence intervals.

(F) The number of species' occurrences out of all species' occurrences per site, with each detected species at each site counted as 1.

bat activity at 12 urban and 15 rural sites across a precipitation range between 200 and 800 mm per year over 2.5 months. We chose urban and rural sites in proximity to each other (within each latitude zone) to reduce environmental confounds. Following previous approaches distinguishing bats along urbanization gradients,^{10,41} we divided bat species into two groups: species that appear at both urban and rural sites (we termed them “generalists”), and species that were only detected at rural sites (which we term rural “specialists”). We hypothesized that when active in urban sites, bats would be less affected by environmental conditions than when active in rural sites both at the night and the seasonal levels.

RESULTS

Of the 23 bat species that we could detect in the area of the study (see [STAR Methods](#) regarding species detection limitations), we

detected a total of 11 species from 7 genera and 4 families across 24 sites (13 rural and 11 urban) of the overall 27 monitoring sites ([Figure 1A](#); [Table 1](#)). No bats were detected at the remaining three sites (sites 1, 10, and 14). In total, we recorded 95,473 bat occurrences across all sites over the 2.5-month period.

Bat occurrence in urban and rural sites

Rural species richness was higher than that in urban sites. In total, eleven bat species were detected at rural sites, while only eight species were detected at urban sites ([Figure 1B](#)), all of which were also detected at the rural sites. The activity (number of encounters) of seven of the species detected at both urban and rural sites was significantly higher at rural sites than at urban sites, while *T. teniotis* was the only species that was significantly more active in urban areas, where it typically roosts (generalized linear mixed model [GLMM], all $p < 0.05$; [Figure 1C](#); [Table 1](#)).

Table 1. GLMM results

Dependent variable	Estimate	z	p
<i>Eptesicus serotinus</i>	−3.20	−7.51	<0.001
<i>Nyctalus noctule</i>	−3.73	−10.11	<0.001
<i>Pipistrellus kuhlii</i>	−0.67	−20.91	<0.001
<i>Pipistrellus pipistrellus</i>	−2.43	−13.15	<0.001
<i>Rhinopoma microphyllum</i>	−5.02	−8.20	<0.001
<i>Taphozous nudiventris</i>	−1.64	−17.97	<0.001
<i>Taphozous perforates</i>	−2.69	−7.32	<0.001
<i>Tadarida teniotis</i>	0.78	16.43	<0.001
<i>Hypsugo savii</i>	detected only at rural sites		
<i>Myotis capaccinii</i>	detected only at rural sites		
<i>Rhinopoma cystops</i>	detected only at rural sites		

All species except *Tadarida teniotis* were more active at the rural sites. Estimates reflect average differences in the number of bat encounters per hour between urban and rural sites for each species (i.e., negative means more in rural).

Interestingly, while bat species richness and activity declined markedly in rural environments toward winter, no significant seasonal variation was observed in the urban sites (Figures 1D and 1E).

As expected, of the six sites with the highest number of species, the first five were in the north of our sampling range (Figure 1F, sites 4, 2, 11, 6, and 3), where annual precipitation is the highest. Indeed, a simple linear regression revealed that species richness positively correlated with the latitude ($t = 2.14$, $p = 0.04$; Figure S3).

The effects of the environment on activity at rural and urban sites

When examining the model's estimates according to the three categories defined above, most environmental parameters showed a similar pattern, with rural specialists (green bars in Figures 2 and S3; Tables 2 and S2) being most affected by weather (temperature, humidity, wind speed, and ambient illumination); generalists at urban sites being least affected (red bars); and generalists at rural sites being intermediately affected (note that in some cases the effect is negative, but urban active bats are always closer to the zero line). On average, bat activity increased with temperature and humidity and decreased with wind speed and illumination, but in all cases, the activity was most affected by ambient conditions in rural specialists and least in generalists at urban sites (Figures 2A–2D). Similar patterns emerged when examining the urbanization parameters (built-up area and height). While average bat activity always decreased with urbanization, it decreased more in rural specialists, which seemed to show an aversive response to urbanization (Figures 2E and 2F). Furthermore, rural specialists were most affected by both the hour of the night and latitude (Figures 2H and 2I). A complementary group-level GLMM analysis yielded patterns broadly consistent with the species-level results. The direction and relative effect sizes of environmental effects among bat groups were largely similar to those inferred from the species-specific analyses (Table S3).

We also ran the model after excluding sites without nearby urban centers (i.e., rural sites 3 and 4), and the results remained very similar (Figure S5). Estimating the environmental noise

above 20 kHz at all monitoring sites revealed no significant difference in high-frequency noise levels between the rural and urban sites (LMM with site ID and date as random factors: $t = -0.92$, $p = 0.37$; Figure S6), suggesting that noise could not have biased our detection of activity. When only moonlight was included in the model, urban bat activity was not significantly affected by this variable, except in *P. pipistrellus*, whereas bat activity in rural sites generally declined with increasing illumination (Table S4).

Examining the environmental conditions during the bats' activity revealed that rural specialists were most restricted in their activity and were active only at higher temperatures and lower humidities than generalist species that were active at the exact same sites. Moreover, bats active in urban habitats extended their activity to much lower temperatures and much higher humidities and wind speeds (see purple brackets in Figures 3A–3C that highlight the differences between generalists in urban and rural species). The activity hours of generalists at both urban and rural sites were also longer in comparison to the rural specialist bats (Figure 3D).

For comparison, we show the ranges of environmental conditions at the urban and rural sites during the same period but over the entire night (dashed lines in Figure 3). On average, urban temperature was $\sim 2^\circ\text{C}$ higher and humidity was $\sim 5\%$ lower than those at rural sites, while wind speed did not differ significantly (Table S5). As shown by the Kullback-Leibler (KL) divergence heatmap in Figure 3C, the disparity between actual environmental conditions and preferred activity conditions was substantially greater for rural specialists than for any other group and was the smallest for generalists active in urban environments, highlighting that specialists require specific weather conditions while generalists don't and that in cities, generalists are even less restricted by weather conditions.

DISCUSSION

With the ongoing intensification and spread of urbanization and other anthropogenic-related changes, urban environments are inhabited, tolerated, or even exploited by more species. How these animals respond to urban conditions and how their behavior differs from that of their rural conspecifics are still not

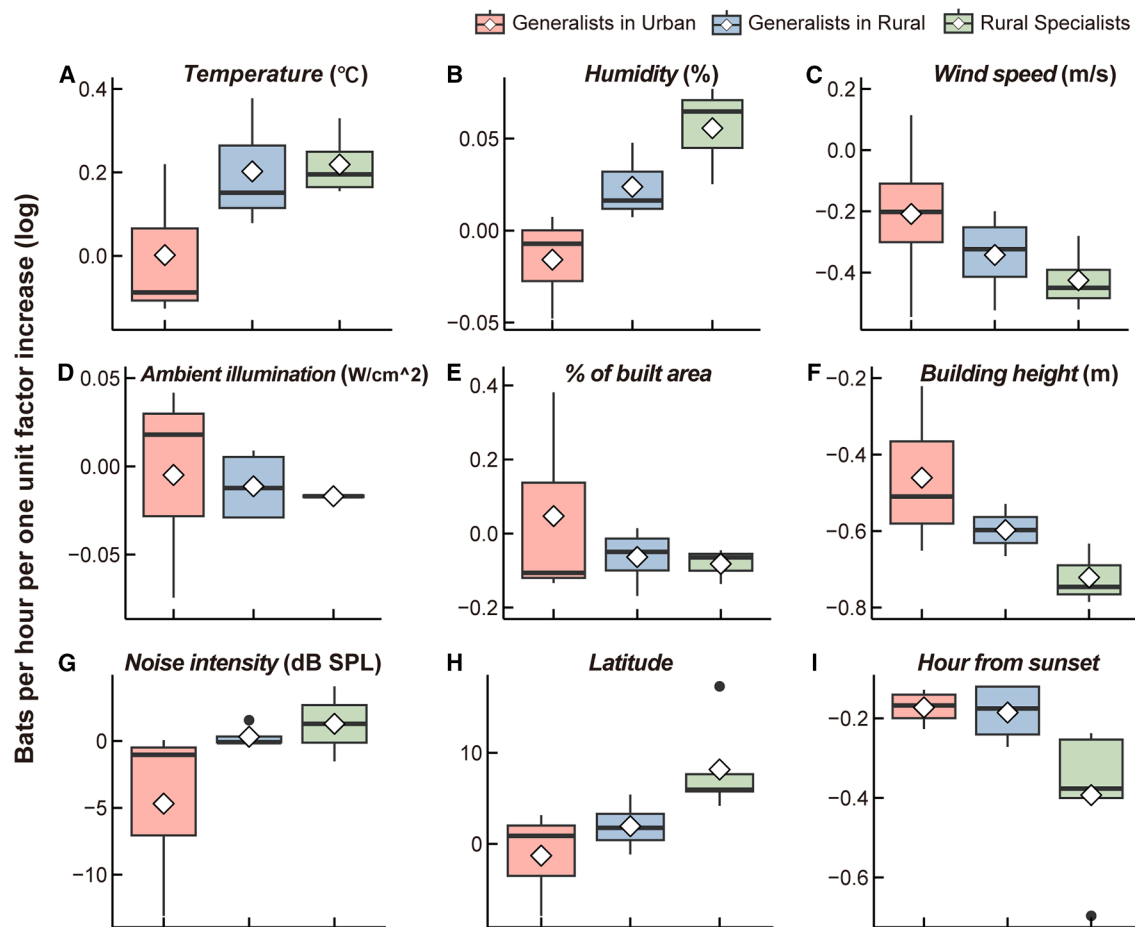


Figure 2. Mean estimates of the effect of different environmental factors on bat activity based on the results of the selected models

Panels show the effects of temperature (A), humidity (B), wind speed (C), ambient illumination (D), proportion of built area (E), building height (F), noise intensity (G), latitude (H), and hour from sunset (I).

(A–I) The estimates were clustered into three groups: generalists at urban sites (4 species), generalists at rural sites (4 species), and rural specialists (5 species). The midlines of the boxplots indicate medians; white diamonds show mean values; the box edges depict the 25th and 75th percentiles; whiskers represent the 5th and 95th percentiles; and values beyond these limits are shown as black points. For visualization, five outliers (2 in (E), 1 in (F), and 2 in (G)) are not displayed.

fully understood.^{20,22,42} In this study, we examined how bats in the urban and rural habitats respond to environmental conditions across a steep aridity gradient, ranging from lush forests to semi-deserts. Even though bat activity was found to be higher at rural sites, both in terms of species diversity and total occurrence, we detected eight species that are routinely active in urban environments.

Weather conditions are among the key factors shaping animal activity.^{27,29,43} In addition to its direct effects on animals through habitat destruction and air pollution, urbanization also alters local weather conditions, mostly by creating urban heat islands^{44,45} and reducing weather variability.¹ A few previous studies have shown that the activity of several bat species can vary markedly across urban-rural gradients, with some species exhibiting higher activity in urban habitats, whereas others are more active in rural environments.^{8,14,46}

We found that the activity of most bat species was strongly affected by environmental factors but that these effects greatly

varied between the urban and rural sites. For all tested environmental parameters, urban bats were less affected by environmental conditions than rural bats. Notably, we identified two groups of species: rural specialists, which avoided urban environments altogether; and generalists, which were found both in cities and rural environments.

Examining the range of environmental conditions under which bats of each group were active supported the conclusion that urban bats benefit from the fact that urban environmental conditions are more stable, which enable them to operate under a wider range of weather conditions. Figure 3 reveals that rural specialists are highly restricted and active only at higher temperatures and lower wind speeds relative to generalists at the same sites, thus narrowing their potential windows of activity (Figure 3D and see KL heatmap).

Generalists, on the other hand, were active at a much wider range of environmental conditions, but interestingly, in urban sites, they were active over a wider range of temperatures and

Table 2. The effects of environmental factors on bat activity based on the best-fit model of each species in rural and urban sites

Rural/Urban	Species	Predictors ^a	Estimate	z	p
Rural	<i>E. serotinus</i>	Temp	0.17	2.84	0.005
		Humid	0.08	4.64	<0.001
		WindSpd	−0.52	−2.64	0.008
		BuildProp	−0.06	−1.74	0.08
		BuildHeight	−0.75	−3.48	<0.001
		Latitude	5.94	8.98	<0.001
		Hour	−0.24	−4.97	<0.001
	<i>N. noctula</i>	Temp	0.16	2.84	0.005
		Humid	0.06	5.51	<0.001
		WindSpd	−0.43	−2.79	0.005
		BuildProp	−0.05	−2.08	0.04
		BuildHeight	−0.63	−3.78	<0.001
		Latitude	7.65	11.02	<0.001
		Hour	−0.38	−7.81	<0.001
	<i>P. kuhlii</i>	WindSpd	−0.27	−13.29	<0.001
		Amblllumi	0.004	2.38	0.02
		BuildProp	0.01	6.99	<0.001
		BuildHeight	−0.67	−39.75	<0.001
		Latitude	0.93	31.37	<0.001
		Hour	−0.23	−37.16	<0.001
		Noise	−0.09	−10.25	<0.001
	<i>P. pipistrellus</i>	Temp	0.08	2.26	0.02
		Humid	0.02	2.50	0.01
		WindSpd	−0.38	−3.07	0.002
		Amblllumi	0.03	−2.85	0.004
		BuildProp	−0.17	−6.93	<0.001
		BuildHeight	0.72	2.65	0.008
		Latitude	5.41	17.38	<0.001
	<i>R. cystops</i>	Hour	−0.27	−9.15	<0.001
		Noise	1.56	10.24	<0.001
		Temp	−0.28	−4.14	<0.001
		WindSpd	0.42	2.16	0.03
		Amblllumi	−0.02	−1.47	0.14
		BuildProp	−2.47	−1.19	0.23
		Latitude	17.30	1.28	0.20
	<i>R. microphyllum</i>	Hour	−0.70	−10.25	<0.001
		Noise	4.09	0.93	0.36
		Temp	0.33	5.04	<0.001
		WindSpd	−0.28	−1.57	0.12
		Amblllumi	−0.02	−1.71	0.09
		BuildProp	−0.14	−2.65	0.008
		BuildHeight	−0.79	−3.74	<0.001
	<i>T. nudiventris</i>	Latitude	4.20	9.72	<0.001
		Hour	−0.40	−7.31	<0.001
		Temp	0.38	17.32	<0.001
		Humid	0.05	8.18	<0.001
		WindSpd	−0.52	−8.54	<0.001

(Continued on next page)

Table 2. Continued

Rural/Urban	Species	Predictors ^a	Estimate	z	p
	<i>T. perforatus</i>	Amblllumi	−0.03	−6.90	<0.001
		BuildProp	−0.02	−3.09	0.002
		BuildHeight	−0.53	−12.19	<0.001
		Latitude	2.61	30.84	<0.001
		Hour	−0.12	−7.02	<0.001
		Noise	−0.11	−4.24	<0.001
		Temp	0.22	3.59	<0.001
		Humid	0.03	1.82	0.07
		WindSpd	−0.47	−3.03	0.002
		BuildProp	0.69	6.59	<0.001
	<i>T. teniotis</i>	BuildHeight	−13.12	−6.45	<0.001
		Latitude	5.76	6.19	<0.001
		Hour	−0.25	−5.03	<0.001
		Noise	−1.52	−5.59	<0.001
		Temp	0.15	11.83	<0.001
		Humid	0.01	2.31	0.02
		WindSpd	−0.20	−4.08	<0.001
		Amblllumi	0.09	2.20	0.03
		BuildProp	−0.07	−6.57	<0.001
		Latitude	−1.15	−16.15	<0.001
Urban	<i>P. kuhlii</i>	Hour	−0.12	−9.02	<0.001
		Noise	−0.08	−4.22	<0.001
		Temp	−0.13	−12.37	<0.001
		Humid	−0.01	−4.52	<0.001
		WindSpd	0.11	5.60	<0.001
		Amblllumi	0.04	21.61	<0.001
		BuildProp	−0.11	−10.57	<0.001
		BuildHeight	−0.23	−10.82	<0.001
		Latitude	0.89	7.24	<0.001
		Hour	−0.23	−27.32	<0.001
	<i>P. pipistrellus</i>	Noise	0.06	2.87	0.004
		Temp	0.22	1.55	0.12
		Humid	−0.05	−2.94	0.003
		WindSpd	−0.54	−4.26	0.80
		Amblllumi	−0.60	−4.25	<0.001
		BuildProp	8.09	0.36	0.72
		Hour	−0.19	−3.90	<0.001
		Noise	−13.09	−0.44	0.66
	<i>T. nudiventris</i>	WindSpd	−0.18	−3.04	0.002
		Amblllumi	0.02	4.24	<0.001
		BuildProp	−0.13	−5.19	<0.001
		BuildHeight	−0.65	−5.13	<0.001
		Latitude	3.15	13.58	<0.001
		Hour	−0.14	−7.46	<0.001
	<i>T. teniotis</i>	Temp	−0.09	−7.36	0.001
		Humid	0.007	3.24	0.001
		WindSpd	−0.22	−8.54	<0.001
		Amblllumi	−0.07	−28.30	<0.001

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Table 2. Continued

Rural/Urban	Species	Predictors ^a	Estimate	z	p
		BuildProp	0.38	24.45	<0.001
		BuildHeight	−0.51	−17.74	<0.001
		Latitude	−7.90	−32.25	<0.001
		Hour	−0.13	−13.14	<0.001
		Noise	−1.04	−25.17	<0.001

Species with a total number of less than one hundred encounters are excluded. *p* values less than 0.05 are in bold.

^aTemp, temperature; Humid, relative humidity; WindSpd, wind speed; Ambllumi, ambient illumination; BuildProp, building proportion; BuildHeight, building height.

wind speeds than in rural sites (notably, these are the same species; see horizontal purple brackets in Figure 3). This might be a result of various urban-related factors, such as the vicinity of available food, or the availability of ample water sources (see more below) or the microclimatic shelter provided by buildings, all of which allow operation under more harsh environmental conditions.

Both urban and rural sites are highly heterogeneous. Thus, rather than modeling all sources of environmental variation, we aimed to identify patterns that are consistent across diverse habitat types. To account for the key parameters of urbanization, we incorporated the proportion of built area and building height into our models, as these factors are likely to interact with local weather conditions and influence bat activity.

Several previous studies have considered the effects of urban micro-climate on animal behavior. Wintering birds are more widely distributed at urban and warmer sites in winter,³² and a survey³⁴ has suggested that both urbanization and weather influence the distribution of the Tawny owl (*Strix aluco*). Urban fruit bats diversify their diet more than their rural counterparts, likely because of urban climate-related fruit availability.²⁴ In the present study, rural bats were shown to prefer low wind speeds, while urban bats did not show any preference. Lower wind speeds might be preferred by rural bats due to their reduced impact on body thermoregulation and, hence, on the animal's energetic demands, as well as the reduced acoustic interference, and increases in insect activity and migration intensity.^{26,29,47–50}

When only moonlight was included as the sole illumination variable in the model, bat activity at rural sites generally declined with increasing moonlight intensity, whereas the activity of most species at urban sites was not significantly associated with moonlight. This pattern suggests that responses to moonlight were more pronounced under rural conditions. Brighter moonlit conditions have been proposed to increase perceived predation risk and reduce activity in some bats, although response to moonlight varies among species and environmental contexts.^{51–56} By incorporating hourly, rather than nightly, illumination values, our analysis captured finer variation that may be overlooked in studies based on nightly averages.

Model fit varied among species and sites. Across the 13 ZINB models, McFadden's pseudo-*R*² ranged from 0.064 to 0.465, with a median of 0.245, indicating variable improvements in log likelihood relative to the corresponding intercept-only models.⁵⁷ We acknowledge that the response of the bats to environmental conditions is likely aimed at optimizing their activity in relation to

food resources, which are known to greatly affect insectivore animals' decision-making and activity and, specifically, their foraging ecology, behavior, and movement.^{24,58,59} In this context, cities sometimes provide new foraging opportunities for animals.^{1,19} In the region, water is often a scarce resource, especially during summer and autumn, and towns often have parks that are irrigated and contain open water sources such as ponds and lakes, which have been shown to attract bats and their insect prey.^{11,60}

Due to the limited sampling rate and microphone sensitivity, we could reliably detect only relatively loud calls below 50 kHz. Consequently, nine local species, including all Rhinolophid species, were not recorded. Although these species may differ in some aspects of behavior, previous studies have consistently identified Rhinolophid as rural specialists that rarely occur in urban environments,^{61–64} suggesting that their responses would likely resemble those of the rural specialists examined here.

Bat diversity remained relatively stable throughout the study period, except in mid-October when a few known migrants (e.g., *T. nudiventris* and *R. microphyllum*) were no longer detected. Seasonal declines in diversity and activity were evident only at rural sites, whereas urban bat activity remained comparatively stable. This pattern suggests that the urban environments may buffer bats against seasonal environmental variation and allow activity to extend later into the year, consistent with previous evidence for urban heat-island effects on bat phenology.⁶⁵

Our study demonstrates the advantage of passive acoustic monitoring that enables long-term continuous research of echolocating bats over a large spatial scale and with no interference to the animals. Combining wide-band acoustic monitoring with automatic species classification has great advantages for future biodiversity research, as well as for behavioral and ecological analyses.^{40,66} Acoustic monitoring also has several disadvantages, such as the inability to distinguish multiple individuals from one individual, but this difficulty is also present in most visual surveys.⁶⁷ Our large-scale acoustic survey demonstrates that bat activity in urban environments is less sensitive to variations in weather and illumination than activity in rural habitats.

Limitations of the study

This study has several limitations. Acoustic monitoring quantified call encounters, rather than the number of individual bats; so, we could not determine whether differences in activity were partly driven by differences in the number of bats present. Monitoring covered 2.5 months from midsummer to autumn; so, the findings

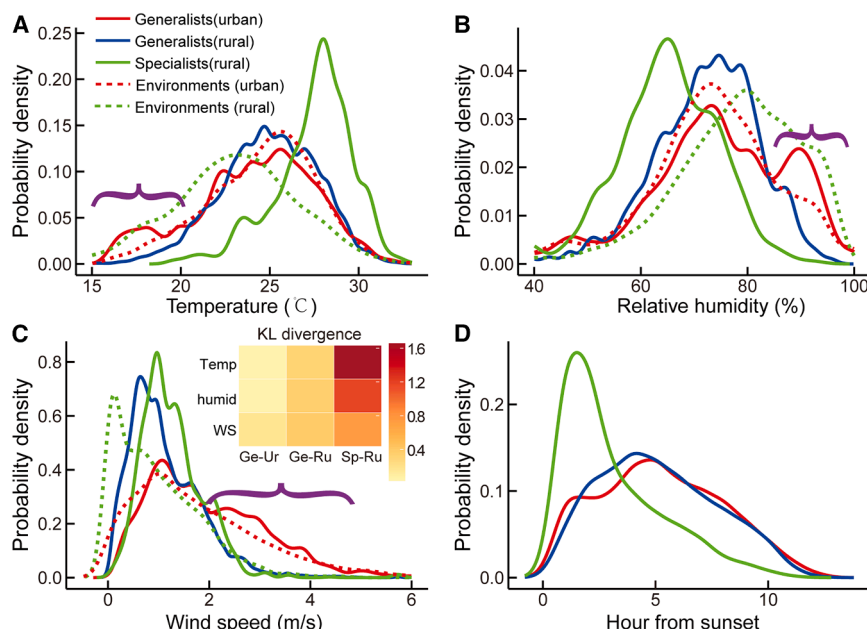


Figure 3. Environmental conditions vs. bat activity for generalists in urban and rural sites and for rural specialists

(A–D) Temperature (A), humidity (B), wind speed (C), and hour from sunset (D). For a valid comparison, only sites at which bats from all categories were active were used (i.e., sites 2, 4–7, 11, 15, 18–21, 23, and 25–27). Solid lines represent environmental distributions during bat activity, and dashed lines represent overall environmental distributions.

Purple brackets in (A)–(C) highlight stronger activity of urban generalists than that of rural generalists. The KL divergence heatmap in (C) illustrates the differences between environmental distributions during bat activity and those across the entire night.

Ge-Ur, generalists in urban sites; Ge-Ru, generalists in rural sites; Sp-Ru, specialists in rural sites. For example, the cell in the upper-left corner shows the KL divergence in temperature between the active-period distributions of urban generalists and the full-night temperature distribution of urban sites.

may not fully represent other seasons or years. In addition, because this was a remote recording study, we cannot directly establish that urban environmental buffering caused bats to remain active across a broader range of environmental conditions. Other factors that we did not measure, such as prey availability and small-scale differences in habitat structure, may also have contributed to the observed urban-rural differences in bat activity.

RESOURCE AVAILABILITY

Lead contact

Requests for further information, resources, and reagents should be directed to and will be fulfilled by the lead contact, Yossi Yovel (yossiyovel@gmail.com).

Materials availability

This study did not generate new unique reagents.

Data and code availability

- The bat species detections datasets supporting this study are publicly available at Zenodo (<https://doi.org/10.5281/zenodo.19216373>).
- The original codes are also available in the Zenodo repository (<https://doi.org/10.5281/zenodo.19216373>) and are also listed in the [key resources table](#).
- Any additional information required to reanalyze the data reported in this paper is available from the [lead contact](#) upon request.

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AUTHOR CONTRIBUTIONS

Y.Y. and N.S. designed the study, supervised the research project, and revised the manuscript; J.D. analyzed the data and drafted the manuscript; A.B.

collected data and wrote the program; O.E., Y.W., and D.T. collected the data and commented on the manuscript. All authors have approved the final version of the manuscript.

DECLARATION OF INTERESTS

The authors declare no competing interests.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

Supplemental information can be found online at <https://doi.org/10.1016/j.isci.2026.117767>.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Software and algorithms		
MATLAB R2020b	MathWorks	https://www.mathworks.com/products/matlab.html
ArcGIS Pro 3.0.3	Esri	https://www.esri.com/en-us/arcgis/products/arcgis-pro/overview
R 4.2.3	R Core Team	https://www.r-project.org/
Custom-written program for species identification	This paper; Zenodo	https://doi.org/10.5281/zenodo.19216373
Other		
AudioMoth	Open Acoustic Devices	N/A
Meteorological data	Israeli Meteorological Service/Meteorology Unit of the Israel Ministry of Agriculture	N/A
Anthropogenic light intensity	VIIRS map	https://www.lightpollutionmap.info
NASA/JPL Horizons ephemeris data for the Moon	NASA/JPL Solar System Dynamics	https://ssd.jpl.nasa.gov/horizons/app.html#/

EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

Omitted as our study does not involve biological models.

METHOD DETAILS

Survey sites and acoustic monitoring

We sampled 27 sites in Israel, of which 15 were rural and 12 were urban sites (Figure 1A; Table S1), distributed across a large aridity gradient, from the temperate forests in the northern region with an annual rainfall of 800 mm, to the semi-arid desert areas in the south with an annual rainfall of 200 mm, nearly 300 km apart (Orni & Efrat 1971). Both the rural and urban sites were selected based on their proximity to nearby weather stations (<20 m), which allowed characterizing the weather at the point of acoustic recording. Furthermore, this design allowed testing environmental effects at close by urban and rural sites, with a minimum distance of 2.4 km and an average distance of 10.2 km between two adjacent rural and urban sites. When rural sites 3 and 4, which were located in regions without nearby urban centers, were excluded, the average distance between adjacent rural and urban sites decreased to 7.5 km. According to the Taub Center (<https://www.taubcenter.org.il/>), Israel has one of the highest population densities worldwide (when ignoring very small countries). Population density was significantly higher at urban sites than at rural sites (Figure S1). Population density data were obtained from WorldPop (<https://hub.worldpop.org/geodata/summary?id=73883>; <https://doi.org/10.5258/SOTON/WP00839>) at a spatial resolution of 100 m, and were calculated at a 1-km-diameter buffer around each monitoring site.

At each site, a full-spectrum acoustic recorder, AudioMoth (Hill et al. 2018), was positioned within 20 m of a weather station of either the Israeli Meteorological Service (IMS) or the Meteorology Unit of the Israel Ministry of Agriculture, at about 2 m above the ground. The recorder was placed in a plastic casing with the microphone fully exposed, aimed skyward. We recorded audio sessions of 30 s every 1 min (50% duty cycle), for 12 h daily from sunset to sunrise. Each site thus generated nearly 720 audio files per night from midsummer (August 1st) until mid-fall (October 13th), when bat activity starts decreasing toward late fall. In total, we recorded and processed 1,151 nights of data (accumulated across all sites), resulting in a very large dataset.

The sampling frequency was set to 96 kHz with a sensitivity setting of medium. Of the 32 bat species in the region, only seven Rhinolophid species, one hipposiderid and *Nycteris thebaica* cannot be detected with our sampling rate. Our extensive experience with acoustic monitoring in the region using higher sampling rates and more sensitive devices (e.g., wildlife acoustics SM4) indicates that these species are hardly ever recorded because of their highly directional and quickly attenuating echolocation - unless the microphones are placed in known foraging habitats or passing routes (our sites were rather open for Rhinolophids). Specifically, in thousands of hours of recordings that we have performed in urban habitats over the years, they have been detected less than a handful of

times. We thus preferred to use a sampling rate which would allow longer recordings (by reducing the battery's power consumption) at the cost of missing these hard-to-detect species. We did not aim to report a full community structure and our result are general for a very large number of species which we have detected.

Automatic species identification and bat activity

A custom-written MATLAB program was used to detect bat echolocation calls and to automatically identify bat species. Specifically, the program divided the entire range into the frequency-bands typically used by the different species of bats and extracted bat calls in segments of 2 s. Species were identified according to their signals' frequency, duration, and harmonic content. If more than one call of a specific species was detected in a 30 s audio file, this was noted as one encounter of the species. We refer to the number of encounters of each species within an hour as its activity.

To verify the reliability of the identification, we manually scrutinized the full recordings of 30 nights at each survey site. We assessed the accuracy of the program as the number of audio files correctly classified, divided by the total number of files for each monitoring site. Following this assessment, we used the automatic classifier only at sites where the accuracy was above 90% (15 sites). If the accuracy was between 70% and 90% (7 sites), we used the automatic classifier, but manually validated all its identifications; while at sites with an accuracy below 70% (2 sites), we manually classified all the audio files. There were no bats detected on three sites. Moreover, the high abundance of *T. nudiventris* was somewhat surprising as there are only a few known colonies of this species at the surveyed sites. We therefore manually validated most of the calls detected for this species.

Environmental parameters data

Recording sites were predefined as urban – within cities – or rural – not within cities (or any other human settlements), as determined from GIS maps and confirmed during field survey. Sites within continuous built-up areas were classified as urban, whereas those surrounded predominantly by agricultural or open land were classified as rural. For all sites, we then computed meteorological, urbanization and illumination parameters. All recording sites were chosen such that they were within 20 m from a meteorological station, thus ensuring that the weather parameters we used accurately reflected the conditions at the bat recording sites. We downloaded meteorological data collected at the nearby station either every 5 or 10 min (based on the available resolution), from the IMS website (https://ims.gov.il/en/data_gov), and extracted temperature, humidity, and wind speed. Cloud cover is typically zero during summer in the region and it was therefore not incorporated, and neither was precipitation. Latitude is highly correlated with aridity in our study area and we therefore used it as a factor in the model (Goldreich & Karni 2001; latitude obtained from smartphone GPS coordinates). The average monthly anthropogenic light intensity within a 500-meter diameter circle around each site was measured from a 2021 VIIRS map (<https://www.lightpollutionmap.info/help.html>).⁶⁸ We also extracted moon irradiance (normalized to a max = 0.4 Lux i.e., 5.9×10^{-8} Watt/cm²) with a 15-min temporal resolution (from NASA: <https://ssd.jpl.nasa.gov/horizons/app.html#/>; Target body: moon), taking into account moon phase, angle, and distance. Typically, anthropogenic light was higher in cities and moon irradiance was higher in rural areas. We thus created a single parameter that comprised the maximum light level for each time point and site (Figure S2), and this measure of ambient light was used in the analysis. We used GIS (ArcGIS Pro 3.0.3) to extract the proxies of the level of urbanization, including the proportion of built-up area, from the Hebrew University GIS Center (<https://cris.huji.ac.il/en/organisations/gis-center>), and the average height of the buildings at a radius of 500 m around the microphone locations (from the National Topographic Database (BNTAL), Survey of Israel). We investigated the potential impact of environmental noise on bat call encounters in urban and rural sites by filtering the audio recordings to isolate frequencies above 20 kHz, and then calculating the noise intensity after excluding segments with bat vocalizations.

QUANTIFICATION AND STATISTICAL ANALYSIS

We quantified weekly species richness and calculated the average daily occurrence of each species per week at each site. Temporal trends in species richness and bat activity were then assessed using linear regression separately for rural and urban sites. To compare hourly bat activity between rural and urban sites, we fitted Generalized Linear Mixed Models (GLMM, “lme4” and “glmmTMB” packages in R) for species with more than 100 recorded encounters. The date and the hour relative to sunset were included as random factors. Nine species met this criterion at the rural sites and four at urban sites.

A Zero-Inflated Negative Binomial model (ZINB, “pscl” package in R) was then used to investigate the effects of environmental parameters on species-specific bat activity. Hourly occurrence was used as the response variable, while temperature, humidity, wind speed, ambient illumination, proportion of built area, average height of buildings, environmental noise intensity, hours from sunset, and latitude were included as predictors. For each species, we evaluated all possible predictor combinations (511 models) and selected the best-supported model based on the Akaike Information Criterion (AIC, Akaike 1974). Best-fit models were built separately for urban and rural sites for each bat species. To examine the effects of weather and urbanization, bat species were divided into two groups: species that appear at both urban and rural sites (we termed them Generalists) and species that were only detected at rural sites (which we term rural Specialists). We further compared the activity of the Generalists when they appeared in urban and in rural sites. In addition, we fitted a group-level GLMM (“glmmTMB” packages in R) with a zero-inflated negative binomial error distribution to test the effects of environmental variables on bat groups identified from the survey data (see results). Hourly occurrence was modeled as a function of group-specific environmental responses, with species identity and site included as random effects.

We used independent samples *t* test (“stats” package in R) to compare mean ambient temperature, relative humidity, and wind speed between rural and urban sites during the study period, and to test differences in their standard deviations. The Kullback–Leibler (KL) divergence (estimated using kernel density functions and numerical integration on a common evaluation grid) was used to quantify differences between environmental conditions during bat activity periods and those across the entire night at rural and urban sites (Lee & Park 2006). All statistical analyses were two-tailed with an α level of 0.05 and were performed in R (version 4.2.3).