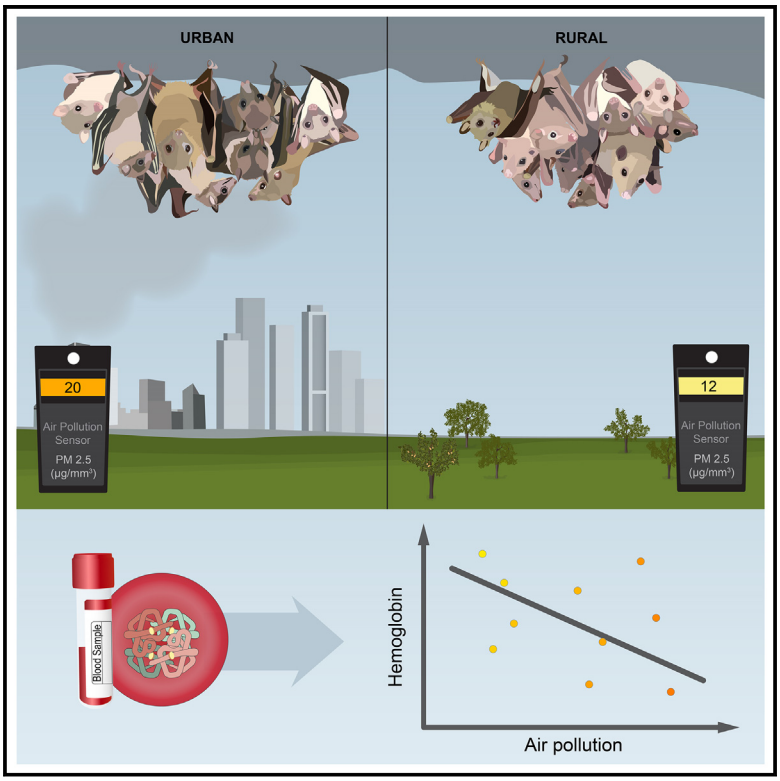
iScience

Article

Air pollution likely reduces hemoglobin levels in urban fruit bats

Graphical abstract



Highlights

- Fruit bats exposed to more pollution have lower blood hemoglobin levels
- The hemoglobin and PM2.5 pollution levels were assessed in urban and rural bats
- In the most polluted areas, hemoglobin levels were 25% lower
- Such differences might affect urban bats' health in the long run

Authors

Omri Gal, Ofri Eitan, Adi Rachum, ..., Reut Assa, Colin Price, Yossi Yovel

Correspondence

omrigal1@mail.tau.ac.il (O.G.), yossiyovel@gmail.com (Y.Y.)

In brief

Environmental science; Pollution; Zoology

Gal et al., 2025, iScience *28*, 111997
March 21, 2025
https://doi.org/10.1016/j.isci.2025.111997

CellPress

iScience

CellPress
OPEN ACCESS

Article

Air pollution likely reduces hemoglobin levels in urban fruit bats

Omri Gal,[1,*] Ofri Eitan,[2] Adi Rachum,[2] Maya Weinberg,[2] Dean Zigdon,[2] Reut Assa,[2] Colin Price,[2] and Yossi Yovel[1,3,4,*]
[1]Porter School of the Environment and Earth Science, Faculty of Exact Sciences, Tel Aviv University, 6997801 Tel Aviv, Israel
[2]School of Zoology, Faculty of Life Sciences, Tel Aviv University, 6997801 Tel Aviv, Israel
[3]The Steinhardt Museum of Natural History, Tel Aviv University, Tel Aviv, Israel
[4]Lead contact
*Correspondence: omrigal1@mail.tau.ac.il (O.G.), yossiyovel@gmail.com (Y.Y.)
https://doi.org/10.1016/j.isci.2025.111997

SUMMARY

Air pollution is one of the world's most substantial environmental problems. Air pollution is more severe in urban environments. Besides humans, other animals also inhabit cities. Despite the significant impact of air pollution on health, there is limited research on its effects on wildlife in general and specifically on bats, which are common in cities. Egyptian fruit bats dwell in both rural and urban environments. We assessed the exposure to particulate matter (PM)2.5 pollution and compared it to blood hemoglobin (HGB) levels in fruit bat populations roosting at different degrees of urbanization. We found a significant negative correlation between PM2.5 exposure and HGB levels. Bats that roost and forage in highly urban-polluted areas exhibited low HGB levels. This is a first attempt to examine the effect of urbanization-related pollution on bat health, revealing a negative correlation between air pollution and HGB levels that might detrimentally affect bats' health in the long run.

INTRODUCTION

Air pollution poses a significant threat to living beings, including humans. In highly polluted countries in Asia, the accumulated damage from air pollution results in a substantial increase in premature death.[1] Moreover, due to the rapid increase in urbanization, air pollution is on the rise in large parts of the world (mostly in developing countries) although some western countries are experiencing a decline. Notably, most of the human population lives in places where air pollution is higher than the guidelines of the World Health Organization.[2–4] The primary source of air pollution is burning fossil fuels, and the major air pollutants include ozone, carbon monoxide, nitrogen dioxide, sulfur dioxide, and particulate matter (PM). PM is a generic term used to describe air pollutants of various sizes and compositions of particles suspended in the air, and it is considered one of the most dangerous types of air pollutants, with significant harmful effects on health.[5–7] These particles can be solid or liquid and include dust, dirt, soot, smoke, or liquid droplets. Their composition includes elemental carbon, organic carbon, sulfate, nitrate, ammonium, and various geological materials (oxides of different metals). PM is commonly divided into two main categories based on particle diameter: PM2.5 and PM10, representing diameters smaller than 2.5 and 10 μm, respectively. Generally speaking, larger particles (greater than 2.5 μm) are generated mainly through natural processes like erosion, while smaller ones are produced from artificial combustion processes. PM is a key indicator used to assess air quality, and it is the primary pollutant used to evaluate the health impact of air pollution on humans.[8–10]

Exposure to air pollution can lead to damage to multiple biological systems including the nervous, respiratory, and cardiovascular systems. In the respiratory system, exposure to pollutants can lead, for example, to nose and throat irritation, bronchoconstriction, dyspnea, lung inflammation, asthma, emphysema, and lung cancer.[7,11]

The health effects of PM pollution depend on parameters such as the duration of exposure, the quantity of matter entering the body, and the composition and size of the particles. The size of the particles determines how deeply they penetrate the body, with PM10 particles primarily reaching the upper respiratory system and fine particles able to penetrate deeper into the lung alveoli (air sacs). Smaller particles also remain in the body for longer periods, making them more hazardous.[7,12]

Research on PM as a major pollutant with significant health impacts is indeed extensive in humans. Estimates have indicated that even short-term exposure to PM is associated with an increase in all-cause mortality. For example, a comprehensive study including data from 24 countries and 652 cities found that an increase of 10-μg-per-cubic-meter in PM10 concentration is linked to a significant 0.44% global increase in all-cause mortality, while the increase is 0.68% for PM2.5.[13]

Moreover, studies have identified a negative correlation between PM concentration and blood hemoglobin (HGB) levels in humans.[2,14] Although the exact mechanism is not entirely clear, it is suggested that PM that penetrates the blood system disrupts heme synthesis, which is necessary for the formation of the HGB molecule. Some research has shown that PM pollution can also lead to a decrease in HGB-related indices, such as MCH (mean corpuscular hemoglobin) and MCHC (mean corpuscular

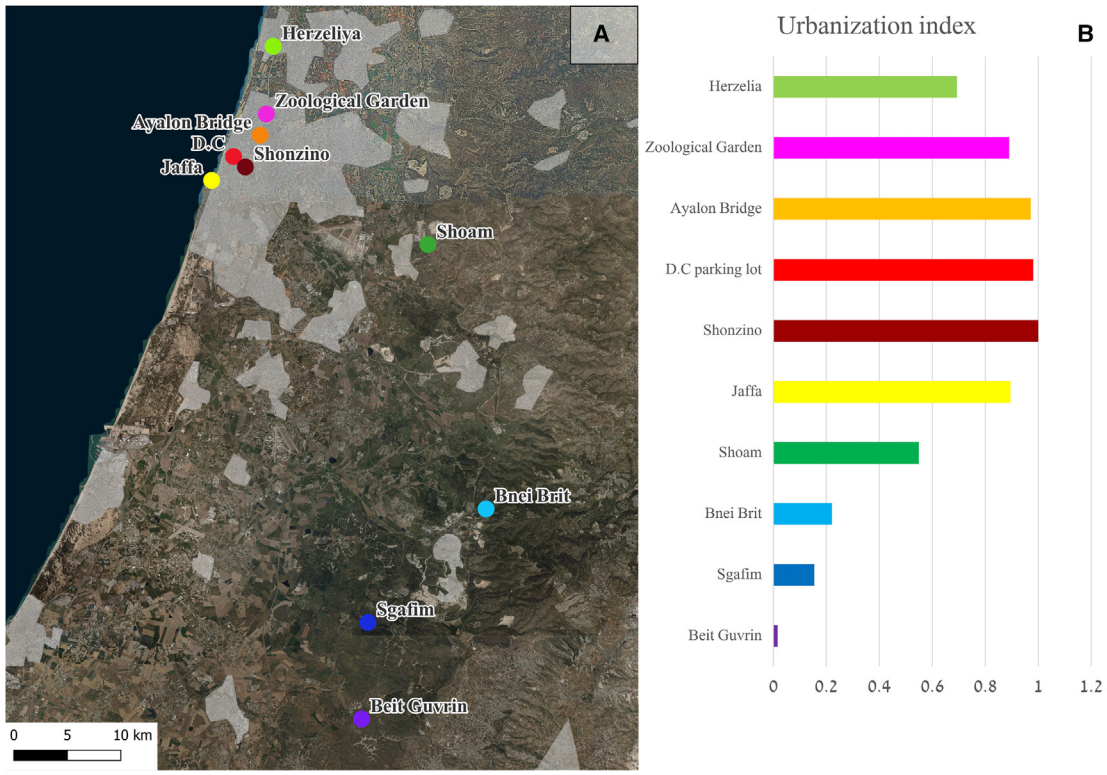


Figure 1. The ten urban and rural colonies that were sampled in the study

(A) The locations of the study colonies are presented on an aerial map. Large urban areas are depicted by gray shadings.

(B) The urbanization index of the different colonies. This normalized index was estimated as the log10 of the population in a 3 km radius around each colony divided by log10 of the estimated population in a 3 km radius around Shonzino colony—the colony situated in the most populated region. The colonies on the map were color-coded accordingly (for the actual estimated population sizes, see Figure S1).

hemoglobin concentration). These effects can persist for various durations, ranging from one day to several years.[15–17] Low levels of HGB are a major cause of anemia and can increase mortality in individuals with conditions such as cancer or myocardial infarction.[18,19]

The urban environment, which continues to grow worldwide, alters resource availability, land use, and community composition, causing negative influences on animals' health.[20] Despite its potential harm, there have not been many studies examining the effect of air pollution on animals. The few studies that have been conducted focused on using animals to monitor pollutants, a method known as "animal sentinel systems",[21,22] or on examining the effects of pollution on animal health to better understand the implications for human health.[8,23] Some of these studies found that long-term and short-term exposure to air pollution in animals damage the nervous system and lungs, causing physiological and behavioral disorders such as inflammation; asthma; dementia; oxidative stress; alterations in their DNA; and disruptions in memory, olfaction, and learning capabilities.[23–26]

Bats are among the most abundant and widely distributed mammalian species. With more than 1,500 species, bats account for more than 20% of mammalian species.[27] Urbanization dramatically affects bats, reducing both their abundance[28] and diversity on the one hand but also creating attractive habitats for a few synanthropic bat species that thrive in human-altered environments.[29,30] Bats often prefer the edges of cities, which are characterized by more vegetation and diverse habitats, while avoiding foraging sites with high traffic and noise.[31]

Only a few studies investigated the effects of urbanization and human-related pollution on bats or on other wild animals. Most studies used bats as bio-indicators for assessing the presence of heavy metals or pesticides. These pollutants can have catastrophic implications, causing genotoxic and mutagenic damage and affecting various body organs and systems.[32,33] The effect of air pollution on bats' activity has rarely been examined with one study revealing more diversity in less polluted forests,[34] but the effect of pollution on bats' health has never been examined. Moreover, it is noteworthy that air pollution can also indirectly affect bats by contaminating their drinking water or by accumulating in insects that they prey on.[26,31,34] Some researchers have even hypothesized a potential link between particulate pollution and the white-nose syndrome, a deadly fungal disease affecting millions of bats in North America.[35]

In this study, we focused on the Egyptian fruit bat (*Rousettus aegyptiacus*), which is one of the most common bat species in Israel and arguably the most abundant one in urban environments. In addition to roosting in rural areas, fruit bats also commonly roost in cities in Israel, enjoying the rich diversity of planted and watered fruit trees[36] and drinking from artificial water sources.[37] Egyptian fruit bats spend many hours foraging every night and can fly up

Table 1. PM2.5 sampling pollution periods inside and outside each colony

Colony	Inside measurement	Outside measurement	Urbanization index	Colony morphology	Estimated number of bats	Total number of bats sampled
DC parking lot	May 2022–June 2023	October 2022–February 2023	0.981	parking lot	500	45
Zoological Garden	May–October 2022	February–May 2023	0.89	artificial room	50	42
Herzeliya	September, October, and November 2022	September, October, and November 2022	0.693	calcarine limestone	2,000	21
Shonzino	October, November, and December 2022	September 2022–August 2023	1	abandoned building	400	20
Shoam	August, November, and December 2022	August, November, and December 2022	0.549	limestone cave	2,300	25
Jaffa	December 2022	March–December 2023	0.895	abandoned building	1,000	21
Beit Guvrin	January 2023	January 2023	0.016	chalk cave	500	19
Bnei Brit	March and July 2023	July and August 2023	0.221	limestone cave	300	17
Ayalon Bridge	January, February, March, and May 2023	May–June 2023	0.971	highway bridge	1,800	18
Sgafim	April and July 2023	August 23	0.154	marl cave	600	18

In Herzeliya, Shonzino, Shoam, Jaffa, Beit Guvrin, Bnei Brit, Sgafim, and inside the Ayalon bridge colonies, the sampling was done using the Pats sensor. In the Zoological Garden and inside the Dizengoff Center parking lot, the measures were done using the PurpleAir sensor. Outside the Dizengoff Center, Shonzino, Jaffa, and Ayalon Bridge colonies, the measures were made by sensors from stations of the Ministry of Environmental Protection (using the closest station to each colony—one of four different stations). The total number of individual blood samples taken in each colony is shown in the right column. For more detailed information including the blood sample dates, see Table S1.

to dozens of kilometers from their roost to reach a foraging tree.[38] While they often return to familiar fruit trees, bats occasionally embark on exploratory flights, which might expose them to much PM pollution when flying in urban environments. Some rural bats also routinely forage in urban areas.[36]

In Israel, the current assessment of air quality indicates that PM levels consistently exceed the established standards. The geographic location of Israel, close to North Africa and the Arab deserts, coupled with PM transport from Europe, contributes to the relatively high PM levels.[39]

In light of all the aforementioned facts, we set to examine whether Egyptian fruit bats that roost and forage in urban environments risk their health due to their exposure to air pollution and specifically if they suffer from low HGB levels. We sampled ten fruit bat colonies located in environments with different levels of urbanization (Figure 1 and Table 1) and found a strong negative correlation between PM 2.5 pollution and HGB levels.

RESULTS

A correlation between urbanization and PM2.5 pollution

There was a strong positive correlation between the colony's degree of urbanization and the PM2.5 pollution level outside it (Figure 2, R = 0.95, $p < 2E{-}05$, Pearson correlation test). PM2.5 levels inside the colonies were also significantly correlated with the urbanization index (R = 0.67, $p = 0.045$) but only after removing the Zoological Garden colony in which pollution inside was remarkably low, probably because of the small entrance size and the artificial air-conditioning (compare pink triangle and circle in Figure 2). Interestingly, the average PM2.5 levels outside the urban colonies were significantly higher than those inside the colonies (except for the Dizengoff Center colony, which is located inside an active suppliers' parking lot where trucks enter routinely to unload supplies, often leaving their engines running). In contrast, pollution levels were higher inside than outside the colonies in rural areas (compare circles to triangles in Figure 2). Notably, fruit bats spend many hours foraging every night (up to 10 h, Harten et al.[38]), and thus they are exposed to external pollution as much as to the pollution inside their colonies.

To account for the effects of both urbanization and the location of the measurement (inside or outside the colony), a generalized linear model was employed.

The model was employed with PM2.5 levels set as the explained parameter and with fixed effects including the colony's normalized urbanization level, the measurement location (in/out, binary with 1 for inside), and their interaction. As expected, the urbanization index had a large significant effect on the pollution levels (with an estimate of 9.97 $\frac{\mu g}{m^3}$ per urbanization unit, $p < 5\ E{-}04$, Table 2). The interaction between urbanization and measurement location was also significant, and the estimate was negative suggesting that, in urban colonies, pollution was significantly higher outside the colony than inside (with an estimate of $-6.93\ \frac{\mu g}{m^3}$, $p = 0.04$, Table 2, see Figure S2). To examine the effect of population density on pollution, we ran the same model with the actual (rather than the normalized) population

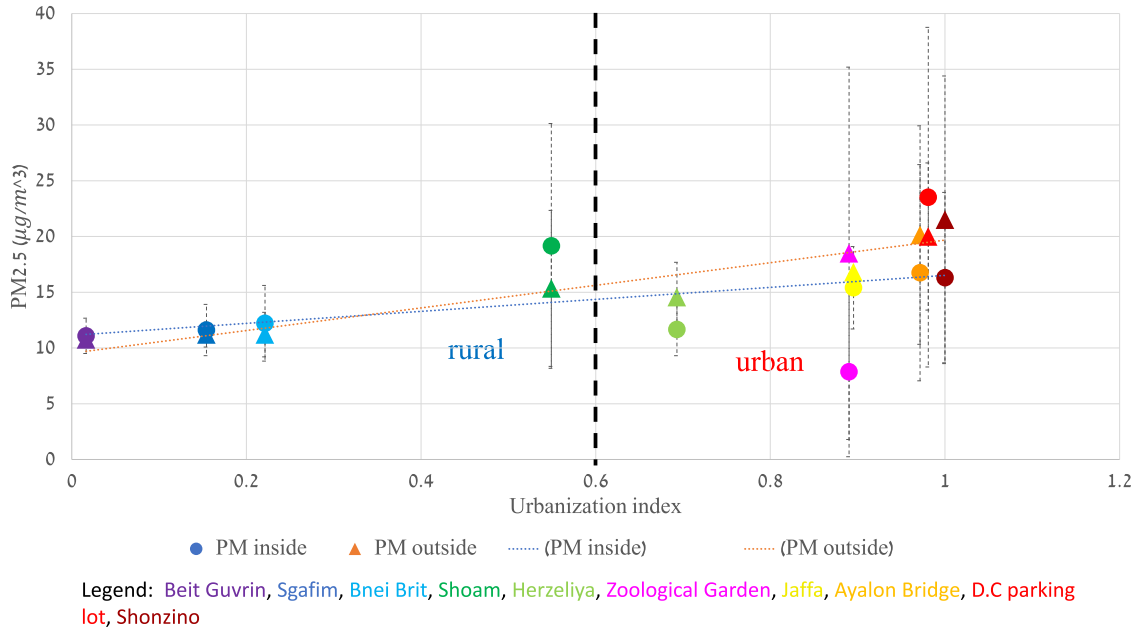


Figure 2. Average PM2.5 levels inside (dots) and outside (triangles) bat colonies located in different urbanization levels

Each point represents one colony, color-coded according to the legend. The dashed red line is the linear fit for the measurements outside y = 10.14x + 9.54, with R^2 = 0.91 (with a Pearson correlation of R = 0.95, and $p < 2E{-}05$). The dashed blue line represents the linear fit of the measurements inside each colony: y = 5.38x + 11.13, with R^2 = 0.20 (the Pearson correlation after removing the Zoological Garden colony was R = 0.67, and $p = 0.045$). The thin vertical dashed lines represent the standard division. The vertical dashed line separates stations in rural and urban locations.

density as a fixed factor and found that pollution increases on average by 2.9 $\frac{\mu g}{m^3}$, for every increase in 100,000 people per km^2 ($p = 0.0005$).

These estimates were computed after excluding the Dizengoff Center colony, where bats roost in an active truck parking lot. Notably, the effect of urbanization remained significant even when including the Dizengoff colony (Table 3). For visualization of the average PM2.5 inside and outside the rural and urban areas (including and excluding the Dizengoff Center colony), see Figure S2.

Bats from more polluted regions have lower HGB levels

After establishing a connection between urbanization and pollution, we examined whether PM2.5 pollution in the colonies was correlated with bats' HGB levels. There was a significant negative correlation between the PM2.5 concentrations (the average of both inside and outside measurements) and HGB levels (Figure 3A, Pearson correlation: R = −0.68 and $p = 0.029$). Similarly, PM2.5 measures exhibited significant negative correlations with HGB-related parameters, including the MCH and the MCHC (Figures 3B and 3C, Pearson correlations of −0.74 and −0.73 and p values of 0.014 and 0.016, respectively). Adding bats' sex (female/male) to the models did not improve their fit.

Bat HGB and HGB-related parameters also negatively correlated with the pollution measured only inside the colonies (Pearson correlation: R = −0.61, −0.61, and −0.5; p = 0.06, 0.061, and 0.146, for HGB, MCH, and MCHC respectively; Figure S3), as well as with the pollution measured only outside the colonies (Pearson correlation: R = −0.57, −0.68, and −0.8; $p = 0.166$, 0.031, and 0.006, for HGB, MCH, and MCHC respectively; Figure S4).

None of the other blood parameters including the red blood cell count (RBC), the white blood cell count (WBC), the mean corpuscular volume (MCV), and the hematocrits showed a significant correlation with pollution.

There was also no significant correlation between blood iron and HGB levels in the 21 bats that we examined (Pearson correlation test, $p > 0.7$, R = 0.09).

Table 2. Fixed effects coefficients for the effect of urbanization and measurement location on pollution (95% CIs)

Name	Estimate values	Standard error	tStat	p value
Intercept	9.6	1.5	6.2	2.26E−05
Norm. density	10	2.2	4.5	4.85E−04
Inside	2.2	2.2	1	0.339
Urban: inside	−6.9	3.1	−2.2	0.044

HGB levels are not correlated to instantaneous exposure to pollution

Finally, we examined the timescale of the effect of pollution on HGB. To this end, we examined the levels of pollution that individuals in one colony (Zoological Garden) were exposed to, over a period of two months by placing multiple sensors along the typical routes they used in flight and continuously measuring pollution in the colony (Figure 4 and see STAR Methods). In parallel to measuring pollution, we routinely (∼once a week) extracted blood samples and estimated their HGB levels. We did

Table 3. Fixed effect coefficients for the effect of urbanization and measurement location (inside/outside) on pollution including the Dizengoff Center colony (95% CIs)

Name	Estimate values	Standard error	tStat	*p* value
Intercept	9.5	1.8	5.2	9.4E−05
Norm. density	10.1	2.5	4	9.9E−04
Inside	1.6	2.6	0.6	0.55
Urban: inside	−4.8	3.6	−1.3	0.201

not find a significant correlation between the specific (3 days and one week) pollution levels to which individuals were exposed and their respective instantaneous HGB levels (Tables S2 and S3, respectively) suggesting that the effects of pollution on HGB accumulate over relatively long periods of months.

DISCUSSION

With the rapid growth in urbanization, we are only beginning to understand its impacts on wildlife. Air pollution is one of the main characteristics of urbanization, but its health impacts

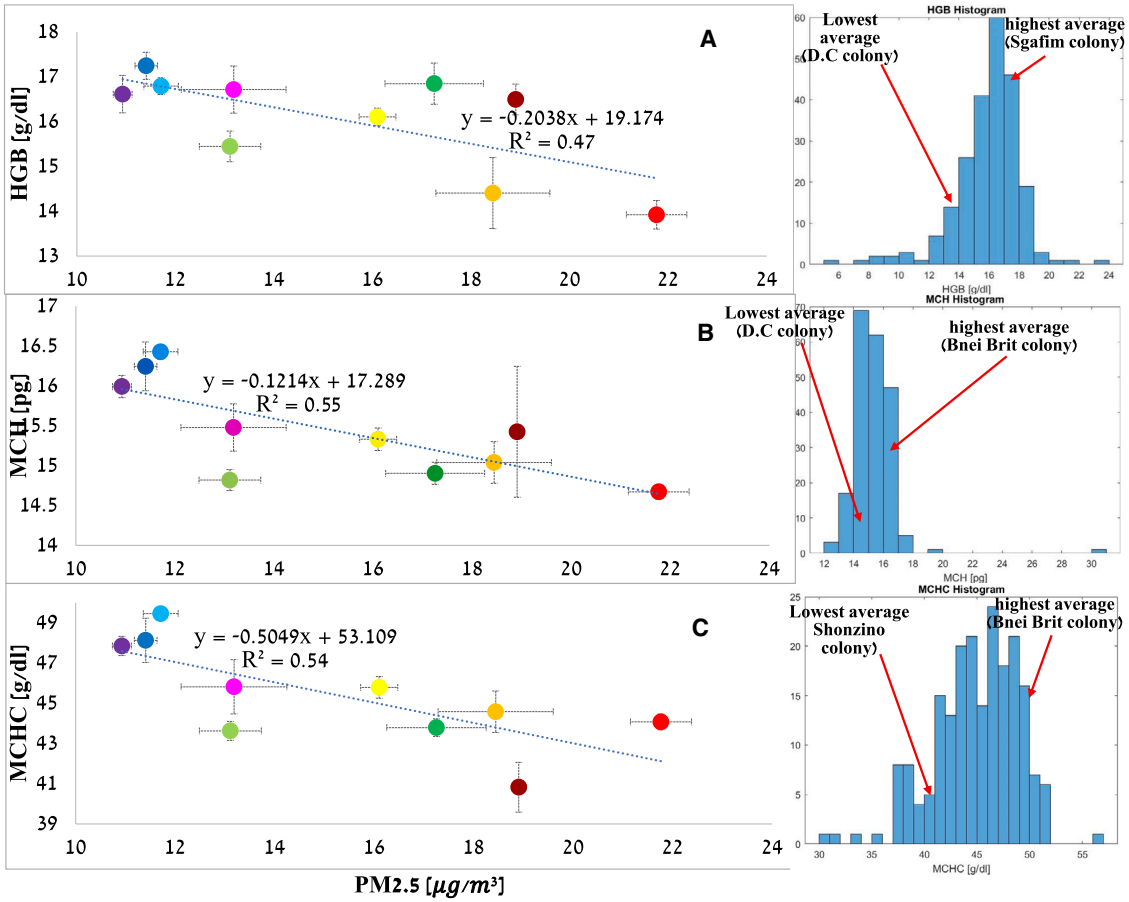


Figure 3. Average colony hemoglobin and blood parameters vs. PM2.5 pollution in the different colonies (average of inside and outside)

Each colored point represents one colony. Dash lines represent standard errors. The right panel in each row shows the distribution of measurements for all colonies together.

(A) Average colony HGB vs. PM2.5 in the different colonies. The equation of its linear fit is $y = -0.2x + 19.17$, with $R^2 = 0.47$. The Pearson correlation between them is −0.68, and the *p* value is 0.029.

(B) Average colony MCH vs. PM2.5 in the different colonies. The equation of its linear fit is $y = -0.12x + 17.29$, with $R^2 = 0.55$. The Pearson correlation between them is −0.74, and the *p* value is 0.014.

(C) Average colony MCHC vs. PM2.5 in the different colonies. The equation of its linear fit is $y = -0.5x + 53.11$, with $R^2 = 0.54$. The Pearson correlation between them is −0.73, and the *p* value is 0.016.

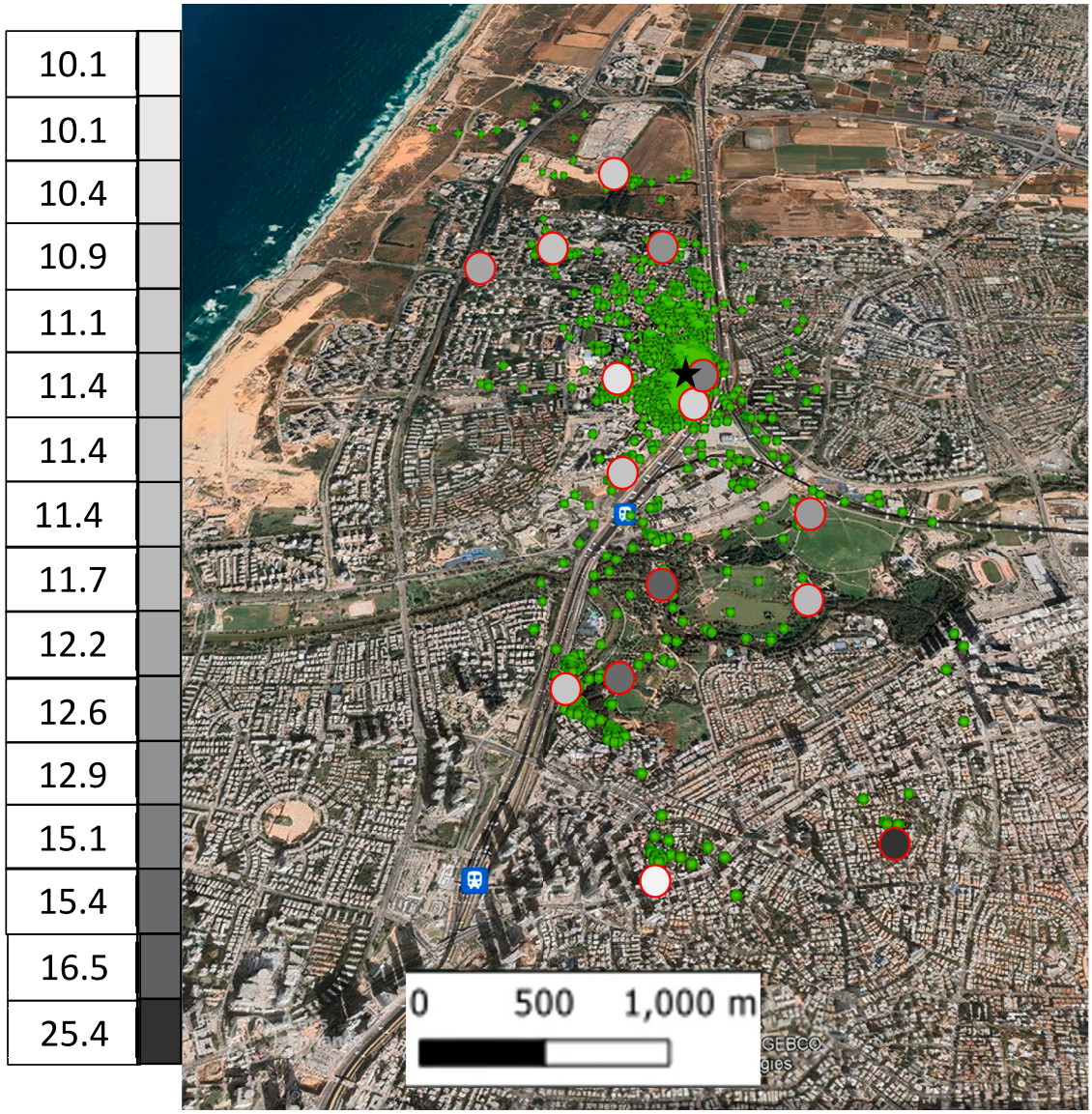


Figure 4. Individual pollution exposure measurements

Circles show the locations where the Pats+ sensors were placed during February–May 2023. They are color-coded according to the median pollution from the lower measurements (white) to higher pollution measurements (dark). Color bar on the left depicts pollution levels in $\mu g/mm^3$. The green dots show the trajectories of 8 bats (overlaid on each other). The Zoological Garden colony is marked by a black star. The circle next to the colony shows the measurements outside the colony (which indicates a relatively high pollution outside).

have mainly been examined on humans. In this study, we reveal a very clear negative correlation between the pollution in the area where the bats roost and their HGB levels. We observe a reduction of approximately 1.8 g/dL in HGB levels with a PM2.5 increase of 10 $\frac{\mu g}{m^3}$. The higher HGB levels measured in the less polluted colonies were in line with previously published values for the species.[40,41] There is no documentation of what HGB level constitutes anemia in bats, but we observe a difference of ~25% between the highest and lowest HGB average colony levels, equivalent to more than 2STDs (standard deviations) relative to the population's mean. Such a decrease in humans would be considered anemia and thus might impact bats' health, especially as bats are highly aerobic creatures with an extended demand for oxygen due to their strenuous metabolic effort of flight. Additional HGB-related parameters (such as the MCH) all showed the same negative correlation with pollution.

Our attempt to find a correlation between individual foraging patterns and individual exposure to pollution with HGB failed, suggesting that HGB levels are determined over long periods of many weeks and maybe months. This is in line with data published for humans where athlete HGB levels increased by only 5% after three weeks at high altitudes.[42]

Because some bats roost in the country but routinely fly to forage in the city and thus experience country colony pollution

levels, but urban environmental pollution levels[36] we also compared the pollution inside and outside the colonies. Indeed, one of the interesting insights we obtained is that, in urban environments, pollution levels inside the colony are usually lower than those outside (unlike in rural areas) suggesting that, in this respect, bats would benefit from shortening their foraging time. The DC (Dizengoff Center) colony was an exception, but bats rarely roost in very active parking lots. The fact that the bats choose to roost in such a polluted spot suggests that they do not assess PM pollution when making roosting decisions or that they cannot assess the pollution level (there are many other roosting possibilities in the city). Notably, when entering the parking lot, we were not disturbed by air quality.

Two additional interesting cases are the relatively low PM2.5 pollution inside the urban Zoological Garden colony, probably because of the narrow entrance to this colony and the artificial air-conditioning, which circulates the air, and the relatively high pollution in the rural Shoham colony probably because of the archeological excavation at the entrance to the cave, which resulted in airborne dust. The bats in the Zoological garden had the highest average HGB levels exemplifying the importance of clean air in the roost.

We excluded the possibility that HGB differences might result from difference in the bats' iron diet as there was no correlation between HGB and blood iron levels. This alternative explanation also seems less likely as colonies that are nearby each other and whose bats thus share a very similar diet exhibited very different HGB levels that correlated with pollution. For example, the DC parking lot and the Jaffa colonies, which are only 3 km apart and where bats forage on very similar trees, differed greatly in both pollution and HGB levels. In fact, one of the suggested mechanisms by which PM2.5 pollution might impact HGB is by bonding to iron atoms in the blood. Moreover, the models' fit (measured based on the Akaike information criterion [AIC]) was better when using pollution rather than human population density (i.e., a proxy of urbanization) as an explaining parameter suggesting that pollution better explains HGB differences than other urban parameters.

A negative correlation between pollution and HGB has been shown for humans, but, to our best knowledge, this is the first study that shows a connection between air pollution and HGB in wild animals. With the ever-increasing spread of urbanization, many animals find themselves living in urban environments exposed to various types of anthropogenic pollution. Low HGB concentrations could lead to anemia and in the long run could impair bats' foraging abilities. As flying mammals, bats require high levels of oxygen to commute and forage. This study thus highlights the cost that urban-dwelling animals must pay while enjoying some of the city's benefits such as warm temperatures, artificial roosts, and an excess in both amount and variability of fruit in the case of fruit bats.

In conclusion, we found a negative correlation between exposure to PM pollution and bats' blood HGB levels (as well as other HGB-related parameters such as MCH and MCHC). Specifically, bats that roost and forage in the cities were exposed to more air pollution and had lower HGB levels, potentially endangering their health. Furthermore, the pollution in urban areas was found to be higher outside than inside the bats' colonies. Hence, the foraging patterns of urban bats will likely affect their health, and, in terms of PM pollution, it is better for them to stay inside their colony as long as possible. This rule of thumb might be wrong in cases where the bats select to roost in a highly polluted root such as an active parking lot.

Limitations of the study

Notably, this is a correlative study, and we have not proven directly that PM pollution is the driver of HGB levels. Controlled laboratory studies are needed in order to generate a direct link between pollution and HGB.

Additional research is also required in order to reveal the impact of the possible effect that we have observed on actual bat health. Such research could include, for example, an assessment of bats' physiological performance under physical activity. Additional GPS tracking is also required in order to examine the relation between individual foraging choices and the individual effects of air pollution.

Moreover, our research is only a starting point for further studies on the impact of air pollution on urban-dwelling animals. Future work can explore not just HGB-related parameters but also other health aspects and foremost the respiratory system. Our research aims to encourage more in-depth exploration with larger sample sizes of the hazards and morbidity of air pollution, primarily caused by humans, on the animals that coexist with us.

RESOURCE AVAILABILITY

Lead contact

Requests for further information and resources 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

- This paper does not report original code.
- Data reported in this paper have been deposited at Mendeley Data (DOI: https://doi.org/10.17632/jx5ggwnypn.1) and are publicly available as of the date of publication.
- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

ACKNOWLEDGMENTS

This research was partially supported by the European Research Council (ERC CoG – Behavior-Island-101001993). Additionally, our thanks go to the management of the Botanic Garden and Dizengoff Center Mall for granting us permission to use their properties for placing our sensors.

AUTHOR CONTRIBUTIONS

Y.Y., C.P., and O.G. designed the experiments. O.E., Y.Y., A.R., M.W., D.Z., R.A., and O.G. collected the data. O.G. analyzed the data. Y.Y. and O.G. wrote the paper.

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:

- KEY RESOURCES TABLE
- EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS
- METHOD DETAILS
  - Bat roosts
  - Pollution measurements
  - Hemoglobin (HGB) and iron assessments
  - Individual bat tracking
- QUANTIFICATION AND STATISTICAL ANALYSIS

SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.isci.2025.111997.

Received: June 26, 2024
Revised: December 6, 2024
Accepted: February 7, 2025
Published: February 17, 2025

REFERENCES

1. Somboonsin, P., and Canudas-Romo, V. (2021). Mortality attributable to fine particulate matter in Asia, 2000-2015: A cross-sectional cause-of-death analysis. BMJ Open *11*, e043605.
2. Seaton, A., Soutar, A., Crawford, V., Elton, R., McNerlan, S., Cherrie, J., Watt, M., Agius, R., and Stout, R. (1999). Particulate air pollution and the blood. Thorax *54*, 1027–1032.
3. Mayer, H. (1999). Mayer: Cities. Atmos. Environ. *33*, 4029–4037.
4. Shima, M. (2017). Health Effects of Air Pollution: A Historical Review and Present Status. Nihon Eiseigaku Zasshi *72*, 159–165.
5. Festy, B. (2013). Review of evidence on health aspects of air pollution - REVIHAAP Project. Technical Report. World Health Organization Regional Office for Europe 2013. Pollut. Atmos. *219*.
6. Mustafić, H., Jabre, P., Caussin, C., Murad, M.H., Escolano, S., Tafflet, M., Périer, M.C., Marijon, E., Vernerey, D., Empana, J.P., and Jouven, X. (2012). Main Air Pollutants and Myocardial Infarction: A Systematic Review and Meta-analysis. JAMA *307*, 713–721. https://doi.org/10.1001/jama.2012.126.
7. Kampa, M., and Castanas, E. (2008). Human health effects of air pollution. Environ. Pollut. *151*, 362–367.
8. Losacco, C., and Perillo, A. (2018). Particulate matter air pollution and respiratory impact on humans and animals. Environ. Sci. Pollut. Res. Int. *25*, 33901–33910.
9. Arias-Pérez, R.D., Taborda, N.A., Gómez, D.M., Narvaez, J.F., Porras, J., and Hernandez, J.C. (2020). Inflammatory effects of particulate matter air pollution. Environ. Sci. Pollut. Res. *27*, 42390–42404.
10. Oanh, N., Pongkiatkul, P., Cruz, M., Dung, N., Phillip, L., Zhuang, G., and Lestari, P. (2012). Monitoring and Source Apportionment for Particulate Matter Pollution in Six Asian Cities. In Integrated Air Quality Management (CRC Press), pp. 97–124.
11. Shahi, A.M., Omraninava, A., Goli, M., Soheilarezoomand, H.R., and Mirzaei, N. (2014). The Effects of Air Pollution on Cardiovascular and Respiratory Causes of Emergency Admission. Emergency *2*, 107–114. http://www.ncbi.nlm.nih.gov/pubmed/26495360%0Ahttp://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=PMC4614571.
12. Schraufnagel, D.E. (2020). The health effects of ultrafine particles. Exp. Mol. Med. *52*, 311–317.
13. Liu, C., Chen, R., Sera, F., Vicedo-Cabrera, A.M., Guo, Y., Tong, S., Coelho, M.S.Z.S., Saldiva, P.H.N., Lavigne, E., Matus, P., et al. (2019). Ambient Particulate Air Pollution and Daily Mortality in 652 Cities. N. Engl. J. Med. *381*, 705–715.
14. Li, Z., Li, X., Song, H., Tao, B., Qiu, B., Tian, D., Zhan, M., Wu, Z., Wu, J., Zhang, Q., and Wang, J. (2021). Effects of short-term ambient PM2.5 exposure on the blood cell count and hemoglobin concentration among 82,431 people in eastern China. Sci. Total Environ. *776*, 146046.
15. Honda, T., Pun, V.C., Manjourides, J., and Suh, H. (2017). Associations between long-term exposure to air pollution, glycosylated hemoglobin and diabetes. Int. J. Hyg Environ. Health *220*, 1124–1132. https://doi.org/10.1016/j.ijheh.2017.06.004.
16. Gao, K., Chen, X., Zhang, L., Yao, Y., Chen, W., Zhang, H., Han, Y., Xue, T., Wang, J., Lu, L., et al. (2022). Associations between differences in anemia-related blood cell parameters and short-term exposure to ambient particle pollutants in middle-aged and elderly residents in Beijing, China. Sci. Total Environ. *816*, 151520. https://www.sciencedirect.com/science/article/pii/S0048969721065980.
17. Tian, L., Sun, M., Lin, L., Wang, Y., Yu, Y., Duan, J., and Sun, Z. (2022). Effects of ambient air pollution on glycosylated hemoglobin: a systematic review and meta-analysis. Environ. Sci. Pollut. Res. Int. *29*, 53954–53966. https://doi.org/10.1007/s11356-022-20728-7.
18. Lipšic, E. (2006). Erythropoietin in Cardiac Ischemia (Groningen University Institute).
19. Littlewood, T.J. (2001). The impact of hemoglobin levels on treatment outcomes in patients with cancer. Semin. Oncol. *28*, 49–53. https://www.sciencedirect.com/science/article/pii/S0093775401902131.
20. Murray, M.H., Sánchez, C.A., Becker, D.J., Byers, K.A., Worsley-Tonks, K.E.L., and Craft, M.E. (2019). City sicker? A meta-analysis of wildlife health and urbanization. Front. Ecol. Environ. *17*, 575–583.
21. Peakall, D. (1992). Animal Biomarkers as Pollution Indicators (Springer-science+ buisness media, B.V).
22. Van der Schalie, W.H., Gardner, H.S., Jr., Bantle, J.A., De Rosa, C.T., Finch, R.A., Reif, J.S., Reuter, R.H., Backer, L.C., Burger, J., Folmar, L.C., and Stokes, W.S. (1999). Animals as sentinels of human health hazards of environmental chemicals. Environ. Health Perspect. *107*, 309–315.
23. Fonken, L.K., Xu, X., Weil, Z.M., Chen, G., Sun, Q., Rajagopalan, S., and Nelson, R.J. (2011). Air pollution impairs cognition, provokes depressive-like behaviors and alters hippocampal cytokine expression and morphology. Mol. Psychiatry *16*, 987-95–973.
24. Block, M.L., Elder, A., Auten, R.L., Bilbo, S.D., Chen, H., Chen, J.-C., Cory-Slechta, D.A., Costa, D., Diaz-Sanchez, D., Dorman, D.C., et al. (2012). The outdoor air pollution and brain health workshop. Neurotoxicology *33*, 972–984. https://www.sciencedirect.com/science/article/pii/S0161813X12002100.
25. Costa, L.G., Cole, T.B., Coburn, J., Chang, Y.C., Dao, K., and Roque, P. (2014). Neurotoxicants are in the air: Convergence of human, animal, and *in vitro* studies on the effects of air pollution on the brain. BioMed Res. Int. *2014*, 736385.
26. Wang, Q., Liu, G., Yan, L., Xu, W., Hilton, D.J., Liu, X., Pei, W., Li, X., Wu, J., Zhao, H., et al. (2023). Short-term particulate matter contamination severely compromises insect antennal olfactory perception. Nat. Commun. *14*, 4112.
27. Fenton, M.B., and Simmons, N.B. (2015). A World of Science and Mystery (University of Chicago Press). https://doi.org/10.7208/9780226065267.
28. Voigt, C.C., and Kingston, T. (2015). Bats in the anthropocene: Conservation of bats in a changing world. In Bats in the Anthropocene: Conservation of Bats in a Changing World (Springer International Publishing), pp. 1–606.
29. Coleman, J.L., and Barclay, R.M.R. (2012). Urbanization and the abundance and diversity of Prairie bats. Urban Ecosyst. *15*, 87–102.
30. Russo, D., and Ancillotto, L. (2015). Sensitivity of bats to urbanization: A review. Mamm. Biol. *80*, 205–212. https://doi.org/10.1016/j.mambio.2014.10.003.

31. Legakis, A., Papadimitriou, C., Gaethlich, M., and Lazaris, D. (2000). Survey of the bats of the Athens metropolitan area. Myotis 38. Greece Bats.PDF, *38*, pp. 41–46, Myotis. 2000.

32. Sotero, D.F., Benvindo-Souza, M., Pereira de Freitas, R., and de Melo e Silva, D. (2022). Bats and pollution: Genetic approaches in ecotoxicology. Chemosphere *307*, 135934. https://www.sciencedirect.com/science/article/pii/S0045653522024274.

33. Zukal, J., Pikula, J., and Bandouchova, H. (2015). Bats as bioindicators of heavy metal pollution: History and prospect. Mamm. Biol. *80*, 220–227. https://doi.org/10.1016/j.mambio.2015.01.001.

34. Rachwald, A., Wodecka, K., Malzahn, E., and Kluziński, L. (2004). Bat activity in coniferous forest areas and the impact of air pollution. Mammalia *68*, 445–453. https://doi.org/10.1515/mamm.2004.045.

35. Marvin Herndon, J., and Whiteside, M. (2020). Unacknowledged Potential Factors in Catastrophic Bat Die-off Arising from Coal Fly Ash Geoengineering. Asian J. Biol. *15*, 1–13.

36. Egert-Berg, K., Handel, M., Goldshtein, A., Eitan, O., Borissov, I., and Yovel, Y. (2021). Fruit bats adjust their foraging strategies to urban environments to diversify their diet. BMC Biol. *19*, 123.

37. Weinberg, M., Nissan, Y., and Yovel, Y. (2022). Egyptian Fruit Bat Rousettus Aegyptiacus (Geoffroy, 1810) (Springer), pp. 1–26.

38. Harten, L., Katz, A., Goldshtein, A., Handel, M., and Yovel, Y. (2020). The ontogeny of a mammalian cognitive map in the real world. Science *369*, 194–197.

39. Netanyahu, S., Magdon, G., Matzner, A., Tzelock, M., Shtainbaum, H., and Avisror, O. (2017). State of Enviornment in Israel, Report (Minist enviornment Prot Isr). http://moodle.telhai.ac.il/pluginfile.php/686290/mod_resource/content/0/enviornmentalstatereport2017.pdf.

40. Korine, C., Zinder, O., and Arad, Z. (1999). Diurnal and seasonal changes in blood composition of the free-living Egyptian fruit bat (Rousettus aegyptiacus). J. Comp. Physiol. B *169*, 280–286.

41. Carpenter, R.E. (1986). Flight physiology of intermediate-sized fruit bats (pteropodidae). J. Exp. Biol. *120*, 79–103.

42. Garvican-Lewis, L.A., Halliday, I., Abbiss, C.R., Saunders, P.U., and Gore, C.J. (2015). Altitude exposure at 1800 increases haemoglobin mass in distance runners. J. Sports Sci. Med. *14*, 413–417.

STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Biological samples		
Blood samples (WBC,RBC,HGB, HCT, MCV, MCH,MCHC tests)	American Medical Laboratories (AML)	N/A
Other		
Mendeley	Elsevier	https://data.mendeley.com/preview/jx5ggwnypn?a=d4b4523f-aa77-405c-a7be-b2eb29d7d158
Experimental models: Organisms/strains		
Rousettus aegyptiacus	Colonies in central Israel	Taxonomy ID: 9407
Software and algorithms		
MATLAB R2022a	MathWorks	https://www.mathworks.com/downloads/;

EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

212 Egyptian fruit bats (*Rousettus aegyptiacus*) were sampled in this study. 131 from them were female, and the majority were adults (208 bats). The detailed information about the colonies of the bats is presented in Table 1. All captures and blood extraction were done with the permission of the National Park Authority (permit 2022-43219(and the institutional IACUC (permit number TAU - LS - IL - 2201 - 114 - 2).

METHOD DETAILS

Bat roosts

We sampled bats at 10 Egyptian fruit bat (*Rousettus aegyptiacus)* colonies located in both urban and rural areas in Israel (Figure 1A). An urbanization index was calculated for each colony (Figure 1B) based on the estimated population density within a 3 km radius around the colony, after excluding non-inhabitable areas such as the Mediterranean Sea and then normalizing by the density of the colony positioned in the most populated region. A radius of 3 km was chosen because bats spend a large amount of their time within this radius.[38] The population data were obtained from the ''demographics variables layer - 2014'' in ARC GIS and from the Tel-Aviv municipal and the Population and Immigration Authority websites.

Pollution measurements

To monitor and measure PM2.5 air pollution levels inside and outside bat colonies and along their flight routes, two main sensors were utilized: (1) The PurpleAir PA-II-SD (https://www2.purpleair.com/products/purpleair-pa-ii) and (2) The PATS+ Monitor (https://berkeleyair.com/wp-content/uploads/2020/02/PATS-Specifications-Oct-2016.pdf) from Berkeley University. The PurpleAir sensor requires high voltage and was employed to measure PM2.5 in locations with electricity availability, while the battery-powered PATS+ sensors were used in all other sites. A comparison had been made between these two sensors at the same location, the measurements were equivalent (see calibration below), but the PATS+ sensor didn't measure values under 10 $\mu g/m^3$. Therefore, at the low PM2.5 concentration levels the PurpleAir sensor will be more accurate.

The PA-II-SD allows measuring three levels of PM pollution (PM10, PM2.5 & PM1) simultaneously every two minutes with an accuracy of 0.01 $\mu g/m^3$. Additional measurements acquired by this sensor include ambient temperature, humidity and pressure. The PATS+ sensor measures PM2.5 concentration with a high accuracy of 10^{-7} $\mu g/m^3$, as well as ambient temperature and relative humidity (sampling once per minute).

In addition to these two sensors, data from two additional publicly available sensors were used: Airlink (Davis Instruments) and sensors from stations of the Ministry of Environmental Protection of Israel. These sensors were used for validation of the measurements of the above sensors above. All sampling periods at the various colonies can be found in Table 1.

To examine the accuracy of the PATS+ sensor we compared its PM2.5 measurements to those of the Ministry of Environmental Protection of Israel sensor in ''Yehuda Maccabi'' station taken over a period of a 4 days in May 2023. The distance between the sensors was 1 km. We found a strong significant correlation between the two sensors: R^2=0.77, and a Pearson correlation of r=0.87 & $p< 10^{-5}$. To compare the PM2.5 measurements of PA-II-SD sensor and the Ministry of Environmental Protection of Israel sensor in

"Yehuda Maccabi" station data was taken over a period of a 30 days in July 2022. The distance between the sensors was 2 km. We found a strong significant correlation between the two sensors: R^2=0.61, and a Pearson correlation of r=0.77 & p< 10-5.

The sensors that were placed inside the colonies were placed as close as possible to the location where the bats roost. The sensors placed outside the colonies were placed near the entrance. The PA-II-SD sensors were placed in the Zoological Garden, D.C parking lot and the Shonzino colonies. The PATS+ sensors were placed in the other colonies.

Hemoglobin (HGB) and iron assessments

Bats (both females and males) were caught using hand- or mist nets at the various colonies (see Tables 1 and S1 for dates and numbers). The bats were gently hand-restrained without using anesthesia. Venipuncture was performed on the antebrachial vein in the wing, and approximately 1,000μl of blood was collected into small EDTA-coated tubes (BD Vacutainer® spray-coated K2EDTA). The tubes were stored inside temperature-controlled boxes and sent within a few hours for analyses at a professional veterinary laboratory (American Medical Laboratories, Herzeliya Israel). At least 17 adult bats were sampled in each colony (see Table S1). Samples with mean corpuscular hemoglobin concentration (MCHC) values of above 100 g/dl were removed from the data set. Such high values suggest an artifactual measurement, probably due to blood clots. After the removal, the minimal sample set per colony was 13.

To account for a potential effect of diet-iron levels on hemoglobin (HGB) levels, we measured and compared iron and HGB concentrations in bats from two colonies: DC and Beit Guvrin, representing low and high air pollution levels, respectively. We collected a total of 21 samples from male bats—9 from Beit Guvrin and 12 from DC. These samples were analyzed at American Medical Laboratories in Herzeliya, Israel. Individual serum iron levels were assessed using assays from Roche Diagnostics, GmbH, Mannheim, Germany.

Individual bat tracking

In addition to the colony level analysis, we assessed how individuals' exposure to pollution affects their HGB levels. To this end, we took advantage of the unique open colony in the Zoological Garden of Tel-Aviv University where the bats are free to forage outside (38).

We GPS-tracked 13 individual bats between January to April 2023 using miniature GPS tags (Vesper tags, ASD Inc). The tags were attached to the bats' backs with a collar, and the data was downloaded daily as described by Harten et al., 2020. (In parallel to the tracking, blood samples were taken from the bats approximately once a week (Table S1). Furthermore, in addition to the fixed air pollution measurements performed inside and outside the colony in the Zoological Garden, sporadic mobile devices were placed in several locations where these bats routinely fly and forage to estimate the individual pollution levels that bats were exposed to. We then examined the correlation between pollution exposure and blood HGB dynamically at the individual level.

QUANTIFICATION AND STATISTICAL ANALYSIS

All statistics were performed using MATLAB and Excel software. We used mixed-effect Generalized linear models (GLMM) to test for correlations between parameters.

All variables used to fit the GLMM models are specified in the main text.

Generalized Linear Mixed Models (GLMMs) extend generalized linear models by incorporating both fixed and random effects, making them ideal for analyzing hierarchical or clustered data. Fixed effects capture relationships between predictors and outcomes, while random effects account for variations across groups or locations. GLMMs handle data dependencies, improve estimation accuracy, and are flexible enough for various dependent variables. They are particularly useful for analyzing pollution levels across urban and rural areas, as they model both the effects of environmental factors and location-specific variations, preventing bias that might arise from ignoring these dependencies, and ensuring more accurate and generalizable results.

Pollution levels used in the models (except for the individual tracking) were the averages over 25 days on average. For the individual tracking models, average pollution levels were estimated during the 3 or 7 days before the blood samples were used.