The Apparent Urban Advance in Juvenile *Vulpes vulpes* Observations Diminishes after Accounting for Switzerland's Elevational Structure

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Urbanization can alter wildlife life cycles, but comparisons between more and less urbanized environments may be confounded by other environmental gradients. This study analyzed 4295 human-reported observations of *Vulpes vulpes* from 496 generalized 5×5 km cells across Switzerland between 2018 and 2024 to estimate when the probability that a spring record contained juveniles increased. Without environmental adjustment, the most built-up cells reached a 30 % probability threshold approximately 4.7 days earlier than the least built-up cells (95 % confidence interval: 0.2–8.4 days earlier). Temperature had little influence on this contrast. However, the most built-up cells were also located at considerably lower elevations, and joint adjustment for temperature and elevation reduced the contrast to 0.7 days in the opposite direction (95 % confidence interval: -3.8 to $+7.7$ days). Analyses using an alternative elevation measure, different probability thresholds, comparable elevation ranges, and a conservative treatment of potential duplicate records produced consistent results. These data therefore provide insufficient evidence for an independent urban advance and instead show how the elevational structure of Switzerland can generate an apparent timing contrast. The result describes the observable timing of records containing juveniles, not the dates of birth or den emergence.

Vulpes vulpes **| urban ecology | juvenile observations | elevation gradient | phenology | public occurrence data | Switzerland**

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Introduction

Hominins began constructing artificial structures long before the emergence of our own species, *Homo sapiens* (1). Over time, humans have used such structures to obtain protection from extreme weather, provide shelter and security, store food and other resources, support social organization, enable production and trade, facilitate movement, and improve living conditions. In doing so, we have transformed our surroundings to an unprecedented extent (2, 3).

This transformation has altered natural ecosystems (4–7), directly affecting the availability and distribution of habitats and resources, as well as the abundance and composition of numerous biological communities.

The red fox, *Vulpes vulpes*, provides a clear example of the effects of urbanization. Its high adaptability has enabled populations to become established in numerous Swiss cities (8) and to exploit food resources of human origin (9).

This study was motivated by research published in 2025 on foxes in Warsaw, where urban foxes began breeding approximately two weeks earlier than foxes in a nearby rural population (10). Switzerland, however, has a distinctive geographical structure: its most built-up areas are concentrated mainly at low elevations, whereas many less built-up areas occur at higher elevations (11). This overlap may produce an apparent timing difference between the two environments even when urbanization is not the underlying explanation. The present study therefore tests whether public records containing juvenile *Vulpes vulpes* occur earlier in the most built-up cells of Switzerland and whether any such difference remains after accounting for temperature and the country's elevational structure.

Methods

Occurrence data and study sample. Records of *Vulpes vulpes* were obtained from the *Swiss National Mammal Databank*, published by InfoSpecies and distributed through GBIF under a CC BY 4.0 license (12). The archive contained 205310 records of the species, of which 63700 provided interpretable information on the life stage of the observed individuals. The original descriptions were parsed into separate counts of adults, juveniles, and subadults.

The analysis was restricted to human-reported observations with a known calendar date, recorded between 2018 and 2024 from 1 March to 1 June. Records containing at least one adult or juvenile were retained. For each record i, $Y_i = 1$ when it contained one or more juveniles and $Y_i = 0$ when it contained adults but no juveniles. Records containing only subadults were excluded. Dates after 29 February in leap years were corrected to obtain a common annual scale. The final sample comprised 4295 records distributed among 496 observation cells. The coordinates released by the database are generalized to cells of approximately 5×5 km; they therefore represent observation areas rather than the exact locations of foxes or their dens. The variable Y_i describes whether a record contained juveniles, not their birth date or the precise timing of den emergence.

Environmental characterization of observation cells. The degree of urbanization of each cell was estimated using the 2020 GHS-BUILT-S R2023A built-up surface layer at a spatial resolution of 30 arcseconds (13). For each generalized coordinate, built-up surface area was summed within an approximate 5×5 km area. The built-up proportion of cell j was defined as $U_j = A_{\mathrm{built},j}/25\,000\,000\ \mathrm{m}^2$. Giving equal weight to each of the 496 cells, the first and third quartiles of U_j were 0.0182 and 0.0648, respectively. Thus, cells in the lower quartile contained at most approximately 1.82 % built-up surface, whereas those in the upper quartile contained at least 6.48 %. These categories represented the least and most built-up reference levels without assuming a strict division between rural and urban environments.

Terrain elevation was obtained from the SRTM 90 m v4.1 digital elevation model (14). For each generalized coordinate, the mean elevation of all pixels within the same approximate 5×5 km area was calculated. This measurement describes the general landscape elevation associated with each cell rather than the exact elevation of the observed animal. As an independent check, the occurrence elevation provided by the database was also retained when available.

Temperature data were obtained from NASA POWER and derived from the MERRA-2 atmospheric reanalysis (15). Each cell-year combination was assigned the nearest available grid point, at a resolution of 0.5° latitude by 0.625° longitude. The thermal covariate was mean daily air temperature at 2 m from 1 February to 31 March of the corresponding year.

Statistical analysis. Logistic regression was used to estimate the probability that each record contained at least one juvenile. Date was expressed as day of year and centered and scaled as $D_i = (d_i - 120)/30$. Because built-up proportion was right-skewed, it was transformed as $\log_{10}(U_i + 0.001)$ and subsequently standardized. The main model was defined as:

$$\begin{aligned}\operatorname{logit}[\Pr(Y_i = 1)] = {} & \beta_0 + \beta_1 D_i + \beta_2 U_i \\ & + \beta_3 D_i U_i + \beta_4 \mathrm{Lat}_i + \beta_5 \mathrm{Lon}_i \\ & + \gamma_{\mathrm{year}(i)},\end{aligned} \tag{1}$$

where Y_i indicates whether record i contained juveniles, D_i represents date, and U_i is the transformed and standardized level of urbanization. The interaction $D_i U_i$ allows the temporal change in probability to differ with the degree of urbanization. Year was included as a categorical effect, and latitude and longitude were included to account for broad geographical differences within Switzerland.

Daily probability curves were derived from the model for the urbanization levels corresponding to the first and third quartiles. Predictions were averaged with equal weight assigned to each year, while geographical position was held at the sample mean. For each curve, the first day on which the estimated probability reached 30 % was calculated by interpolation between consecutive days. The timing contrast was defined as $\Delta t = t_{\text{most built-up}} - t_{\text{least built-up}}$; a negative value of Δt therefore indicates that the threshold was reached earlier in the most built-up cells.

To evaluate the influence of environmental conditions, the model was repeated with temperature, terrain elevation, and both variables jointly. These variables were standardized and included both as main effects and through their interactions with date, allowing them to modify the temporal change in probability. The 95 % confidence intervals were calculated from 300 bootstrap replicates, using the 5×5 km cell as the resampling unit so that all records from the same cell remained grouped.

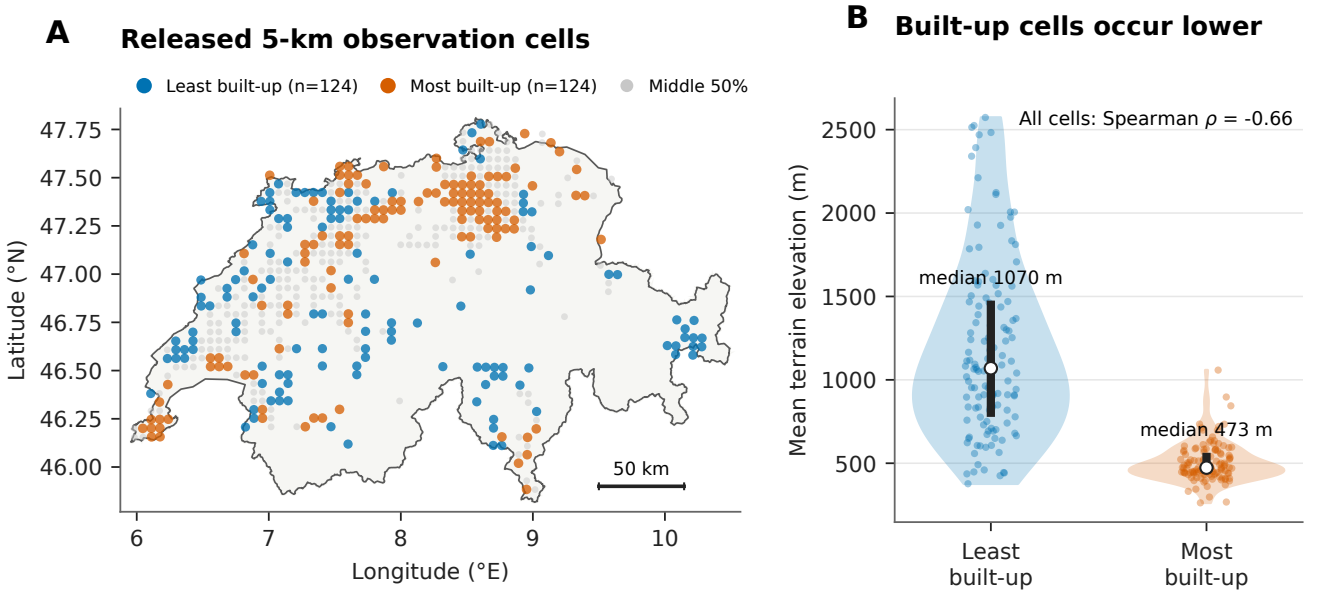
Sensitivity analyses. To test whether the timing contrast depended on the selected probability threshold, the unadjusted and jointly temperature- and elevation-adjusted models were repeated using thresholds of 20 %, 30 %, and 40 %. Sensitivity to the elevation measure was examined by replacing mean terrain elevation with the original occurrence elevation provided by the database, which was available for 3400 records. The analysis was also restricted to 400–800 m, the range containing the principal elevational overlap between cells with lower and higher built-up surface. This restricted sample comprised 3988 records from 344 cells.

Within the 400–800 m range, cells were further divided into four 100-m elevation bands. Within each band, cells were classified as relatively more or less built-up according to whether their built-up surface was above or below the band-specific median. A joint model included date, relative urbanization, elevation, temperature, year, and geographical position. The final contrast was obtained by averaging the estimated differences across the four bands with equal weight.

Finally, to evaluate the influence of potential duplicate records, the analysis was repeated after retaining one observation per cell and date. A cell-date combination was considered positive when at least one of its records contained juveniles, producing a conservative sample of 3949 observations. Confidence intervals for these checks were calculated using bootstrap resampling clustered by cell, with 300 replicates for the nationwide models and 400 for the comparison within elevation bands. All analyses were conducted in Python using NumPy, pandas, and scikit-learn. Logistic models were fitted with the L-BFGS solver and weak L2 regularization ($C = 1000$).

Results

The released 5×5 km observation cells covered much of Switzerland, although the least and most built-up quartiles had different spatial distributions (Fig. 1A). The most built-up cells occurred at lower elevations than the least built-up cells (medians of 473 and 1070 m, respectively), and built-up proportion was negatively correlated with elevation across all cells ($\rho = -0.66$; Fig. 1B).



Coordinates are generalized observation cells, not exact fox or den locations. Elevation summaries give each released cell equal weight.

Fig. 1. Geographical and elevational distribution of observation cells. (A) Distribution across Switzerland of generalized 5×5 km cells classified by built-up surface. (B) Elevation distributions of the least and most built-up quartiles; $\rho = -0.66$ across all cells.

As an initial timing contrast, the probability that an observation contained juveniles was estimated across the spring. The most built-up cells reached the 30 % threshold approximately 4.7 days earlier than the least built-up cells (95 % confidence interval: 0.2–8.4 days earlier; Fig. 2). This estimate was adjusted for year and geographical position, but not for elevation or temperature.

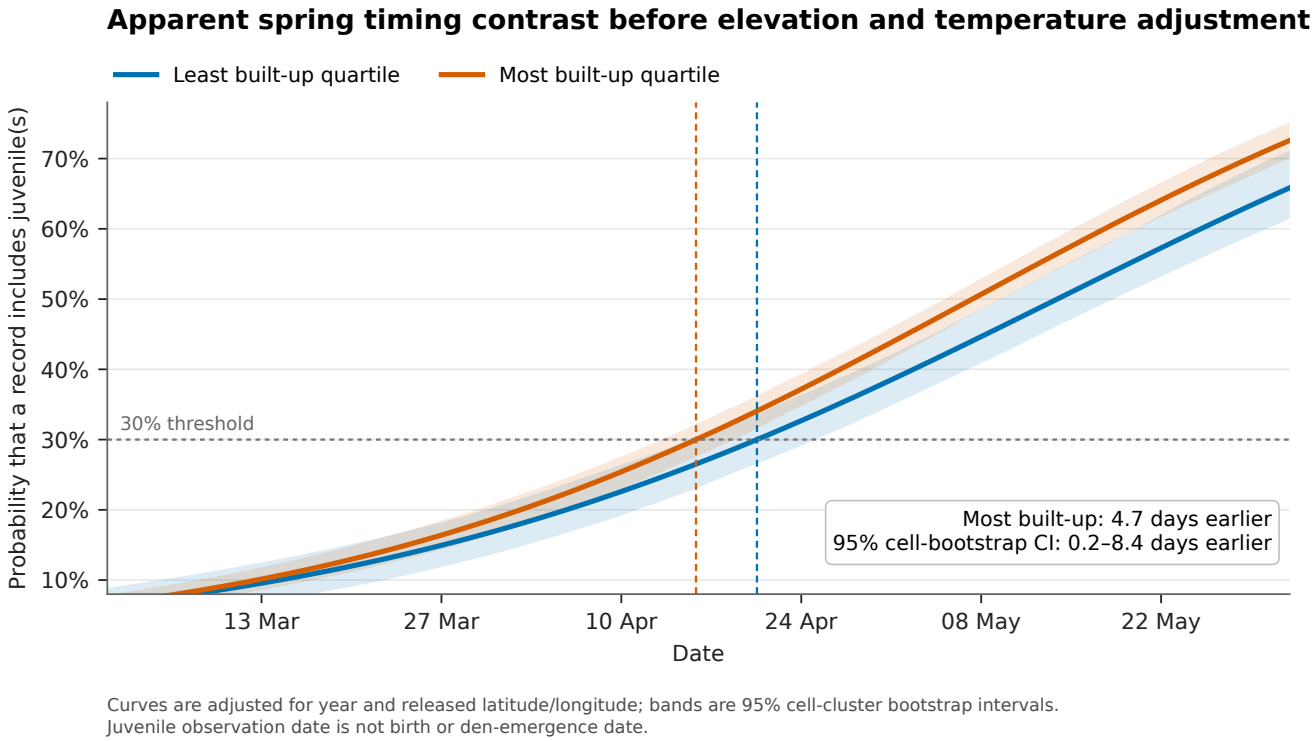


Fig. 2. Estimated probability that an observation contains juveniles across the spring in the least and most built-up quartiles. Vertical lines indicate when each curve reaches the 30 % threshold, yielding an apparent difference of 4.7 days. Shaded bands represent 95 % confidence intervals. Estimates are adjusted for year and geographical position, but not for elevation or temperature.

To evaluate the stability of the initial timing contrast, estimates without environmental adjustment were compared with estimates obtained after incorporating temperature, elevation, and both variables jointly. The analysis used terrain elevation for the complete set of records and was repeated, as an independent check, in the subset containing original occurrence-elevation information (Fig. 3).

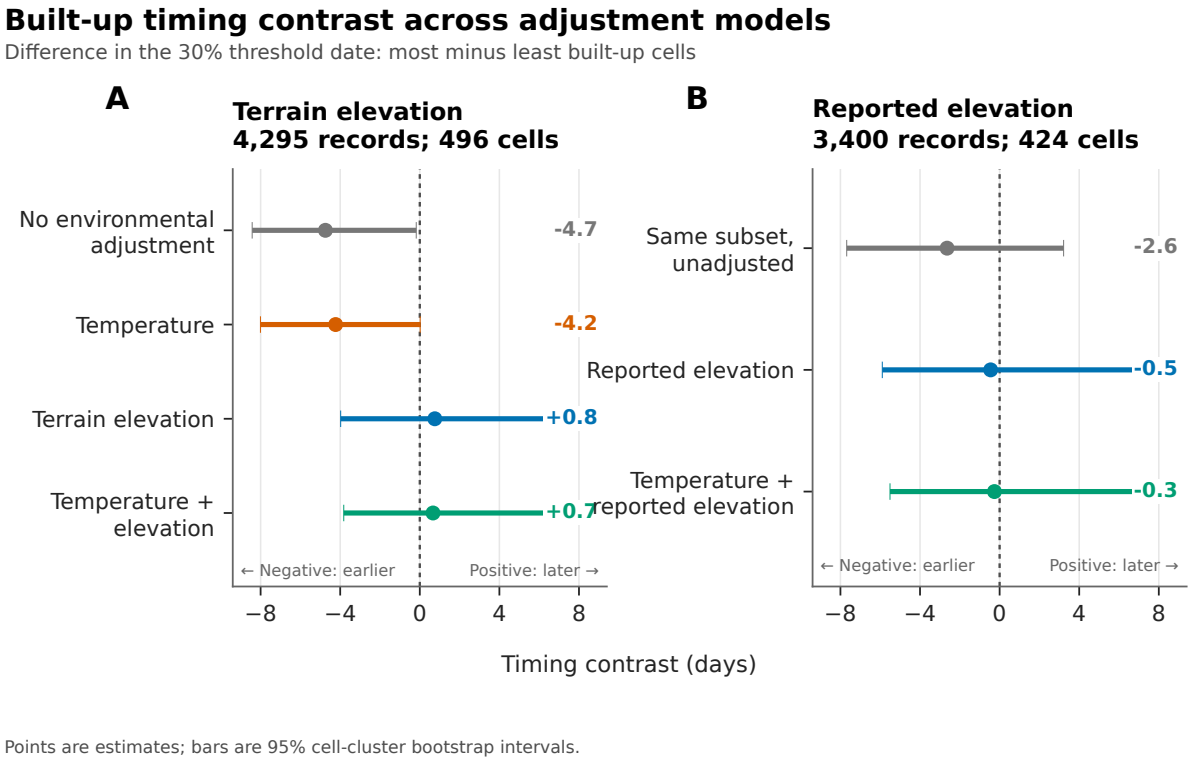


Fig. 3. Timing contrast between the most and least built-up cells under different environmental adjustments. (A) Complete-sample analysis using terrain elevation. (B) Check in the subset with reported occurrence elevation. Points represent differences in the date on which the estimated probability reaches 30 %; bars show 95 % confidence intervals obtained by bootstrap resampling clustered by generalized 5×5 km cell.

To determine whether the result depended on specific analytical choices, the contrast was re-estimated using alternative thresholds, different elevation measures and restrictions, a relative classification of urbanization, and a conservative treatment of potential duplicate records. Confidence intervals included zero in every environmentally adjusted analysis (Table 1).

Table 1. Sensitivity analyses of the timing contrast between the most and least built-up cells.

Analysis	Records	Difference (days)	95% CI (days)
No environmental adjustment; 20% threshold	4295	-3.6	$-7.9, +1.7$
No environmental adjustment; 30% threshold	4295	-4.7	$-8.4, -0.2$
No environmental adjustment; 40% threshold	4295	-5.7	$-9.3, -1.5$
Temperature and terrain-elevation adjustment; 20% threshold	4295	$+1.9$	$-4.4, +10.8$
Temperature and terrain-elevation adjustment; 30% threshold	4295	$+0.7$	$-3.8, +7.7$
Temperature and terrain-elevation adjustment; 40% threshold	4295	-0.3	$-4.4, +5.2$
Reported occurrence elevation and temperature	3400	-0.3	$-5.5, +7.3$
Common elevation range of 400–800 m; temperature and terrain elevation	3988	$+0.3$	$-5.1, +6.8$
Relative built-up level within 100-m elevation bands	3988	$+4.0$	$-3.1, +11.4$
One record per cell and date; temperature and terrain elevation	3949	$+0.5$	$-4.5, +7.6$

Differences are defined as the date on which the estimated probability of observing juveniles reaches the stated threshold in the most built-up cells minus the corresponding date in the least built-up cells. Negative values indicate earlier juvenile-containing records in more built-up cells, whereas positive values indicate later records. Confidence intervals were obtained by bootstrap resampling clustered by generalized 5-km cell.

Discussion

Figure 1 provides geographical context for the analysis. Panel A maps three categories of observation cells across Switzerland, each covering approximately 5×5 km, or 25 km^2. Blue cells represent the least built-up quartile, defined by the proportion of each cell occupied by artificial structures according to the GHSL (*Global Human Settlement Layer*) built-up surface estimate, whereas orange cells represent the most built-up quartile. Gray cells represent the intermediate 50 % of the urbanization distribution.

Panel B shows that the most built-up cells in this dataset generally occur at lower elevations than the least built-up cells. This pattern is consistent with the locations of several major Swiss cities, including Zurich (∼410 m), Bern (∼550 m), Geneva (∼375 m), Basel (∼260 m), and Lausanne (∼500 m), whereas higher-elevation localities such as Splugen (∼1475 m), Bosco/Gurin (∼1500 m), and Guarda (∼1650 m) illustrate Switzerland's strong topographic gradient. These examples are illustrative; the statistical contrast is based on all released cells rather than on the named localities.

This overlap requires related environmental factors to be considered before interpreting the study question. In Switzerland, highly built-up surfaces are concentrated at lower elevations, where spring conditions are generally reached earlier (16). In one alpine comparison, red fox dens also occurred at lower elevations than Arctic fox dens (17), although this does not establish a general den-site preference for the species. Urbanization, elevation, and seasonality may therefore be difficult to separate in a mountainous landscape.

Figure 2 describes the unadjusted spring change in the probability that a *Vulpes vulpes* record contained at least one juvenile. A 30 % probability threshold was used to summarize the separation between the two curves. Alternative thresholds did not change the direction of the unadjusted point estimate, although uncertainty was greater at the 20 % threshold (Table 1). The 30 % threshold was reached approximately 4.7 days earlier in the most built-up cells than in the least built-up cells. One possible interpretation is that cities provide more abundant and predictable food and numerous sheltering opportunities, which could favor reproduction and juvenile rearing (9, 10); this mechanism was not tested here. Importantly, the contrast in Fig. 2 is not adjusted for temperature or the elevational structure of Switzerland, whose influence is evaluated in Fig. 3.

Figure 3 examines whether the apparent 4.7-day advance in the 30 % threshold date for juvenile-containing records in the most built-up cells persists after accounting for temperature and terrain elevation.

Adding temperature shifted the timing contrast by only $+0.5$ days, from -4.7 to -4.2 days. Temperature therefore did not account for most of the initial contrast in these models. This does not imply that temperature is unimportant to red fox reproduction; it means only that adding this thermal measure had little influence on the estimated difference between the least and most built-up cells. The estimate changed much more substantially when terrain elevation was included.

After adjustment for the elevational structure of Switzerland, the initial 4.7-day advance in the most built-up cells became an estimated 0.8-day advance in the least built-up cells. The initial apparent advance therefore disappeared and the point estimate reversed slightly, although its confidence interval included zero. Joint adjustment for temperature and elevation produced a nearly identical estimate of $+0.7$ days.

Panel B showed similar attenuation in the 3400 records with reported occurrence elevation: the contrast changed from -2.6 days without environmental adjustment to -0.5 days after adjustment for occurrence elevation and to -0.3 days after temperature was added, with confidence intervals that included zero. Agreement between the two elevation measures indicates that the apparent urban advance is closely associated with the elevational structure of Switzerland and cannot be attributed independently to urbanization in these data. The analysis does not demonstrate that elevation is the direct biological cause, nor does it rule out a smaller urban effect.

Conclusions

Public records of *Vulpes vulpes* initially showed an apparent timing contrast: the probability that an observation contained juveniles reached the 30 % threshold approximately 4.7 days earlier in the most built-up cells. These cells, however, were also located at considerably lower elevations. Temperature had little influence on the initial estimate, whereas incorporating elevation reduced the difference to less than one day and slightly reversed its direction, with confidence intervals that included zero. Sensitivity analyses were consistent with this interpretation.

The analyzed data therefore provide insufficient evidence to attribute the apparent advance of juvenile-containing records to an independent effect of urbanization. The main contribution of this study is to show that, in Switzerland, the close relationship between built-up surface and elevation can generate an apparent urban timing contrast when geographical structure is not considered explicitly. This result concerns the observation dates of records containing juveniles, not their dates of birth or den emergence; it neither demonstrates a direct causal effect of elevation nor excludes a smaller urban effect. Future studies should compare environments at equivalent elevations or incorporate elevation before interpreting differences in the observable timing of the species, particularly in mountainous regions such as Switzerland.

Data and code availability

The occurrence data are publicly available from the *Swiss National Mammal Databank* through GBIF (GBIF dataset). Built-up surface data are available from GHS-BUILT-S R2023A (GHS-BUILT-S dataset), elevation data from SRTM

90 m v4.1, and temperature data from NASA POWER. Analysis code and derived data underlying the figures and table are available from the corresponding author upon reasonable request.

Ethics statement

This study used previously collected, publicly available occurrence records and involved no capture, handling, or experimental manipulation of animals.

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Competing interests

The author declares no competing interests.

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