Title: Introduced urban lizards (*Podarcis muralis*) exhibit environmentally plastic activity patterns and precise behavioral thermoregulation

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Highlights:

- In the field, wall lizards thermoregulated close to lab-measured thermal preferences.
- Lizard field body temperatures did not vary by size, sex, or reproductive status.
- Plastic individual behaviors produce emergent population level patterns in activity.
- Activity is coregulated by responses to air temperature and ultraviolet radiation.
- Effective thermoregulation in urban zones may enable establishment of populations.

Abstract

The ability to effectively thermoregulate is important for most ectotherms, as body temperature determines the rate of nearly all physiological processes. However, for most organisms we lack understanding of which environmental factors affect thermoregulatory behaviors, especially outside of a laboratory setting, and how individual behaviors scale over an entire day and at the population level. Introduced populations of the common wall lizard (*Podarcis muralis*) in Cincinnati, Ohio, USA are thriving after an introduction almost 75 years ago. To non-invasively quantify daily thermoregulatory behaviors, thermoregulatory effectiveness, and variation across sites, we used infrared thermography (a thermal imaging camera) to conduct repeated standardized sampling every 30 minutes across the lizard’s normal activity period (0800 to 2000) at multiple urban locations. We also measured air temperature, UV radiation, and wind speed while 3-D printed operative temperature models assessed available temperatures throughout the activity period. We found that lizard activity varied throughout the day and peaked in the early afternoon. Further, activity patterns were associated with the interaction of temperature and ultraviolet (UV) radiation intensity such that predicted activity at high temperatures is greatest when UV is low and at low temperatures predicted activity is greatest when UV is high. Activity was limited by cool environmental temperatures, even on hot days in mid-summer. When lizards were active, they thermoregulated precisely and achieved body temperatures closely matching preferred temperatures as selected in a laboratory gradient in a previous study. Furthermore, field body temperatures did not vary due to sex, reproductive status, or size. Data on daily activity and thermoregulatory decision-making, especially in an urban habitat, provide valuable insight into how an ectothermic organism integrates multivariate sensory inputs from the environment to make behavioral decisions. The role of environmental conditions in behavioral decision-making is especially relevant in predicting geographical range expansions, particularly in the context of changing urban environments and introduced species.

Resumen

La capacidad de termorregular eficazmente es importante para la mayoría de los ectotermos, ya que la temperatura corporal determina la taza de casi todos los procesos fisiológicos. Sin embargo, para la mayoría de los organismos, desconocemos qué factores ambientales afectan los comportamientos termorreguladores, especialmente fuera del laboratorio, y cómo se escalan los comportamientos individuales a lo largo de un día entero y a nivel poblacional. Las poblaciones introducidas de la lagartija roquera común (*Podarcis muralis*) en Cincinnati, Ohio, EE. UU., prosperan tras su introducción hace casi 75 años. Para cuantificar de forma no invasiva los comportamientos termorreguladores diarios, su eficacia y la variación entre sitios, utilizamos termografía infrarroja (una cámara termográfica) para realizar muestreos estandarizados repetidos cada 30 minutos durante el período de actividad normal de la lagartija (de 8:00 a 20:00) en múltiples ubicaciones urbanas. También medimos la temperatura del aire, la radiación UV y la velocidad del viento, mientras modelos impresos en 3D de temperatura operativa evaluaban las temperaturas disponibles durante todo el período de actividad. Observamos que la actividad de la lagartija variaba a lo largo del día y alcanzaba su punto máximo al principio de la tarde. Además, los patrones de actividad se asociaron con la interacción de la temperatura y la intensidad de la radiación ultravioleta (UV), de modo que la actividad prevista a altas temperaturas es máxima cuando la UV es baja, y a bajas temperaturas la actividad prevista es máxima cuando la UV es alta. La actividad se vio limitada por las bajas temperaturas ambientales, incluso en los días calurosos de mediados de verano. Cuando las lagartijas estaban activas, termorregulaban con precisión y alcanzaban temperaturas corporales que coincidían estrechamente con las temperaturas preferidas seleccionadas en un gradiente de laboratorio en un estudio previo. Además, las temperaturas corporales en el campo no variaron en función del sexo, el estado reproductivo, o el tamaño. Los datos sobre la actividad diaria y decisiones termorreguladoras, especialmente en un hábitat urbano, proporcionan información valiosa sobre cómo un organismo ectotérmico integra las entradas sensoriales multivariadas del ambiente para tomar decisiones comportamentales. El papel de las condiciones ambientales en las decisiones comportamentales es especialmente relevante para predecir las expansiones del rango geográfico, en particular en el contexto de cambios en áreas urbanas y especies introducidas.

INTRODUCTION

Understanding how animal behaviors respond to multiple intrinsic and extrinsic factors is a major goal in behavioral ecology (Bateson & Laland, 2013; Endler, 2025). Environments vary through space and time at different scales, but multimodal sensory inputs are received by individual organisms (Mathot et al., 2024; Munoz & Blumstein, 2020). It is at the individual level that decisions to react – or not – to sensory inputs are made. This behavioral plasticity is the condition-sensitive action or ability of organisms to react to environmental inputs (Forsman, 2015; West-Eberhard, 2003). Many behaviors exhibit such flexibility (within limits; Sih et al., 2010, 2012; Wolf & Weissing, 2012) and often represent the first-line response to new or changing environments (Huey et al., 2012, 2018; Mayr, 1963; Seebacher, 2005). Characterizing the range and limits of behavioral responses is crucial for predicting how organisms will respond to anthropogenically-driven changes in climate, habitat structure, and biotic interactions. One axis of environmental variation to which behavioral responses have been particularly well-studied is temperature (Abram et al., 2017; Hutchison & Maness, 1979). Behavioral thermoregulation is the primary mechanism by which most terrestrial ectothermic organisms both avoid potentially detrimental extreme temperatures or optimize temperature-dependent physiological processes (Angilletta et al., 2002; Seebacher, 2005). As such, behavioral thermoregulation is essential to consider when predicting how organisms will respond to new or changing environments over both short ecological time scales or longer macroevolutionary time scales (Bodensteiner, Agudelo-Cantero, et al., 2021; Huey et al., 2003; Muñoz, 2022).

Lizards consist of nearly 8,000 species (Uetz et al., 2025), with many species exhibiting diverse thermoregulatory behaviors (Dubiner et al., 2024). The rich literature on this topic in lizards demonstrates the ecological importance of these behaviors (Fey et al., 2019; Gunderson & Leal, 2016) and the evolutionary role they play (Black et al., 2019; Bodensteiner, Agudelo-Cantero, et al., 2021; Muñoz, 2022). Despite the established importance of thermoregulatory behavior, studies of behavioral thermoregulation have developed primarily outside the traditional animal behavior literature. In lizards specifically, this is likely due to the fact that much previous work has sought to draw conclusions about thermoregulation at the population (Gvoždík, 2002; Pafilis et al., 2024) or species level (Muñoz et al., 2014; Muñoz & Bodensteiner, 2019) rather than quantify patterns among individuals. For example, few studies have quantified thermoregulatory behaviors among individuals or examined how different aspects of thermoregulation may be correlated within and among individuals. That is to say, few studies have treated thermoregulation as a behavior to be quantified in the same way social behaviors or ‘behavioral syndromes’ might be. The notable exceptions have clearly established that there is among-individual consistency in behavioral differences (Alujević et al., 2024; Goulet, Thompson, & Chapple, 2017; Livingston et al., 2025; Stapley, 2006) and that thermoregulatory behaviors may be correlated with other aspects of behavior, such as boldness, in different contexts (Goulet, Thompson, Michelangeli, et al., 2017; Michelangeli et al., 2018). However, evidence for such behavioral syndromes is inconsistent across taxa (Stellatelli et al., 2025). Furthermore, few studies have quantified patterns of individual thermoregulatory behaviors *in situ* by repeatedly measuring the same individuals over time. These field observations are essential for examining the influence of the immediate environment on thermoregulatory behavior, linking laboratory measurements to natural behaviors, and assessing how individual decisions contribute to population- or species-level patterns. Such field-based studies are especially important to understand how organisms operate and the importance of behavioral plasticity in human-built environments, which may present novel challenges or opportunities (Battles et al., 2019; Campbell-Staton et al., 2020).

As an extreme example of human-built environments, urbanization provides novel structural habitat (Battles et al., 2019; Falvey et al., 2020; Winchell et al., 2016) and alteration of thermal environments, such as the urban heat island effect (Campbell-Staton et al., 2020; Diamond & Martin, 2021). Furthermore, living in cities exposes organisms to disturbances like artificial light (Kolbe et al., 2021; Thawley & Kolbe, 2020) and different forms of pollution (Fernández-Juricic et al., 2005; Higham et al., 2021; Johnson et al., 2024; M. M. Moore et al., 2025), all of which influence behavior. Despite these challenges, some organisms thrive in urban environments, with some being more successful in cities than in 'naturalistic' environments (Ouyang et al., 2018). One influential factor in ectothermic animals for successfully residing in urban settings is the ability to effectively thermoregulate through behavior. Behavioral thermoregulation buffers organisms from exposure to suboptimal conditions (e.g., extremely high or low temperatures; Kearney et al., 2009; Kirchhof et al., 2017; Ortega, Mencía, & Pérez-Mellado, 2016) and can also prompt exploitation of novel habitat (Muñoz & Losos, 2018). In the case of urbanization, actively thermoregulating lizards may be presented with challenges in the form of increased environmental temperatures but also opportunity in the form of novel structural habitat. Thermoregulatory behaviors are simultaneously simultaneously influenced by many factors aside from temperature, including human disturbance (Frid & Dill, 2002; Rodríguez-Prieto et al., 2010), extrinsic environmental variation (e.g., ultraviolet radiation, wind, hydric conditions; Conley & Lattanzio, 2022; Sannolo & Carretero, 2019; Spears et al., 2024; Virens & Cree, 2022), and biotic interactions (Herczeg et al., 2008). Notably, thermoregulatory decisions may also vary throughout the day, as a result of fine-scale changes in the environment. Currently, there is little understanding of how environmental factors besides temperature affect individual thermoregulation, as well as how individual behavioral responses to multiple axes of environmental variation might scale up to patterns at the population level throughout the day.

The common wall lizard (*Podarcis muralis*) is a useful organism when observing the confluence of activities impacting wildlife in the Anthropocene, including responses to variation in climate (Bodensteiner, Gangloff, et al., 2021; While et al., 2015), propensity for human-aided introductions (Kowalik et al., 2024; Oskyrko et al., 2020), and great success in urban environments (Beninde et al., 2016; Davis et al., 2021; Speybroeck et al., 2016). Common wall lizards are diurnally active heliotherms, capable of using the sun to thermoregulate effectively and maintain field body temperatures within a narrow range (Bodensteiner, Gangloff, et al., 2021; Sagonas et al., 2017) that optimizes traits such as sprint speed and aerobic scope (Telemeco et al., 2022). This work focuses on populations of common wall lizards from Cincinnati, Ohio, United States which originated from a single introduction of approximately ten individuals in the early 1950s (Davis et al., 2021; Hedeen, 1984). From this initial founder event, populations have expanded across the greater Cincinnati area, with lizards found in high densities within many urban areas (Brown et al. 1995). Notably, lizards from this introduced population are larger in absolute size and exhibit preferences for much higher temperatures when tested in a thermal gradient, compared than those in European populations (Bauwens et al., 1996; Bodensteiner, Gangloff, et al., 2021; Gangloff et al., 2025; Spears et al., 2024; Trochet et al., 2018). As such, these populations of wall lizards specifically provide a valuable case study of an organism's intrinsic characteristics (phenotype) underlying behavioral mechanisms that enable the introduction, establishment, and continued success of non-native ectotherms in or near human-built environments (Wirga & Majtyka, 2015).

The goal of this study is to address the knowledge gap of how variation in daily activity periods and thermoregulatory behaviors are related to successful urban invasions. Specifically, we aim to quantify population-level patterns emerging from individual behaviors (activity and thermoregulation) and how this depends on both intrinsic traits (size, sex) as well as extrinsic environmental factors (wind, UV radiation, and temperature). In addition to data on lizard activity and body temperature, we quantify the effectiveness of thermoregulation by comparing body temperatures to environmental temperatures.

We conducted repeated, non-disruptive surveys at replicate sites consisting of human-constructed walls in urban habitat. Importantly, our use of infrared thermography (i.e., thermal imaging) allowed us to non-invasively monitor individuals over the activity period of entire days. We hypothesized that in introduced urban populations, common wall lizards will demonstrate effective thermoregulation even as behaviors vary due to both intrinsic and extrinsic factors. We predicted that (1) lizards will be most active when the thermal quality of the environment is optimal for thermoregulation (e.g., when wind speed is low and air temperature is high) and that lizards would avoid overexposure to UV radiation and (2) activity times and body temperatures will be dependent on size, sex, and reproductive status due to both differences in physiological demands associated with growth, reproductive stages, and size-dependent heat transfer rates. By quantifying these important aspects of behavioral thermoregulation across replicate populations sharing similar structural habitat, we aim to provide insights into the variation of these regulatory behaviors and how these behaviors may facilitate the successful introduction and establishment of species in new or urban environments (Ryan & Gunderson, 2020; Wright et al., 2010).

METHODS

Ethical Note

All research was conducted under Ohio Division of Wildlife Wild Animal Permit (SC220002) and all procedures were approved by Ohio Wesleyan University IACUC (02-2024-03_2). Careful consideration was made during all animal interactions and observations to ensure the safety of the organism, including proper handling techniques and rapid processing for release at the precise point of capture. Our observational surveys using infrared thermography were explicitly intended to minimize potential disturbance to the animals.

Study Species

The common wall lizard (*Podarcis muralis* Laurenti, 1768) is endemic across a broad range of southern and central Europe, with new populations established via human-mediated transport in both Europe and North America (Engelstoft et al., 2020; Kowalik et al., 2024; Oskyrko et al., 2020; Santos et al., 2019). Common wall lizards were introduced to Cincinnati, Ohio, USA from a source population in northern Italy in the 1950s and quickly established populations and expanded in this urban environment (Davis et al., 2021; Deichsel & Gist, 2001; E. Bode et al. in review). Cincinnati is located within a humid continental climate zone, sitting close to a humid subtropical climate zone (*NOAA NCEI U.S. Climate Normals Quick Access*, 2025), with temperature and precipitation patterns very similar to Milan, Italy, the city nearest to the source population (Davis et al., 2021). These lizards are small (median adult snout-vent length ~60-65 mm) and are active during daylight hours when they often forage and thermoregulate (Davis et al., 2021; Speybroeck et al., 2016). We measured animals and performed surveys across three locations in Cincinnati, Ohio, USA that shared comparable structural habitat (a human-built stone wall; Fig. 1). This structural habitat provides similarities across sites and permits conspicuous activity so that we could accurately observe the number of active lizards in each survey. We performed surveys at each of three locations for 12 hours each in 2023 and 2024, for six total surveys totalling 72 hours of behavioral observations (see Table 1 sampling dates and habitat details).

Morphological Data Collection

To avoid affecting lizard behavior through capture and handling, we collected adult body size and sex data 1–2 days before conducting activity surveys (see below). We caught adult lizards (minimum adult snout-vent length [SVL] 50 mm; Gangloff et al., 2025) with a thread lasso or by hand. We measured snout-vent length (SVL; distance from the tip of the snout to the posterior end of the anal scale) with digital calipers (Model CD-6, Mitutoyo, Japan) and weighed lizards to the nearest 0.01 g using a digital scale (Weigh Gram Top-100, Pocket Scale, Tulelake, California, USA). Sex was determined by relative head size, the presence of femoral pores, and/or by hemipenes eversion. We gently palpated females to determine gravidity. Each animal was then marked with a unique color code at the lateral junctures of each limb using non-toxic paint (POSCA Acrylic Paint Pen, Japan) and released at the precise point of capture.

Survey Protocols

We conducted intensive surveys of diel activity patterns, body temperatures, and environmental conditions on a single day following morphological data collection and marking with paint. Each day we recorded lizard activity every 30 minutes from 0800 to 2000 hours (25 samples per day; Table 1). We quantified diel activity by walking slowly along the stone wall from a distance of about 2-3 meters and counting the number of lizards on the stone wall. The stone walls provide generally linear habitat structure which facilitates observation of these active, conspicuous lizards. During these surveys we measured body temperatures without disturbing the animals by capturing digital and infrared thermal images of lizards, identifying individuals by paint ID when possible (often with the aid of binoculars). Lizards that were observed but not imaged (see below) were still documented as active lizards for that time period. Juvenile lizards were included in the total active lizard counts, but were not included in the body temperature data due to methodological limitations in obtaining reliable body temperatures, given their small body size. Specifically, small lizards do not yield enough pixels to accurately define a region of interest (ROI) used to extract temperatures from thermal images (see details of thermal imaging processing below). At the start of each 30 minute sampling period, we measured air temperature adjacent to the wall and 5 cm off the ground in the shade (PTH8708 Digital Temperature & Humidity Pen, General Tools, New York, USA), UV index 1.5 m off the ground in full sun when available (Solarmeter 6.5R, Solartech, Inc., Glenside, Pennsylvania, USA), and wind speed 1.5 m off the ground and in the direction of wind (Kestrel 3000 Weather Meter, Nielsen-Kellerman, Boothwyn, Pennsylvania, USA).

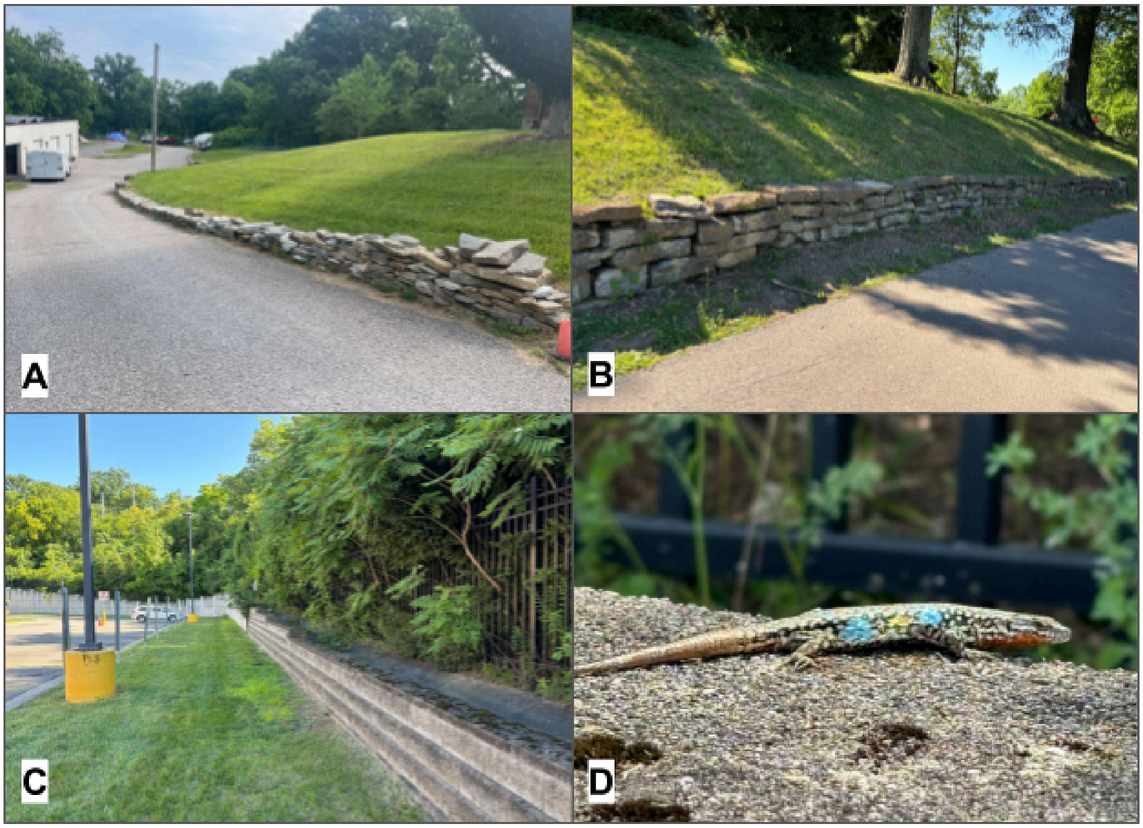

Figure 1. Sampling locations and study species in Cincinnati, Ohio, USA. A. Ault Park (AUL), B. Alms Park (ALM), and C. Walmart (WAL). D. Adult common wall lizard (*Podarcis muralis*) on a stone wall marked with paint (blue-yellow-blue) found at the WAL site.

Infrared Thermography

Infrared thermography provides a useful tool for collecting body temperature data on organisms noninvasively (Bonar & Petre, 2015; Goller et al., 2014; Tattersall, 2016) and provides reliable data on internal body temperature (Barroso et al., 2016; Spears et al., 2024). When a lizard was observed, we took a thermal image of the body from an optimal dorsal angle (Teledyne FLIR T540, Wilsonville, Oregon, USA; as in Spears et al., 2024). We used a 29 mm lens, providing a field angle of 14°, and captured images at a pixel resolution of 464 x 338. Image distance ranged from 0.15 - 10.90 m (median = 2 m) and we attempted to take multiple images of each lizard. Digital images were used to assist in animal identification using paint IDs. We extracted lizard body temperature from thermal images with FLIR Research Studio (v. 2.0.0). Software parameters were set to reflect the air temperature and relative humidity measured at the start of each survey period and the emissivity was set to 0.97 (Luna & Font, 2013; Spears et al., 2024). We drew an ellipsis over the torso region of each lizard, and we recorded the average temperature and pixel number for each Region of Interest (ROI). We extracted body temperature using the ellipses ROI tool on the image that provided the sharpest focus of the lizard (median ROI value: 75.5 pixels; range: 10 - 954 pixels). We excluded from analysis all images that lacked clear resolution of the subject's torso.

Operative Temperature Models

We utilized operative temperature models to quantify the potential range of temperatures available to lizards (OTMs; Bakken, 1976; Taylor et al., 2021). Specifically, OTMs approximate a non-thermoregulating lizard's internal body temperature in a given micro-habitat. We deployed 16 3D-printed OTMs (Alujević et al., 2023; Watson & Francis, 2015) before 0800 hours on each survey day. We placed the OTMs in a variety of microhabitats in which we observed lizards, including under rocks, in and on top of stone walls, and in association with adjacent vegetation. A probe inserted into the abdomen of each model recorded internal temperature every 10 minutes to a Pace data logger system (XR5-SE-20 mV, Boone, North Carolina, USA).

Table 1. Survey, habitat, and environmental data from all conducted surveys in Cincinnati, Ohio, USA. Wall length refers to the length of the stone wall surveyed (see Fig. 1); T_b refers to lizard body temperature.

Population (Abbreviation)	**Latitude / Longitude**	**Wall Length (m)**	**Survey Dates**	**N Activity observations**	**N T_b observations**	**Air Temperature (°C) mean ± sd**	**UV Index (Index) mean ± sd**	**Wind Speed (ms^{-1}) mean ± sd**
Ault Park (AUL)	39°08'06.7" N 84°24'24.1" W	79.2	14 June 2023	46	14	27.44 ± 4.68	3.52 ± 3.29	0.65 ± 0.30
			30 May 2024	27	9	26.08 ± 4.92	2.32 ± 1.82	1.02 ± 0.89
Alms Park (ALM)	39°06'41.1" N 84°25'49.3" W	62.4	21 June 2023	90	50	26.12 ± 2.74	3.28 ± 2.90	0.68 ± 0.41
			12 June 2024	44	22	23.91 ± 2.33	4.64 ± 3.23	0.37 ± 0.36
Walmart (WAL)	39°08'54.8" N 84°24'1.1" W	122.4	12 July 2023	75	32	29.78 ± 4.76	3.90 ± 3.56	0.82 ± 0.60
			18 July 2024	118	59	25.36 ± 3.44	3.18 ± 2.69	1.03 ± 0.90

Statistical Analyses

Data structure

We collected varying amounts of data for each lizard observation during surveys. While we attempted to record temperature data using thermal imaging for each individual, this was not always possible due to animal orientation or rapid fleeing. As such, the datasets used for each analysis are nested. See Fig. 2 for a visual representation of data used for each analysis.

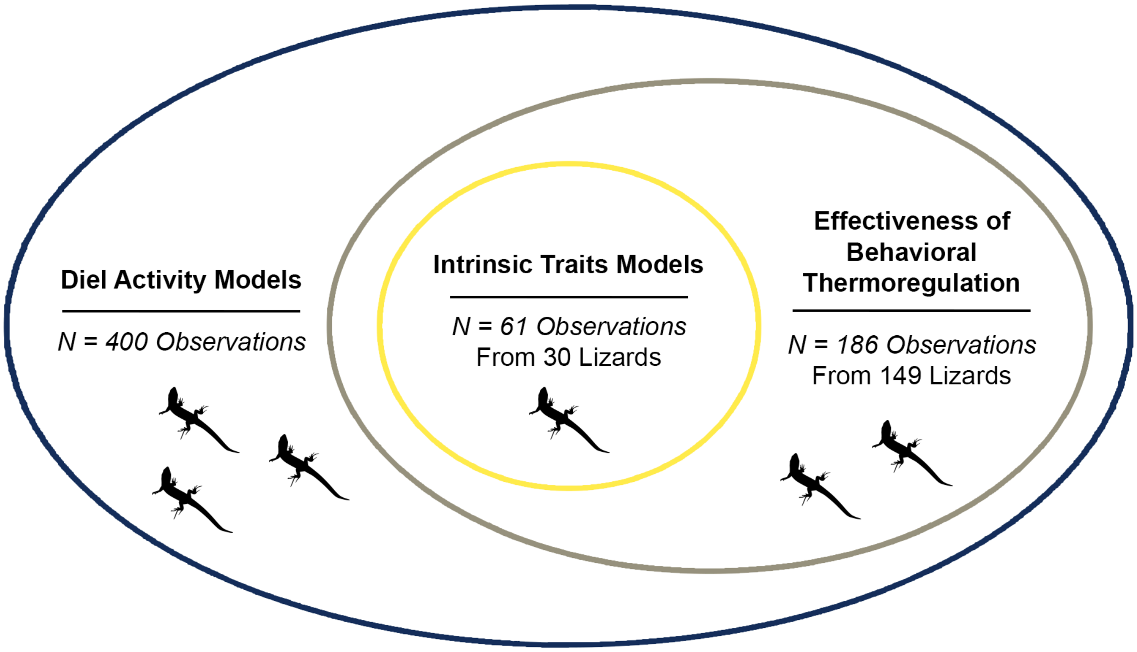

Figure 2. Venn diagram showing the relationships and sample sizes among analyses. Intrinsic traits models refer to modelling temperatures and activity times as functions of size, sex, and reproductive status. Of 400 total observations, 186 observations are included in the effectiveness of thermoregulation calculations and 61 of those observations were included in the intrinsic traits models. The silhouettes of *Podarcis muralis* were obtained from PhyloPic, designed by Titouan Montessuit, and used under a CC BY 4.0 International license (https://creativecommons.org/licenses/by/4.0/).

Diel activity models

We performed all data visualization and analyses using the programming language R (v. 4.5.0, R Core Team, 2025). To determine the relationship between the number of lizards active through time and environmental factors (temperature, UV index, and wind speed) throughout the day, we implemented a generalized linear mixed model in the poisson family using a likelihood framework. Models included a single random effect composed of all combinations of site and year as we were interested in the population-level effects of different environmental traits, irrespective of location and year. This random effect helps to account for randomness in which locations were sampled on what date, relative to other locations and dates we could have sampled. We accounted for autocorrelation from taking repeated samples of activity throughout the day by incorporating a first order autoregressive (AR1) covariance structure into the model (Box et al., 2015; Brooks et al., 2017; Pinheiro & Bates, 2010) and we used the Akaike Information Criterion-corrected for small sample size (AICc) to evaluate the relative performance of four candidate models (Anderson & Burnham, 2004; Burnham et al., 2011; Hurvich & Tsai, 1989). All four models included an interaction between temperature and UV. However, the four models differed in whether they included or excluded: 1) a triple interaction among temperature, UV, and wind speed, and 2) a zero-inflation fixed effect correlated with time of day. We excluded constant (uncorrelated) zero-inflation factors because they resulted in poor model fits with convergence issues. Adding a zero-inflation component turns the base model into a mixture model that mixes regression for main effects and logistic regression for the zero-inflation component (Lim et al., 2014). The four candidate models were fit using the glmmTMB package (v. 1.1.11, Brooks et al., 2017) and we performed model diagnostics using the diagnose, simulateResiduals, and testResiduals functions in the DHARMa package (v. 0.4.7, Hartig, 2024). We then estimated adjusted predictions (marginal means) for the population-level fixed effects using the ggeffects package 2.2.1 (v. 2.2.1, Lüdecke, 2018) by setting the method argument to “zero_inflated” to make predictions based on the fixed effects and zero-inflation components, adjusting for bias associated with showing the responses on the raw scale (bias_correction = TRUE) and estimating margins (margin = “empirical”) through empirical averaging (Dickerman & Hernán, 2020). We also plotted the fit of the zero-inflation component (a logistic regression) where inactivity is regressed onto sampling time.

Effectiveness of behavioral thermoregulation

We used data from operative temperature models (N = 16) for each survey date, but eliminated data from two models at the WAL site in 2023 because temperature probes became dislodged, resulting in N = 14 operative temperature models for this survey day. Following Hertz et al., 1993, we estimated environmental and body temperature deviations (d_e and d_b) which are the absolute deviations between the model (d_e) or lizard (d_b) temperatures and the closest point to the range of preferred temperatures. We used a preferred temperature range of 35.57–37.62°C, representing the interquartile range of selected temperatures in a lab-based experimental gradient on lizards from the same source populations we sampled in the current study (Spears et al., 2024). We next calculated two indices of thermoregulatory effectiveness (E). First, we used the equation of Hertz et al., 1993:

$$E_H = 1 - \overline{d}_b/\overline{d}_e.$$

Values of E_H describe a continuum from thermoconformers (values near zero) to precise thermoregulators (values near one). Additionally, we estimated an alternative index of thermoregulatory effectiveness as proposed by Blouin-Demers & Weatherhead (2001), defined as:

$$E_B = \overline{d}_e - \overline{d}_b.$$

We estimated both indices of thermoregulatory effectiveness (E_H and E_B) for each population independently and for all data combined and estimated 95% confidence intervals around each value through 1,000 iterations of bootstrap resampling of our empirical distributions (Muñoz and Losos, 2018).

Intrinsic traits models

Our dataset of observations for which we had body size, sex, reproductive status, and body temperature includes N = 61 observations across N = 30 lizards (14 males, 11 gravid females, and 5 non-gravid females; Fig. 2). We modelled body temperature and activity time (minutes past midnight) separately by regressing each onto body size (SVL), a single categorical factor denoting sex-reproductive status (with three levels: male, gravid female, and non-gravid female), and the two-way interaction between body size and sex-reproductive status using linear mixed models with the *lmer* function in the package lme4 (v. 1.1–37, Bates et al., 2015). The model for body temperature also included linear and quadratic terms for the covariate of minutes past midnight. These time effects were necessary to account for changes in body temperature throughout the day (as lizards warm toward their preferred temperature); omitting the terms resulted in a poor model fit. Both models included a random effect of survey day and a random effect of individual to account for observations occurring on the same survey day and on the same individual. We assessed significance with *F*-tests calculated with Type III sums of squares and corrected the denominator degrees of freedom for random effects using the Kenward-Roger algorithm (Kenward & Roger, 1997), which is a more conservative approach relative to the default Satterthwaite algorithm. Both models displayed appropriate model diagnostics which we confirmed using Shapiro-Wilks tests on model residuals and by evaluating residual plots.

RESULTS

Summary statistics

In total, we collected size (SVL and mass), sex, and reproductive status data for N = 138 lizards (on the days prior to the surveys), including 67 males, 31 non-gravid females, and 40 gravid females, though many of these lizards were not seen again during surveys. The diel activity surveys yielded N = 400 observations of active lizards over 72 total hours (Table 1). Generally, we found fewer lizards at AUL (N = 73) and the most lizards at WAL (N = 193) and sites were comparable in average air temperature, UV index, and wind speed (Table 1). Plots of the number of lizards caught and all environmental traits through time separated by site and year are found in the Supplementary Material (Figs. S1-4). Additionally, we recorded 186 body temperatures (T_b) in the field from at least 149 unique lizards, including 61 observations of 30 lizards for which we had collected morphological data previously (see Table 1, Fig. 2). Lizards for which we obtained both body temperature and morphology data had a body size (SVL) of 64.18 ± 5.24 mm (mean ± sd), a median of 65.79 mm, and range of 51.21–70.25 mm. Across all samples, lizard body temperatures were 35.5 ± 4.1°C (mean ± sd), with a median of 36.3°C, and range of 17.3–43.1°C. The OTM temperatures were 28.9 ± 7.5°C (mean ± sd), with a median of 27.6°C, and range of 13.0–55.4°C.

Diel activity is plastic and coregulated by temperature and UV

The best model predicted that lizard activity is significantly related to air temperature and UV index, but not wind speed (Table 2; AICc = 545.39). The next best model had a ΔAICc >2 (2.27) indicating the lack of viability for all alternative candidate models (Table S1). We found a significant interaction between air temperature and UV index, despite heterogeneity in individual behavioral responses at the 30-minute scale (i.e., the confidence intervals overlap; Fig. 3). Predicted lizard activity was highest (on average) when air temperature is high and UV is low (Fig. 3). Notably, air temperature had the largest effect (z-value) on activity compared to all other variables in the model (Table 2). The random effect containing population and year explained almost no variation in lizard activity (standard deviation < 0.0001). Additionally, the model showed appropriate model diagnostics including stationarity ($-1 < \varphi < 1$) where the mean, variance, and autocorrelation structure is constant over time. The modelled temporal structure accounted for repeated samples of lizard activity which had an (auto)correlation of $\varphi = r = 0.89$ at the 30-minute scale.

Table 2. Best model of diel activity in *Podarcis muralis* across surveyed years and populations in Cincinnati, Ohio, USA. Model performance was determined using AICc. The conditional model fits non-zero data only; it is statistically conditional on zeroes generated through the poisson and zero-inflation processes. Std. Error is the standard error. Pr(>|z|) is the p-value. *,**, and *** denote the < 0.05, 0.01, and 0.001 levels of significance, respectively. Air Temp × UV is the interaction of air temperature and UV index. Sampling Time is a continuous variable representing measurements taken every 30 minutes from 8:00 to 20:00.

Conditional Model				
Coefficient	**Estimate**	**Std. Error**	**z-value**	**Pr(>|z|)**
Intercept	-2.6914	1.0911	-2.47	0.014*
Air Temperature (℃)	0.1270	0.0394	3.22	0.001***
UV Index	0.4517	0.1903	2.37	0.018*
Wind Speed (m/s)	0.0924	0.0849	1.09	0.277
Air Temp × UV	-0.0157	0.0064	-2.44	0.015*
Zero-inflation Model				
Intercept	2.2655	0.9727	0.33	0.020*
Sampling Time	-0.5482	0.1791	-3.06	0.002**

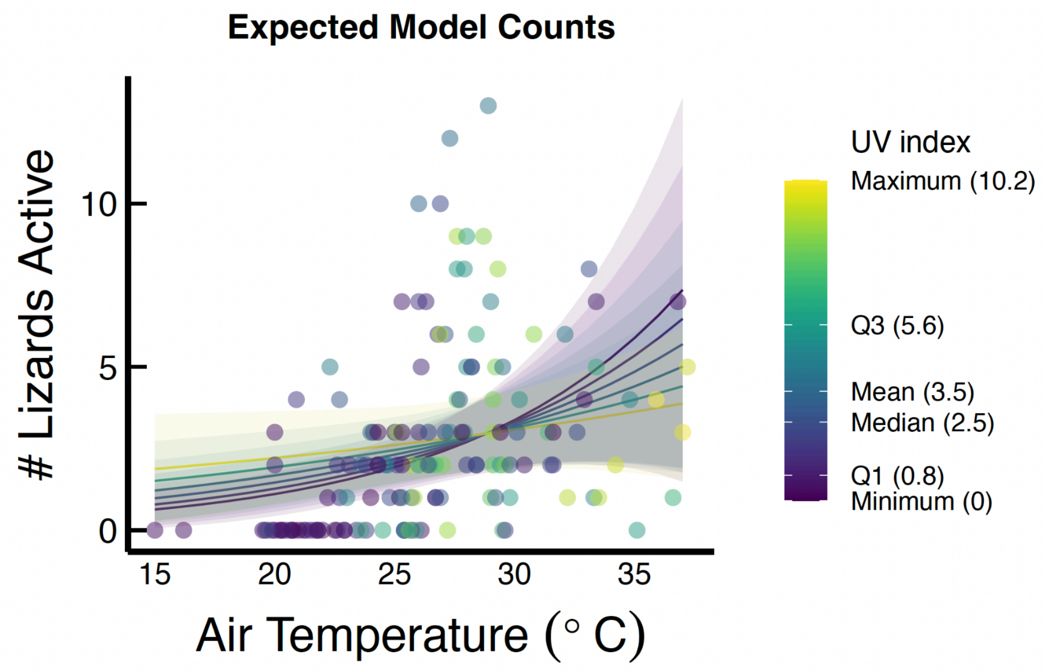

Figure 3. Diel activity is coregulated by air temperature and UV index in common wall lizards (*Podarcis muralis*) from Cincinnati, Ohio, USA. The plot shows the interactive effects of air temperature and UV index on the number of lizards active. The interaction is shown across all values of temperature and six margins (values) of the UV index chosen to represent the full distribution of the UV index, i.e. the minimum, mean, maximum, and the 1st–3rd quartiles. The corresponding UV index values are in parentheses. Colored points are the raw data colored by the UV index at the sampling time.

Common wall lizards are effective behavioral thermoregulators

Our observations show that lizards maintain body temperatures within a relatively narrow range compared to the available environmental temperatures during the daylight activity period (Table 3, Figs. 4–5). Operative temperature models indicated that daytime hours with temperatures available for use within the preferred temperature range (T_{Pref}) of common wall lizards was 6.50 hours per day (range: 5.02–7.65 h/d) on average. In 2023, sites varied in hours available for activity based on OTMs within T_{Pref}. While the Walmart site had 7.65 hours with suitable temperatures within the T_{Pref}, the Alms site only had 5.02 hours. Deviations of operative temperatures from preferred temperatures (d_{e}) were generally consistent across surveys (range: 6.52–10.46°C) and were consistently higher than deviations of body temperatures from preferred temperatures (d_{b}; range: 0.76–4.25°C). Interestingly, only 33.9% of observed body temperatures were within T_{Pref}. Calculations of thermoregulatory effectiveness following Hertz et al. 1993 (E_H) show that lizards were generally effective thermoregulators ($0.5 < E_H < 1$) with estimates for E_H per site ranging from 0.54–0.88, with an average value of 0.76 (Table 1). Calculations of E_B following Blouin-Demers & Weatherhead (2001) averaged 6.52 (range: 4.91–7.59). Notably, 75% of lizard body temperatures are in the upper 25% of OTM temperatures (Fig. 5).

Table 3. Thermoregulatory effectiveness details for each survey day. Hours within T_{pref} are based on operative temperature model (OTM) temperatures using the range of preferred temperatures from Spears et al. 2024. *E* calculation statistics represented by common wall lizard (*Podarcis muralis*) body temperature averages (T_b), d_e, d_b, E_H (defined in Hertz et al. 1993), and E_B (defined in Blouin-Demers & Weatherhead 2001).

Population	Survey Date	T_b (°C) [mean ± sd]	Hours within T_{pref}	d_e	d_b	E_H (95% CI)	E_B (95% CI)
Ault Park (AUL)	14 June 2023	31.95 ± 5.72	1131 - 1752 (6.35 Hours)	9.16	4.25	0.54 (0.24 - 0.79)	4.91 (2.21 - 7.30)
	30 May 2024	32.72 ± 2.23	1050 - 1750 (7.00 Hours)	10.46	2.87	0.73 (0.59 - 0.85)	7.59 (6.09 - 8.93)
Alms Park (ALM)	21 June 2023	34.96 ± 3.32	1134 - 1635 (5.02 Hours)	7.63	1.72	0.77 (0.69 - 0.87)	5.91 (5.20 - 6.65)
	12 June 2024	34.39 ± 5.86	0943 - 1540 (5.95 Hours)	7.89	2.63	0.67 (0.36 - 0.89)	5.25 (2.85 - 6.97)
Walmart (WAL)	12 July 2023	37.21 ± 1.83	1219 - 1958 (7.65 Hours)	6.52	0.76	0.88 (0.84 - 0.93)	5.76 (5.38 - 6.17)
	18 July 2024	36.69 ± 3.68	1207 - 1907 (7.00 Hours)	9.35	1.81	0.81 (0.74 - 0.86)	7.54 (6.83 - 8.16)
Overall (All sites)	–	35.49 ± 4.08	Mean: 6.49 Hours	8.54	1.94	0.77 (0.72 - 0.82)	6.60 (6.13 - 7.02)

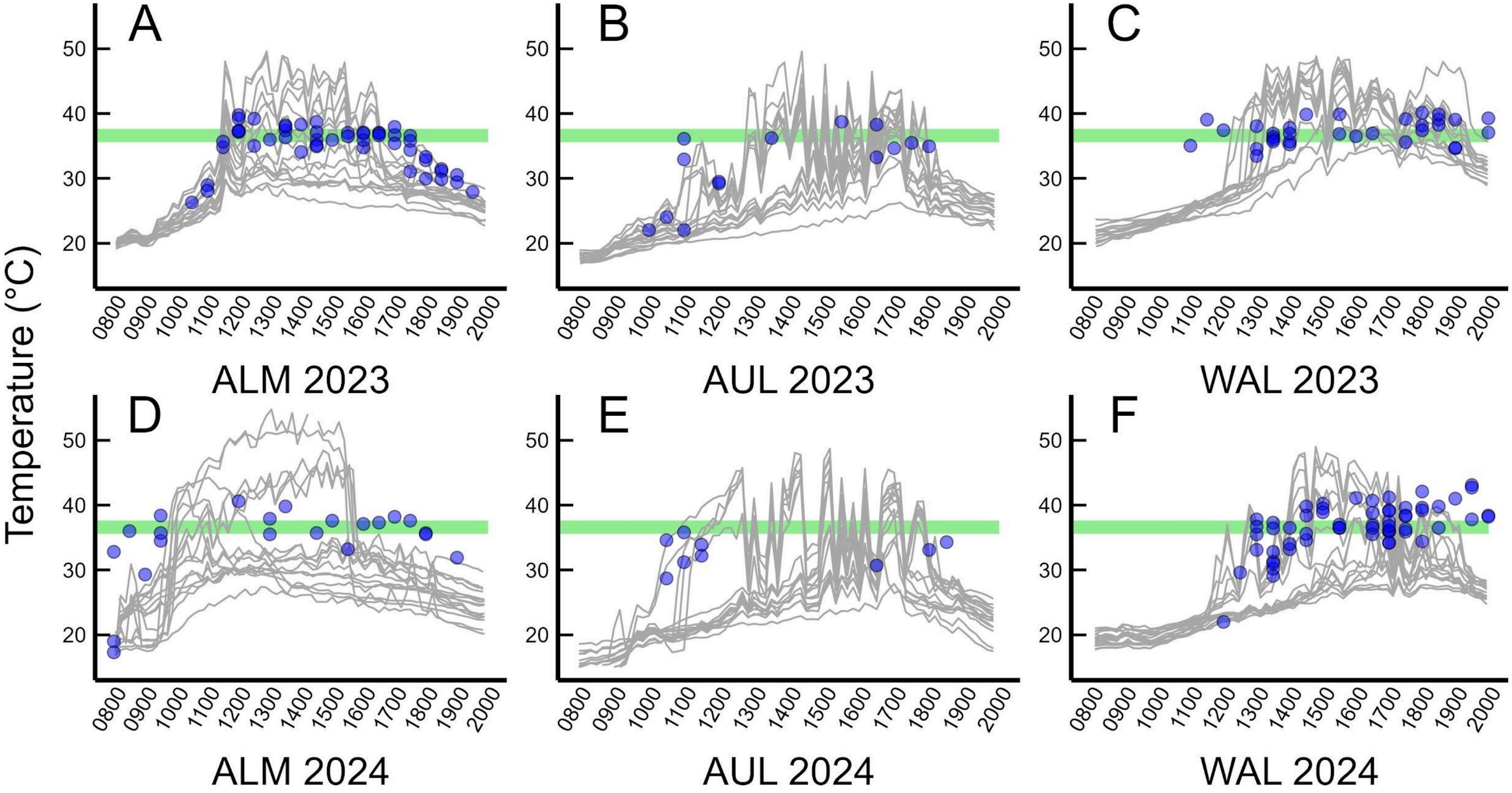

Figure 4. Common wall lizard (*Podarcis muralis*) T_b and operative temperature model (OTM) T_e observed throughout thermal surveys in Cincinnati, Ohio, USA. Lizard body temperature (blue points) overlaid on the operative temperature model (OTM) collected temperature data (grey lines) through time (by site). The green bar represents the preferred temperature range for lizard body temperature (from Spears et al. 2024). The x-axis shows the survey times across the locations: ALM is Alms Park, AUL is Ault Park, and WAL is Walmart.

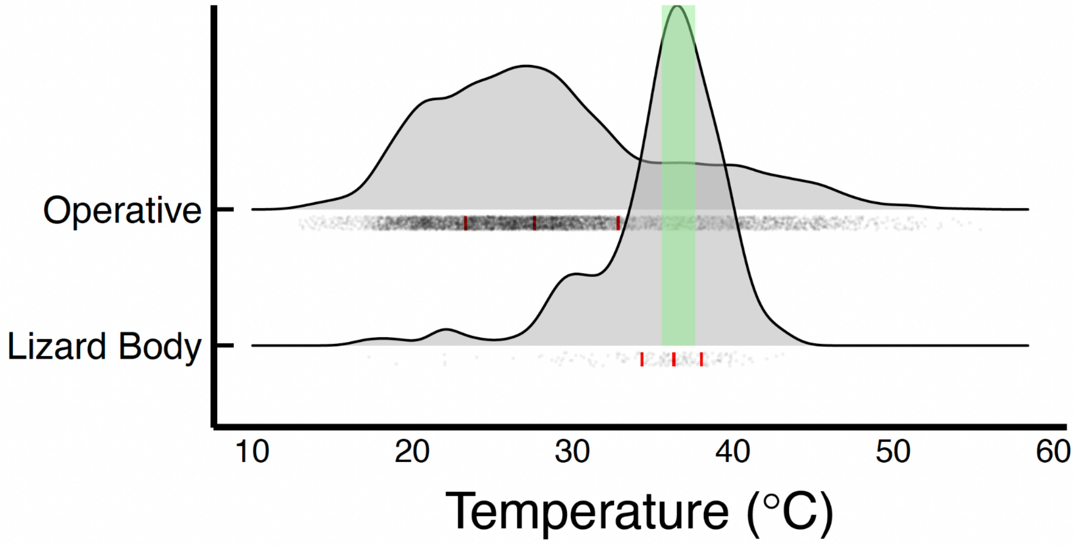

Figure 5. Comparison of Operative Temperature Model (Operative) and lizard body temperatures (Lizard Body). The distributions (gray) are densities, the jittered (black) points are the raw data, the red bars correspond to the quartiles of each distribution, and the green indicates the lizard's preferred temperature range (from Spears et al. 2024; see text).

Diel activity patterns and body temperatures do not differ in adults

Common wall lizards were active from 930 to 1900 hours with a mean activity time of approximately 1445 and a spread (standard deviation) of 2.5 hours. For lizards for which we had morphology data, field body temperatures were 34.8 ± 3.6°C (mean ± sd), with a median of 35.7°C and a range of 22.0–40.2°C. Neither size nor sex/reproductive category affected the times at which lizards were active or the selected field body temperatures (Table 4). However, we found body temperatures were influenced by the quadratic effect of time of day. Using body mass instead of SVL as the estimate of body size did not qualitatively change these results.

Table 4. Results of models testing the effect of sex/reproductive status and body size on activity time (minutes past midnight) and field body temperatures (°C) of adult common wall lizards (*Podarcis muralis*). * denotes the < 0.05 level of significance. See text for statistical details. T_b is body temperature, SE is the standard error, *F* is the *F* statistic, df_n and df_d are the numerator and denominator degrees of freedom, respectively, *P* is the *P*-value, and SVL is snout-vent length.

Model Terms	**Time of Activity Model**	**Field T_b Model**
Intercept		
Estimates (± SE)	1027.17 ± 299.76	38.57 ± 6.23
Sex		
Estimates (± SE)	Gravid Female: 31.35 ± 817.73 Male: -186.50 ± 624.25	Gravid Female: -11.15 ± 17.19 Male: -4.64 ± 13.38
F (df_n, df_d)	0.044 (2, 19.4)	0.23 (2, 4.9)
P	0.96	0.80
SVL		
Estimate (± SE)	-2.02 ± 4.77	-0.058 ± 0.10
F (df_n, df_d)	0.097 (1, 20.6)	0.03 (1, 15.1)
P	0.76	0.87
Sex × SVL		
Estimates (± SE)	Gravid Female × SVL: -1.64 ± 12.85 Male × SVL: 2.75 ± 9.61	Gravid Female × SVL: 0.17 ± 0.27 Male × SVL: 0.066 ± 0.21
F (df_n, df_d)	0.053 (2, 17.9)	0.20 (2, 13.7)
P	0.95	0.82
Time		
Estimates (± SE)	–	Linear: 6.29 ± 3.33 Quadratic: -8.60 ± 3.42
F (df_n, df_d)	–	4.53 (2, 49.1)
P	–	**0.016***

DISCUSSION

Common wall lizards (*P. muralis*) in introduced, urban populations generally thermoregulated effectively, obtaining field body temperatures very close to those selected in a laboratory thermal gradient (Spears et al., 2024). While field observations of body temperature mostly matched estimates of preferred temperature in a lab, we also discovered that lizard activity patterns are environmentally plastic such that lizards at the population level (across sites and years) are most active at high temperatures with low ultraviolet (UV) radiation intensity. This is an intriguing result given that this species is generally described as heliothermic and prefers sunny basking spots (Žagar et al., 2015). At the individual level, the lizards showed large variation in their response to environmental conditions, especially at mid-range temperatures. The number of lizards active gradually increased through the day, reached a peak in mid-afternoon (about 1445), and decreased later in the day. In adult lizards, neither activity periods nor body temperatures depend on size, sex, or reproductive status (gravidity). Taken together, these results suggest that wall lizards behaviorally thermoregulate to buffer their exposure to suboptimal environmental conditions, including both low and high temperatures and levels of UV, and that individual thermoregulatory behaviors explain population-level diel activity behaviors. Such buffering behaviors can be considered a form of niche construction (Kearney & Porter, 2004) and, in turn, can affect broad evolutionary patterns (Muñoz, 2022).This capacity to modulate the environmental conditions to which individuals are exposed through active behavioral regulation plausibly contributes to the success of this species introduced to urban habitats.

Overall, our findings are consistent with our hypothesis that population-level statistics (e.g., measures of thermoregulatory effectiveness) indicate that lizards are thermoregulating precisely and this behavior varies in response to immediate environmental conditions. Lizards avoided critically high temperature extremes through precise thermoregulation; for example operative temperatures during the middle of the day in our ALM 2024 survey (Fig. 4D) were well above the critical thermal maximum (41.3°C; Bodensteiner, Gangloff, et al., 2021). Our data demonstrate that activity levels increased with increasing air temperature, but this effect is non-linear when extreme temperatures are included in the range of measured temperatures. Importantly, the relationship between air and microhabitat temperatures is largely dependent on the physical structure of the microhabitat and is an important area for future research. Unlike air temperature and UV, wind speed had no effect on lizard activity. The lack of influence of wind was somewhat surprising considering that in a laboratory experiment wind equivalent to a light breeze prompted lizards to select higher temperatures (Spears et al., 2024). Notably, we measured wind speed at a height of 1.5 m off the ground in open space; lizards may be utilizing habitat that is at least partially buffered from wind currents, such as leeward facing walls or crevices between stones (Ortega et al., 2017). This finding highlights the importance of conducting studies of thermoregulation *in situ*, where aspects of microhabitat structure or the behavioral response to other environmental factors can modulate conclusions drawn from laboratory-based studies. Lizards are not simply just thermoregulating, but performing behaviors that modulate exposure to a wide range of environmental variables. Considering these factors beyond temperature becomes especially important when data on temperature selection and thermal buffering are used to inform predictive models of the response to future environments (Clusella-Trullas et al., 2011; e.g., Huey et al., 2012).

Lizards in the field obtained body temperatures remarkably similar to those obtained in a laboratory gradient, despite the potential for confounding factors (e.g., predator presence, human activity) to limit thermoregulation. Our estimates of thermoregulatory effectiveness are nearly identical to low and high-elevation populations of this species in the native range (from this study: E_H = 0.77, low-elevation French populations; E_H = 0.82, high-elevation French populations E_H = 0.77, with all confidence intervals showing substantial overlap; Bodensteiner et al., 2021). For comparison, however, studies in other Lacertid species demonstrate a much greater capacity for thermoregulatory effectiveness, though in apparently harsher (i.e., warmer) thermal environments (e.g., Ortega, Mencía, & Pérez-Mellado, 2016; Pafilis et al., 2024). For instance, a study in the congener *P. lilfordi* demonstrates that thermoregulatory effectiveness increases in warmer summer months, even as achieved body temperatures do not change (Ortega et al., 2014). In our study, increased thermoregulatory effectiveness may not have been necessary to achieve preferred body temperatures given the number of hours for which suitable temperatures were available (Table 4). Microhabitats to obtain body temperatures within the preferred range were available on average for just under seven hours per day across our surveys, as indicated by operative temperature model data (Table 4), with at least some lizard activity observed for about 10 hours a day (Fig. 4). This is comparable to the activity periods for lizards in the native range (in Italy, Avery, 1978), despite that lizards in introduced populations have significantly higher preferred body temperatures compared to populations in the native European range (by ~4°C, Bauwens et al., 1996; Bodensteiner, Gangloff, et al., 2021; Sagonas et al., 2017; Spears et al., 2024). This clear pattern of lizards from introduced populations selecting higher preferred temperatures in laboratory gradients and achieving higher body temperatures in the field suggests that the thermal dependence of performance or physiological traits may have shifted as well if thermoregulatory behaviors are co-adapted (Blouin-Demers et al., 2003; Huey & Bennett, 1987). We are directing current work to creating thermal performance curves to assess and compare the thermal optima for such fitness-relevant traits (e.g., locomotion, digestion; see Telemeco et al., 2022).

Importantly, our survey protocols differed from most other studies quantifying lizard thermoregulation in that we began surveys before lizards were active, permitting data collection on animals just as they emerged from shelter before reaching preferred body temperatures. In mornings before about 1100, lizards were limited from achieving temperatures within the preferred range by available temperatures in the environment (Fig. 4), which may be misleading in suggesting suboptimal thermoregulation. Close inspection of our data also reveals that some lizards early in the day were able to find and exploit patches of warm microhabitat (i.e., sunny spots) that we did not capture with our operative temperature models. For example, early in the day of the WAL 2023 survey, several animals achieved body temperatures within the preferred range even as no operative temperature models indicated that such temperatures were available (Fig. 4C). These observations highlight the importance of sampling environmental temperatures with operative temperature models and the likelihood that, even with sufficient numbers of models and intentional placement, lizards are likely to identify and exploit thermal resources beyond those recorded by researchers. Importantly, the distribution of microhabitats sampled by operative temperature models can affect the calculation of deviance of environmental temperatures from the preferred temperature range (d_e), which in turn can influence estimates of thermoregulatory effectiveness (E; Currin & Alexander, 1999). Often, inferences about a species' or population's thermoregulatory capacity are based on a single survey or estimate of E. Our study highlights the potential for single surveys to be misleading, as we found that E can vary substantially (Table 4) across replicate studies at similar sites under similar environmental conditions. Additionally, two commonly-used metrics of thermoregulatory effectiveness in the field revealed distinct patterns. Post-hoc analysis of these estimates across surveys showed only a weak and non-significant correlation between these metrics (Spearman's $\rho = 0.49$, S= 18, $P = 0.36$). In particular, despite estimates of E_H (following Hertz et al., 1993) being comparable across the two WAL site surveys (Table 4), the estimate of E_B (following Blouin-Demers and Weatherhead, 2001) was significantly higher in the second survey than in the first one (non-overlapping confidence intervals). Lizards on average maintained an approximately 2°C greater difference between body temperatures and environmental temperatures in the second compared to the first survey, even as they achieved similar mean body temperatures. This difference was likely driven by lower ambient temperatures in the second survey, which allowed microhabitats (e.g, cracks in the stone wall) to maintain cooler temperatures in the heat of the day. Recent work in island populations of a congener wall lizard species exemplified similar discordance among metrics of thermoregulatory effectiveness and prompted researchers to standardize their interpretation (Pafilis et al., 2024). We suggest that future studies of thermoregulatory effectiveness should: (1) include repeated sampling across sites and time, (2) standardize placement of operative temperature models across the environment, and (3) consider carefully how variation in environmental and body temperatures can influence interpretations of different thermoregulatory metrics.

The extent to which ectothermic animals can effectively thermoregulate, as well as the factors facilitating or limiting this thermoregulation, has been the topic of intense study, especially in the context of changing climates and the expected impacts on ectotherm physiology and distribution (Huey et al., 2012; Kearney et al., 2009). In particular, lizards have been well-studied, with their thermoregulatory capacities expected to provide some buffering from climate change (Black et al., 2019; Muñoz et al., 2021; Ortega, Mencía, & Perez-Mellado, 2016; Ortega, Mencía, & Pérez-Mellado, 2016). However, few studies have repeatedly measured the thermoregulatory abilities of individuals over time across populations. Field-based data are increasingly important to gaining a deeper understanding of how lizard thermoregulatory behaviors are influenced not just by environmental temperature, but by other axes of environmental variation and intrinsic physiological state. These factors can produce variation in thermoregulatory behaviors across time, space, and taxonomic group. For example, a recent laboratory study demonstrated that fence lizards (*Sceloporus undulatus*) actively increase their exposure to UV radiation even as this requires exposure to suboptimal temperatures (Conley &

Lattanzio, 2022). The activity of lizards in our study was greatest when temperatures were high but UV was low, suggesting that lizards might avoid overexposure to UV. While UV can cause cellular damage in many taxa (Hird et al., 2024), UV exposure does not necessarily increase oxidative stress in lizards (Reguera et al., 2015) and is essential for some metabolic pathways, such as Vitamin D synthesis (Vergneau-Grosset & Péron, 2020). Our results suggest that lizards may be avoiding UV exposure on the most intense days, but seeking it out when conditions are overcast. It would be useful to direct future studies toward understanding the optimal levels of UV exposure in this species relative to the levels available in different habitat types and seasonal cycles.

Two aspects of our results suggest that these introduced lizards will continue to be successful in their anthropogenically-structured environment. First, lizards were effective thermoregulators and achieved active body temperatures in the field nearly identical to those selected in a lab gradient, where they were presumably free of ecological constraints (Fig. 5). Second, suitable temperatures for activity were available for most daylight hours (Fig. 4), even during midsummer in urban environments, which are warmer than surrounding areas (Campbell-Staton et al., 2020; Mohajerani et al., 2017). In fact, cool temperatures limited lizard activity in the mornings while suitable refuges were available even through the warmest parts of the afternoon. As such, diurnal activity even in midsummer does not appear limited by high temperatures in our focal populations, which will likely continue to exploit suitable thermal niches even as climates continue to warm. Importantly, lizards are likely to exploit deeper crevices in the rocks and ground than we could reach with our operative temperature models, likely providing an even greater buffer from daytime temperature extremes. We also found that neither body size, sex, nor reproductive status (in the case of females) affected the body temperatures or activity periods of adult lizards (Table 3). This result suggests that intersexual differences and intraspecific social interactions (possibly including competition) may not be limiting the ability of lizards to successfully exploit the thermal environment to achieve preferred body temperatures. In other words, suitable thermal habitat during active daytime hours does not appear to be a limiting resource within this ecological context. While behavioral thermoregulation may buffer these lizards from high daytime temperatures, an important question that remains is whether they will be exposed to detrimentally warmer temperatures at night, where they may not be able to avoid suboptimal temperatures via thermoregulation (Muñoz et al., 2014; Muñoz & Bodensteiner, 2019). Recent work on this species in the native range suggests that such warmer nighttime temperatures – even those that do not approach thermal limits – pose risks to long-term physiological condition and may act as an evolutionary trap (Perry et al., 2025).

Our results suggest several potentially fruitful research avenues to address important questions on how organisms can behaviorally respond to dynamic or novel environments, especially important in the contexts of ongoing climate change and urbanization. Wall lizards are successful in urban environments in both their native and introduced range (Amer et al., 2023; Beninde et al., 2016; Brown et al., 1995; Davis et al., 2021; Speybroeck et al., 2016). Such urban-adapted species often possess characteristics that favor continuing spread (Borden & Flory, 2021; Diamond & Martin, 2021). Our recent surveys demonstrate that wall lizards are living and reproducing in forest patches within the urban matrix. Assessing the viability of populations in these forested habitats, where the thermal environment is substantially cooler and less favorable (unpublished data) than on stone walls, is essential to predict if wall lizards may spread to more naturalistic areas and disrupt local ecosystems. Namely, can wall lizards in these thermally suboptimal environments thermoregulate more effectively to achieve preferred body temperatures? Or will thermal optima for performance or physiological traits shift downward? Importantly, forested habitats differ in additional abiotic factors such as humidity, wind speed, and shelter. However, accounting for all of these variables is challenging when estimating thermoregulatory effectiveness (E) as current methods lack built-in controls for confounding abiotic variables that can affect temperature. For instance, the use of OTMs does not account for evaporative cooling, which may lead to lower body temperatures (Loughran & Wolf, 2020).

Furthermore, while we know that environmental factors beyond temperature are important in determining activity patterns and thermoregulatory behaviors (Conley & Lattanzio, 2022; Sannolo & Carretero, 2019; Spears et al., 2024; Virens & Cree, 2022), we have a limited understanding of how organisms integrate this multimodal sensory data to determine behavioral outcomes (Angilletta et al., 2019; Rivest et al., 2019). Such neural models become especially important as climate change impacts different aspects of the environment in distinct ways (e.g., D. Moore et al., 2018). However, following the ‘multiple stressors framework’ of Hale et al. (2017), air temperature and UV radiation are two important stimuli that have antagonistic effects on behavioral thermoregulatory decisions in common wall lizards; the marginal effects (z-values) of temperature and UV each have a positive impact on activity but their interactive effect is less than the sum of its parts. Finally, the expansion of wall lizards into new environments will also generally involve a shift in type and quantity of biotic interactions. New predators may present different activity times and hunting modes, prey species composition and density will be altered, and intraspecific interactions will vary with population density. While environmental temperatures are an important – and perhaps even the most important – driver of ectotherm behavioral patterns, forecasting responses to future environments requires knowledge of how organisms sense their multivariate environment, integrate this complex information, and then respond to this heterogeneity across time.

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Supplementary Material

Table S1. Relative model comparisons of environmental controls on lizard diel activity. Double interaction refers to a model with only an air temperature by UV index interaction. Triple interaction refers to a model with interactions between air temperature, UV index, and wind speed. Zero-inflation refers to a zero-inflation factor that is correlated with sampling time.

Model	DF	AICc	ΔAICc
Double interaction, no zero-inflation	8	549.67	6.28
Triple interaction, no zero-inflation	11	554.46	11.07
Double interaction, zero-inflation	10	543.39	0
Triple interaction, zero-inflation	13	545.66	2.27

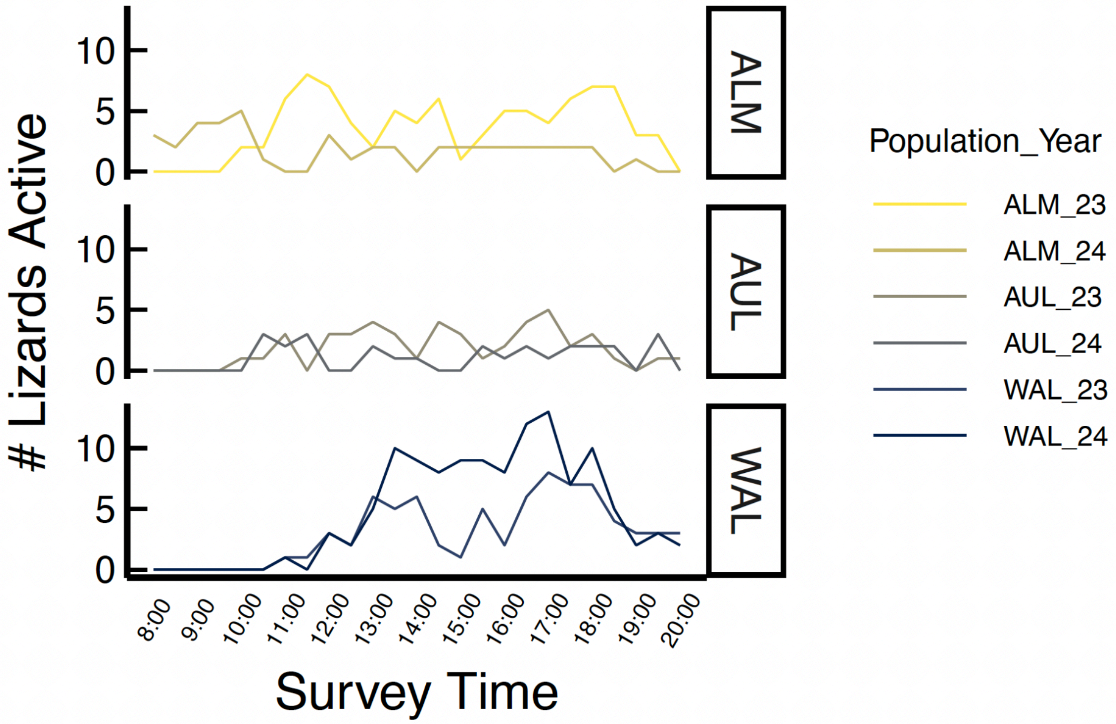

Figure S1. Lizard diel activity at sampled populations and years. AUL is Ault Park, ALM is Alms Park, and WAL is Walmart.

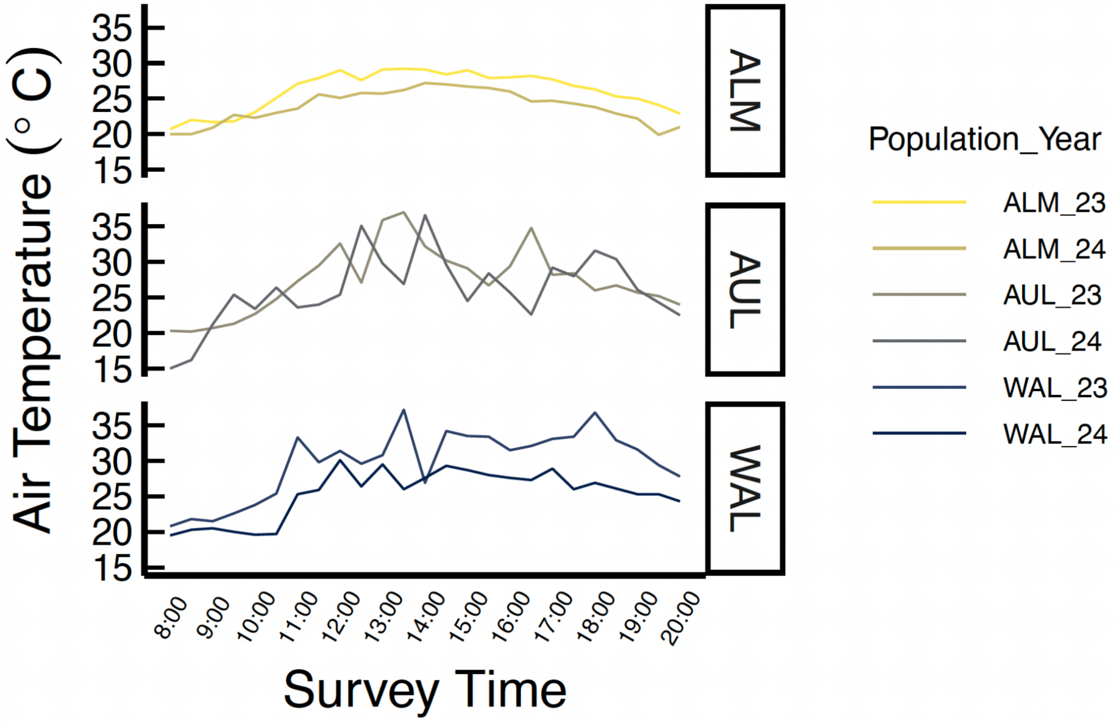

Figure S2. Air temperature through time at sampled populations and years. AUL is Ault Park, ALM is Alms Park, and WAL is Walmart.

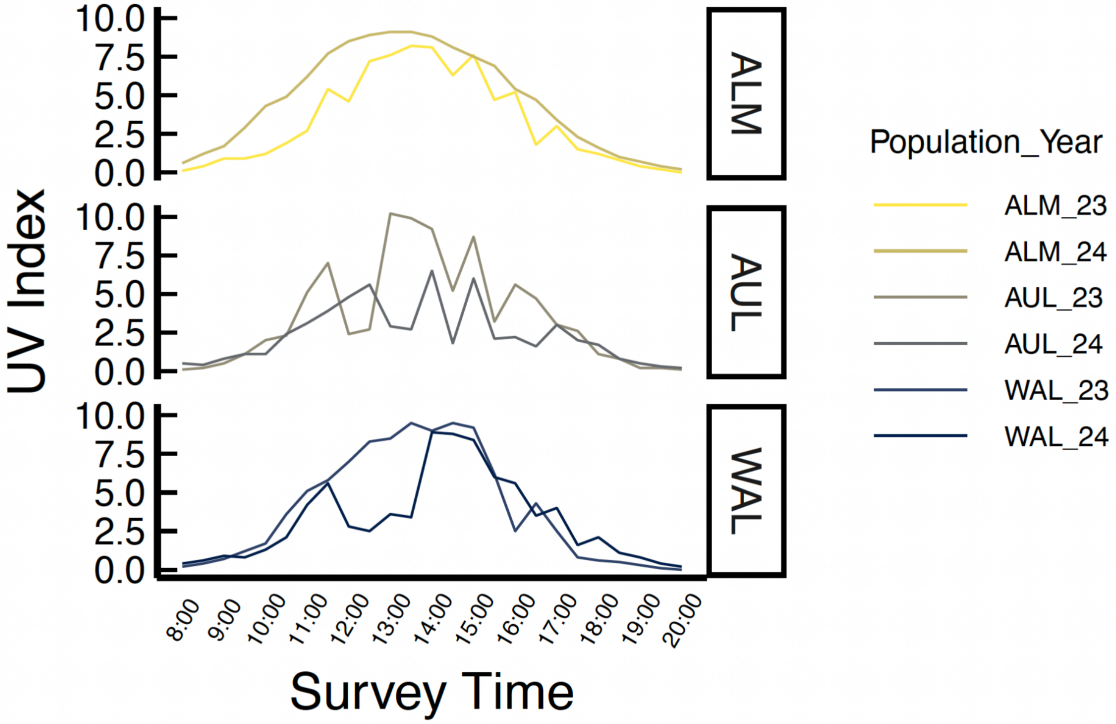

Figure S3. UV index through time at sampled populations and years. AUL is Ault Park, ALM is Alms Park, and WAL is Walmart.

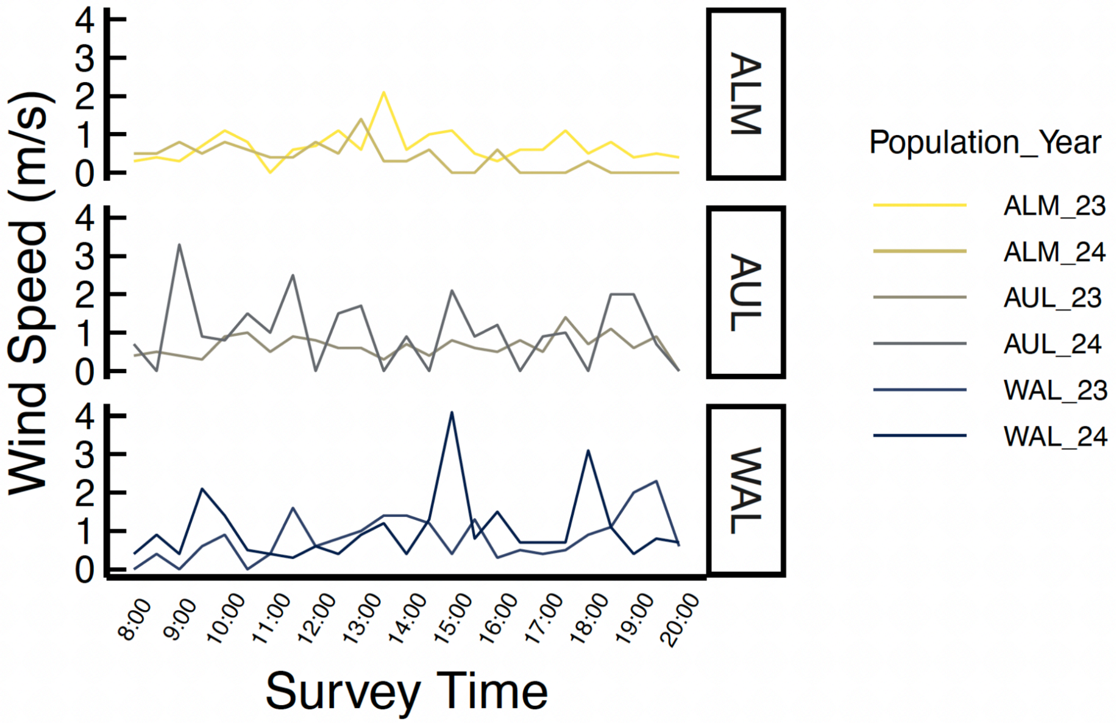

Figure S4. Wind speed through time at sampled populations and years. AUL is Ault Park, ALM is Alms Park, and WAL is Walmart.