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Weather-related detection probability of *Lacerta agilis* LINNAEUS, 1758 within the core range in western Germany

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Weather conditions are important factors determining the activity, and consequently detection probability of animals. Especially in ectotherms from temperate habitats, activity can vary strongly depending on weather. The sand lizard *Lacerta agilis* is a wide-ranging lizard that is often subject to environmental impact assessments due to its proximity to humans and prevalence as a candidate for compensatory measures according to the Flora and Fauna Habitat Directive of the European Union. *Lacerta agilis* has been studied extensively at certain edges of its distribution, but studies focusing on the core range have been rare. We use Bayesian models in order to identify the best explaining weather variables out of a large variety of available variables for a population of *Lacerta agilis* in western Germany. We furthermore depict their interactions with an easy-to-understand regression tree model. Sand lizards have shown to be more active during dry conditions with low windspeeds. They further are best found after sunny weather with temperatures around 20°C. Rainfall in the previous 24 hours also increases the detection probability. An unpruned regression tree reaffirms the results while giving concrete variable values and exploring how the values influence each other. Overall, the method delivers a decision tree based on easy-to-obtain weather variables that allows for post-survey analysis and for determination of the best survey conditions.

Key words: Bayesian model, Lacertidae, CART model, activity pattern, thermal ecology, European lizard.

Weather conditions play an important role on every ecological scale. The effects of climate change and global warming have been shown to affect ecological communities on large scales (e.g., GILMAN *et al.*, 2010; KORDAS *et al.*, 2011), while local weather fluctuations can, for example, affect the ecology and phenotype of individuals (e.g., VANNINI *et al.*, 2021; WINTER & SHIELDS, 2021). The influence of weather conditions on animal populations and communities is an important subject in the study of ecology and the practice of conservation as weather conditions can influence population dynamics in numerous ways. Weather conditions can influence the phenotype of individuals in a population. Western diamond back rattlesnakes (*Crotalus atrox*) in Arizona have been shown to become larger in colder, wetter environments than in dry and hot environments, presumably because hotter weather limits foraging time for the animals (AMARELLO *et al.*, 2010). Similarly, weather can influence

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prey availability as has been shown for frog eating keelbacks (*Tropidonophis mairii*), which have more reproductive success in hot and wet years, when frogs are more abundant (BROWN & SHINE, 2002; BROWN & SHINE, 2007). It has also been shown that weather conditions can directly influence movement patterns of lizards like the western green lizards (*Lacerta bilineata*) (SOUND & VEITH, 2000), and the Cuban brown anole (*Anolis sagrei*) (LOPEZ-DARIAS *et al.*, 2012), as well as influence fecundity and survival rate (ADOLPH & PORTER, 1993). So, especially for ectothermic species, day to day weather plays an important role.

Consequently, weather conditions also have a strong influence on encounter rates during any type of field study involving ectotherms (e.g., ADOLPH & PORTER, 1993; BROWN & SHINE, 2002; SPENCE-BAILEY *et al.*, 2010). Be it general ecological field work or targeted environmental impact assessments made in advance of a large developmental project, many fieldwork studies on animals require visual encounter surveys or procedures otherwise dependent on the animal activity at the time of field work. For example, according to §16 of the UVPG (Gesetz für die Umweltverträglichkeitsprüfung/Law for the environmental impact assessment) of the Federal Republic of Germany, part of an environmental impact assessment is the inventory and assessment of concerned species. It is therefore important to consider detection probability at the time of the surveys to correctly estimate population size. Furthermore, knowing that detection probability within a population in advance can help schedule surveys on days at which conditions suggest detection probability is highest and thus maximize sample size. Existing literature on activity periods and detection probability of a species cannot be expected to accurately predict the phenology of particular populations. Phenology, and therefore detection probability, are likely to differ among populations especially in wide ranged species (KÜHNELT, 1965). For those species, unless a study has been conducted specifically in the target area, previously reported activity patterns give no more than a rough idea at best.

Lacerta agilis LINNAEUS, 1758 is one of such widespread ectothermic species, occurring in vast parts of the Palaearctic (EDGAR & BIRD, 2006). It is listed as "Least Concern" internationally in the IUCN red list but is locally threatened, especially in its north-western range (IUCN, 2020). As a synanthropic species, this mid-sized member of the Lacertidae often lives near humans as it benefits from the open, bushy habitats humans create (HOUSE & SPELLERBERG, 1983; DENT & SPELLERBERG, 1987; BISCHOFF, 1988; NEMES *et al.*, 2006). However, due to its proximity to humans it is also often victim of developmental expansion and therefore, subject to environmental impact assessments and subsequent compensatory measures after Appendix IV of the FFH Guidelines of the Natura2000 Project (RÖDDER *et al.*, 2016). It is therefore, a likely candidate to be subject to numerous visual encounter surveys in a variety of drastically different areas.

Even though activity patterns of *Lacerta agilis* have been studied in the past, many of those studies focus on the edges of their distribution, where *Lacerta agilis* is restricted to montane areas (AMAT *et al.*, 2003) or sand dunes (HOUSE *et al.*, 1979;

House & Spellerberg, 1983; Dent & Spellerberg, 1987; Edgar & Bird, 2006), providing little insight into its ecological potency within the core range. For the closely related *Lacerta viridis*, it has already been shown that populations at the core and periphery of its distribution range differ in their realized niches (Prieto -Ramirez *et al.*, 2018).

To summarize known weather preferences, *Lacerta agilis* within the mountainous habitats in the Pyrenees favour air temperatures between 17°C and 20°C (Amat *et al.*, 2003), while an activity peak at 31°C-32°C has been reported for populations in Hungary near Budapest albeit here, temperatures 5 cm above ground level were measured (Heltai *et al.*, 2015). In Latvia, warm and dry habitat has been reported as the most important factor (Čeirâns, 2006) as well. Sand lizards in lower Saxony, Germany, have been reported to be most active around 20°C (Blanke, 1999). Sand lizards in a South-West Siberian coniferous forest are mainly dependent on low humidity and sunshine, while temperature only plays a role if it fluctuates strongly (Kuranova *et al.*, 2003). However, populations from southern England are by far the most extensively studied. Here, it was reported that temperatures have to reach 18°C before sand lizards come out and start basking (House *et al.*, 1979; Edgar & Bird, 2006; Fearnley, 2009). At 23° C, basking is greatly reduced and lizards tend to retreat into burrows (House *et al.*, 1979; Edgar & Bird, 2006; Fearnley, 2009), and *Lacerta agilis* retreat into their burrows at night at 19°C (House *et al.*, 1979). Sand lizards have a bimodal activity pattern, hiding during the hot hours at noon but they can switch to a unimodal pattern on colder days (House *et al.*, 1979). Sand lizards are generally more thermophilic than sympatrically occurring lizards like *Zootaca vivipara, Anguis fragilis* or *Podarcis muralis* (House *et al.*, 1979; Litvinov & Ganshchuk, 2003; Heltai *et al.*, 2015). Furthermore, sand lizards have been shown on multiple occasions to be heliothermic (Fearnley, 2009) and usually bask either by radiation alone, or by radiation and convection (Saint Girons, 1976). To that end, *Lacerta agilis* usually bask in full sunlight, sheltered from the wind (Edgar & Bird, 2006), and favour high heat capacity spots for basking (House *et al.*, 1979). Furthermore, activity declines when conditions are overcast or raining (House *et al.*, 1979). Fearnley (2009) suggests that there are shifts in weather variable importance before, during, and after breeding season. Over time, temperature, sunshine intensity and duration and humidity seem to play a role for sand lizards (Fearnley, 2009), which are the variables we see reoccurring in other studies.

In this study, we assess weather dependent detection probabilities that identify key weather contributors. These can be used before a study to maximize encounter rates, as well as after or during a study to set encounter rates into context. We combine visual encounter surveys with the weather data of a nearby weather station, to identify weather components influencing the activity pattern of a population of *Lacerta agilis* in the Dellbrücker Heide in Northeast Cologne, Germany. We use a Bayesian model framework to identify the influence of the most important weather variables. Knowing the best explaining

terms, we also compute a CART model, a decision tree that can be used to determine the best overall weather conditions for high encounter rates. CART models use these explanatory variables to split the data into more homogenous groups (DE'ATH & FABRICIUS, 2000). In this case, the CART model groups subsets of similar encounter rates, based on weather variables. Based on what is known on weather dependent activity patterns of sand lizards elsewhere, we expect that important factors will be temperature, sunshine duration and intensity, humidity and rainfall. We expect that ideal temperatures to be similar to other parts of Europe, between 17°C and 23°C, and detection probability to be highest when sunshine duration and intensity are strongest, and conditions are dry.

MATERIALS AND METHODS

Data Collection

Data on the activity of *L. agilis* was collected in the Dellbrücker Heide, a heathland nature reserve in northeast Cologne (approximate corners in WGS 84: NW: 50.9836°N, 7.0514°E; NE: 50.9848°N, 7.0611°E; SE: 50.9808°N, 7.0646°E; SW: 50.9788°N, 7.0541°E). Data was collected from 02.05.2018 to 26.09.2018, from 14.04.2019 to 03.09.2019, and from 07.06.2020 to 11.09.2020. The same population was studied in two further papers, which characterize the population (CLEMENT *et al.*, 2022; SCHMITZ *et al.*, 2022). The area was split into three parts of roughly equal size (Fig. 1A). We randomly generated 100 points in ArcMap 10.6 (ESRI, 2018) and went to the field to check them for accessibility, and potential suitability for *L. agilis*. We chose 10 points in each third that were accessible and suitable for sand lizards (Fig. 1A). One random point became inaccessible in the central area as the area was fenced off as a pasture for goats and sheep. Afterwards, it was largely stripped of the needed vegetation and hence discarded. Within each week, each area was visited once, and lizards were registered around every point in a 10m – 20m radius depending on vegetation density. One to two people spent around 15 minutes at a point. Areas were visited either in the morning (09:00 – 12:00), during midday (12:00 – 15:00), or in the afternoon (15:00 – 18:00). Within the framework of another study (SCHMITZ *et al.*, 2022), lizards were registered along transects 65 times as well to assess the distribution across the area (Fig. 1B). Time to traverse the transects was taken and paused whenever a lizard was located. On average, one transect took 20-30 minutes to complete without stopping. Once a lizard was detected, date and time were noted as well as the time interval for the sampling interval (morning, midday, or afternoon). GPS Coordinates were recorded with the "My GPS Coordinates" app by GPS Tools. Relocations on the same day were avoided by keeping an eye on lizards recorded in close proximity and making special notice of striking features or particular back patterns. If there was uncertainty about a lizard already being recorded on that day, it was not recorded to avoid pseudoreplications. Usually, sampling was not initiated on rainy days but was continued if it started to rain during sampling. Each encounter was assigned with a

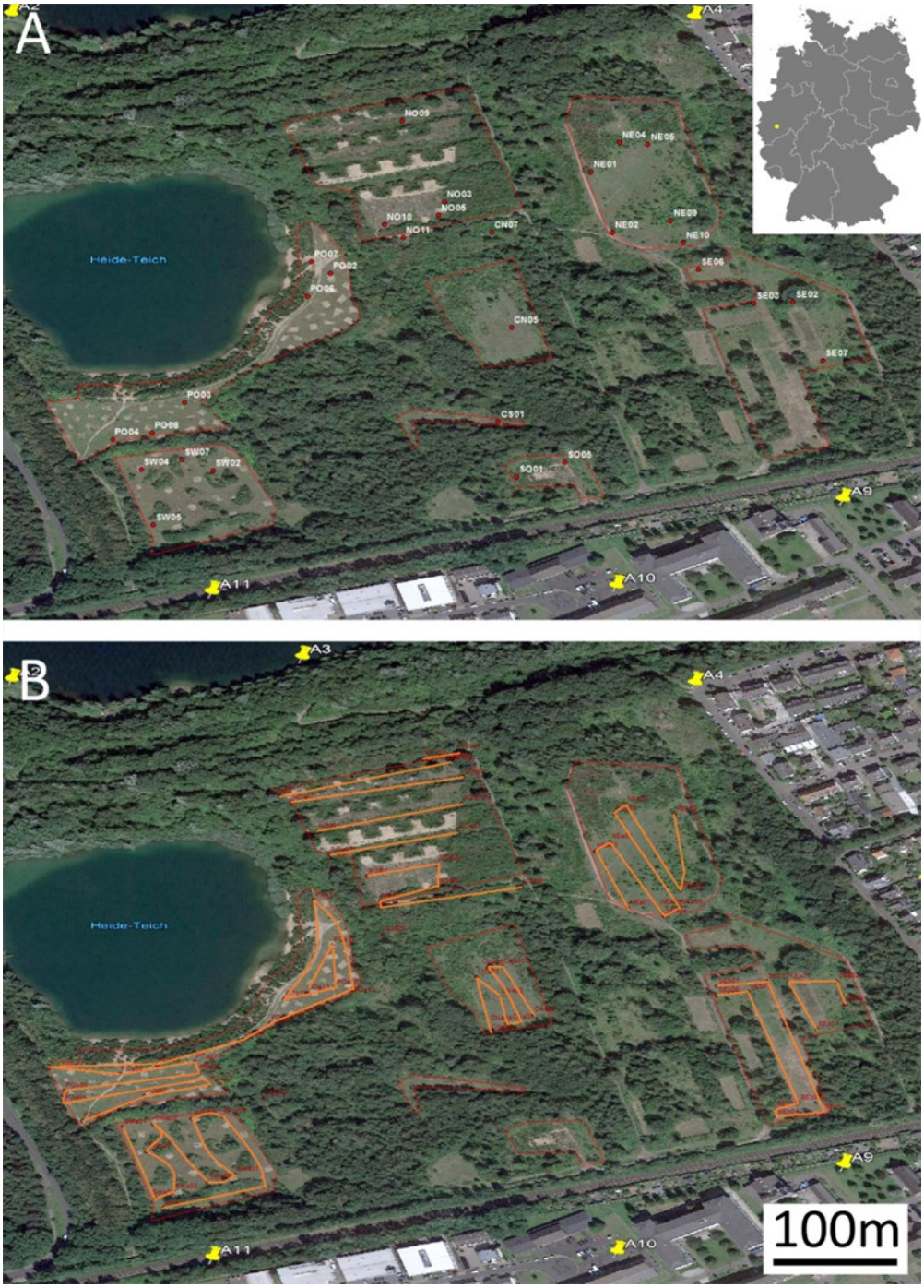

Figure 1: Study area in the Dellbrücker Heide with marked sampling points (A) and transects (B). Yellow pins were used to georeference the footage. Satellite photo taken with Google Earth. Top right shows the location within Germany. Map provided by https://simplemaps.com

Table 1: Explanation of weather variables used with units.

Variable Name	Description	Unit
max_temp	Highest temperature recorded at 1m above ground within the last 10 minutes	°C
min_temp	Lowest temperature recorded at 1m above ground within the last 10 minutes	°C
min_temp_5cm	Lowest temperature recorded at 5cm above ground within the last 10 minutes	°C
air_press	Mean air pressure recorded at 1m above ground within the last 10 minutes	hPa
air_temp	Air temperature recorded at 1m above ground at that moment	°C
air_temp_5cm	Air temperature recorded at 5cm above ground at that moment	°C
rel_humidity	relative humidity recorded at 2m above ground at that moment	%
Tau_temp	Dew point at that moment	°C
diffuse_radiation	diffuse radiation at that moment	J/cm^2
global_rad	global radiation at that moment	J/cm^2
sunshine_duration	duration during which the sun shone unblocked within the last 10 minutes.	hour
precip_duration	duration during which it rained within the last 10 minutes.	minute
precip_height	Sum of precipitation height of the last 10 minutes.	mm
max_wind_speed	Highest wind speed within the last 10 minutes	m/s
min_wind_speed	lowest wind speed within the last 10 minutes	m/s
mean_max_wind_speed	highest 10 minute average wind speed within the last 10 minutes.	m/s
mean_wind_speed	mean wind speed within the last 10 minutes	m/s

unique ID. Overall, we recorded 1115 encounters (679 on random points and 436 on transects) over a course of 205 days.

Weather data for the time period was acquired from the Deutscher Wetterdienst (DWD). We used weather data recorded by the weather station "Köln-Bonn" (ID2667), which is situated at 50° 51'N and 7°09'E and is hence, the closest weather station to the study area only being about 16km away. Table 1 shows a description of the used weather variables as well as their respective units. Weather data was recorded every 10 minutes and all variables can be found in the electronic supplement (Table S1).

Data processing

We estimated the relationship between temporal and environmental variables and the detection probability of sand lizards in a sampling interval using binomial generalized linear models in a Bayesian framework. The general workflow follows FALASCHI (2021), with the following refinements: As environmental predictors, we

used the local weather data obtained from the DWD (Fig. 2A). As we expect time lags between some of the weather events such as rain or windspeed, we calculated the average of all values during the observation interval and during the three, six, twelve, and twenty-four hours prior to the beginning of the interval, identified by the suffixes_int (for averages during the observation interval), _3h, _6h, _12h, _24h (for averages in the 3/6/12/24 hours prior to the beginning of the observation interval) (Fig. 2A→B). Hence, the total set of predictors comprised 85 variables as well as the Julian date, which was added as a temporal variable to include the possibility, that lizards are influenced by length of day or show seasonal shifts in their activity patterns, which may change over the year (Fig. 2B). To estimate the distribution of likely coefficients of each term, the original variables were standardized using the *bestNormalize* function of the bestNormalize package for R (PETERSON & CAVANAUGH, 2020; PETERSON, 2021), automatically selecting the optimal settings to reduce skewness and to scale the variables to a mean of zero and a standard deviation of one.

As a first step, we analyzed the explanative power of each candidate term separately, by estimating the coefficients (a-d) for each variable (x) of the Bayesian model with the following structure (Fig. 2B→C):

y = intercept + a * x + b * x^2 + c * x * julian date + d * x^2 * julian date

The priors of the regression coefficients were set to uniform, ranging from -10 to 10, and three chains were run (each 20,000 interactions, discarding the first 10,000 as burn-in) following (FALASCHI, 2021). Convergence was checked visually and by assessing Rhat values (<1.01 for each parameter). Significance of each term per variable was assessed by evaluating the region of practical equivalence (ROPE) and pd (≥ 0.99) parameters, and the associated p-values using the bayestestR package (MAKOWSKI *et al.*, 2019), which were corrected for potential alpha-error inflation using a Bonferroni correction ($p < 0.05$). ROPE represents a null hypothesis to test if a parameter is significant, i.e., important enough to be included in the final model. The proportion of the whole posterior distribution that does not lie within the ROPE interval can then be used to assess significance in terms of p-values (MAKOWSKI *et al.*, 2019). The final set of terms comprised 38 potential candidates (Fig. 2C). To further reduce the number of candidates, we used the variance inflation factor with a cut-off of 10 to select the best suitable subset to compute the final model (Fig. 2C→D), as we expected some collinearity issues among the temporal subsets of the potential terms. The final set comprised 12 candidate terms (Fig. 2D), which were used to build a new binomial generalized linear model with the following structure (Fig. 2E):

y = intercept + a*global_rad_3h + b*global_rad_int + c*mean_wind_speed_int + d*min_wind_speed_6h + e*precip_duration_24h + f*rel_humidity_int + g*sunshine_duration_12h + h*sunshine_duration_3h + i*sunshine_duration_int + j*(julian_date)^2 + k*(max_temp_6h)^2 +l*(precip_duration_6h)^2

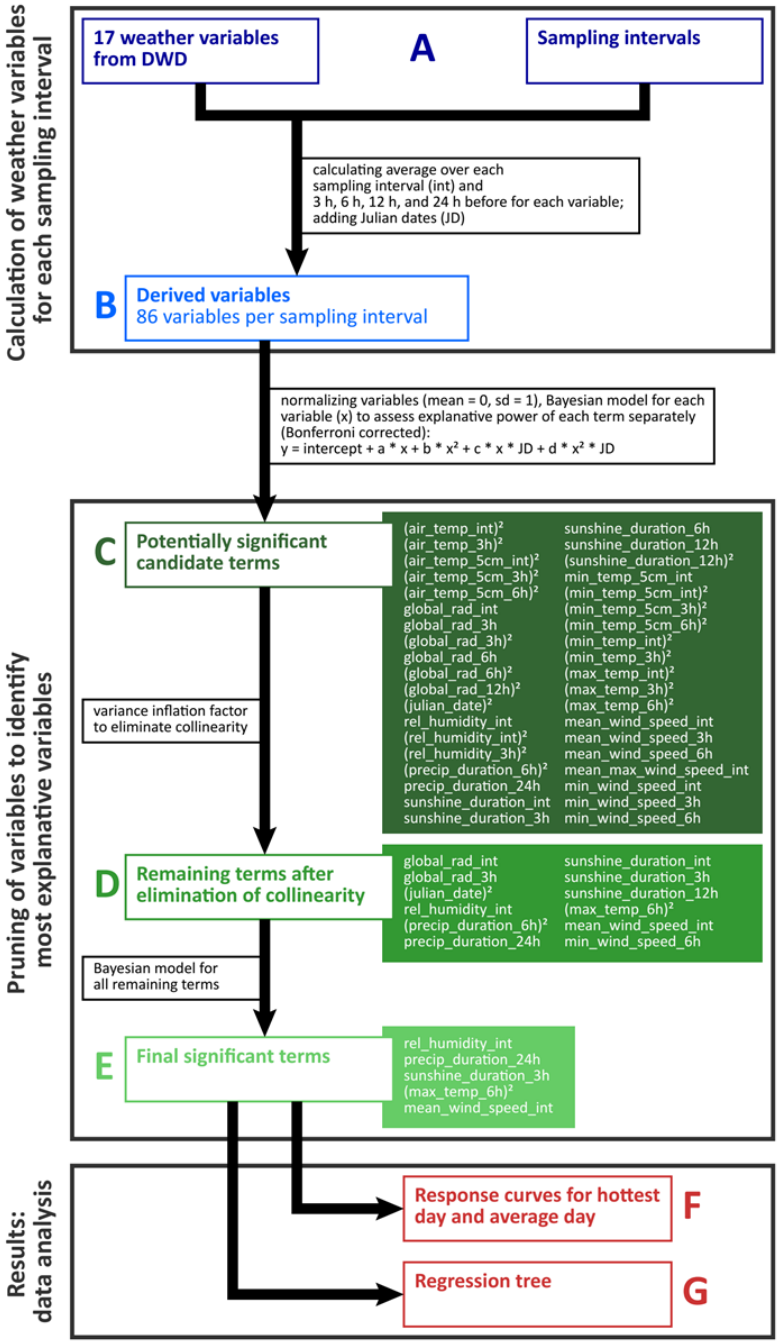

Figure 2: Workflow of methods, processing raw weather data into the final most significant terms. First by calculating average weather data for every sampling interval, then pruning the data by eliminating insignificant terms and eliminating collinearity and finally examining the most explanatory terms.

This was analyzed in the same Bayesian framework as explained above, and only significant terms were further analyzed (Fig. 2E→F and Fig. 2E→G). All analyses were conducted in R (R Core Team, 2020) using adapted scrips provided by FALASCHI (2021) and the package R2jags (SU & YAJIMA, 2015). The package bayestestR was used to assess significances (MAKOWSKI *et al.*, 2019). Results were visualized via response curves, plotting the detection probability as a function of one variable while keeping all other variables at their averages (Fig. 2F). Resulting terms were also visualized in a descriptive graph as to represent the weather conditions during the study period (Fig. S1).

Additionally, using these remaining significant terms, a regression tree was constructed in R using the function *rpart* from the package rpart (THERNEAU *et al.*, 2019; Fig. 2G). This allows for an easy-to-follow decision process predicting expected detection probability based on the best explaining variables only. We left trees unpruned to examine activity patterns in relation to the five terms resulted from the Bayesian model (TREILIBS *et al.*, 2016).

RESULTS

Overall, 238 sampling intervals were conducted over 156 days. All sampling points with coordinates as well as time and date of sighting, and the duration of the sampling intervals can be found in the supplementary material (Table S2). Furthermore, weather conditions during the sampling intervals can also be found in the supplementary material Fig. S1.

Weather conditions throughout the months of the sampling intervals are for the most part quite similar. The general trends are similar between the years (Fig. S1).

Pruning of variables

Pruning of variables revealed 38 candidate terms with significant influence on the number of lizards found during a survey trip after conducting the multiple, Bonferroni corrected Bayesian models for every set of variables. The resulting potentially significant candidate terms are found as a list in Fig. 2C and details are provided in Table 2. Complete results of the Bayesian models can be found in the appendix (Table S3, terms with significant influence on number of lizards found are identified by the first column). After calculating the variance inflation factor to eliminate collinearity in the independent variables (Fig. 2C→D), twelve final variables were left for the refined Bayesian model, which are listed in Fig. 2D.

Model analysis

Using the 12 variables in combination (Fig. 2D→E), only five remained significant which had a strong effect on detection probability (Fig. 2E and Fig. 3). These terms are the 10-minute averages of relative humidity during the observation interval (rel_humidity_int), precipitation duration within the 24 hours before the observation interval (precip_duration_24h), sunshine duration within the 3 hours before the observation interval (sunshine_duration 3h), the square of the maximum temperature within the 6 hours before the observa-

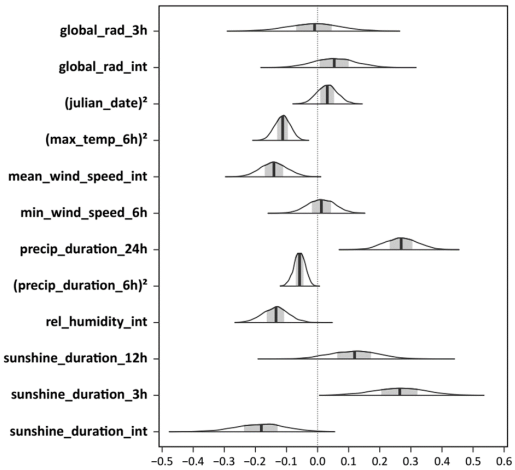

Figure 3: Density plots of the posterior distribution for the terms of the final Bayesian Model. Thick vertical lines represent the median estimated effect for each term, shaded areas represent the 80% confidence interval.

tion interval [(max_temp_6h)^2], and mean wind speed during the observation interval (mean_wind_speed_int). The final formula for the model equation is:

$$y = -2.902 - 0.011*\text{global\_rad\_3h} + 0.054*\text{global\_rad\_int} - 0.140*\text{mean\_wind\_speed\_int} + 0.012*\text{min\_wind\_speed\_6h} + 0.269*\text{precip\_duration\_24h} - 0.135*\text{rel\_humidity\_int} + 0.118*\text{sunshine\_duration\_12h} + 0.263*\text{sunshine\_duration\_3h} - 0.183*\text{sunshine\_duration\_int} + 0.031*(\text{julian\_date})^2 - 0.113*(\text{max\_temp\_6h})^2 - 0.058*(\text{precip\_duration\_6h})^2$$

The terms that best explain detection probability are (max_temp_6h)^2, mean_wind_speed_int, precip_duration_24h, rel_humidity_int, and sunshine_duration_3h. Average 10-minute maximum temperature in the six hours before sampling (meaning the average of the maximum temperature within 10-minute intervals over the 6 hours prior to sampling) showed a squared relationship with detection probability with the probability being highest at 20°C (Fig. 4A). Mean wind speed and relative humidity during the sampling interval show a negative relationship with detection probabil-

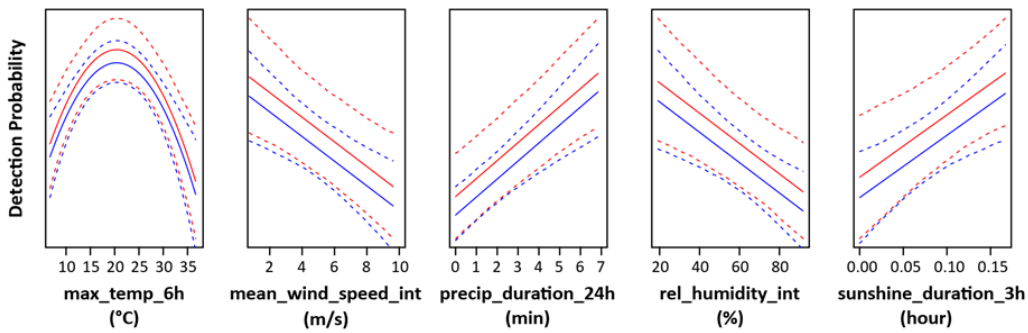

Figure 4: Response curves showing the detection probability as a function of one term if all other terms are kept to the average. Dotted lines represent the 95% confidence intervals. Red lines indicate the hottest day (julian day 268) and blue lines for an average temperature day (julian day 183).

Table 2: Summary statistics of significant candidate variables and terms obtained from Bayesian modeling. Model status indicates if the respective candidate variable entered the final model (final), while significance in the final model is indicated as bold. For each candidate, the term structure is indicated as linear or quadratic and the probability of direction (pd) and the Bonferroni corrected significance level are provided (p_ROPE_bf). For the full list of statistical results see appendix Table S3.

Variable	Model status	term	estimate	std.error	pd	p_ROPE_bf
global_rad_3h	final	linear	0.46	0.06	1	<0.001
global_rad_int	final	linear	0.30	0.05	1	<0.001
julian_date	final	squared	-7.39	1.83	1	<0.001
max_temp_6h	**final**	squared	-0.28	0.05	1	<0.001
mean_wind_speed_int	**final**	linear	-0.29	0.05	1	<0.001
min_wind_speed_6h	final	linear	-0.30	0.05	1	<0.001
precip_duration_24h	**final**	linear	0.40	0.08	1	<0.001
precip_duration_6h	final	squared	-0.39	0.08	1	<0.001
rel_humidity_int	**final**	linear	-0.52	0.06	1	<0.001
sunshine_duration_12h	final	linear	0.35	0.06	1	<0.001
sunshine_duration_3h	**final**	linear	0.44	0.06	1	<0.001
sunshine_duration_int	final	linear	0.39	0.06	1	<0.001
air_temp_3h	canditate	squared	-0.33	0.06	1	<0.001
air_temp_5cm_3h	canditate	squared	-0.45	0.06	1	<0.001
air_temp_5cm_6h	canditate	squared	-0.41	0.06	1	<0.001
air_temp_5cm_int	canditate	squared	-0.27	0.05	1	<0.001
air_temp_int	canditate	squared	-0.32	0.06	1	<0.001
global_rad_12h	canditate	squared	-0.42	0.06	1	<0.001
global_rad_3h	canditate	squared	-0.37	0.06	1	<0.001
global_rad_6h	canditate	linear	0.35	0.06	1	<0.001
global_rad_6h	canditate	squared	-0.39	0.06	1	<0.001
max_temp_3h	canditate	squared	-0.40	0.06	1	<0.001
max_temp_int	canditate	squared	-0.28	0.05	1	<0.001
mean_max_wind_speed_int	canditate	linear	-0.27	0.05	1	<0.001
mean_wind_speed_3h	canditate	linear	-0.27	0.04	1	<0.001
mean_wind_speed_6h	canditate	linear	-0.27	0.04	1	<0.001
min_temp_3h	canditate	squared	-0.32	0.05	1	<0.001
min_temp_5cm_3h	canditate	squared	-0.49	0.06	1	<0.001
min_temp_5cm_6h	canditate	squared	-0.37	0.06	1	<0.001
min_temp_5cm_int	canditate	linear	0.34	0.07	1	<0.001
min_temp_5cm_int	canditate	squared	-0.24	0.05	1	<0.001
min_temp_int	canditate	squared	-0.28	0.05	1	<0.001
min_wind_speed_3h	canditate	linear	-0.36	0.04	1	<0.001
min_wind_speed_int	canditate	linear	-0.36	0.05	1	<0.001
rel_humidity_3h	canditate	squared	-0.39	0.06	1	<0.001
rel_humidity_int	canditate	squared	-0.44	0.06	1	<0.001
sunshine_duration_12h	canditate	squared	-0.35	0.05	1	<0.001
sunshine_duration_6h	canditate	linear	0.42	0.06	1	<0.001

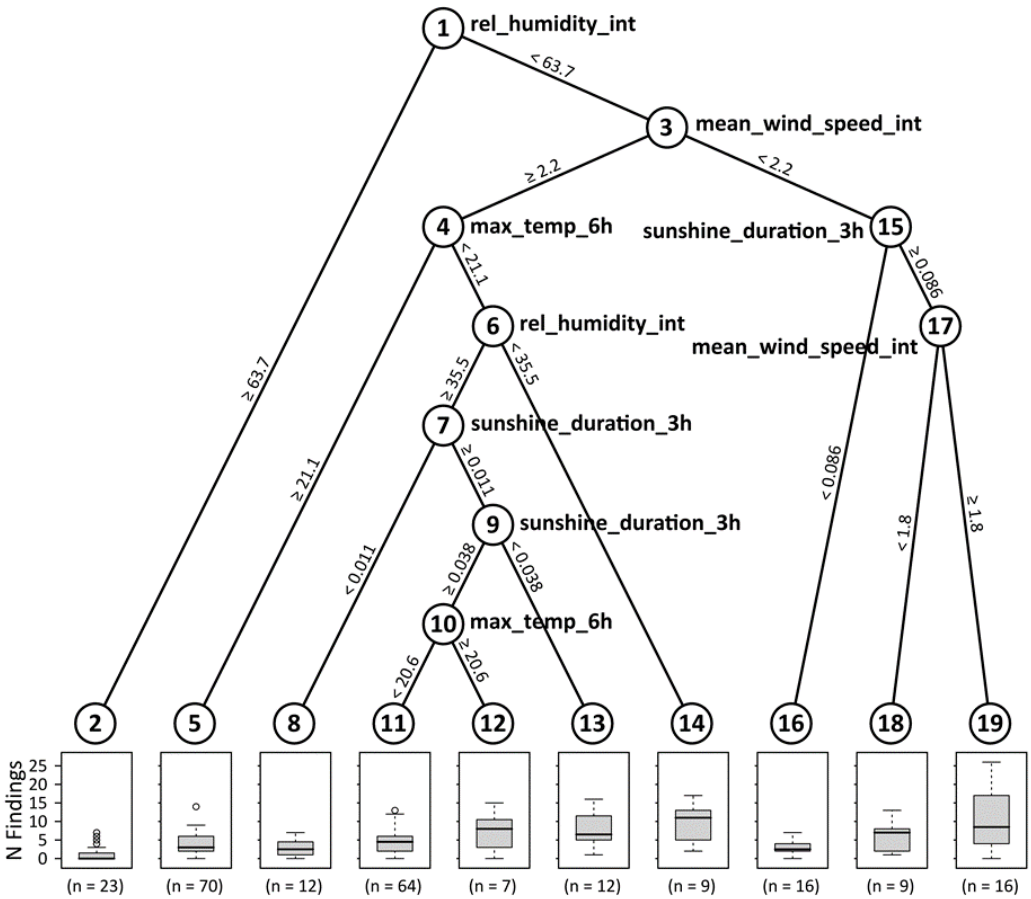

Figure 5: Regression tree for encounter rate of *L. agilis*. Data are partitioned by the five weather variables with the highest explanatory effect. Non-terminal nodes are numbered in boxes above the variable names. Terminal nodes are numbered above the boxplots. Terminal nodes are labelled with the number of sampling intervals for the corresponding conditions, and display the distribution of lizard counts in a boxplot. Variables have the same units as shown in figure 2.

ity, while precipitation duration in the 24 hours preceding the sampling interval and average 10-minute sunshine duration in the 3 hours preceding the sampling interval (meaning the average time the sun shone during 10-minute intervals over the 3 hours prior to sampling) show a positive relationship (Fig. 4B-E). This suggests that lizards are less likely to be found in humid and windy conditions while rainy weather the day before and sunny weather immediately preceding the collecting period, increase the encounter rate.

Regression tree analysis

The regression tree (Fig. 5) suggests that over the course of the experiment, encounter rate was lowest when relative

humidity during the sampling interval was above or equal to 63.7% (Node 2). Contrary, encounter rate was among the highest recorded, albeit with lots of variance, when relative humidity during sampling interval was below 63.7%, mean wind speed during sampling interval was smaller than 2.2 m/s, mean sunshine duration per 10 minutes in the 3 hours before sampling was above 0.086 hours (meaning on average, the sun shone during 5.16 minutes out of 10 minutes during those 3 hours), and mean wind speed was larger or equal to 1.8 m/s (Node 19). Compared to that path in the tree, encounter rate is somewhat reduced when mean wind speed was instead smaller than 1.8 m/s (Node 18), while it was greatly reduced when average sunshine duration in 10 minutes during the 3 hours prior was smaller than 0.086 hours (Node 16). It was still possible to get high encounter rates if mean wind speed was larger than 2.2 m/s as long as relative humidity during the sampling interval remained below 63.7%. For this, 10-minute average maximum temperature during the six hours preceding the sampling interval had to remain below 21.1°C and relative humidity during the sampling interval had to be below 35.5% (Node 14). If the 10-minute average maximum temperature was higher or equal to 21.1 °C, encounter rate was low (Node 5). If the 10-minute average maximum temperature remained below 21.1 °C but relative humidity was above or equal to 35.5% there were three possibilities depending on sunshine duration. If 10-minute average sunshine duration was below 0.011 hours, encounter rate was low (Node 8) while for a 10-minute average sunshine duration between 0.011 hours and 0.038 hours, encounter rate was higher (Node 13). For a 10-minute average sunshine duration above 0.038 hours, encounter rate was higher, when the average maximum temperature during 10 minutes for the 6 hours prior to the sampling interval was higher or equal to 20.6°C (Node 12) and low when it is below that threshold (Node 11).

Table 3: Ranges of the five terms best explaining the detection probability.

Interval	maximum	minimum	unit
rel_humidity_int	91.9	19.1	%
precip_duration_24h	6.8	0.0	min
sunshine_duration_3h	0.167	0.000	h
max_temp_6h	36.7	6.7	°C
mean_wind_speed_int	9.6	1.1	m/s

Since a regression tree partitions data according to the recorded variables, it is important to note that encounter rate outside the recorded range of these variables, can be inferred but has not been considered by the model. Therefore, an expression like > X for any variable really means a value between X and the largest recorded value for the tree. To identify the values, where the model ends and speculation begins, the range of the variables used for the model have to be considered (Table 3) (Complete summary of the regression tree can be found in the supplementary material Text S1).

Discussion

Interpreting the best explanatory terms

The step by step pruning of variables revealed that the majority of *L. agilis'* detection probability can be explained by five

weather variables: average maximum temperature six hours prior to the sampling interval, mean wind speed and relative humidity during the sampling interval, mean precipitation duration in the 24 hours before the sampling interval and sunshine duration in the three hours prior to the sampling interval. Temperature has a squared relationship with detection probability, peaking around 20°C, while wind speed and relative humidity have a negative linear relationship and precipitation duration and sunshine duration have a positive linear relationship with detection probability.

The 10-minute average of max temperature over the six hours before the sampling period shows, that both temperatures deviating too much from 20°C can lead to reduced detection probability and hence, reduced activity in *L. agilis*. *Lacerta agilis* has been shown to avoid temperatures below 17°C while spending prolonged periods at temperatures above 23°C, whether active in the shade under dense vegetation or inactive in hiding, leading to decreased detection probability (House *et al.*, 1979; Edgar & Bird, 2006; Fearnley, 2009). Sand lizards, consequently, have a bimodal activity pattern which can on colder days become unimodial (Saint Girons, 1976; House *et al.*, 1979), sharing this pattern with many other European reptiles (Böhme, 1981; Grimm *et al.*, 2014; Grimm *et al.*, 2015). However, we found maximum temperature in the six hours proceeding the sampling interval to be a better indicator than temperature during the sampling interval. We can assume a time lag between temperature fluctuations and lizard behaviour. According to Blanke (1999), *L. agilis* in lower Saxony, Germany start basking at temperatures near 20°C. While basking, lizards remain largely immobile making them harder to detect, explaining the increased detection rate due to higher activity some hours after temperatures reached that point. Lizards in hiding could especially need some time to become active as temperature fluctuations might take some time to reach hiding spots.

The negative linear relationship between detection probability and mean wind speed and humidity during the sampling interval are what is to be expected for a small heliophile lizard (Fearnley, 2009). Increased humidity is correlated with increased wetness in the environment and is also related to rain probability. A wet environment reduces basking capabilities by convection, as evaporation cooling of surfaces and the skin of the lizard occurs. Meanwhile, overcast or rainy skies reduce basking capabilities by radiation as clouds block the sun. As sand lizards are known to bask via those two mechanisms, the negative correlation of humidity to detection probability appears to be reasonable. It is possible, that lizards use the opportunity to hydrate but forego prolonged periods of activity due to the aforementioned reasons, making them in turn hard to detect. Sand lizards have been shown on multiple occasions to be mostly active when conditions are dry (House *et al.*, 1979; Kuranova *et al.*, 2003; Čeirâns, 2006). Lower activity during humid and overcast conditions distinguishes *L. agilis* from the sometimes sympatrically occurring *Zootaca vivipara*, which is more tolerant to

those conditions (House *et al.*, 1979; Kuranova *et al.*, 2003). Wind on the other hand, is rarely mentioned as a contributor to lizard activity in other studies. It has even been cited specifically as avoidable by the lizards (Edgar & Bird, 2006). However, high wind speed can make life hard for small animals as bushes are rattled, alarming sounds are masked, and air temperature tends to sink. As higher wind speeds increase convective heat transfer (Porter *et al.*, 1973), the animals cool down faster in windy conditions leading to more time spend basking or hiding. This is especially true in wet conditions due to the aforementioned cooling effects of evaporation. Additionally, fewer insects might be found during higher wind speeds (Williams, 1961). High wind speeds have been shown to be avoided by another lacertid, *Podarcis guadarramae* in spring, autumn and winter (Ortega & Pérez-Mellado, 2016). There is also a possibility, that lizards are not affected by wind speeds directly but instead, detection capabilities of researchers could be impacted as lizards were best detected by the rustling sound of their movements.

The importance of sunshine duration three hours prior the surveys can be explained by the heliothermic nature of *L. agilis* (Avery, 1979; Fearnley, 2009). The more the sun shines, the better for thermoregulation, as surfaces heat up, while long periods of shaded conditions could lead to the lizards cooling out faster and taking more breaks to bask and longer to heat up (House *et al.*, 1979). Both ways, sand lizards' basking is directly reliant on sunlight as both basking by radiation and basking by convection need sunlight to heat up the lizard or the surfaces it basks on. Sand lizards have been observed to have shorter activity periods on overcast days, possibly not even emerging at all (House *et al.*, 1979). As with temperature, there is a time lag between achievement of optimal conditions and increase of detection probability as lizards need time to heat up. The time lag is smaller for sunshine than for temperature, possibly hinting at the importance of sunshine in the activity of the heliophile lizard. *Lacerta agilis* has been shown to be more reliant on sunlight than *Zootoca vivipara* who often occurs in the same areas (House *et al.*, 1979; Kuranova *et al.*, 2003).

Finally, the positive relationship of detection probability and precipitation duration 24 hours prior to the sampling interval might seem contradictory to our interpretations of relative humidity thus far but can be explained by lower physiological performance during rainy days. It has been shown that during rain, lizards rarely appear (House *et al.*, 1979; Čeirâns, 2006). So, after the rains stopped, lizards could be inclined to venture out even in conditions they would normally deem sub-optimal to make up for lost time. Increased activity after rainfall in the 24 hours prior has been shown for *Podarcis muralis* by (Falaschi, 2021), who also hypothesised the animals making up for lost time or suggested, that prey insects could be more abundant after rainfall according to Williams (1951).

Regression tree analysis

Analysis of the regression tree shows that lizard activity is not dependent on a single variable but rather can be dependent on multiple variables. While CART models

can deal with a large number of covariates and can therefore stand on their own (TREILIBS *et al.*, 2016), they are helpful in visualising the complex relationship between the best explaining variables resulting from a data-reduction technique.

An overall important factor for detection probability of *Lacerta agilis* is relative humidity remaining below 63% as higher humidity leads to the lowest encounter rate in the study (Fig.6 Node 2). Humidity being a limiting factor for sand lizard activity has been proven in the past as discussed above (HOUSE *et al.*, 1979; KURANOVA *et al.*, 2003). Whenever humidity remained below that threshold, most lizards were encountered on sunny days with very light breezes. Under these conditions, detection probability is highest, but also shows high variance (Node 19). Alternatively, comparatively high encounter rates are also found on more windy days as long as temperature was below 21 °C six hours prior to sampling and either very dry during the sampling or at least moderately sunny three hours before. The tree reinforces the results of the Bayesian model that sunny and dry conditions overall increase encounter rates. While encounter rates are best during low wind speeds, it is possible to encounter lots of lizards when wind speeds are higher. This may suggest, that the negative effects of wind might be offset by especially low humidity or sunny weather, further reinforcing the importance of dry, sunny weather for sand lizards. Evaporation cooling, which was discussed above as one adverse effect of high wind speeds when combined with humid condition would not be a problem in dry, sunny weather. As *Lacerta agilis* spends a considerable amount of time basking, dry surfaces heated up by sunlight are important for the animals to finish basking quickly (GLANDT, 1979; HOUSE *et al.*, 1979; HEYM *et al.*, 2013). Furthermore, by basking in spots sheltered from the wind, sand lizards can offset high wind speeds while wet or overcast weather is much harder to escape. Temperatures diverging too far from 20-21 °C in the six hours prior to the sampling interval led to lower encounter rates again reinforcing the results of the Bayesian model.

In conclusion, the relations from the Bayesian model are reflected overall in the CART model but might diverge in the cases of wind speed and sunshine duration later in the tree, when the algorithm was already trained with a subset of the data the Bayesian model used. These subsets might have different relationships towards encounter rate than the original complete set of encounters. The absence of precipitation duration during the preceding 24 hours from the tree suggests that, although the positive effect of rainfall in the preceding day has been shown, other variables might have a more immediate effect on lizard activity, as discussed above. If lizards are making up for lost time as proposed by FALASCHI (2021), it is possible that rainfall duration in the past 24 hours might be more of an additional encouragement for lizards, while other factors could impact the lizard's performance more directly, for example through basking efficiency. The CART model is not only a comprehensive decision-making tool but it also highlights the interactions between the best

explaining variables in a way the Bayesian model could not.

Conclusion

Overall, our results suggest that *L. agilis* in the Dellbrücker Heide prefer dry and sunny weather conditions with temperatures around 20 °C prior to their activity phase, and low wind speeds. Additionally, lizards are even more exposed if it rained a lot in the 24 hours prior. Our hypotheses concerning temperature, sunshine duration and humidity were confirmed, although we did not expect windspeed to play a defining role and did not find sunshine intensity among the best explaining variables. Our results are in line with other studies, especially in northern and central Europe, suggesting weather dependent activity of *Lacerta agilis* is similar. Bayesian models are a great tool to identify the terms that best explain encounter rate but fail to comprehensibly depict the complex relationship of these related weather variables. Regression trees therefore, complement the Bayesian model by delivering an easy-to-understand depiction of which relationships lead to which encounter rates. Regression trees of variables that can realistically be predicted by consulting weather forecasts, can be a great help in finding optimal conditions for field studies or predict encounter rate within a population. Aside from the post field work analytical aspects, this method can also be an enormous help in studies involving field work, especially if field work opportunities are limited. The combination of methods between the Bayesian model framework and the CART tree are computationally fairly straightforward and rely solely on the number of encounters during fieldwork and the availability of weather data for the corresponding time periods. The method is also not species or habitat specific and works with any visual encounter survey, even post-survey. We therefore, think it is of great value in conservation, monitoring and wildlife management. While the big disadvantage of the method is that it needs a rather large sample size, it can be helpful for populations that are regularly checked on or studied over a long period of time, for example in the context of long-term monitoring projects.

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Electronic Supplement

Supplementary material can be found on FigShare under https://figshare.com/articles/dataset/Supplementary_Material/21948236

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Weather-related detection probability of *Lacerta agilis* LINNAEUS, 1758 within the core range in western Germany

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SUPPLEMENTARY MATERIAL

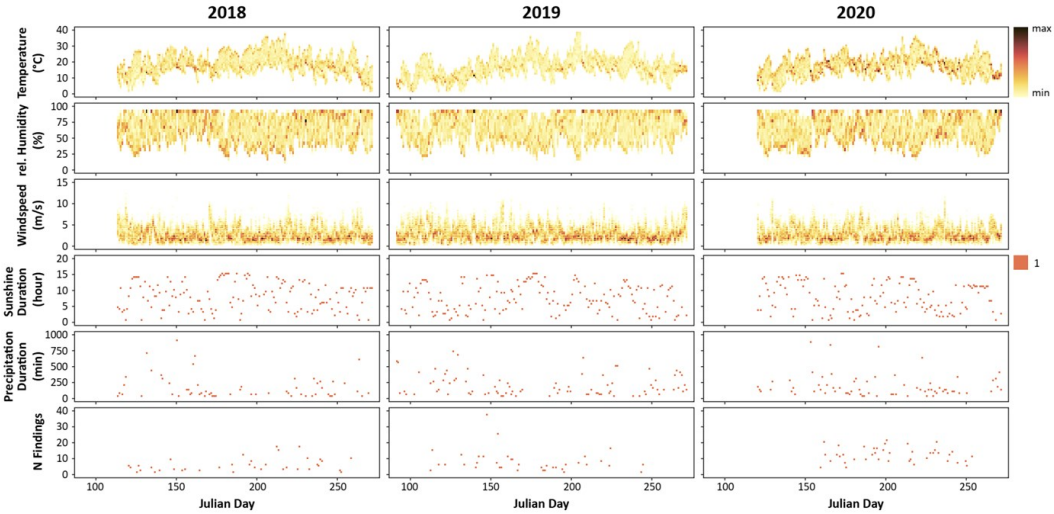

Figure S1: Weather conditions during the sampling times for 2018 (A), 2019 (B) and 2020 (C). Temperature shows the distribution of values for maximum air temperature since the last measurement taken every 10 minutes. Relative humidity shows the humidity at the time of measuring, taken every 10 minutes. Windspeed shows the average windspeed since the last measurement taken every 10 minutes. Sunshine duration and precipitation duration are cummulative for the entire 24 hour day, as are number of findings.

Text S4: Results of the CART model with errors and alternative splits.

```
Call:
rpart(formula = Species ~ rel_humidity_int + mean_wind_speed_int +
   sunshine_duration_3h + max_temp_6h + precip_duration_24h,
   data = pca.tree, method = "anova")
  n= 238

         CP nsplit rel error   xerror      xstd
1 0.06490276      0 1.0000000 1.011221 0.1646115
2 0.04869952      1 0.9350972 1.024799 0.1567676
3 0.02988345      3 0.8376982 1.061378 0.1632443
4 0.02373533      5 0.7779313 1.087653 0.1668668
5 0.01643948      6 0.7541960 1.106785 0.1656221
6 0.01011343      8 0.7213170 1.134243 0.1663088
7 0.01000000      9 0.7112036 1.163458 0.1673224

Variable importance
   rel_humidity_int sunshine_duration_3h  mean_wind_speed_int  precip_duration_24h
max_temp_6h
               31                26                19                13                11

Node number 1: 238 observations,    complexity param=0.06490276
  mean=4.684874, MSE=17.87969
  left son=2 (23 obs) right son=3 (215 obs)
  Primary splits:
     rel_humidity_int     < 63.675      to the right, improve=0.064902760, (0 missing)
     sunshine_duration_3h < 0.01097368  to the left,  improve=0.059297110, (0 missing)
     mean_wind_speed_int  < 2.174107    to the right, improve=0.030177580, (0 missing)
     max_temp_6h          < 25.91216    to the right, improve=0.015264000, (0 missing)
     precip_duration_24h  < 3.486207    to the right, improve=0.007282954, (0 missing)
  Surrogate splits:
     precip_duration_24h < 4.265517    to the right, agree=0.916, adj=0.13, (0 split)

Node number 2: 23 observations
  mean=1.391304, MSE=4.325142

Node number 3: 215 observations,    complexity param=0.04869952
  mean=5.037209, MSE=18.04513
  left son=6 (174 obs) right son=7 (41 obs)
  Primary splits:
```

```
    mean_wind_speed_int  < 2.174107    to the right, improve=0.027476880, (0 missing)
    sunshine_duration_3h < 0.01097368  to the left,  improve=0.026387590, (0 missing)
    max_temp_6h          < 25.91216    to the right, improve=0.025695190, (0 missing)
    rel_humidity_int     < 35.52917    to the right, improve=0.020518910, (0 missing)
    precip_duration_24h  < 2.568966    to the right, improve=0.007382531, (0 missing)
  Surrogate splits:
    precip_duration_24h < 3.486207    to the left,  agree=0.823, adj=0.073, (0 split)
    max_temp_6h         < 11.25135    to the right, agree=0.814, adj=0.024, (0 split)

Node number 6: 174 observations,    complexity param=0.02988345
  mean=4.695402, MSE=12.59113
  left son=12 (70 obs) right son=13 (104 obs)
  Primary splits:
    max_temp_6h          < 21.14189    to the right, improve=0.04285845, (0 missing)
    rel_humidity_int     < 35.52917    to the right, improve=0.01581210, (0 missing)
    sunshine_duration_3h < 0.01369298  to the left,  improve=0.01402203, (0 missing)
    mean_wind_speed_int  < 3.49        to the right, improve=0.01191176, (0 missing)
    precip_duration_24h  < 0.003448276 to the left,  improve=0.01175907, (0 missing)
  Surrogate splits:
    rel_humidity_int     < 45.87619    to the left,  agree=0.678, adj=0.200, (0 split)
    sunshine_duration_3h < 0.1656579   to the right, agree=0.655, adj=0.143, (0 split)
    precip_duration_24h  < 0.003448276 to the left,  agree=0.621, adj=0.057, (0 split)
    mean_wind_speed_int  < 2.20625     to the left,  agree=0.603, adj=0.014, (0 split)

Node number 7: 41 observations,    complexity param=0.04869952
  mean=6.487805, MSE=38.59131
  left son=14 (16 obs) right son=15 (25 obs)
  Primary splits:
    sunshine_duration_3h < 0.0865      to the left,  improve=0.19457580, (0 missing)
    mean_wind_speed_int  < 1.75        to the left,  improve=0.16781950, (0 missing)
    precip_duration_24h  < 0.6310345   to the right, improve=0.08315863, (0 missing)
    rel_humidity_int     < 52.20234    to the right, improve=0.05969091, (0 missing)
    max_temp_6h          < 20.93108    to the left,  improve=0.03671477, (0 missing)
  Surrogate splits:
    precip_duration_24h < 0.006896552 to the right, agree=0.854, adj=0.625, (0 split)
    mean_wind_speed_int < 1.72381     to the left,  agree=0.805, adj=0.500, (0 split)
    rel_humidity_int    < 48.95       to the right, agree=0.780, adj=0.438, (0 split)
    max_temp_6h         < 14.08378    to the left,  agree=0.683, adj=0.188, (0 split)

Node number 12: 70 observations
  mean=3.8, MSE=7.274286
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Node number 13: 104 observations,    complexity param=0.02988345
  mean=5.298077, MSE=15.26692
  left son=26 (95 obs) right son=27 (9 obs)
  Primary splits:
      rel_humidity_int     < 35.52917    to the right, improve=0.10104380, (0 missing)
      max_temp_6h          < 20.83514    to the left,  improve=0.05987520, (0 missing)
      sunshine_duration_3h < 0.01142105  to the left,  improve=0.04845186, (0 missing)
      mean_wind_speed_int  < 3.821591    to the right, improve=0.02006089, (0 missing)
      precip_duration_24h  < 2.568966    to the right, improve=0.01093660, (0 missing)

Node number 14: 16 observations
  mean=3.0625, MSE=3.433594

Node number 15: 25 observations,    complexity param=0.02373533
  mean=8.68, MSE=48.7776
  left son=30 (9 obs) right son=31 (16 obs)
  Primary splits:
      mean_wind_speed_int  < 1.805556    to the left,  improve=0.08282695, (0 missing)
      max_temp_6h          < 23.22568    to the right, improve=0.03080675, (0 missing)
      rel_humidity_int     < 39.91111    to the left,  improve=0.01760462, (0 missing)
      sunshine_duration_3h < 0.1599211   to the right, improve=0.01104749, (0 missing)
  Surrogate splits:
      sunshine_duration_3h < 0.1634474   to the left,  agree=0.80, adj=0.444, (0 split)
      max_temp_6h          < 19.62838    to the left,  agree=0.72, adj=0.222, (0 split)
      rel_humidity_int     < 44.52143    to the right, agree=0.68, adj=0.111, (0 split)

Node number 26: 95 observations,    complexity param=0.01643948
  mean=4.915789, MSE=12.68765
  left son=52 (12 obs) right son=53 (83 obs)
  Primary splits:
      sunshine_duration_3h < 0.01142105  to the left,  improve=0.045540840, (0 missing)
      max_temp_6h          < 16.17838    to the left,  improve=0.035044950, (0 missing)
      rel_humidity_int     < 51.9487     to the right, improve=0.027624440, (0 missing)
      mean_wind_speed_int  < 3.8525      to the right, improve=0.021437550, (0 missing)
      precip_duration_24h  < 0.5068966   to the left,  improve=0.008500535, (0 missing)
  Surrogate splits:
      precip_duration_24h < 3.282759    to the right, agree=0.884, adj=0.083, (0 split)

Node number 27: 9 observations
  mean=9.333333, MSE=24.66667
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Node number 30: 9 observations
  mean=6, MSE=15.33333

Node number 31: 16 observations
  mean=10.1875, MSE=61.27734

Node number 52: 12 observations
  mean=2.916667, MSE=5.243056

Node number 53: 83 observations,    complexity param=0.01643948
  mean=5.204819, MSE=13.10263
  left son=106 (71 obs) right son=107 (12 obs)
  Primary splits:
      sunshine_duration_3h < 0.03771053  to the right, improve=0.07817840, (0 missing)
      rel_humidity_int     < 51.97727    to the right, improve=0.03904708, (0 missing)
      mean_wind_speed_int  < 3.821591    to the right, improve=0.03442652, (0 missing)
      max_temp_6h          < 16.17838    to the left,  improve=0.03288963, (0 missing)
      precip_duration_24h  < 2.568966    to the right, improve=0.01517618, (0 missing)

Node number 106: 71 observations,    complexity param=0.01011343
  mean=4.788732, MSE=10.61734
  left son=212 (64 obs) right son=213 (7 obs)
  Primary splits:
      max_temp_6h          < 20.57162    to the left,  improve=0.05709018, (0 missing)
      mean_wind_speed_int  < 3.461429    to the right, improve=0.04439311, (0 missing)
      sunshine_duration_3h < 0.07986842  to the left,  improve=0.02327315, (0 missing)
      rel_humidity_int     < 50.33       to the right, improve=0.02023827, (0 missing)
      precip_duration_24h  < 0.5724138   to the left,  improve=0.01006022, (0 missing)

Node number 107: 12 observations
  mean=7.666667, MSE=20.72222

Node number 212: 64 observations
  mean=4.53125, MSE=8.311523

Node number 213: 7 observations
  mean=7.142857, MSE=25.55102
```