BRILL

Amphibia-Reptilia (2021) DOI:10.1163/15685381-bja10051

brill.com/amre

Phenology and temperature are the main drivers shaping the detection probability of the common wall lizard

Mattia Falaschi*

Abstract. Measuring the abundance of organisms is essential to provide information to ecology and biodiversity conservation. Hardly ever, the probability of detecting an animal during a survey is near one. Overlooking this observational process can lead to biased estimates of population size and vital rates. In this study, through Bayesian modeling, I evaluated the effects of temperature, precipitation, wind, humidity, and phenology in determining changes in the detection probability of the common wall lizard, for which studies on the factors determining detection probability are currently not available. Additionally, I tested for two possible interactions: date-temperature and date-humidity, in order to assess if the relationships of these variables with detection probability vary through the sampling season. Detection probability was highest earlier in the season (April) and between 24 and 28 degrees. Rainfall during the survey showed a negative effect on detection probability. In contrast, cumulative precipitation in the 24 hours before the survey showed a positive relationship, indicating that lizards are easier to detect in surveys after rainy days. Furthermore, date and temperature showed a positive interaction, indicating that the relationship between detectability and temperature changed over the sampling season. Date and humidity showed a negative interaction: late in the sampling season, detectability was higher with lower humidity, however, this relationship was not found in the early season. Future studies can consider multiple sites to evaluate the extent of variation in the drivers of detection probability and to assess the factors related to abundance.

Keywords: detection probability, N-mixture models, northern Italy, *Podarcis muralis*.

Introduction

Measuring the abundance of organisms is essential to provide information to ecology and biodiversity conservation. While simple counts of population size can be easy to obtain, the probability of detecting an individual during a survey is usually less than one. Imperfect detection can be the results of different factors acting jointly, such as environmental conditions, observer skill, or species traits (Mazerolle et al., 2007; Kellner and Swihart, 2014). Not including this observational process into models can lead to biased estimates of population size, vital rates such as survival probability, and of relationships with covariates driving these parameters (Kéry and Schaub, 2012). Since the early 2000s, there has been a considerable increase in methods able to include detection probability into models and in their use (MacKenzie et al., 2003; Royle, 2004; Manenti et al., 2020). However, many studies still do not consider imperfect detection, even if this pattern can vary across taxa (Kellner and Swihart, 2014).

Species with a cryptic behavior or a cryptic color pattern can be particularly hard to detect, and this is the case for many reptiles (Mazerolle et al., 2007; Ficetola et al., 2018, 2020). Many factors can influence the probability of seeing an individual during a survey. These factors can be either site-specific, such as the vegetation type, survey-specific, such as weather conditions during the survey, or may depend on individual heterogeneity, such as life-stage or sex. For instance, the activity of ectothermic vertebrates can be strongly influenced by abiotic factors such as temperature, humidity, and precipitation (Daltry et al., 1998; Sun et al., 2001). Another factor that can affect activity patterns is phenology. Many species are more active and easier to detect during the breeding season, reducing activity in other periods of the year (Braña, 1991; Zamora-Camacho et al., 2013). If few surveys are available to assess the

Department of Environmental Science and Policy, Università degli Studi di Milano, Via Celoria 10, 20133 Milano, Italy

*E-mail: matt_fala@hotmail.it

status of a species in a certain area, it is best to carry out those surveys when the probability of finding the target species is highest. For this reason, knowing the factors that influence species' detection probability is crucial to optimize the monitoring of both rare and common species.

In this study, I focused on the common wall lizard *Podarcis muralis*, a lacertid lizard distributed in central and southern Europe (Sillero et al., 2014). Many aspects of the ecology and ethology of this species have been intensively studied, including its polymorphism, aggressive behavior, hematology, and demography (Gracceva et al., 2008; Scali et al., 2016, 2019; Pérez i de Lanuza and Carretero, 2018; Sacchi et al., 2020). However, so far, no study has ever focused on the factors related to detection probability in this species, even if it is a widespread and common reptile. For this reason, I estimated the relative effect of several candidate drivers of detection probability in the common wall lizard. By performing a large number of surveys at a site in northern Italy, I evaluated the effects of temperature, precipitation, wind, and humidity in determining changes in detection probability. Additionally, I considered the effect of the date of the survey to consider the phenology. Furthermore, I tested for two possible interactions: between date and temperature, and between date and humidity, in order to assess if the relationship between these two variables and detectability varied over the sampling season.

Material and methods

Study area and sampling

The study was carried out in Cardano al Campo, Lombardy, northern Italy, coordinates: 45.6367N, 8.7710E. The study site is a residential area composed of roads, houses, private gardens, and meadows (supplementary fig. S1). Walking around the streets, it is easy to spot the common wall lizard, a small lacertid lizard with a maximum snout-vent length of ∼75 mm (Biaggini et al., 2011), mating, hunting, or basking onto the walls. I performed repeated counts of lizards within this area by walking along a pre-defined path of ∼1.1 km in length (supplementary fig. S1). The path was walked at a slow speed (between 2 and 3 km/h) to allow a careful inspection of both sides of the roads. A total of 117 surveys were performed between 12 April and 6 October 2020, a period covering the peak of activity of this species (Biaggini et al., 2011). On some days, I carried out two surveys, while in others, no survey was carried out. The average frequency of surveys was one every 1.5 days (supplementary appendix S1). The time of the survey ranged between 08:01 and 20:00 daylight savings time. To respect the assumption of population closure (Royle, 2004), newly hatched individuals (total length 5-6 cm; Biaggini et al., 2011) were excluded from the analyses.

Environmental data

Environmental data were gathered from a weather station of the regional agency for the protection of the environment (https://www.arpalombardia.it/Pages/Meteorologia/Richiesta-dati-misurati.aspx). The station is located near the study site (station coordinates: 45.61924N, 8.75697E) and registers weather data every 10 minutes. Temperature and precipitation are two crucial variables shaping reptiles' activity (Zamora-Camacho et al., 2013; Cunningham et al., 2016). Additionally, humidity and wind can be important determinants of activity patterns (Daltry et al., 1998; Sun et al., 2001). Hence, for each survey, I extracted values of mean temperature, mean humidity, mean wind speed, and cumulative precipitation. As the duration of a survey was 25-30 min, weather data values were averaged across the 30 min timespan corresponding to the time when each survey was carried out. Additionally, I calculated the cumulative precipitation in the 24 hours before the survey to test for a possible effect of rainfall on the activity of the following day.

Statistical analyses

N-mixture models can reliably estimate population abundance and detection probability of vertebrates (Ficetola et al., 2018). However, estimating values of abundance and detection probability is not possible with data from a single site. Nevertheless, it is still possible to estimate the relationships between covariates and detection probability and also to compare the relative importance of these covariates. For this reason, in order to estimate the effect of abiotic factors on detection probability, I used a binomial generalized linear model in a Bayesian framework, specifically written for this analysis (supplementary appendices S1 and S2). The following covariates of detectability were included in the model: average temperature during the survey (both quadratic and linear terms), average humidity during the survey, average wind speed during the survey, cumulative precipitation during the survey, cumulative precipitation in the 24 hours before the survey; additionally, I included the date, expressed as Julian day, to consider the effect of phenology, and two interactions: date-temperature and date-humidity. Before running the model, I log-transformed precipitation and wind variables to reduce skewness, and then scaled all independent variables of detection with mean of 0 and a standard deviation of 1 (Sokal and Rohlf, 2012). Correlations among independent variables were weak ($|r| < 0.57$; supplementary table S1), hence I decided to keep all

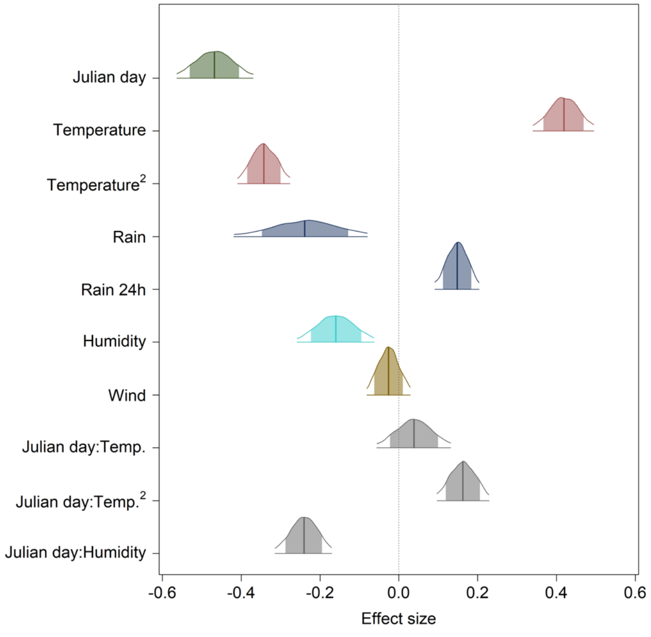

Figure 1. Density plots of the posterior distribution for the variables related to detection probability. Thick vertical lines represent the average estimated effect for each variable, outer lines represent the 95% credible interval and shaded areas represent the 80% credible interval. The superscript "^{2}" indicates a quadratic relationship.

the predictors in the model. The priors of regression coefficients of the variables related to detection probability were uniform, ranging from −10 to 10. The model was run with three chains and for 20 000 iterations for each chain, discarding the first 10 000 iterations as a burn-in. The distribution of posteriors was sampled with a thinning of 10, resulting in 1000 samples for each chain. Parameter convergence was checked both visually and by looking at the Rhat value, which was <1.01 for all parameters. Analyses were run in the R environment (R Core Team, 2018) using the package R2jags (Su and Yajima, 2015). A script of the model and data used to run the analyses are available in supplementary appendices S1 and S2.

Results

Over the 117 surveys, the number of detected lizards ranged from 0 to 49 (supplementary fig. S2). Julian day showed a negative relationship with average detection probability (fig. 1), indicating that lizards were easier to detect earlier in the sampling season (fig. 2a). Detection probability showed a quadratic relationship with temperature (fig. 1). On average, the highest detection probability was observed at 25.6°C. The effect of precipitation showed a bimodal pattern. Rainfall during the survey showed a negative relationship with detection probability (fig. 1), while rainfall in the 24 hours before the survey showed an average positive relationship (figs 1 and 2b). This indicates that lizards are less detectable during rains but easier to detect after rainy days. Humidity showed a negative relationship with detection probability, indicating that detection probability was lower during surveys with higher relative humidity (fig. 1). The average effect of wind was close to zero, with 95% CIs widely overlapping zero, suggesting no effect of wind on detection probability (fig. 1). The quadratic effect of temperature showed an interaction with Julian day, indicating that the temperature at which detection probability was the highest varied over the sampling season (fig. 1). For instance, in the early season (mid-April), detection probability was highest at 24.3°C (fig. 2c), while later in the season (beginning of August), detection prob-

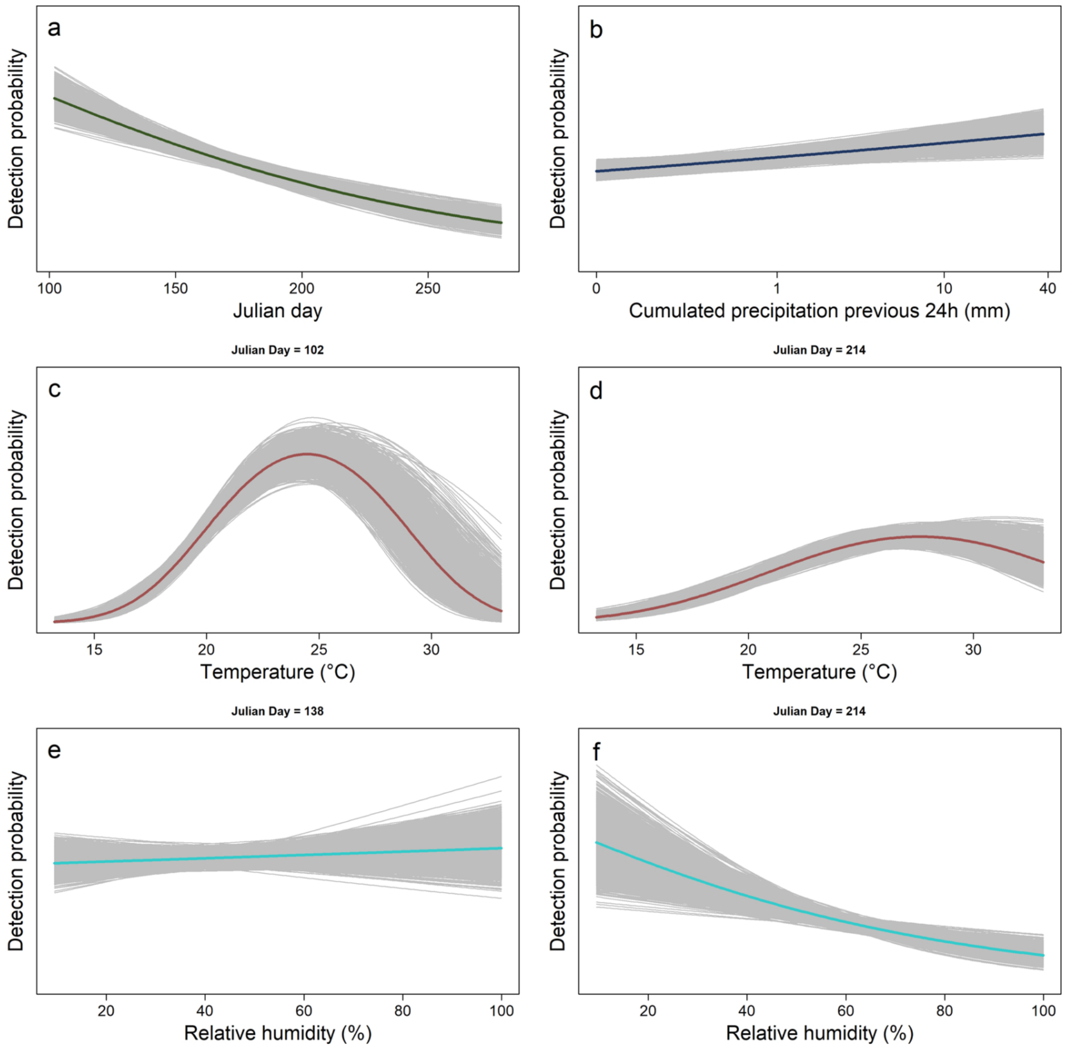

Figure 2. Relationship between detection probability and some of the most influential variables. In each plot, the thick colored line represents the average predicted relationship, while the thin grey lines represent 3000 samples of the posterior distribution (1000 for each chain). a) Relationship between detection probability and Julian day; b) Relationship between detection probability and cumulated precipitation during the 24h before the survey; The interaction between Julian day and temperature is showed in c and d. c) Relationship between detection probability and temperature during the survey, with Julian day fixed at 102 (mid-April); d) Relationship between detection probability and temperature during the survey, with Julian day fixed at 214 (beginning of August). The interaction between Julian day and humidity is showed in e and f. e) Relationship between detection probability and humidity during the survey, with Julian day fixed at 138 (mid-May); d) Relationship between detection probability and humidity during the survey, with Julian day fixed at 214 (beginning of August).

ability was highest at 27.6°C (fig. 2d). On the contrary, Julian day showed a negative interaction with humidity: the negative relationship between humidity and detection probability was not present in the early season (fig. 2e and 2f).

Discussion

Despite being a very common and widespread species, so far, no study assessed the factors driving the detection probability of the common wall lizard. In this study, through Bayesian modeling, I showed that the most influential drivers of the detection probability of this species are temperature and phenology, followed by precipitation and humidity. Temperature showed a quadratic relationship with detection probability, indicating that the activity of the common wall lizard is highest between 25 and 28 degrees, decreasing at lower or higher temperatures (fig. 2c and 2d). Previous studies found the body temperature of active common wall lizards around 34°C (Avery, 1978; Braña, 1991). This is not in contrast with the results of this study, since the common wall lizard shows an active thermoregulatory behavior, allowing individuals to reach body temperatures higher than the air temperature (Braña, 1991). Obtaining information about the environmental temperatures which maximize the probability of detecting individuals gives useful, practical information to plan the monitoring of this species.

The date of the survey (Julian day) showed a strong negative relationship with detection probability (fig. 2a). This indicates that, even after accounting for the effect of temperature, phenology plays a significant role in shaping the activity patterns of the common wall lizard. This species usually breeds between March and June (Biaggini et al., 2011), which can explain the higher detectability earlier in the season. However, this relationship might change across life stages or based on other individual characters. For instance study on aggressive behavior showed a contrasting effect of phenology based on lizard color morph (Coladonato et al., 2020). The picture is further complicated by the interaction between date and temperature (fig. 2c and 2d). Many studies found a shift in body temperature of reptiles over the sampling season (Castilla, Van Damme, and Bauwens, 1999). However, interactions are often not considered in models with detection probability, either because including additional variables is data-demanding or because it produces model convergence issues. Additionally, through the usage of cosinor models, previous studies showed a strong effect of circadian rhythm on hematological variables and protein secretion in this species (Mangiacotti et al., 2019; Sacchi et al., 2020). Implementing cosinor models into N-mixture/occupancy models could be the focus of future research and can potentially improve the precision of estimates of the factors related to detection probability.

Humidity can significantly influence reptiles' activity because of physiological constraints or because it can be related to other biotic factors, such as prey availability (Sun et al., 2001; Bulova, 2002). For example, some species can prefer higher humidity to avoid the risk of dehydration (Daltry et al., 1998), while others might prefer lower humidity to optimize the heat gain (Sun et al., 2001; Spence-Bailey et al., 2010). Here we showed that adult common wall lizards are more detectable when humidity is low (fig. 2f). However, this relationship might change among sexes or with age (Sannolo, Barroso, and Carretero, 2018; Sannolo et al., 2020). For instance, smaller individuals might prefer higher humidity to avoid the risk of dehydration due to a higher surface/volume ratio (Sannolo, Barroso, and Carretero, 2018). Further studies are needed to assess if there is intraspecific variation in the factors driving detection probability. Moreover, the presence of a negative interaction between date and humidity suggested that the negative relationship between humidity and detection probability appears only in the late season (fig. 2e and 2f). A possible explanation is that the preference for low humidity values is overrun by the advantages of being more active during breedings in the early season.

Precipitation can be a key factor influencing the activity of ectotherms (Rozen-Rechels et al., 2019). Rainfall during the survey showed a negative relationship with detection probability (figs 1 and 2b), in agreement with the known ecology of the species (Avery, 1978). However, it has to be remarked that only three surveys (2.5% of total surveys) were performed during rains (supplementary appendix S1). Contrary to rainfall during the survey, a higher proportion of surveys (35%) showed precipitation in the previous 24 hours. Interestingly, cumulative precipitation in the 24 hours before the survey showed a positive relationship with detection probability (fig. 1). This suggests that after rainy days, the activity of this species is enhanced, perhaps to regain the time spent inactive or because invertebrate prey is more abundant after rains (Williams, 1951).

In this study, I assessed the effect of abiotic factors on the detection probability of the common wall lizard. Performing a large number of surveys at the same study site allowed me to identify temperature and phenology as the most influential drivers of detection probability, followed by precipitation and humidity. Knowing the factors that affect the probability of detecting an individual of a given species is of primary importance to avoid bias in population size and vital rates estimates (Kéry and Schaub, 2012). Since with a single site, it is not possible to estimate values of abundance and detection probability, future studies can apply this sampling method to multiple sites. Previous capture-mark-recapture studies showed that demographic parameters of the common wall lizard can vary widely at different sites (Gracceva et al., 2008). Performing counts at multiple sites would allow us to estimate population abundance and to evaluate how microhabitat or landscape characteristics can influence it.

Acknowledgements. I want to thank D. Delle Monache for the help in writing the model and for the discussion about statistical issues. I am grateful to Federica, Juno, and Zeus for help in planning and performing the fieldwork. The comment of two anonymous reviewers and the associate editor helped improve a first version of the manuscript.

Supplementary material. Supplementary material is available online at:
https://doi.org/10.6084/m9.figshare.14134997

References

Avery, R.A. (1978): Activity patterns, thermoregulation and food consumption in two sympatric lizard species (*Podarcis muralis* and *P. sicula*) from central Italy. J. Anim. Ecol. **47**: 143-158.

Biaggini, M., Bombi, P., Capula, M., Corti, C. (2011): *Podarcis muralis* (Laurenti, 1768). In: Reptilia. Fauna d'Italia, vol. XLV, p. 391-401. Corti, C., Capula, M., Luiselli, L., Razzetti, E., Sindaco, R., Eds, Calderini, Bologna, Italy.

Braña, F. (1991): Summer activity patterns and thermoregulation in the wall lizard, *Podarcis muralis*. Herpetol. J. **1**: 544-549.

Bulova, S.J. (2002): How temperature, humidity, and burrow selection affect evaporative water loss in desert tortoises. J. Therm. Biol. **27**: 175-189.

Castilla, A.M., Van Damme, R., Bauwens, D. (1999): Field body temperatures, mechanisms of thermoregulation and evolution of thermal characteristics in lacertid lizards. Nat. Croat. **8**: 253-274.

Coladonato, A.J., Mangiacotti, M., Scali, S., Zuffi, M.A.L., Pasquariello, C., Matellini, C., Buratti, S., Battaiola, M., Sacchi, R. (2020): Morph-specific seasonal variation of aggressive behaviour in a polymorphic lizard species. PeerJ **8**: 1-16.

Cunningham, H.R., Rissler, L.J., Buckley, L.B., Urban, M.C. (2016): Abiotic and biotic constraints across reptile and amphibian ranges. Ecography **39**: 1-8.

Daltry, J.C., Ross, T., Thorpe, R.S., Wüster, W. (1998): Evidence that humidity influences snake activity patterns: a field study of the Malayan pit viper *Calloselasma rhodostoma*. Ecography (Cop.). **21**: 25-34.

Ficetola, G.F., Barzaghi, B., Melotto, A., Muraro, M., Lunghi, E., Canedoli, C., Lo Parrino, E., Nanni, V., Silva-Rocha, I., Urso, A., Carretero, M.A., Salvi, D., Scali, S., Scarì, G., Pennati, R., Andreone, F., Manenti, R. (2018): N-mixture models reliably estimate the abundance of small vertebrates. Sci. Rep. **8**: 10357.

Ficetola, G.F., Fanell, M., Garizio, L., Falaschi, M., Tenan, S., Ghielmi, S., Laddaga, L., Menegon, M., Delfino, M. (2020): Estimating abundance and habitat suitability in a micro-endemic snake: the Walser viper. Acta Herpetol. **15**: 73-85.

Gracceva, G., Bombi, P., Luiselli, L., Bologna, M.A. (2008): Do demographic aspects of neighbouring lizard populations differ? A case study with the common wall lizard, Podarcis muralis. Amphib. Reptil. **29**: 443-448.

Kellner, K.F., Swihart, R.K. (2014): Accounting for imperfect detection in ecology: a quantitative review. PLoS One **9**: e111436.

Kéry, M., Schaub, M. (2012): Bayesian Population Analysis Using WinBUGS: a Hierarchical Perspective. Academic Press.

MacKenzie, D.I., Nichols, J.D., Hines, J.E., Knutson, M.G., Franklin, A.B. (2003): Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. Ecology **84**: 2200-2207.

Manenti, R., Falaschi, M., Monache, D.D., Marta, S., Ficetola, G.F. (2020): Network-scale effects of invasive species on spatially-structured amphibian populations. Ecography **43**: 119-127.

Mangiacotti, M., Pezzi, S., Fumagalli, M., Coladonato, A.J., D'Ettorre, P., Leroy, C., Bonnet, X., Zuffi, M.A.L., Scali, S., Sacchi, R. (2019): Seasonal variations in femoral gland secretions reveals some unexpected correlations between protein and lipid components in a lacertid lizard. J. Chem. Ecol. **45**: 673-683.

Mazerolle, M.J., Bailey, L.L., Kendall, W.L., Royle, J.A., Converse, S.J., Nichols, J.D. (2007): Making great leaps forward: accounting for detectability in herpetological field studies. J. Herpetol. **41**: 672-689.

Pérez i de Lanuza, G., Carretero, M.A. (2018): Partial divergence in microhabitat use suggests environmental-dependent selection on a colour polymorphic lizard. Behav. Ecol. Sociobiol. **72**: 138.

R Core Team (2018): R: a Language and Environment for Statistical Computing. R Found. Stat. Comput., Vienna, Austria.

Royle, J.A. (2004): N-mixture models for estimating population size from spatially replicated counts. Biometrics **60**: 108-115.

Rozen-Rechels, D., Dupoué, A., Lourdais, O., Chamaillé-Jammes, S., Meylan, S., Clobert, J., Le Galliard, J.F. (2019): When water interacts with temperature: ecological and evolutionary implications of thermo-hydroregulation in terrestrial ectotherms. Ecol. Evol. **9**: 10029-10043.

Sacchi, R., Mangiacotti, M., Scali, S., Coladonato, A.J., Pitoni, S., Falaschi, M., Zuffi, M.A.L. (2020): Statistical methodology for the evaluation of leukocyte data in wild reptile populations: a case study with the common wall lizard (*Podarcis muralis*). PLoS One **15**: e0237992.

Sannolo, M., Barroso, F.M., Carretero, M.A. (2018): Physiological differences in preferred temperatures and evaporative water loss rates in two sympatric lacertid species. Zoology **126**: 58-64.

Sannolo, M., Civantos, E., Martín, J., Carretero, M.A. (2020): Variation in field body temperature and total evaporative water loss along an environmental gradient in a diurnal ectotherm. J. Zool. **310**: 221-231.

Scali, S., Sacchi, R., Falaschi, M., Coladonato, A.J., Pozzi, S., Zuffi, M.A.L., Mangiacotti, M. (2019): Mirrored images but not silicone models trigger aggressive responses in male common wall lizards. Acta Herpetol. **14**: 35-41.

Scali, S., Sacchi, R., Mangiacotti, M., Pupin, F., Gentilli, A., Zucchi, C., Sannolo, M., Pavesi, M., Zuffi, M.A.L. (2016): Does a polymorphic species have a 'polymorphic' diet? A case study from a lacertid lizard. Biol. J. Linn. Soc. **117**: 492-502.

Sillero, N., Campos, J., Bonardi, A., Corti, C., Creemers, R., Crochet, P.A., Isailović, J.C., Denoël, M., Ficetola, G.F., Gonçalves, J., Kuzmin, S., Lymberakis, P., De Pous, P., Rodríguez, A., Sindaco, R., Speybroeck, J., Toxopeus, B., Vieites, D.R., Vences, M. (2014): Updated distribution and biogeography of amphibians and reptiles of Europe. Amphibia-Reptilia **35**: 1-31.

Sokal, R.R., Rohlf, F.J. (2012): Biometry: the Principles and Practices of Statistics in Biological Research, 4th Edition. W.H. Freeman and Company, New York, USA.

Spence-Bailey, L.M., Nimmo, D.G., Kelly, L.T., Bennett, A.F., Clarke, M.F. (2010): Maximising trapping efficiency in reptile surveys: the role of seasonality, weather conditions and moon phase on capture success. Wildl. Res. **37**: 104-115.

Su, Y.-S., Yajima, M. (2015): R2jags: using R to Run 'JAGS'. R package version 0.5-7.

Sun, L.X., Shine, R., Debi, Z., Zhengren, T. (2001): Biotic and abiotic influences on activity patterns of insular pit-vipers (*Gloydius shedaoensis*, Viperidae) from north-eastern China. Biol. Conserv. **97**: 387-398.

Williams, C.B. (1951): Changes in insect populations in the field in relation to preceding weather conditions. Proc. R. Soc. B Biol. Sci. **138**: 130-156.

Zamora-Camacho, F.J., Reguera, S., Moreno-Rueda, G., Pleguezuelos, J.M. (2013): Patterns of seasonal activity in a Mediterranean lizard along a 2200 m altitudinal gradient. J. Therm. Biol. **38**: 64-69.

Submitted: November 20, 2020. Final revision received: February 19, 2021. Accepted: February 20, 2021.
Associate Editor: Miguel A. Carretero.