How effectively do European skinks thermoregulate? Evidence from *Chalcides ocellatus*, a common but overlooked Mediterranean lizard

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Abstract. Effective thermoregulation is of vital importance since body temperature affects virtually all physiological and biochemical processes. Yet, our current knowledge in reptilian thermoregulation is largely based on a few, well-studied taxonomic groups. This is especially true in Europe, where our insights derive primarily from studies on the numerous lacertids of the continent. Skinks on the other hand remain understudied despite being abundant around the Mediterranean. In this paper we examine the thermoregulation effectiveness of the Ocellated Skink, a common lizard whose thermal biology has been overlooked, focusing on a population from a typical Mediterranean habitat in mainland Greece. We recorded body temperatures in the field and the lab and assessed the thermal quality of the habitat through operative temperatures. Our findings suggest that *Chalcides ocellatus* is a poor thermoregulator that stands very close to thermoconformity. The high thermal quality of the habitat allows the Ocellated Skink to regulate its temperature with less effort and lower accuracy. This indicates that *C. ocellatus* may have adopted a distinct thermoregulation strategy, most probably due to the particular life style of skinks.

Keywords. Lizard, Scincidae, temperature, habitat quality, thermal biology, Greece.

INTRODUCTION

The regulation of body temperature is arguably one of the most vital processes in reptilian life since most physiological and biochemical processes are temperature-dependent (Angilletta et al., 2002; Angilletta, 2009). Unlike endotherms, reptiles do not rely on metabolism for thermoregulation but utilise their thermal environment instead: most species shuttle constantly within various microhabitats in search of favourable temperatures, while others move slowly between microhabitats and perform within a wide range of body temperatures (Pough and Gans, 1982; Stevenson, 1985).

The question of "how effectively does a lizard thermoregulate?" preoccupies herpetological research for decades (e.g., Baldwin, 1925; Sagonas et al., 2017). Limi-

tations in assessing reptilian thermoregulation were described in detail by Hertz et al. (1993), who proposed an index of effectiveness using three variables: field body temperatures (T_b), i.e., temperatures that lizards achieve in the field, operative temperatures (T_e), i.e., temperatures that non-regulating animals would achieve in the field, and preferred temperatures (T_{pref}), i.e., the temperature (or range of temperatures, the set-point range T_{set}) that animals select in the lab in an unconstrained thermal experimental setting. This approach, taken together with more recent modifications (e.g., Blouin-Demers and Weatherhead, 2001) is widely accepted as the most accurate and exhaustive methodology and has been applied in numerous lizard species.

In Europe, lacertids comprise the largest lizard group (Arnold and Ovenden, 2002; Uetz, 2017) and studies on

their thermoregulation have been on the front line for the past 30 years, yielding valuable insights. Case studies that include viviparous (Van Damme et al., 1986; Gvoždík and Castilla, 2001) or oviparous species (Díaz et al., 2005; Sagonas et al., 2013a), gravid or non-gravid females (Braña, 1993; Veríssimo and Carretero, 2009), populations that live on tiny islets (Ortega et al., 2014; Pafilis et al., 2016) or in alpine habitats (Monasterio et al., 2009; Ortega et al., 2016) describe in detail various alternative thermoregulatory patterns. However, in a striking contrast, all the other European lizard families remain largely understudied in terms of their thermal biology, and this applies to Scincidae as well. The reason for this discrepancy should be sought primarily in the number of species: of the more than 1600 skinks currently described, only eight species occur in Europe (Uetz, 2017). Additionally, the cryptic lifestyle of skinks and their low population densities limit thermoregulatory studies even more. As a result, only a handful of papers provide some, mostly descriptive, data on European skinks' temperatures (Al-Sadoon and Spellerberg, 1985; Hailey et al., 1987; Daut and Andrews, 1993; Herczeg et al., 2007) and, to the best of our knowledge, there are no works investigating their thermoregulation effectiveness *sensu* Hertz et al. (1993).

In this study we examine for the first time the thermoregulation of a European skink, the Ocellated Skink (*Chalcides ocellatus*), the species with the widest range within the genus (Schneider, 1997; Lymberakis et al., 2009). Taking into account that the species' biology deviates in many ways from that of the lacertids (e.g., mainly fossorial life style with limited climbing abilities, viviparity) it would be presumable that its thermal physiology would also differ. Our aim was on the one hand to provide the first systematically collected field and lab thermal data for a European skink, filling a knowledge gap on the ecophysiology of a common but understudied lizard group, and on the other hand to quantitatively assess the species' thermoregulatory effectiveness (Hertz et al., 1993; Blouin-Demers and Weatherhead, 2001).

MATERIAL AND METHODS

Study system

Chalcides ocellatus (Forskål, 1775) (Squamata, Scincidae) is a common viviparous skink of the Mediterranean. Though its distribution is wide, including large parts of Africa and southwestern Asia, in Europe it occurs mainly on Mediterranean islands such as Sardinia, Sicily and Malta and their surrounding islets (Schneider, 1997). Its distribution in Greece comprises a few disconnected areas in the mainland and many islands (e.g., Crete, Rhodes, Karpathos, Chios) (Valakos et al., 2008). Inter-

estingly, new records come to enhance the insular range of the species (Belasen et al., 2012; Itescu et al., 2016), most probably due to human transportation (Kornilios et al., 2010). *Chalcides ocellatus* is a fairly robust lizard, with a cylindrical body, a thick tail, short limbs, a relatively small head and a snout to vent length (SVL) of up to 15 cm. It inhabits a variety of habitats including shrublands, sandy areas and farmlands and mainly feeds on Coleoptera, Formicidae, various larvae and snails (Valakos et al., 2008; Carretero et al., 2010). It is active during the day, but usually hides underneath rocks or buries itself in the sand (Al-Sadoon and Spellerberg, 1985; Valakos et al., 2008).

On 23 April 2016, field work was conducted on the campus of the National and Kapodistrian University of Athens in Greece (37°58'01"N, 23°47'20"E). Located at the foothills of Mount Hymettus, the study site consists of an extensive area of maquis vegetation dominated by kermes oak (*Quercus coccifera*), Aleppo pine (*Pinus halepensis*), gum tree (*Eucalyptus* sp.) and green olive tree (*Phillyrea latifolia*), as well as patches of open grassland and phrygana. The terrain is fairly rough and rocky, providing ideal hiding spots for the skinks. Apart from *C. ocellatus*, two more lizards are present on the site, the Balkan green lizard (*Lacerta trilineata*) and the European snake-eyed skink (*Ablepharus kitaibelii*).

Adult male lizards were captured by hand after overturning stones, rocks and tree trunks, and were subsequently taken to the facilities of the Faculty of Biology at the National and Kapodistrian University of Athens. Female lizards were not used in the experiment to avoid possible effects of gravidity on thermoregulation (Daut and Andrews, 1993; Corso et al., 2000; Carretero et al., 2005). The captured lizards were housed for one week in individual glass terraria (80 × 30 × 40 cm) with a sand substrate before the experiment started. Stones and bricks were placed on the substrate to serve as hiding spots. Access to water was provided *ad libitum* and mealworms (*Tenebrio molitor*) were fed to the lizards every other day. The lizards were held at 25°C under a controlled photoperiod (12L:12D). A 60 W incandescent lamp over each terrarium allowed the animals to thermoregulate for 8 hours per day. The animals were released back to the study site after the end of the experiment.

Field temperatures (T_b and T_e)

We measured the body temperature of 14 males in the field. T_bs were measured to the nearest 0.1 °C, using a quick-reading cloacal thermometer (T-4000, Miller & Weber Inc., Queens, NY) within 10 sec after capture (Veríssimo and Carretero, 2009; Osojnik et al., 2013). Air temperature (T_{air}) at the capture point of each individual was also recorded. The relatively small sample size reflects the sparse population density of *C. ocellatus* on the site and its cryptic lifestyle.

We recorded operative temperatures using 28 hollow copper models that approximated the size and reflectance of *C. ocellatus* (Bakken, 1992; Dzialowski, 2005). The models were closed at both ends and filled with 2.5-3 ml of water in order to replicate the heat storage capacity of the lizards (Grbac and Bauwens, 2001; Lutterschmidt and Reinert, 2012). At one end of the models a narrow slot was left open where the log-

ger probes (HOBO U12-008 4-Channel External Data Logger) were plugged in (Díaz, 1997). The models were placed to cover as many of the microhabitat types available to lizards as possible (Huey, 1991), which in this case were grouped in four different microhabitats: open ground, on relatively flat medium-sized rocks (Vasconcelos et al., 2012), inside shrubs and underneath rocks. Operative temperatures were recorded at 30 min intervals from 10:30 to 17:30 on the same day that field body temperatures (T_b) were measured.

To ensure the similarity of the temperature responses between models and lizards (Hertz, 1992), we performed a laboratory experiment comparing their heating rates, before placing the models in the field (Lutterschmidt and Reinert, 2012). A lizard and a model were placed side-by-side under a 150 W lamp. We then measured their temperature every 5 min for a 45 min period. A linear regression of T_b on T_e (slope = 0.84 ± 0.14, intercept = 4.68 ± 4.59, R^2 = 0.83, n = 10) suggests that the copper model temperature is a significant predictor of the animal body temperature ($F_{1,8}$ = 38.04, P = 0.0003).

Lab measurements (T_{pref} and T_{set})

We measured the preferred temperature and set-point range of 12 males in a specially designed terrarium (100 × 25 × 25 cm) that had two ice bags at one end and a 150 Watt heating lamp at the other end, thus providing a thermal gradient ranging from 15 to 50 °C (Van Damme et al., 1986). Prior to the experiment, the SVL of each individual was recorded using a digital caliper (Silverline 380244, accurate to 0.01 mm). Each lizard was then allowed to acclimate inside the thermal gradient for 60 min prior to the actual measurements (Sagonas et al., 2013a) and subsequently its body temperature was recorded every 30 min for an 180 min period (Hertz et al., 1993). The measurements took place from 09:00 to 13:00, which coincides with the animal's activity period based on our observations in the field. We calculated T_{pref} for each individual as the mean of the body temperatures that the individual selected in the thermal gradient and then calculated the population T_{pref} as the mean of individual T_{pref}s.

We estimated T_{set} for each individual by using the lower and upper bounds of the central 50% of values (1st and 3rd quartile respectively) of the body temperatures that each individual selected in the thermal gradient. The T_{set} for the population was subsequently calculated as the mean lower and mean upper bound of individual T_{set}s (Hertz et al., 1993; Christian and Weavers, 1996).

Effectiveness of thermoregulation

The effectiveness of thermoregulation was assessed with the formula proposed by Hertz et al. (1993), $E = 1 – (\overline{d_b}/\overline{d_e})$, where $\overline{d_b}$ is the mean deviation of field T_b from T_{set} and denotes the accuracy of thermoregulation and $\overline{d_e}$ is the mean deviation of T_e from T_{set} and describes the thermal quality of the habitat. The values of E range from zero (perfect thermoconformers) to one (perfect thermoregulators) (Hertz et al., 1993).

E has some limitations though: being a ratio, the index is sensitive to extreme values and, additionally, different $\overline{d_b}$ and $\overline{d_e}$ combinations may yield equivalent estimates of thermoregulation effectiveness (Christian and Weavers, 1996; Blouin-Demers and Weatherhead, 2001). Thus, we implemented a complementary method proposed by Blouin-Demers and Weatherhead (2001) to quantify the extent of departure from perfect thermoconformity $(\overline{d_e} – \overline{d_b})$. In this approach, a value of zero indicates a perfect thermoconformer, positive values describe a thermoregulator, whereas negative values denote animals that actively avoid habitats of high thermal quality. The magnitude of the difference between $\overline{d_b}$ and $\overline{d_e}$ provides an index of the effectiveness of thermoregulation (Blouin-Demers and Weatherhead, 2001).

Statistics

The Shapiro-Wilk test was used to test for normality. The non-parametric Kruskal-Wallis rank sum test was used to test T_e differences between microhabitats, since the assumption of normality was violated (P < 0.05). The relationship between T_b and T_{air} was assessed using linear regression. 95% confidence intervals for E were determined using bootstrap resampling: 1000 values of E were computed using random sampling with replacement from the observed T_b and T_e distributions and subsequently the 2.5th and 97.5th percentiles were used as confidence interval limits (percentile method, Hertz et al., 1993). The same procedure was also applied to the index $\overline{d_e} – \overline{d_b}$ (Blouin-Demers and Weatherhead, 2001). All tests were performed in R 3.3.2 (R Core Team, 2016).

RESULTS

The mean preferred temperature was 31.8°C, ranging from 27.9 to 34.6 °C (Table 1). Set-point range was estimated at 30.4 to 33.6 °C. The mean field body temperature was 27.2°C, ranging from 23.1 to 30.6 °C (Table 1). $\overline{d_b}$ and $\overline{d_e}$ were 3.2 and 4.6 °C respectively (Table 1).

The placement of the lizard models in the field covered successfully the thermal diversity of the habitat, as revealed by the T_es (Table 2) recorded across different microhabitat types (Kruskal-Wallis rank sum test, χ^2 = 39.229, df = 3, P < 10^{-6}). The mean operative temperature was 30.1 °C, ranging from 18.2 °C at 11:00 (lowest T_e) to 57.0 °C at 15:30 (highest T_e) (Table 1).

Field body temperature (T_b) was positively correlated with air temperature (T_{air}) at the point of capture (Pearson's r = 0.709) and the linear model that describes the relationship between the two variables had a strong fit (T_b = 1.04 * T_{air} + 2.6, R^2 = 0.502, $F_{(1,12)}$ = 12.1, P = 0.0046, Fig. 1). The effectiveness of thermoregulation *sensu* Hertz et al. (1993) was estimated as E = 0.31 (bootstraped mean: 0.31, 95% confidence intervals: 0.03-0.56, n = 1000). Thermoregulation effectiveness *sensu* Blouin-

Table 1. Variables used in this paper for the study of thermoregulation. T_b: field body temperatures, T_e: operative temperatures, T_{pref}: preferred temperatures, d_b: deviation of T_b from T_{set}, d_e: deviation of T_e from T_{set}.

Variable	n	Mean	Range	SD	SE
T_b	14	27.23	23.10-30.60	2.41	0.64
T_e	28	30.05	18.22-56.98	7.24	0.35
T_{pref}	12	31.83	27.93-34.58	2.03	0.59
d_b	14	3.19	0-7.30	2.39	0.64
d_e	28	4.62	0-23.41	4.21	0.21

Table 2. Operative temperatures (T_e) across microhabitat types within the study site.

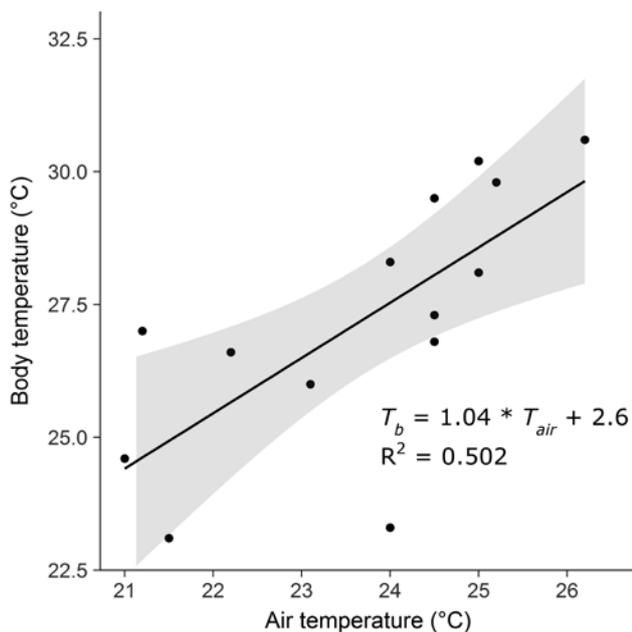| Microhabitat	n	Mean	Range	SD	SE
Open ground	6	33.18	21.82-56.98	9.23	0.97
Rock surface	9	31.18	19.39-44.38	6.27	0.54
Inside shrubs	9	28.14	20.48-53	6.33	0.54
Under rocks	4	27.06	18.22-36.47	5.29	0.68

Fig. 1. Linear regression of field body temperature (T_b) on air temperature (T_{air}). Shaded area denotes 95% confidence intervals.

$$T_b = 1.04 * T_{air} + 2.6$$
$$R^2 = 0.502$$

Demers and Weatherhead (2001) was evaluated at 1.44 (bootstraped mean: 1.44, 95% confidence intervals: 0.21-2.72, n = 1000).
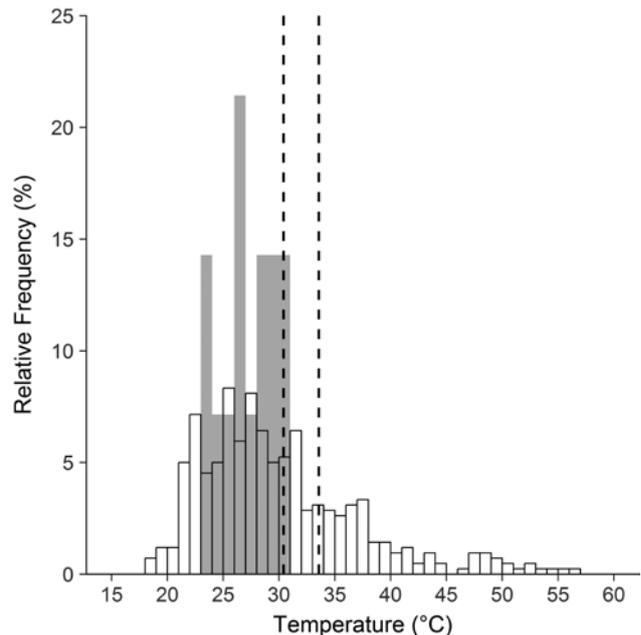

Fig. 2. Relative frequency of field body temperatures (T_b, grey shade), operative temperatures (T_e, solid line) and set-point range (T_{set}, dotted lines) for the Ocellated Skink.

DISCUSSION

In this study we assessed for the first time the thermoregulatory profile of a European skink. We recorded body temperatures in the field and the lab and, taking into account the thermal availability of the environment (T_e), we estimated the accuracy, precision and effectiveness of thermoregulation. Only a few descriptive studies have dealt with aspects of the thermal biology of *C. ocellatus*: to the best of our knowledge this is the first time that thermoregulation effectiveness (Hertz et al., 1993) was assessed for this species. Because of the scarcity of thermal data for *C. ocellatus* from Europe, we also compare our findings with conspecific populations outside Europe and with other European *Chalcides* as well.

Body temperatures in the field reached a mean value of 27.2 °C (Table 1). Lo Cascio and Corti (2008) reported similar T_bs from an insular population in Italy in the springtime (Lampedusa Island: 26.9 ± 1.7 °C), with T_bs rising higher in the summer (Lampedusa Island: 32.0 ± 0.6 °C, Isola dei Conigli: 31.3 ± 1.2 °C). The congeneric *Chalcides bedriagai* from Spain achieved higher T_bs and a wider range (mean T_b = 30.5 °C, range = 25-35 °C; Hailey et al., 1987). Since there are no other T_b measurements for *C. ocellatus*, it is hard to estimate the nature of these results. However, the diel variation of T_bs was limited, a finding that suggests high precision in thermoregulation.

Preferred temperatures were higher than T_bs and achieved a mean value of 31.8 °C (Table 1). Interestingly, T_{pref} had a wider range of variation compared to lacertids. Nonetheless, the T_{pref}s of the Greek population were lower than the values reported from Egyptian populations. Al-Sadoon (1986) measured a mean T_{pref} of 34°C, similarly to Pough and Andrews (1985) who found a mean T_{pref} of 34.4 °C. Also, the range of T_{pref} has been reported to vary from 28 to 37 °C (Al-Sadoon and Spellerberg, 1985). These deviations in T_{pref} between the European and African populations could be attributed to environmental conditions. Preferred temperatures depend on the particular conditions of the habitat (Scheers and Van Damme, 2002; Pafilis et al., 2016). Populations from warmer habitats are known to achieve higher T_{pref} (Sagonas et al., 2013b), though thermal optima have been also reported to show resilience despite environmental divergence in temperature (Osojnik et al., 2013; Clusella-Trullas and Chown, 2014). We believe that the lower T_{pref} of the Ocellated Skink in Greece is due to the temperate, cooler climate of the north Mediterranean costs. Nonetheless, we cannot rule out that methodological differences (e.g. sex, size class, time, season) with the above-mentioned papers might be responsible for the observed deviations.

Operative temperatures ranged within a broad thermal window, varying from 18.2 to 57.0 °C (Table 1). This wide range indicates high thermal heterogeneity, in other words a diverse thermal mosaic where lizards can shuttle between different microhabitats (Table 2). The mean T_e was 30.1 °C, which lies within the values that have been reported from other Greek habitats (Adamopoulou and Valakos, 2005; Sagonas et al., 2013 a, b; Kapsalas et al., 2016; Pafilis et al. 2016; Belasen et al., 2017; Sagonas et al., 2017). Based on these operative temperatures, the thermal quality index (*sensu* Hertz et al., 1993) received a low value ($\overline{d_e}$ = 4.6), which is actually among the lowest ever reported in the north Mediterranean (see Table 1 at Pafilis et al., 2016). The low $\overline{d_e}$ indicates a habitat of high quality (Hertz et al., 1993) that provides many thermal opportunities for successful thermoregulation.

Contrary to the low $\overline{d_e}$, $\overline{d_b}$ received a value of 3.2, which is rather medial according to Hertz et al., (1993). Low $\overline{d_b}$ implies high accuracy, since most of the observed field body temperatures fall within the animal's preferred temperature range. In the case of the Ocellated Skink, T_bs fell outside the set-point range in 93% of the cases (all of which were below T_{set}) (Fig. 2), resulting in the observed $\overline{d_b}$. This value suggests low accuracy in thermoregulation. However, we have to stress out the relativity of the latter notion. The lack of thermoregulatory studies on European skinks or within the genus *Chalcides*, precludes us

from understanding the magnitude of the observed $\overline{d_b}$ value. For instance, a $\overline{d_b}$ of 3.2 is rather high for lacertids (Díaz et al., 2006; Monasterio et al., 2009; Ortega et al., 2016; Sagonas et al., 2017) but not particularly high for certain anoles (Hertz et al., 1993, Woolrich-Pina et al 2015), monitor lizards (Christian and Weavers, 1996) or geckos (Rock et al., 2002, Hitchcock and McBrayer, 2006).

The wide spectrum of operative temperatures and the low $\overline{d_e}$ sketch out a rather benign thermal habitat. This fact is reflected in the low index of thermoregulation (E = 0.31). According to theory, E values close to zero stand for animals that do not thermoregulate actively whereas values close to one describe animals that thermoregulate carefully (Hertz et al., 1993). *Chalcides ocellatus* appears to be a poor thermoregulator, at least during this given period of the year. This finding is further supported by the alternative approach proposed by Blouin-Demers and Weatherhead (2001). Although their index ($\overline{d_e} - \overline{d_b}$) does not take values within a specific range (contrary to E, Hertz et al., 1993), the value reported here (1.44) points to a poor thermoregulator as well. Low thermoregulatory effectiveness might be the norm for *Chalcides* lizards. Hailey et al. (1987) categorized the congeneric *Chalcides bedriagai* as a thermoconformer, interpreting the high correlation between field body temperatures and substrate temperatures. This finding is in agreement with the observed thermoregulatory behaviour of the Ocellated Skink in our study, as seen both by the correlation of the Ocellated Skink's T_b with air temperature, as well as by the values of E and $\overline{d_e} - \overline{d_b}$.

According to our results, the focal population lives in a habitat of high thermal quality and heterogeneity. Thermally challenging habitats dictate high thermoregulatory effectiveness to guarantee survival under extreme conditions (Hertz et al., 1993; Ortega et al., 2016; Pafilis et al., 2016). This is not the case for *C. ocellatus*, which thanks to the aforementioned favourable habitat, can afford a less effective thermoregulation. Its thermoregulation is also characterized by high precision and low accuracy. Further studies that would include more species and populations and different seasons are required to thoroughly understand the thermal biology of European skinks. Thermoregulation may vary with season (Huey and Pianka, 1977; Hertz et al., 1993; Díaz and Cabezas-Díaz, 2004), altitude (Spencer and Grimmond, 1994; Zamora-Camacho et al., 2016), insularity (Sagonas et al., 2013b) and body size (Sagonas et al., 2013a). It may also change according to organism needs depending on internal factors (e.g. pregnancy, body condition and water loss rate) (Carretero et al., 2005). Thus, the species' thermoregulation strategy on Mediterranean islands, in high-

er altitudes, in different latitudes or even at our study site during different seasons, may deviate from the present results.

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