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Do the thermal and hydric physiologies of *Zootoca* (*vivipara*) *carniolica* (Squamata: Lacertidae) reflect the conditions of its selected microhabitat?

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Organisms possess a set of physiological traits that define the limits of their fundamental niche (Kearney et al. 2013). In lizards, one of the most important ecophysiological traits is the preferred body temperature (Tp) (Huey 1982). Values in the range of a species' Tp are recorded while a lizard is allowed to thermoregulate without potentially restrictive factors like predation, social interactions, foraging, etc. (e.g., Huey 1982). Tp directly correlates with lizards' maximum performance like sprint speed, prey manipulation, or speed of energy assimilation through metabolism (van Damme et al. 1991, Angilletta 2001, Angilletta et al. 2002), which impact on a whole array of a lizard's vital activities and processes (e.g., Carretero et al. 2005, Husak et al. 2006, Sacchi et al. 2014) and thus affect individual fitness. When lizards bask, they will at the same time be exposed to cutaneous water loss (Shoemaker & Nagy 1977, Mautz 1982) and respiratory and/or ocular water loss (Mautz 1982). Together with the thermal traits, the rate of water loss adds another aspect to the lizard's ecophysiological fundamental niche (Osojnik et al. 2013, Caldwell et al. 2015). However, the hydric physiology of lizards has been studied to a lesser extent than thermoregulation and has received more attention only recently (e.g., Gunderson et al. 2011, Osojnik et al. 2013, Kolbe et al. 2014, Caldwell et al. 2015, Carneiro et al. 2015, Rato & Carretero 2015).

The common lizard, *Zootoca vivipara* (Lichtenstein, 1823), is the representative of the family Lacertidae (Squamata) with the widest distribution of a member of this family, extending from the northern Iberian Peninsula in the south and west to northwestern Japan in the east and beyond the Arctic circle in the north (Sillero et al. 2014). Although the species has been intensively studied, remarkably, almost no studies have been conducted on populations in the southeastern parts of its range in Europe, i.e., the Balkan Peninsula. Populations in the north of the Balkan Peninsula were ascribed to the (sub)species *Zootoca* (*v.*) *carniolica* (Mayer, Böhme, Tiedemann & Bischoff 2000), which has conserved oviparity (Heulin et al. 2000, Heulin et al. 2002, Surget-Groba et al. 2006) as a plesiomorphic character and belongs to a separate phylogenetic clade (Surget-Groba et al. 2002, Arribas 2009). *Zootoca* (*v.*) *carniolica* exhibits sexual dimorphism (Guillaume et al. 2006). While the thermal and water ecology have been analysed in *Z.* (*v.*) *vivipara* long ago (e.g., van Damme et al. 1986, van Damme et al. 1990, 1991, Gvoždik & Castilla 2001, Carretero et al. 2005), we are not aware of any such studies on populations of *Z.* (*v.*) *carniolica*. Extrapolation of results from viviparous populations could not possibly be straightforward, not only because of the considerable phylogenetic separation of this lineage from *Z. vivipara* sensu lato (Surget-Groba et al. 2002), but also because complete reproductive isolation was found in a contact zone between both forms in northern Italy, advocating a full specific status for *Z.* (*v.*) *carniolica* (Cornetti et al. 2015). These facts provide a need for ecophysiological, ecological, behavioural, and other life-history trait-related data separately for these populations.

In this paper we assess two widely used ecophysiological traits, preferred body temperature (Tp) and water loss rate (EWL) for the first time for *Z.* (*v.*) *carniolica*. Our aims were to analyse intrapopulation (sexual) variations in Tp and EWL rates. Secondly, we investigated if the species' ecophysiology parallels its climatic microhabitat conditions. To this end, we describe the thermal and hydric properties of the species' typical microhabitat in the northern Dinaric Mountains (S Slovenia). Thirdly, we compare ecophysiological traits of *Z.* (*v.*) *carniolica* to two sympatric saxicolous lizards in the area (Žagar et al. 2013): *Iberolacerta horvathi* (Méhely 1904) and *Podarcis muralis* (Laurenti 1768) by adopting Tp and EWL data from Osojnik et al. (2013).

All individuals of *Z.* (*v.*) *carniolica* used in experiments were collected in the second half of July 2014. They were captured in the Kočevsko region, SE Slovenia (45°28'37" N, 14°48'34" E), which is characterized by high forest cover (Puncer 1980) and a mosaic of natural areas and man-made open spaces and offers habitats suitable for reptiles (Žagar et al. 2013). The climate here is temperate continental with an Alpine climate trend at higher altitudes (Kordiš 1993). Captured individuals were placed in a transport box and quickly taken to housing facilities. Females were checked for possible gravidity by assessing belly size, signs of copulation marks, and palpating for eggs around the belly region (Arnold & Ovenden 2004). Snout–vent lengths (SVL) were measured to the nearest 0.01 mm after the experiments using a digital calliper. Prior to conducting experiments, the lizards were kept individually in terraria and provided with food (*Tenebrio molitor* larvae) and water ad libitum under a natural regime of light at temperatures that would allow active thermoregulatory behaviour for a maximum of three days. Each lizard was first used in our thermal gradient experiment, then granted a 2–4 day break, and then used again for our EWL experiment. The lizards were fed during the break save for the day prior to the EWL experiments. They were sexed by assessing their colour patterns, the cloacal region, and the presence/absence of femoral pores (Arnold & Ovenden 2004). Experimental procedures followed standardised protocols for Tp and EWL (García-Muñoz & Carretero 2013, Osojnik et al. 2013) and were conducted using the same terraria and facilities as in the study of Osojnik et al. (2013). Both our Tp and EWL experiments were conducted during 11 consecutive hours from 8:00 through 19:00 h CET, which is the period of diel activity of this species (Salvador et al. 2014). Every hour, the individual boxes containing the lizards were removed from the chamber, weighed with the box for 12 consecutive times with a digital scale (precision 0.0001 g) and placed back in the chamber. Each measuring procedure did not take longer than 20 seconds. All lizards were released at the capture site after our experiments had been concluded. Following Osojnik et al. (2013), we calculated the accumulative water loss (EWl_a) per hour (from 8:00 to 18:00 h CET) of the experiment applying the formula $EWl_a = (W_0 - W_n)/W_0 \times 100$, and the instantaneous EWL (EWl_i) from the formula $Wl_i = ((W_n - W_{n+1})/W_0) \times 100$ (see Osojnik et al. 2013 for details).

To evaluate the thermal and humidity characteristics of the typical microhabitat used by *Z.* (*v.*) *carniolica* in the study area we placed data-loggers (Thermochron iButton DS1922L, Embedded Data Systems, KY, USA) on ground with a cover of herbaceous vegetation in three locations during August 2013. These devices record temperature in predefined intervals with an accuracy of ± 0.5°C from -10 to +65°C. The data-loggers used were of similar height as adults of the studied species and therefore collected temperatures from a similar level above the surface where individual lizards would be. The data-loggers were programmed to record temperature and humidity values once every 20 minutes and left in place for 30 consecutive days. We used only measurements of five days with clear sky and without wind, between 8:00 and 18:00 h, corresponding to the daily activity period of the species observed in the field (Salvador et al. 2014). We calculated the mean values of three data-loggers for each sampling interval (20 min) to obtain daily temperature and relative humidity fluctuations. Secondly, we used the mean hourly temperature measurements from data loggers to calculate the thermal quality index of the microhabitat using the formula by Hertz et al. (1993):

$$\delta ls = \frac{|Tm - Tp|}{Tm + Tp} ,$$

where Tm is the temperature of the microhabitat and Tp the preferred temperature of a given species.

Intraspecific (between sexes) differences in SVL and initial weights (W_0) were tested through a one-way ANOVA with 'sex' as a factor. The distribution of Tp and EWL_i values at each hour did not deviate from normality (Shapiro–Wilk's test, $P < 0.05$ in all cases), were homoscedastic (univariate Levene's tests and multivariate Box M, $P < 0.05$ in all cases), and the variances and means were also uncorrelated; hence, we did not transform the values before analysis. Since measurements were repeated for the same individual for each hourly interval, our statistical analysis was based on an Analysis of Variance for Repeated Measures (ANCOVA-rm) of Tp with 'sex' as a between-subjects factor, 'time interval' as a within-subject factor, and 'SVL' as the continuous predictor to account for size differences (Carretero et al. 2005). Instantaneous water loss rates (EWl_i) were also subjected to ANCOVA-rm, using 'sex' as between-subjects factors, 'time interval' as the within-subject factor, and 'SVL' as the continuous predictor. For the three-species comparison, we focused our comparison on males. We adopted the hourly measurements of Tp and EWL_a for males in summer from the study of Osojnik et al. (2013) to investigate interspecific variation in Tp. We performed statistical analysis of ANCOVA-rm with 'species' as a between-subjects factor, 'time interval' as a within-subject factor, and 'SVL' as the continuous predictor. As for comparisons of accumulative water loss rates (EWl_a) after each hour of the experiment, we ran 11 one-way ANOVA analyses using 'species' as factors. Subsequently, P-values were adjusted for multiple tests using a false discovery rate (FDR) procedure (Benjamini & Hochberg 1995). All analyses were conducted in Statistica 12 software (Statsoft, 2013), except FDR, which was run in R software (R Development Core Team).

Females (N = 9) exhibited a longer SVL than males (N = 11) (one-way ANOVA, sex: $F_{1,18} = 8.56$, $P = 0.009$). However, females were lighter than males of the same SVL (one-way ANOVA, 'SVL' as the continuous predictor, factor 'sex': $F_{1,17} = 6.11$, $P = 0.024$). We obtained preferred body temperatures (Tp) for males, gravid females, and non-

Table 1. Results of ANCOVA analyses of the repeated measurements for preferred body temperatures (Tp) (left) and instantaneous water loss (EWl_i) (right) for *Zootoca* (*vivipara*) *carniolica* males and females using 'sex' as between-subjects factors, 'time interval' as within-subject factor, and 'snout–vent length (SVL)' as covariate. Significant results are printed in bold.

	Tp			EWl_i		
	F	df	P	F	df	P
Sex	11.79	13	< 0.01	0.80	8	0.40
Time	0.86	117	0.56	0.36	72	0.95
Time × Sex	0.63	117	0.77	0.54	72	0.84

gravid (post-oviposition) females (descriptive data available in Appendix 1), but our comparisons between sexes were restricted to males and non-gravid females (N = 6) to avoid gravidity effects on Tp (Carretero et al. 2005). The mean Tp ± SE of *Z.* (*v.*) *carniolica* males was 30.78 ± 0.29°C (range 29.24–32.21°C), which was significantly higher than that of females (mean Tp ± SE: 28.89 ± 0.91°C, range 25.95–32.54°C, Table 1, Fig. 1). However, the diel fluctuation of Tp showed the same pattern for both sexes (Table 1); both attained their highest Tps in the early morning hours with a gradual decline in the afternoon (Fig. 1). As far as water loss rates (EWL_i) were concerned, we did not find any difference between females and males and they did not change with time interval of the experiment (Table 1). Accumulative water loss rates (EWl_a) showed a linear trend of increase with time and a gradual increase in inter-individual variability (Fig. 2).

In the field, microhabitat temperatures (T) were more variable than relative humidity (RH), which remained almost constant (Fig. 3a). T gradually rose during the first third of the day (8–11 h) followed by a steeper slope of increase until 13 h, when the maximum T measured was 53.9°C (Fig. 3a). T remained high until 16 h and then decreased steadily (Fig. 3a). The values of the thermal quality index were low (i.e., microhabitat T was similar to species' Tp) only for a short mid-morning period (10–11 h), whereas the microhabitat was colder than the Tp of the lizards in the morning and became hotter than their Tp after midday and thus produced high thermal quality index values (Fig. 3b).

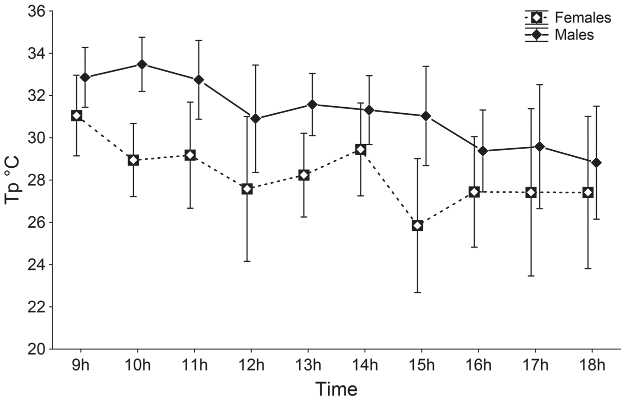

Figure 1. Daily variation in preferred body temperatures (Tp) for males and females of *Zootoca* (*vivipara*) *carniolica*. Displayed are median and 0.95 confidence intervals.

The mean Tp was similar between the three sympatric species, but the diel patterns of Tp differed (Table 2); in summer, *I. horvathi* and *P. muralis* attain Tps within a similarly narrow and constant range (Osojnik et al. 2013), while *Z.* (*v.*) *carniolica* had a higher Tp in the first half of the day and a lower Tp in the second half of the day (Fig. 1). Regarding water loss, results showed that *Z.* (*v.*) *carniolica* lost less water than the other two species, but especially so compared to *P. muralis* (Table 2). Between-species differences in EWL_a became significant in the last three hours of the experiment (Table 2).

In summary, the ecophysiological traits studied in *Z.* (*v.*) *carniolica* revealed a sexual dimorphism in Tp, with females attaining lower Tps than males. This was likely because females were close to their post-oviposition phase (see similar results obtained by Carretero et al. (2005) for the oviparous *Z. v. louislanzi* from the Pyrenees). We also observed a clear diel variation of Tp in both males and females of *Z.* (*v.*) *carniolica*; higher Tps in the morning than in the afternoon. When we examined temperatures in the typical microhabitat that *Z.* (*v.*) *carniolica* uses in the study area, we observed that this species would at this time of the year (late summer) be exposed to very hot temperatures between midday and 16 h. Temperatures on the ground rose to an average of 47°C (maximum 54°C), which is already above or close to the species' critical thermal maximum (CTmax, the temperature defined as the upper limit of the thermal tolerance range within which an

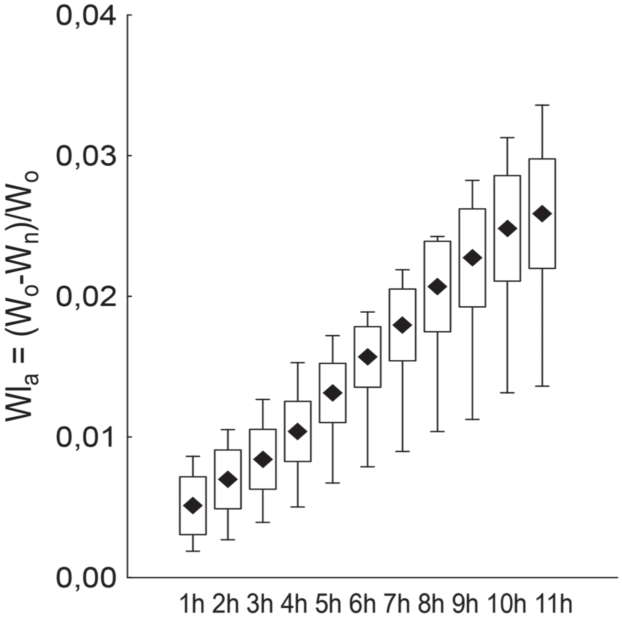

Figure 2. Mean accumulative water loss (EWl_a) of *Zootoca* (*vivipara*) *carniolica*, after 1–11 hours of the experiment (X-axis). Displayed are means (symbols) with standard errors (boxes), and non-outlier minimum and maximum values (whiskers).

organism is able to continue activity necessary for survival; Kearney & Porter 2004, 2009). The CTmax described for viviparous *Z. vivipara* from four populations along the altitudinal gradient in Czech Republic was between 43.8 and 44.1°C (Gvoždik & Castilla 2001). Hence, the ground represents a thermally stressful environment for *Z.* (*v.*) *carniolica* during this period, which likely limits its activity in order to avoid them. Remarkably, the hottest period of the day in the field (12–16 h) also coincided with a selection for lower body temperatures in the thermal gradient; the lizards maintained lower than mean Tp during the afternoon. Moreover, the lizards were observed remaining immobile in the cooler part of their terraria in the late afternoon and seemed to have abandoned thermoregulation. Overall, the association found between restrictive (too hot) thermal properties of the microhabitats and lizard behaviour along the thermal gradient in the afternoon (reflected in lower Tp) suggested an intrinsic thermoregulatory behavioural response to temperatures that might cause lizards to become overheated either by selecting cooler microhabitats or/and by remaining inactive. Being inactive inside burrows or other refuges also keeps lizards from other activities such as feeding, territorial competition, reproduction, etc. (e.g., Aguado & Braña 2014). It has already been demonstrated that shorter daily periods during which lizards are able to reach their Tp will directly reflect in reduced energy consumption (via thermally sensitive metabolizable energy intake [Angilletta 2001]).

Contrary to our initial expectation, *Z.* (*v.*) *carniolica* lost relatively small amounts of water in dry conditions even though this species lives in microhabitats with high and constant relative humidity (mean RH was 66%). This is in fact contrary to the results of some previous studies of EWL in lizards (genus *Anolis* and *Neoscincus*) that have demonstrated that species inhabiting drier and/or warmer localities exhibited reduced water loss rates compared to their counterparts inhabiting moist and/or cooler sites (e.g., Hillman & Gorman 1977, Perry et al. 2000, Caldwell et al. 2015). Furthermore, our expectations were that EWL rates would be highest in *Z.* (*v.*) *carniolica* when compared with sympatric saxicolous *I. horvathi* and *P. muralis* that mostly occupy drier rocky habitats (Žagar et al. 2013). We found the opposite to be true; it seemed that the species inhabiting the most humid microhabitat was losing the least water compared to two species inhabiting rocky microhabitats with drier conditions. On the other hand, the interspecific differences in thermal physiology found between the ground-dwelling *Z.* (*v.*) *carniolica* and the two saxicolous lizards did seem to reflect a difference in their microhabitat use. Restrictive environmental temperatures in the *Z.* (*v.*) *carniolica* habitat (too hot in the afternoon) were responded to by abandoning thermoregulation in the

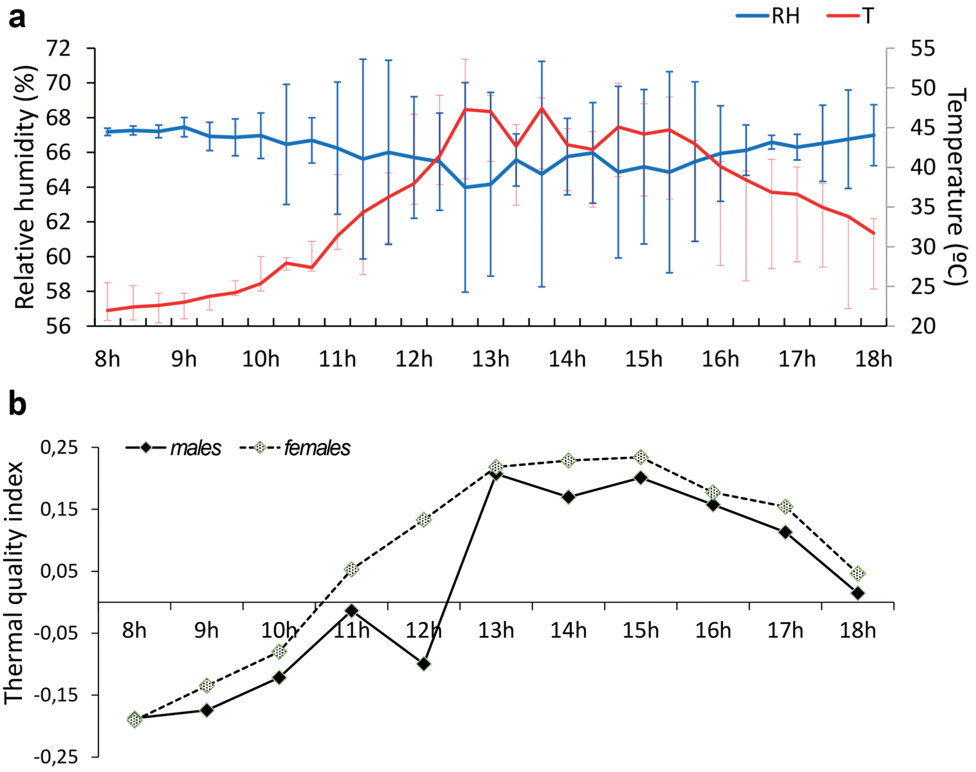

Figure 3. (a) Diel fluctuations of temperature (T) and relative humidity (RH) (median and quartile values, recorded with three dataloggers placed on ground covered with herbaceous vegetation, the typical microhabitat of *Zootoca* (*vivipara*) *carniolica* at the study site in southern Slovenia. (b) Diel variation of the mean absolute thermal quality index values for *Z.* (*v.*) *carniolica* on the ground, calculated as the relative difference between mean temperatures in the microhabitat (T) and mean preferred body temperatures (Tp).

Table 2. The left side of the table represents the mean accumulated water loss rates (EWL$_a$) with results of 11 one-way ANOVA analyses using 'species' as factor and false discovery rate (FDR) values after each hour of the experiment for males of three sympatric species, *Zootoca* (*vivipara*) *carniolica* (ZVC, this study), *Iberolacerta horvathi* (IH, from Osojnik et al. 2013), and *Podarcis muralis* (PM, from Osojnik et al. 2013), measured in summer. On the right side of the table are ANCOVA results of the repeated measurements for preferred body temperatures (Tp) using 'species' as between-subjects factors, 'time interval' as within-subject factor, and 'snout–vent length (SVL)' as covariate. Significant results are printed in bold.

EWL$_a$	Mean			ANOVA			FDR	Tp	ANCOVA-rm		
Num. of hours	ZVC	IH	PM	F	df	P			F	df	P
1	0.005	0.003	0.004	1.43	2	0.25	0.31	species	2.92	2	0.07
2	0.007	0.006	0.007	0.37	2	0.69	0.69	time	0.30	9	0.97
3	0.008	0.009	0.010	0.47	2	0.63	0.69	time × species	3.44	18	< 0.001
4	0.010	0.011	0.014	1.50	2	0.23	0.31				
5	0.013	0.015	0.018	1.84	2	0.17	0.27				
6	0.016	0.018	0.022	2.39	2	0.10	0.18				
7	0.018	0.022	0.026	2.99	2	0.06	0.13				
8	0.021	0.024	0.031	4.19	2	0.02	0.06				
9	0.023	0.028	0.036	**5.88**	**2**	**0.006**	**0.02**				
10	0.025	0.030	0.040	**6.29**	**2**	**0.004**	**0.02**				
11	0.026	0.033	0.043	**8.03**	**2**	**0.001**	**0.01**				

afternoon (diel pattern of Tp), which was a trait not found in *I. horvathi* and *P. muralis* that both occupy exposed rocks with lower and more constant surface temperatures (pers. obs.). The narrow and constant daily range of mean Tp in *I. horvathi* and *P. muralis* suggests that these species are more precise thermoregulators that do not abandon thermoregulation in the afternoon (Osojnik et al. 2013). These results could suggest that hydric physiology plays a subordinate role to thermal physiology in connection with microhabitat use in these three sympatric lizard species in the studied community. Or, to the contrary, these results could suggest that humidity plays an variable role in the physiology of lizards depending on the microhabitat type (stronger role in humid vs dry microhabitats), but more systematic research on the topic of hydric physiology is still needed to understand the results so far found for different species and populations. Moreover, the heterogeneity of microhabitats has recently been demonstrated to also play a role in the effectiveness of thermoregulation of small lacertids (Sears & Angilletta 2015), which suggests that not only average and daily variation of environmental conditions are important, but also the distribution and heterogeneity in space that could impact on thermal and hydric properties.

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Appendix 1

Descriptive statistics of preferred body temperatures (°C) considering sex, time, and gravidity in females of *Zootoca* (*vivipara*) *carniolica* from southern Slovenia. Legend: N – sample size; SE – standard error; * calculated average from the individual means of the 10 time intervals.

	Males			Females non-gravid			Females gravid		
Time	N	Mean	SE	N	Mean	SE	N	Mean	SE
9:00	10	32.09	0.56	6	32.33	1.38	3	28.93	0.46
10:00	10	32.74	0.53	6	30.17	1.28	3	29.00	2.20
11:00	10	32.39	0.61	6	29.77	1.39	3	26.73	2.40
12:00	10	30.52	0.98	6	28.22	1.62	3	26.40	1.66
13:00	10	31.09	0.54	6	29.03	1.17	3	29.97	0.66
14:00	10	30.88	0.69	6	30.17	1.05	3	28.00	0.40
15:00	10	30.41	0.85	6	26.88	1.76	3	27.13	2.89
16:00	10	29.39	0.62	6	27.42	1.36	3	25.70	2.57
17:00	10	29.18	1.25	6	28.03	1.60	3	29.27	1.13
18:00	10	29.17	1.19	6	26.83	1.31	3	30.47	2.24
total*	10	30.79	0.78	6	28.89	1.39	3	28.16	1.66