Consistent individual differences in temperament at different temperatures in

*Leiocephalus schreibersii*

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**Abstract**

Temperament (also referred to as behavioural syndrome, coping style, and personality) is a consistent behavioural difference between individuals. Studying temperament may help understand important aspects of ecology, such as population dynamics, community ecology, speciation, and even adaptations. I investigated how temperature influences temperament, measured by locomotor activity level and exploratory behaviour, in *Leiocephalus schreibersii*. Very few studies have looked at how a change in temperature can affect temperament in ectotherms. The purpose of this study was to examine how temperament varies at different temperatures in a terrestrial vertebrate ectotherm, *Leiocephalus schreibersii*. Lizards were submitted to a novel environment and novel object test three times per temperature at three temperatures (30°C, 34°C, and 38°C). Temperature had an effect on activity, but not on exploration. As temperature increased, locomotor activity decreased. Although there were significant differences among lizards at a given temperature, individual responses to changes in temperature did not differ for locomotor activity. For exploration, none of the variables tested had a significant effect on latency but for the novel object trials, only the trial order had a marginally significant effect. The results for locomotor activity were not as expected since locomotion decreased with temperature and none of the tested variables could explain exploration. Nonetheless, the results demonstrate that there are consistent individuals differences in locomotor activity but not in exploration in *L. schreibersii*.

**Introduction**

Temperament in an animal is a behavioural response that differs between individuals, and these differences between individuals are consistent over time and/or situations (Réale *et al.* 2007). Réale *et al.* (2007) divided temperamental traits into five categories: (1) shyness-boldness, (2) exploration-avoidance, (3) activity, (4) aggressiveness, and (5) sociability. Temperament can help understand important aspects of ecology such as population dynamics, community ecology, speciation, and adaptations (Réale *et al.* 2007). Dall *et al.* (2004) suggested that differences in temperament could be an adaptation itself and stated that: "[…] personality differences can be selected for if the fitness payoffs of the actions available to individuals are dependent on both the frequencies with which they are performed, and the behavioural history of individuals".

Individuals vary in their behavioural responses (Sih *et al.* 2004, Dingemanse and Réale 2005, Sih & Bell 2008). In Iberian wall lizards (*Podarcis hispanica*), individuals that explore more are able to habituate to new environmental cues faster than individuals that do little exploring, and less social individuals habituate faster than more social individuals (Rodriguez-Prieto *et al.* 2011). Variation in behavioural responses can be caused by differences between individuals, variation in the environment, or the interaction between individuals and the environment (Carter *et al.* 2012). Behavioural traits are phenotypically plastic, which allows for individuals to vary their response to changing environmental conditions. For example, vigilance varies depending on group size and perceived predation risk (Roberts 1996). An individual's capacity to respond to a change in a situation depends on the individual's personality and behavioural plasticity, and these traits may be under selective pressure (Sih *et al.* 2004). Carter *et al.* (2012)

looked at the effect of a rapid change in environmental conditions on a set of behavioural traits in the Namibian rock agama (*Agama planiceps*) and suggested that with reliable environmental cues, individual plasticity will be favoured over consistency in behaviour.

In endotherms, behavioural changes can be related to metabolic rate (Careau *et al.* 2008). Expression of temperamental traits such as boldness, exploration, and aggressiveness are energetically costly, and therefore can be correlated to metabolic activity. Often, individuals that have high resting metabolic rates are more active and have a tendency to explore more than individuals with lower resting metabolic rates (Careau *et al.* 2008).

Because metabolic rate is strongly dependant on temperature, it is assumed that an increase in temperature will increase resting metabolic rate and therefore increase behavioural activity in ectotherms (Biro *et al.* 2013). Two studies by Biro *et al.* (2010, 2013) underline the importance of temperature in ectothermic animals in terms of their temperament and behavioural plasticity. Biro *et al.* (2010, 2013) suggested that differences in behavioural responses between individuals at a given temperature may be related to differences in metabolic rates, but they did not test this hypothesis. In damselfish, *Pomacentrus bankanensis*, Biro *et al.* (2010) demonstrated that individuals respond greatly to a change in temperature, even if these changes in temperature are within the normal range of temperatures experienced by these fish in their natural environment. Boldness and aggressiveness in damselfish increased 2.5 to 6-fold with a difference of 3°C in water temperature. Individuals differed in their response to temperature. Most individuals became more active, aggressive and bold as temperature increased, but others did not (Biro *et al.*, 2010). In marine crabs (*Ozius truncates*),

behavioural responses between individuals differ at a given temperature and the rate of change of behavioural responses with changes in temperature also differs among individuals (Biro *et al.* 2013). In the social spider (*Anelosimus studiosus)* the most active, aggressive, and sociable individuals remained the most active, aggressive, and sociable individuals across temperature regimes (Pruitt *et al.* 2011).

The aim of my study was to determine how temperature influences temperament, as measured by locomotor activity and exploration in *Leiocephalus schreibersii*, using a novel environment and a novel object test. This study is the first to look at how temperament varies at different temperatures in a terrestrial vertebrate ectotherm. I expect that there will be consistent differences in activity and exploration between individuals and that these differences vary with temperature. Individuals can differ in their metabolic sensitivity to temperature (e.g. Careau, Gifford, & Biro, 2014; Nespolo *et al.*, 2003), which suggests that behavioural responses expressed at different temperatures might also vary across individuals (Biro *et al.*, 2013). Furthermore, because metabolic rate increases with temperature (Halsey *et al.* 2015), I also expect correlations between temperature, activity, and exploratory behaviour: with an increase in temperature, individuals will have a tendency to be more active and explore more.

**Methods**

Twenty-one *Leiocephalus schreibersii* were obtained from Mirdo Importations Canada Inc. *Leiocephalus schreibersii* are found in the coastal regions of Hispaniola, are ground dwellers, territorial, and favour semi-open habitat with scattered, moderate-sized rocks which they use for surveillance and basking (Marcellini & Jenssen 1989). Males

(max. SVL = 92 mm) are brightly coloured and larger than females (max. SVL = 71 mm) (Marcellini & Jenssen 1989). The lizards were individually housed in plastic containers (21 cm × 11.5 cm × 33 cm) that were lined with newspaper. The temperature in the environmental chamber was set at 30°C during the day from 8:00 to 16:00 and from 16:00 to 20:00 the temperature decreased to 21°C. Overnight, from 20:00 to 6:00 the temperature stayed at 21°C and from 6:00 to 8:00 temperature rose to 30°C. Temperature cycled to reduce stress on individuals by imitating temperature fluctuation that is observed in a natural environment. UVB lights supplemented fluorescent lights. All lights turned on at 8:00 and turned off at 20:00. Flexwatt heat tape was placed beneath half the container to give the lizard a chance to thermoregulate and a half PVC pipe (8-15 cm) was provided as cover. Lizards were fed three times per week with mealworms (*Tenebrio molitor*) and crickets (*Gryllodes sigillatus*) that were dusted in calcium powder with vitamin D3 and multivitamins, and water was available constantly.  Lizards were sexed according to colour and size (Gifford & Powell, 2007). Every week, the cages were shuffled to avoid any potential bias that may be associated with neighbours and their position on the shelf. Lizards were allowed to acclimate to their new environment for two weeks before the trials started. Every two weeks, lizards were weighed using a digital scale (Sartorius TE1502S). When metabolic rates of individuals of different sizes of same species or different species are compared, small animals are found to have the highest metabolic rate (Whitford & Hutchison, 1967). I measured mass, as an indication for size, to be able to determine if in this case, size could influence locomotor activity and exploration because metabolic rate varies with temperature and therefore temperament may also vary with temperature.

*Experimental Design*

To quantify activity and exploration in *L. schreibersii,* I used a novel environment test (Dingemanse, 2002; Rodriguez-Prieto, Martin, & Fernandez-Juricic, 2011; Walsh & Cummins, 1976) and a novel object test (Sambrook & Buchanan-Smith, 1997; Wemelsfelder et al. 2000). For both the novel environment and the novel object trials, the individuals were tested at three temperatures: 30°C, 34°C, and 38°C. These temperatures were selected because previous studies (Marcellini & Jenssen, 1989; Phillips & Howes, 1988) suggested that the preferred body temperature of *Leiocephalus* sp. was 36-38°C.

*Novel Environment*

Trials took place from 8:00 to 13:00. Twenty-four hours before the trial, individuals were placed in a second environmental chamber in which the temperature had been set for the trial so the individuals could acclimate to that temperature. The side of their cages were covered with newspaper to isolate the individuals from one another. For the trial, individuals were transferred from their individual cage into a larger environment.  Handling time was less than a minute. The environment for the novel environment consisted of a rectangular metal arena that measured 50 cm $\times$ 99 cm $\times$ 50 cm. An area of 16 cm by 16 cm at the edge of the environment was delimited where the focal individual was released at the start of each test. I recorded the individual's behaviour for a time span of 15 minutes using a camera (Nikon Coolpix P500) set on a tripod.

*Novel Object*

After the novel environment trial, individuals were given an extra 15 minutes to habituate to the new environment before the novel object test began. After the habituation

time, I introduced a novel objet, a pink round EOS lip balm container, in the environment at three marked squares 48 cm from the individual. To encourage the individual to approach the object, food (one mealworm) was added within 1 cm of the novel object. Once the object was introduced, I used the same recording method as above to analyse the individual's behaviour for five minutes. In-between trials the novel environment and object were disinfected using an ACCEL wipe (active ingredient: hydrogen peroxide 0.5% w/w). The trials were spaced by 7 days. Every individual was tested at three temperatures three times for a total of nine observations per individual.

*Video Analysis*

I viewed the recording for the novel environment and the novel object trials using QuickTime (QuickTime Player v. 10.4) and JWatcher (JWatcher v. 1.0, http://www.jwatcher.ucla.edu/index2.htm). For the novel environment trials, I took note of the time (milliseconds) it took for the lizard to leave the release area, the time the individual spent in the open, corner or edge, the amount of time the individual was stationary, moving, and trying to escape the enclosure (climbing). For the novel object trials, I took note whether or not the individual touched the novel object, the time (milliseconds) of latency to approach the object, and the total time spent near the object. Time spent "near" the object was determined according to the size of the environment; a radius of 16 cm around the object was determined before the test and was used as reference for "near".

*Analyses*

I analyzed the data using linear mixed-effects models (LMMs) and generalized linear mixed-effects models (GLMMs) in the libraries nlme and lme4 in R (Pinheiro *et*

*al.*, 2016; R Core Team, 2015; Bates *et al.*, 2005). I used time spent moving as an indication of locomotion, the time it took to leave the starting point as "latency", and whether or not an individual came into contact with the object as "novel object". Data for locomotion were transformed using the square root to satisfy the assumption of normality. Latency was treated as a binomial factor: individuals that left the starting point in less than 5 seconds received a score of 1 and individuals that left the starting point after 5 seconds received a score of 0. Novel object was also treated as a binomial factor: 1 = touched the object and 0 = did not touch the object. Variables that were considered as fixed effects in the models were: the order at which the trials took place (order), sex, mass (g) and temperature (°C). The lizards' unique identification number (UID) was considered as a random effect in the models. I also looked at the interaction between temperature and UID in the random effects. To select the best-fit model, I started with the most complete model, with all of the fixed effects and an interaction between temperature and UID for the random effects. From there, I eliminated the variable that had the highest p value from the model and ran a new model with one less factor until all remaining variables were significant. Thereafter, I compared the AICc of each model and chose the model that had the smallest AICc value and that was the most parsimonious (Burnham & Anderson, 2002). Repeatability for activity and exploration was calculated using the ICC package in R and following Lessells and Boag (1987).

**Results**

*Novel Environment*

For locomotion, the model with the lowest AICc was the model that included temperature, order, sex and mass as fixed effects and the UID as a random effect (Table 1). Within this model, locomotion declined with trial order (estimate = -5.186, standard error = 1.49, t value = -3.48, p <0.001) and temperature (estimate = -3.29, standard error = 1.18, t value = -2.79, p = 0.0058) and the effect of mass was marginally significant (estimate = -3.47, standard error = 1.70, t value = -2.04, p = 0.056). UID also had a significant effect (variance = 2112, standard error = 45.95, p<0.0001). Sex did not have a significant effect on locomotion (estimate = 11.42, standard error = 31.18, t value = 0.32, p = 0.72).

For latency, the model with the lowest AICc was the model that included mass as a fixed effect and UID as a random effect (Table 2). Mass had no significant effect on latency (estimate = -0.029, standard error = 0.048, z value = -0.60, p = 0.55). The second model with the lowest AICc, which is comparable to the first because it is within 2 AICc, had order and mass as fixed effects and UID as a random effect. In this case, neither factor had a significant effect (mass, p = 0.22 and order, p = 0.23). UID also had no significant effect on latency (variance = 1.53, standard error = 1.24, p = 0.54).

*Novel Object*

The model with the lowest AICc included order as a fixed effect and UID as a random effect (Table 3). The effect of order was marginally significant (estimate = -0.41, standard error = 0.22, z value = -1.92, p = 0.055). The second model with the lowest AICc had order and mass as fixed effects and UID as a random effect. Again, order was marginally significant (p = 0.057). On the other hand, mass had no significant effect

(p = 0.18). UID also had no significant effect (variance = 0.98, standard error = 0.99, p = 0.20).

*Repeatability*

Intraclass correlation coefficient (ICC) was calculated with the ICC package in R. For locomotor activity, the ICC obtained was 0.46 (N = 21, K = 9). The variance within individuals is 3076.97 and the variance among individuals is 2585.89. For latency, the ICC obtained was 0.14 (N = 21, K = 9). The variance within individuals is 0.090 and the variance among individuals is 0.014. As for exploration, the ICC obtained was 0.0162 (N = 21, K = 9). The variance within individuals is 0.0304 and the variance among individuals is 0.0005.

**Discussion**

I looked at how temperature influences temperament in *L. schreibersii* by measuring locomotor activity and exploration. I was expecting that, as temperature increased there would be an increase in both locomotor activity and exploration. Yet, for each increase of 1°C in temperature, lizards moved approximately 0.011 seconds less (Figure 1). Furthermore, the order of the trials also influenced activity. Locomotion decreased by 0.026 seconds per trial (Figure 2). Locomotion could have decreased throughout the trials because as individuals were more and more exposed to the novel environment they became more habituated. Rodriguez-Prieto, Martin, & Fernandez-Juricic (2011) looked at the direct and indirect effects of boldness, exploration and sociability on habituation in Iberian wall lizard (*Podarcis hispanica*). They found that habituation index was significantly associated with the exploration behaviour and

sociability of lizards while boldness, sex and body size did not significantly affect habituation. Fast explorers and less social individuals habituated faster than slow explorers and more social individuals (Rodriguez-Prieto, Martin, & Fernandez-Juricic, 2011). For exploration, temperature did not have a significant effect. Trial order, however, had a marginally significant effect on exploration. As trial order increased, fewer individuals came into contact with the object.

I had also expected that individuals would have consistent differences in their responses within and among temperatures. UID had a significant effect on locomotion. On the other hand, the interaction between UID and temperature did not have a significant effect. Thus, there are significant differences in activity among lizards at a given temperature, individual responses change with temperature, but their responses to changes in temperature did not differ. As the results for the intraclass correlation coefficient (ICC) for locomotor activity, it suggests that individual differences in behavioural tendency are fairly consistent. These results are similar to what Pruitt *et al*. (2011) found in social spiders, but different to what Biro *et al*. (2013) and Biro *et al*. (2010) found in marine crabs. For Pruitt *et al*. (2011) study, animals were only measured once at each temperature, which might have limited their ability to detect differences (Biro *et al.* 2013), but that is not the case in this study as individuals were measured three times at each temperature.

Changes or flexibility in temperament as temperature increases may be energetically costly. Flexibility is likely to be costly in a world that changes continuously regardless of individual actions and behaviour (Dall, Houston, & McNamara, 2004). Although responding adaptively (e.g., change in behaviour) to a portion of an

environment is likely to improve expectations about local conditions, it might increase uncertainty about the rest of the environment. This will increase the chances of responding inappropriately, or take longer to respond appropriately, under alternative conditions that will not have been experienced as recently (Dall, Houston, & McNamara, 2004). Therefore, in this case, it might have been more beneficial for individuals to have a flexible response to a change in temperature because other factor such as food, water availability and the novel environment did not change and could therefore spend the energy necessary to be flexible.

Difference in response might be due to differences in metabolic rate at a given temperature. Metabolic rate could explain the behavioural differences observed between individuals (Biro and Stamps, 2010). Individuals with higher metabolic capacity will be able to sustain more vigorous activities and behaviour such as foraging, growth, and exploring (Biro et al. 2013, Careau et al. 2008). Activity in ectothermic animals increases with temperature because metabolic rate also increases with temperature (Halsey *et al*. 2015). Biochemical reaction rates increase with temperature because higher temperatures increase the proportion of enzymes that have reached their activation level, which allows for more reactions to occur. Therefore, metabolic rate is closely related to temperature in ectotherms (Halsey et al. 2015). However, in this case I have observed that activity decreases with an increase in temperature. This might be due to the fact that the highest temperature (38°C) used in these trials was too high for *L. schreibersii* to sustain high levels of activity, although it has been suggested that the preferred temperature of *Leiocephalus* sp. was 36-38°C (Marcellini & Jenssen, 1989; Phillips & Howes, 1988). As described by Huey (1991), thermal performance curves are a representation of an

individual's performance as a function of temperature. Performance curves have characteristic shape, in which performance increases with temperature until it reaches a maximum and then rapidly declines. In this case, because the thermal performance curve for locomotion has not been established in *L. schreibersii,* the temperatures that were chosen for the trial may not have been the ideal temperature for these lizards. The highest temperature of 38°C may have been beyond the maximum within the region where performance rapidly declines which would explain the decrease in locomotion we see between the highest temperature (38°C) and the other two temperatures (30°C and 34°C) in Figure 1.

For latency in *L. schreibersii*, the best-fit models had no significant variables. Because UID was not significant and the ICC obtained was very, this indicated that there are no consistent differences between individuals, and so this may not be personality trait. Because the other variables were not significant, no affirmative conclusion can be made on why some individuals leave the starting area earlier than other. During the trials, most individuals seemed eager to leave the start point, not to explore, but to escape from my hand. A study using Iberian wall lizard (*Podarcis hispanica*) had shown that less social individuals were out of the refuge faster and explored more than more social individuals (Rodriguez-Prieto, Martin, & Fernandez-Juricic, 2011). In their study, they did not mention how lizards were released in the novel environment. In this case, handling may have affected latency although I tried to limit handling time at less than a minute. As for the novel object test, order was marginally significant. As individuals were more exposed to the object, fewer individuals came in contact with the object. Individuals might not have reacted to the object because it simply did not interest them (no visual stimuli),

although food was nearby, perhaps the lizards were not hungry and were not interested in approaching the object. Due to the outcome of the novel object trial, this type of exploratory test may not be appropriate for these lizards.

**Conclusion**

In conclusion, I showed that *L. schreibersii* differ in their behaviour responses in activity and but not in exploration. There are consistent individuals differences in locomotor activity at different temperature, which have not been observed in exploration. Temperament was measured through activity and exploration with a novel environment and a novel object trial. For the novel environment trials, as temperature and trial order increased, activity decreased in *L. schreibersii*. Furthermore, individual responses changed with temperature, but their responses to changes in temperature did not differ. None of the factors tested had a significant effect on latency and with a low ICC, these results indicates that it may not be a personality trait in these lizards. As for exploration (novel object trials), only trial order had a marginally significant effect, as order trial increase fewer individuals came in contact with the object. In this case, flexibility in locomotor activity as temperature increases is advantageous in this situation, although it is energetically costly, which is why they are consistent differences in individuals' behavioural responses. Other factors, such as metabolic rate, could have offered some insight as to why some individuals are more active than others (Biro & Stamps, 2010). It might also be of interest to do the trials at more than three temperatures: to add a fourth, cooler temperature to see if activity and exploration would decrease. Finally, the results

of this study showed that in *Leiocephalus schreibersii* there is evidence of temperament for one of the traits studied which is locomotor activity.

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**APPENDICES:**

Table 1: Comparison of the linear mixed-effects models that describe activity (locomotion) in *L. schreibersii*. Best model is in bold.

| Models | Effects | | AICc[a] | ΔAICc[a] | K[b] |
|---|---|---|---|---|---|
| | Random | Fixed | | | |
| 1 | Temperature\|UID | Temperature<br>Order<br>Sexe<br>Mass | 2066.07 | 3.61 | 9 |
| **2** | UID | Temperature<br>Order<br>Sexe<br>Mass | 2062.46 | 0 | 7 |
| 3 | UID | Temperature<br>Order<br>Mass | 2069.14 | 6.68 | 6 |
| 4 | UID | Temperature<br>Order | 2074.92 | 12.46 | 5 |
| 5 | UID | Order | 2082.64 | 20.18 | 4 |

[a]ΔAICc is the difference between the model's second order Akaike's information criterion (AICc) and the smallest AICc.
[b]K is the number of parameters in the model.

Table 2: Comparison of the linear mixed-effects models that describe the time it took for individuals to leave the starting point (latency) in *L. schreibersii.* Best model is in bold.

| Models | Effects | | AIC[a] | ΔAIC[a] | K[b] |
|---|---|---|---|---|---|
| | Random | Fixed | | | |
| 1 | Temperature\|UID | Temperature Order Sexe Mass | 142.01 | 7.35 | 8 |
| 2 | UID | Temperature Order Sexe Mass | 139.38 | 4.72 | 6 |
| 3 | UID | Order Sexe Mass | 137.25 | 2.59 | 5 |
| 4 | UID | Sexe Mass | 135.15 | 0.49 | 4 |
| **5** | UID | Mass | 134.66 | 0 | 3 |

[a]ΔAICc is the difference between the model's second order Akaike's information criterion (AICc) and the smallest AICc.
[b]K is the number of parameters in the model.

Table 3: Comparison of the linear mixed-effects models that describe exploration (novel object trials) in *L. schreibersii.* Best model is in bold.

| Models | Effects | | AIC[a] | ΔAIC[a] | K[b] |
|---|---|---|---|---|---|
| | Random | Fixed | | | |
| 1 | Temperature\|UID | Temperature | 61.57 | 7.34 | 8 |
| | | Order | | | |
| | | Sexe | | | |
| | | Mass | | | |
| 2 | UID | Temperature | 58.26 | 4.03 | 6 |
| | | Order | | | |
| | | Sexe | | | |
| | | Mass | | | |
| 3 | UID | Temperature | 56.13 | 1.90 | 5 |
| | | Order | | | |
| | | Mass | | | |
| 4 | UID | Order | 54.69 | 0.46 | 4 |
| | | Mass | | | |
| **5** | UID | Order | 54.23 | 0 | 3 |

[a]ΔAICc is the difference between the model's second order Akaike's information criterion (AICc) and the smallest AICc.
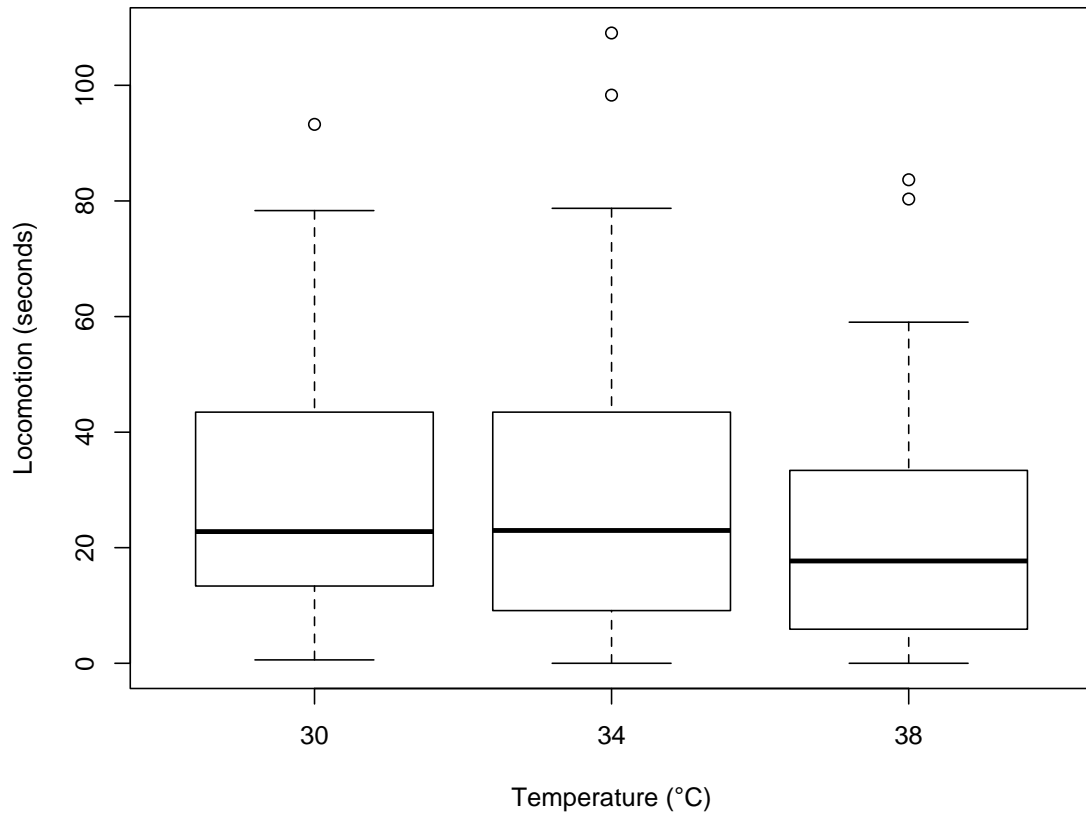[b]K is the number of parameters in the model.

Figure 1: Average time (seconds) spent moving (locomotion) during the novel environment trial (15 minutes) for 21 *Leiocephalus schreibersii* at three temperatures (°C).
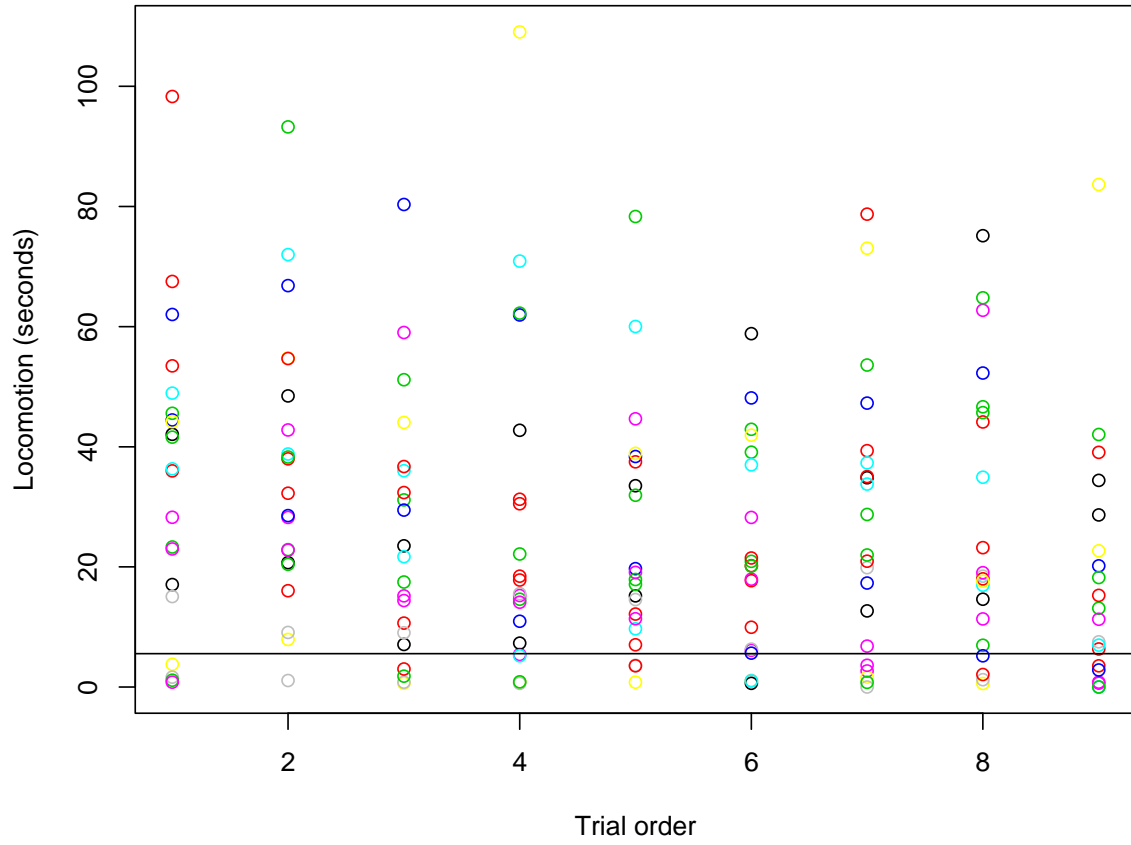
Figure 2: Time (seconds) spent moving (locomotion) during the novel environment trial (15 minutes) for 21 *Leiocephalus schreibersii* for each trial order.
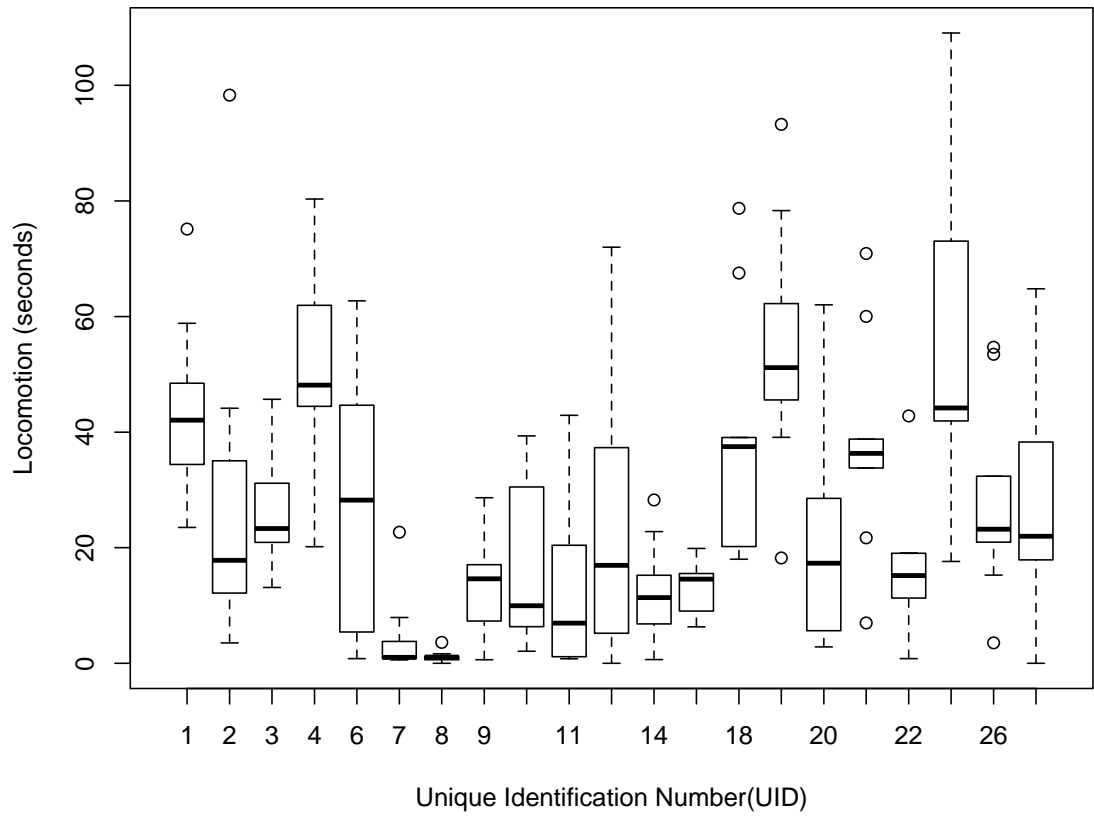
Figure 3: Average time (seconds) spent moving (locomotion) during the novel environment trial (15 minutes) for 21 *Leiocephalus schreibersii* at all of the temperature intervals.