

## Aspects of the thermal ecology of the European tree frog *Hyla arborea* (Linnaeus, 1758) (Anura: Hylidae) in Western France

by

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**Summary** – Body temperatures of the tree frog *Hyla arborea* were measured over a six-year period during overcast and sunny weather in Vendée of Western France. Body temperatures were higher during sunny weather but there was no difference in body temperature variance. Body temperature variance was lower in comparison to the variance of leaf temperatures in sunlit areas but in agreement with leaf temperature variance in shaded areas irrespective of weather conditions. Regression analysis of body temperatures with leaf temperatures in shade or open locations during both sunny and cloudy weather indicated the closest association was with shaded leaf temperature regardless of weather conditions. Frogs were located at median distances of 2-12 m from the nearest water mostly in shaded areas, but a smaller number were observed in sunlit areas during sunny weather in mid-afternoon. The results suggest control of body temperature in *H. arborea* by microhabitat selection, with shaded areas selected to avoid potentially critical high temperatures during sunny weather. However, occasional basking in open locations, even during hot weather, suggests an attempt to elevate body temperature.

**Key-words:** *Hyla arborea*, body temperatures, weather conditions, microhabitat selection.

**Résumé** – Aspects de l'écologie thermique de la Rainette européenne *Hyla arborea* (Linnaeus, 1758) (Anura: Hylidae) dans l'Ouest de la France. Les températures corporelles de la rainette *Hyla arborea* ont été mesurées sur le terrain sur une période de six ans par temps couvert et ensoleillé en Vendée. La température du corps était plus élevée par temps ensoleillé mais il n'y avait pas de différence dans la variance de la température corporelle. La variance de la température corporelle était inférieure par rapport à la variance de la température des feuilles dans les zones ensoleillées, mais comparable à la variance de la température des feuilles dans les zones ombragées, indépendamment des conditions météorologiques. L'analyse de régression de la température du corps avec les températures à l'ombre des feuilles ou des lieux ouverts durant les journées ensoleillées et nuageuses ont indiqué une association plus proche avec la température des feuilles ombragées, indépendamment des conditions météorologiques. Les grenouilles étaient situées à des distances médianes de 2-12m du point d'eau le plus proche pour la plupart dans des zones ombragées, mais un plus petit nombre a été observé dans des zones ensoleillées par temps ensoleillé en après-midi. Les résultats suggèrent le contrôle de la température corporelle chez *H. arborea* par la sélection du microhabitat, avec des zones ombragées dans les arbres sélectionnés afin d'éviter les situations potentiellement critiques des températures élevées par temps ensoleillé. Toutefois, des expositions occasionnelles dans des endroits ouverts, même par temps chaud, suggèrent une tentative pour accroître la température corporelle.

**Mot-clés :** *Hyla arborea*, températures corporelles, conditions météorologiques, sélection du microhabitat.

## I. INTRODUCTION

The body temperature of ectotherms is a key factor in their ecology since many physiological functions are temperatures dependent – e.g. locomotory movement, digestion and growth (Huey 1991). In amphibians the permeable integument and subsequent high rates of evaporative water loss imposes the dual regulation of attempting to maintain body temperatures that are optimal for physiological processes whilst maintaining water balance. This may constrain body temperature selection but in the presence of water many amphibians are able to bask with evaporative water losses contributing to body temperature control (Shoemaker *et al.* 1992, Snyder & Hammerson 1993). Basking in water frogs of the *Pelophylax lessonae/ridibunda/perezi* complex beside ponds or other water bodies even when environment temperatures are high is possible because of the immediate access to water (*e.g.* Meek 1983). When hydration is a limiting factor evaporative water loss may be controlled through postures, employment of special skin secretions or microhabitat selection (review *in* Wells 2007), adaptations often found in tree frogs. Arboreal habitats are particularly challenging for amphibian physiology, especially when the climate is hot with low humidity. This may impose constraints on achieving body temperatures that are optimal for physiological processes, for example, locomotory capacity has been found to be maximal at mean field body temperature in tree frogs (Knowles & Weigl 1990).

The tree frog *Hyla arborea* is a widespread species in Europe although in some areas it has been reported to be in decline (*e.g.* Fog 1995, Baker 1997). It is listed on Appendix II of the Berne Convention and Annex IV of the EU Natural Habitats Directive. It can be a difficult species to locate even when detected from calls, which is temperature dependent (Pellet & Schmidt 2005), but additionally year to year numbers in some areas differ considerably due to migratory movement and/or reproductive success (Baumgartner 1986, Stumpel 1987, Pellet *et al.* 2006). Little information on field body temperature is currently available although according to Stumpel (1987, 1993) it does occasionally bask. This paper presents baseline information on aspects of *H. arborea* thermal ecology in Vendée, western France from data collected over a six-year period mainly between May-September, the months with lowest rainfall/humidity and highest temperatures. During summer ambient air temperatures may regularly exceed 30-35°C and humidity levels descend to less than 40%.

## II. MATERIALS AND METHODS

Data were opportunistically collected between 2004 and 2009 in gardens and surrounding woodlands of the villages of Chasnais, Lairoux, and Saint-Denys-du-Payre (46°27'N). Body temperatures ( $T_b$ ) were recorded from 108 tree frogs, 86 during sunny weather, 22 when the weather was overcast or mostly overcast (s.v. length taken after  $T_b$  was recorded gave  $mean \pm standard\ deviation = 39.3 \pm 5.1$  mm). A further 6 were located during sunny weather in summer but not measured for  $T_b$  although their distances from the nearest water bodies were recorded. Most frogs were located from vocal calls; others were found visually on the leaves of bushes or trees. All individuals measured were close to the ground (3-4 metres) in both shaded and sunlit areas. Body temperatures are defined as skin surface temperatures recorded with an Electronique Frontal infrared detector (model TS112) to within 10-20 mm from the skin surface. This instrument is non-invasive and detects infrared energy emitted from the skin surface and has an error of less than 0.01°C. There will be, however, some additional error due to the emissivity of *H. arborea* skin and also due to the distance that the device is held from the skin surface, as it is possible to measure some of the surrounds. The 10-20 mm distance employed here and size of the frogs minimizes the latter potential. Measurements were made as quickly as possible, usually within several seconds from initial sightings. No handling was involved; the infrared detector was pointed at the animal and its skin surface temperature recorded. Frogs appeared to respond only to measurement if the instrument touched the skin surface and on the few occasions when this occurred the data point was ignored. To provide insight into the available range of temperatures, several leaf surface temperatures next to the frog were simultaneously recorded in the same way, both in shade ( $TL_{Shade}$ ) and in fully sunlit areas ( $TL_{Sun}$ ) and the means of both used for comparison with  $T_b$ . During overcast or mostly overcast weather  $TL_{Sun}$  is defined as leaves on the margins of fully shaded and fully exposed areas. Animals recorded as situated in full sun or partial sun (part of the body in sunshine) does not necessarily imply active basking. For instance, a shift in position from a partial or shaded area to sunlit location does not always require animal movement, it can be a consequence of a shift in the angle of the sun.

*Statistical analysis.* Body temperatures were tested for normality using the Anderson-Darling test. This test assumes the null hypothesis and the results showed no significant departure from normality either during overcast weather ( $a^2 = 0.38$ ,  $p = 0.36$ ) or when sunny

and hot ( $a^2 = 0.69$ ,  $p = 0.07$ ). Leaf temperatures were normally distributed during sunny weather but non-parametric when the weather was overcast and hence Mann Whitney  $U$ -tests were used. Non-parametric tests for equality of variance were made with Levene's test and  $F$ -tests when data were parametric. The adjusted  $r^2$  values are shown, which is independent of sample size – increases in sample size alone will not increase the  $r^2$  value. Tests were made for thermoregulation using regression analysis of body temperature with leaf temperatures. In this test thermoconformity requires a coefficient of 1, which was evaluated using  $t$ -tests at  $n-2$  degrees of freedom (Bailey 1981).

### III. RESULTS

Frogs were measured between 1030-2215 hrs but the majority were found in the afternoon; *median* =1500hrs, *interquartile range* = 1350-1823 hrs. Table I shows the distances they were located from water bodies during different weather conditions and season. The median distances from the nearest pond during sunny weather and overcast weather was not significant ( $w = 5462.5$ ,  $p = 0.21$ ). The distances recorded during spring (late April-May) were significantly shorter than found in summer (June-early October;  $w = 1035.0$ ,  $p = 0.005$ ).

**Table I:** Distances between *H. arborea* and water bodies during different weather and seasons.

Tableau I : Distances entre *H. arborea* et les plans d'eau selon la météorologie et la saison.

	median	interquartile range	<i>n</i>	<i>p</i>
sunny	12	5 - 13	92	n.s.
overcast	9.5	5 - 13	22	
spring	2	2 - 13	25	0.005
summer	12	7 - 13	89	

*Microhabitat selection.* During sunny weather most animals were found in shaded locations on the leaves of trees or other plants (60.5%) followed by partially shaded areas (27.9%). Only 11.6% were located in direct sunshine. When the weather was overcast a relatively greater number of frogs were found in partially sunlit locations (55.6%) compared to sunny weather ( $z = 1.998$ ,  $p = 0.045$ ;  $Q = 0.022$ ). Table II shows the changes in exposure to

**Table II:** Hourly differences in exposure (percent) to sunshine in *H. arborea* during different weather conditions. ND indicates no data available.

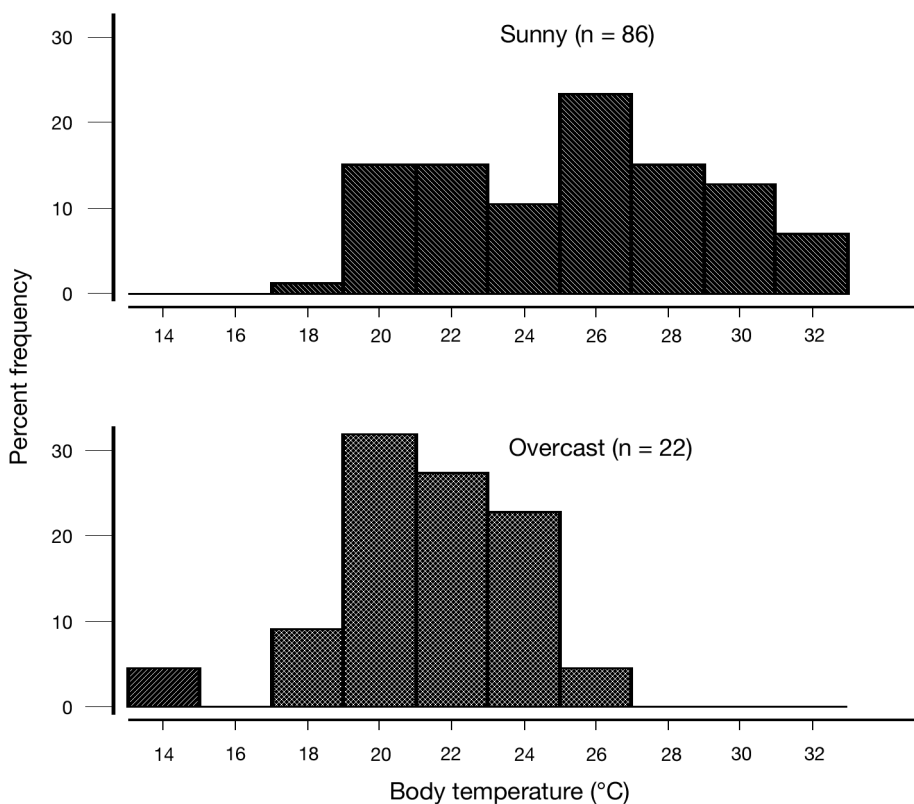
Tableau II : Différences horaires d'exposition (pourcentage) au soleil chez *H. arborea* sous différentes conditions météorologiques. ND indique l'absence de données disponibles.

Time of day (x 100)	Sun ( $\Sigma n = 86$ )				Overcast ( $\Sigma n = 22$ )			
	shade	partial shade	sun	<i>n</i>	shade	partial shade	sun	<i>n</i>
10 - 11	71.4	28.6	0.0	7	ND	ND	ND	0
11 - 12	100.0	0.0	0.0	4	75.0	25.0	0.0	4
12 - 13	100.0	0.0	0.0	6	75.0	25.0	0.0	4
13 - 14	100.0	0.0	0.0	3	75.0	25.0	0.0	4
14 - 15	28.6	52.3	19.1	21	0.0	100.0	0.0	1
15 - 16	38.8	23.1	46.1	13	100.0	0.0	0.0	3
16 - 17	60.0	40.0	0.0	5	100.0	0.0	0.0	1
17 - 18	100.0	0.0	0.0	4	ND	ND	ND	0
18 - 19	100.0	0.0	0.0	8	33.4	66.6	0.0	3
19 - 20	100.0	0.0	0.0	6	ND	ND	ND	0
20 >	55.5	44.4	0.0	9	0.0	100.0	0.0	3

sunlight with time of day when the data are sectioned into hourly time periods. Due to small sample sizes, data for animals found after 2000 hrs have been pooled. Data are absent for several of the hourly periods during overcast weather and indicated as ND. When the weather was sunny most exposure to sunshine was between 1400-1600hrs (partial sun = 42.4%; in full sun = 30.3%).

*Body temperatures.* During sunny weather  $T_b$  (mean±standard deviation =  $25.4 \pm 3.7$ , range = 18.9-32.9°C) was higher than when overcast (mean±standard deviation =  $21.9 \pm 3.5$ , range = 14.0-25.2°C) with the difference significant ( $F_{(1,106)} = 16.1$ ,  $p < 0.0001$ ). Variance of  $T_b$  was not significantly different between weather conditions ( $F = 1.73$ ,  $p = 0.15$ ). Frequency histograms of  $T_b$ s during different weather are shown in Figure 1.

*Body temperatures in relation to  $TL_{Sun}$  and  $TL_{Shade}$ .* Overcast weather  $T_b$  was significantly lower than  $TL_{Sun}$  (mean ± standard deviation =  $26.6 \pm 6.3^\circ\text{C}$ ;  $w = 345.0$ ,  $p = 0.0004$ ) but not significantly different from  $TL_{Shade}$  (mean ± standard deviation =  $20.7 \pm 2.2^\circ\text{C}$ ;  $w = 526.0$ ,  $p = 0.47$ ). Sunny weather  $T_b$  was significantly lower than  $TL_{Sun}$  (mean ± standard deviation =  $32.2 \pm 4.7^\circ\text{C}$ ;  $F_{(1,170)} = 110.9$ ,  $p < 0.0001$ ) but higher than  $TL_{Shade}$  (mean ± standard deviation =  $23.9 \pm 4.1^\circ\text{C}$ ;  $F_{(1,170)} = 5.21$ ,  $p = 0.024$ ). When the weather was overcast variance

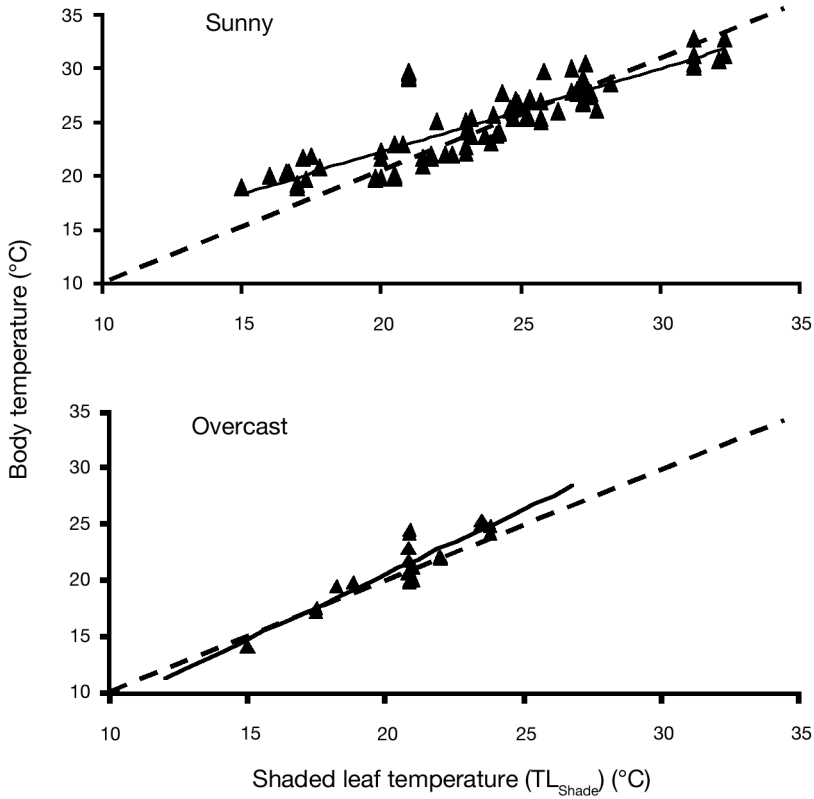


**Figure 1:** Frequency distributions of *H. arborea* body temperatures during sunny and overcast weather.

Figure 1 : Distribution des températures corporelles chez *H. arborea* par temps ensoleillé et nuageux.

of  $T_b$  was significantly smaller than variance of  $TL_{Sun}$  (Levene's test  $L = 4.32$ ,  $p = 0.04$ ) but in agreement with variance of  $TL_{Shade}$  ( $L = 2.76$ ,  $p = 0.10$ ). During sunny weather a similar statistical pattern was found with  $T_b$  variance significantly smaller than  $TL_{Sun}$  variance ( $F = 0.65$ ,  $p = 0.04$ ) but not significantly different from  $TL_{Shade}$  variance ( $F = 0.83$ ,  $p = 0.38$ ).

*Regressions of  $T_b$  versus  $TL_{Shade}$  and  $TL_{Sun}$ .* When the weather was hot and sunny regression analysis indicated a strong association of  $T_b$  with  $TL_{Shade}$  and gave:  $T_b = 6.6 + 0.78 \pm 0.05 TL_{Shade}$  ( $r^2 = 73.2\%$ ) (1). However, the test against a hypothetical value of 1 indicated a significant departure from thermoconformity ( $t = 4.31$ ,  $p < 0.0001$ ). Less agreement was found with  $TL_{Sun}$  (regression coefficient =  $0.42 \pm 0.07$ ;  $r^2 = 26\%$ ). When the weather was overcast



**Figure 2:** Graphs of body temperatures plotted against shaded leaf temperatures during sunny and overcast weather. The lines running through the data represent equations (1) for sunny weather and (2) for overcast weather given in the text and the broken lines that expected from a hypothetical thermoconformer.

Figure 2 : Graphiques de la température corporelle déterminée en fonction de la température des feuilles ombragées par temps ensoleillé et nuageux. Les lignes continues représentent les droites ajustées (1) par temps ensoleillé et (2) par temps couvert (équations indiquées dans le texte) et la ligne discontinue indique le profil hypothétique d'un "thermoconformer".

the closest association was again found with  $TL_{Shade}$  with:  $T_b = -2.6 + 1.16 \pm 0.13TL_{Shade}$  ( $r^2 = 77.9\%$ ) (2), with the regression not significantly different from 1 ( $t = 1.23$ ,  $p = 0.22$ ). The regression coefficient  $TL_{Sun}$  at this time was  $0.37 \pm 0.06$  ( $r^2 = 64.7\%$ ). Figure 2 shows graphs of  $T_b$  plotted against  $TL_{Shade}$  under cloudy and sunny weather with regression lines calculated from equations (1) and (2). The broken lines represent that expected of a hypothet-

ical thermoconformer and indicate departure from thermoconformity during sunny weather is a consequence of elevated  $T_b$  in relation to  $TL_{Shade}$  when  $TL_{Shade}$  is low with  $T_b$  lower than  $TL_{Shade}$  when  $TL_{Shade}$  is high.

#### IV. DISCUSSION

The results suggest that  $T_b$  in *H. arborea* is regulated mainly by selection of microenvironments; the selection of leaves that are in shaded areas when the weather is sunny and hot with some limited movement onto leaves in more open areas during hot sunny weather (perhaps indicating basking behaviour), a trend that increased when the weather was overcast. Therefore in either sunny or overcast weather  $TL_{Shade}$  was the best predictor of  $T_b$ , which is in good agreement with other studies of tree frog  $T_b$ s (e.g. Wygoda & Williams 1991). This is not always the case. For example, in *Hyla arenicolor*, a basking tree frog living beside permanent waterways in North America,  $T_b$  is independent of air temperature and other environmental variables (Snyder & Hammerson 1993). Thermoregulation in ectotherms depends on spatial and temporal availability of suitable microclimates and hence hourly or seasonal  $T_b$  can vary as a consequence (Angilletta *et al.* 2002). Observations of diurnal movement in *H. arborea* indicated some limited activity in trees including, apparently, shade seeking as a consequence of solar movement resulting in lower  $T_b$  variance in respect to variance of  $TL_{Sun}$ . Selection of shaded areas in a sunny and hot environment may enable increased activity and access to food and hence net energy gain, as has been shown in other ectotherms (Riechert & Tracy 1975, Huey 1991).

In tree frogs the impact of evaporative water loss on an ability to thermoregulate in the absence of water is mitigated by reduced rates of evaporative water loss (Wells 2007). In certain hylids this has been shown to be as much as 7 times lower than in typical frogs (e.g. *Hyla arenicolor*; Snyder & Hammerson 1993) facilitating long-term occupancy of elevated habitats at high  $T_b$ s (e.g. *Hyla cinerea*; Wygoda & Williams 1991). Tree frogs, however, must at some point undertake some migratory movement, either to suitable water bodies for reproduction or hibernation. In this study, *H. arborea* were located at much shorter distances from water bodies than found in *H. arborea* in the Netherlands (up to 300 m; Stumpel 1987) and Switzerland (more than 800 m; Pellet *et al.* 2006). In the latter study tree frogs migrated from the breeding area to summer territories where movement was more limited, which is



consistent with the Stumpel (1987) study and the present findings. Road-killed *H. arborea* in the study area were mostly found between October and December (59.5% of 42 individuals), the majority after rain (85.7%); less road-kill (14.6%) was found between April and June. The period between October and November has the highest precipitation and it is therefore possible that the hotter and drier Vendéen climate and/or abundance of water bodies may impact on movement behaviour with hydric conditions particularly constraining longer distance movement.

Elevated  $T_b$ s confer the same physiological benefits to amphibians as they do in reptiles (Brattstrom 1979, Duellman & Trueb 1986). Physiological performance has been shown to be sensitive to  $T_b$  in anurans (Navas 1996) including tree frogs, for instance, jump distances in North American tree frogs increased over temperatures from 0-35°C (John-Alder *et al.* 1989). Elevated  $T_b$ s increase growth in juvenile amphibians and in adult's food turnover, which enhances reproduction (Wells 2007). The  $T_b$ s recorded for *H. arborea*, although at the lower end of the  $T_b$  range for hylids, are in general agreement with those found for North American species (e.g. Wygoda & Williams 1991, Lillywhite *et al.* 1998, Tracy & Christian 2005). For example, *H. cinerea* has been observed in sunlight with  $T_b$ s as high as 36°C (Wygoda & Williams 1991), which exceeds the maximum of 32.9°C found in this study. The Australian tree frogs (*Litoria sp.*) have greater resistance to water loss than hylids and experience  $T_b$ s up to 38°C with the waterproof tree frogs (e.g. genus *Chiromantis* and *Phyllomedusa*) even higher (Shoemaker *et al.* 1987, Geise & Linsenmair 1988, Wells 2007). The mean diurnal  $T_b$  of *H. arborea* in sunny weather was almost identical to those found in sympatric *Pelophylax lessonae* that were measured whilst basking beside ponds or on pond surfaces ( $mean \pm standard deviation = 25.9 \pm 2.5^\circ C, n = 23$ ) and higher than in a small sample of sympatric *Rana dalmatina* diurnally foraging in woodland ( $24.1 \pm 4.6^\circ C, n = 9$ ). However, diurnal  $T_b$ s in sympatric *B. bufo* were higher ( $mean = 30.2^\circ C$ ) and in agreement with shaded air temperatures close to the ground (Meek & Jolley 2006). The ability of *H. arborea* to operate in arboreal habitats presumably reduces predation from terrestrial predators and competition from sympatric terrestrial anurans, for instance from *P. lessonae*, which are abundant around water bodies throughout the active year.

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## REFERENCES

- Angilletta M.J., Niewiarowski P.H. & Navas C.A. 2002 – The evolution of thermal physiology in ectotherms. *J. Therm. Biol.*, 27: 249-268.
- Bailey N.T.J. 1981 – Statistical Methods in Biology. London, English Universities Press, 216 p.
- Baker J. 1997 – Stability for Swedish treefrogs? *FrogLog*, 20: 2-3.
- Brattstrom B.H. 1979 – Amphibian temperature regulation studies in the field and laboratory. *Am. Zool.*, 19: 345-356.
- Baumgartner H. 1986 – Amphibia der Schweiz. Zurich, Panda: 1-31.
- Duellman W.E. & Truebb L. 1986 – Biology of Amphibians. McGraw-Hill, New York, 670 p.
- Fog K. 1995 – Amphibian conservation in Denmark. *FrogLog*, 13: 1-2.
- Huey R.B. 1991 – Physiological consequences of habitat selection. *Am. Nat.*, 137: 91-115.
- Geise W. & Linsenmair K.E. 1988 – Adaptations of the reed frog *Hyperolius viridiflavus* (Amphibia, Anura, Hyperoliidae) to its arid environment. IV. Ecological significance of water economy with comments on thermoregulation and energy allocation. *Oecologia*, Berlin, 77: 327-338.
- John-Alder H.B., Morin P.J. & Lawler S. 1988 – Thermal physiology, phenology and distribution of tree frogs. *Am. Nat.*, 132: 506-520.
- Knowles T.W. & Weigl P.D. 1990 – Thermal dependence of anuran burst locomotor performance. *Copeia*, 1990: 796-802.
- Lillywhite H.B., Mittal A.K., Garg T.K. & Das I. 1998 – Basking behavior, sweating and thermal ecology of the Indian tree frog, *Polypedates maculates*. *J. Herp.*, 32: 169-175.
- Meek R. 1983 – Body temperatures of two species of desert amphibians *Rana perezi* and *Bufo mauritanicus*. *Brit. J. Herp.*, 6: 284-286.
- Meek R. & Jolley E. 2006 – Body temperatures of the common toad, *Bufo bufo*, in the Vendée, France. *Herp. Bull.*, 95: 21-24.
- Navas C.A. 1996 – Metabolic physiology, locomotory performance and thermal niche breadth in neotropical anurans. *Physiol. Zool.*, 69: 1481-1501.
- Pellet J. & Schmidt B.R. 2005 – Monitoring distributions using call surveys: estimating site occupancy, detection probabilities and inferring site absence. *Biol. Cons.*, 123: 223-234.
- Pellet J., Rechsteiner L., Skrivervik A.K., Zuercher J.-F. & Perrin N. 2006 – Use of the Harmonic Direction Finder to study the terrestrial habitats of the European tree frog (*Hyla arborea*). *Amphibia-Reptilia*, 27: 138-142.
- Pellet J., Schmidt B.R., Fivaz F., Perrin N. & Grossenbacher K. 2006 – Density, climate and varying return points: an analysis of long term population fluctuations in the threatened European tree frog. *Oecologia*, Berlin, 149: 65-71.
- Riechert S.E. & Tracy C.R. 1975 – Thermal balance and prey availability – bases for a model relating web site characteristics to spider reproductive success. *Ecology*, 56: 265-284.
- Shoemaker V.H., Hillman S.S., Hillyard S.D., Jackson D.C., McClanahan L.L., Withers P.C. & Wygoda M.L. 1992 – Exchange of water, ions and respiratory gases in terrestrial amphibians. In Feder M.E. & Burggren W.W. (Eds): Environmental Physiology of the Amphibians, p. 125-150. Chicago, University of Chicago Press, 697 p.

Shoemaker V.H., McClanahan L.L., Withers P.C., Hillman S.S. & Drewe R.C. 1987 – Thermoregulatory response to heat in the waterproof frogs *Phyllomedusa* and *Chiromantis*. *Physiol. Zool.*, 60: 365-372.

Snyder G.K. & Hammerson G.A. 1993 – Interrelationships between water economy and thermoregulation in the Canyon tree-frog *Hyla arenicolor*. *J. Arid Environ.*, 25: 321-329.

Stumpel A.H.P. 1987 – Distribution and present numbers of the tree frog *Hyla arborea* in Zeeland Flanders, the Netherlands. *Bijdr. Dierkd.*, 57: 151-163.

Stumpel A.H.P. 1993 – The terrestrial habitat of *Hyla arborea*. In Stumpel A.H.P. & Tester U. (Eds): *The Ecology and Conservation of the European tree frog*, p. 47-54. Wageningen, Netherlands, Institute for Forestry and Nature Research.

Tracy C.R. & Christian K.A. 2005 – Preferred temperature correlates with evaporative water loss in Hylid frogs from Northern Australia. *Physiol. Biochem. Zool.*, 78: 839-846.

Wells K.D. 2007 – *The Ecology and Behaviour of Amphibians*. Chicago, University of Chicago Press, 1400 p.

Wygoda M.L. & Williams A.A. 1991 – Body temperatures of free-ranging green tree frogs (*Hyla cinerea*): a comparison with typical frogs. *Herpetologica*, 47: 328-335.

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