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# SIZE INFERENCES BASED ON SKELETAL FRAGMENTS OF THE COMMON EUROPEAN FROG *RANA TEMPORARIA* L.

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Based on a museum collection of skeletons of adult *Rana temporaria* (Ranidae) from a single population in the French Doubs region, equations for regression that predict the size (total length) and mass (total weight) of the animals are presented. Twenty- six measurements based on skeletal elements were selected as independent variables for the regressions, representing the most common fragments recovered in ecological and palaeontological studies. Equations are given for males on all variables, and for males and females jointly in the 11 variables that showed no significant sexual dimorphism in the three-year age class subsample. Proximo-distal lengths are better predictors in general than transverse.

## INTRODUCTION

The common frog, *Rana temporaria* L., is widespread throughout Europe, and is probably the most frequent amphibian prey item (Martín & López, 1990). It also has a substantial fossil record in the European Quaternary (e.g. Rage, 1974). Nevertheless, remains of predated frogs, as well as fossils, are usually broken and composed of disarticulated skeletal elements, and until now an estimate of frog size has rarely been possible with such material.

Based on a collection of numerous skeletons from a single French population of the nominal subspecies, it is the purpose of this paper to give some estimates of the regression parameters that could be used for determining frog size, if only skeletal fragments are available.

## MATERIALS AND METHODS

The *Rana temporaria temporaria* sample was from a population in the French region of Doubs, near Besançon (altitude 550 m) and was collected in late autumn just before their hibernation. It comprises 49 dry skeletons of adult frogs (32 males and 17 females), stored at the Laboratory of Comparative Anatomy, University of Paris VII. A detailed account of the techniques used for the preparation of the skeletons, previously used for other research purposes, is given in Castanet & Caetano (in press) and no specimen has been sacrificed for our study. The data collected include the snout-vent lengths (SVL) and total weight (TWeight) of the specimens, taken immediately after death, as well as their age class inferred from skeletochronology. The skeletons are disarticulated and nearly complete, but some elements (in particular, tibiofibulae) were used for histology and bone density estimations and are not available.

The different bones were measured either directly using a digital Nikon Measurescope 10 (up to 0.01 mm) or indirectly through scale projections made with a binocular drawing tube. The twenty-six selected variables are represented in Fig. 1, and were described in Sanchiz (1984) and Esteban & Sanchiz (1985) (ilium). On account of their potential preservation as prey remains or fossils, only bone fragments are considered, but not their surrounding cartilaginous or calcified tissues. The complete data are available from the Secretary, Department of Biodiversity, at the address of one of the authors (BS).

Least squares regressions for predicting size were selected following Smith (1994). The statistical package Statgraphics (Anonymous, 1991) was used for the calculations (significance level, $P = 0.05$). The osteological criteria of Rage (1974) and Böhme (1977) were used for species determination. Sexes were determined directly in the cases of humeri and radioulnae (males having sexual crests) or indirectly through measurements (Table 1).

## RESULTS

As the age class of individual frogs is known from previous skeletochronological studies, the estimation of the sexual dimorphism of the different measurements can be tested for the same age class, in our case the three-year-old cohort, having two lines of winter-arrested growth. Testing of dimorphism at the same age class contributes to the elimination of a biased representation of unequal age subsamples. Kolmogorov-Smirnov tests indicate that none of the selected variables significantly differ from normality (grouped, by sexes or by sexes and age classes). Nevertheless, since the female sample is rather small, non-parametric approaches (Mann-Whitney *U* tests) were used to compare males and females. Significant differences ($P<0.05$) were found in 15 variables, including, as expected, all those functionally related to amplexus. There are no significant size (SVL) differences between sexes in the three-year-old subsample.

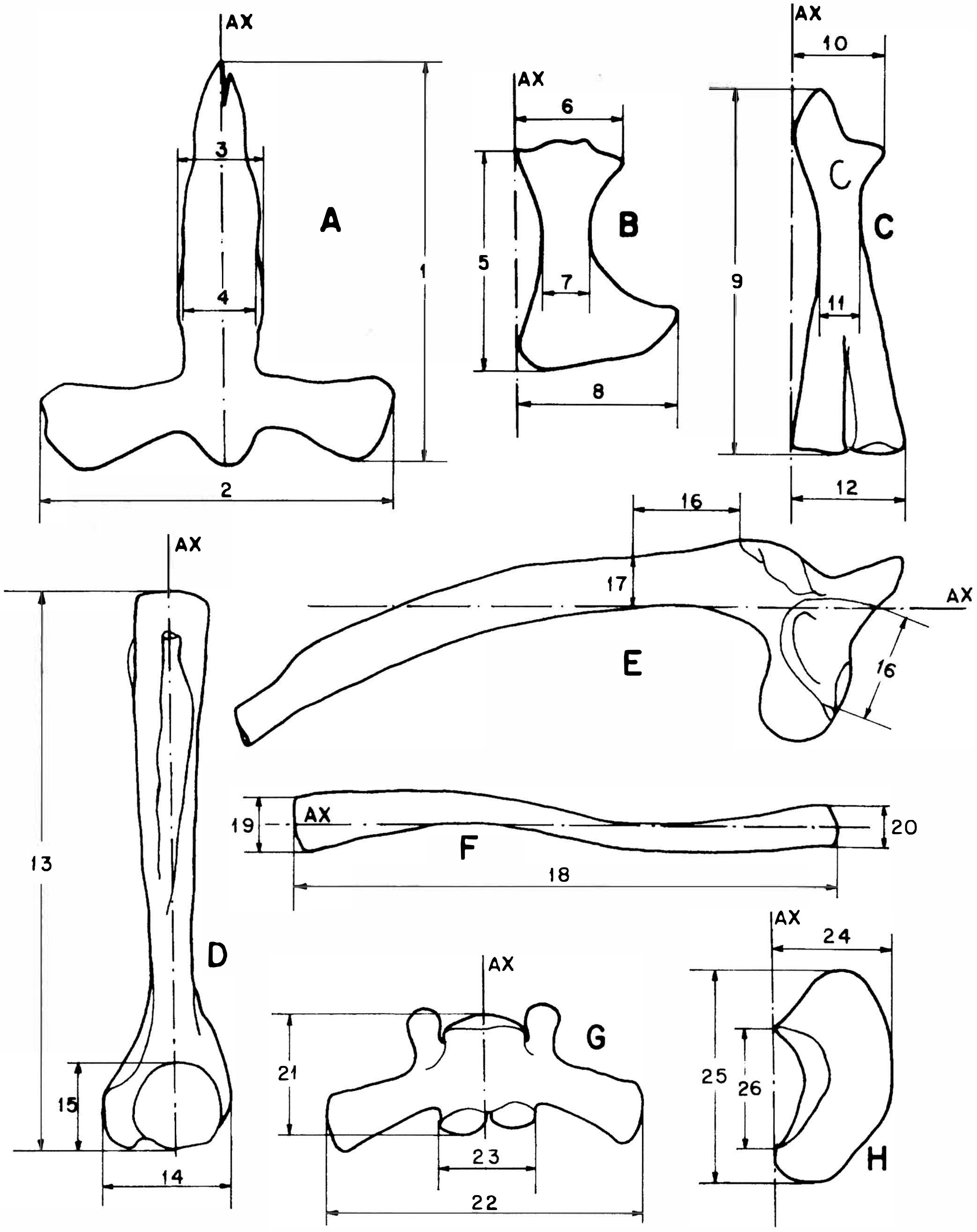

FIG 1. Schematic shapes showing the measurements used. (Their numbers are in parentheses in Table 1). *AX*: main orientation axis for each bone. With the exception of the ilium, measurements are either orthogonal or parallel to the axis. A: parasphenoid. B: coracoid. C: radioulna. D: humerus. E: ilium. F: femur. G: sacrum. H: ischium. Not to scale.

TABLE 1. Basic statistics of the sample. *n*: number of specimens. SD: standard deviation. T: type of measurement (L: length, W: width at the proximal or distal ends of the bone, Z: other measurements). $P_D$ :approximate two-tailed probability in the Mann-Whitney *U* test for sexual dimorphism. Variables are defined in Figure 1; numbers in parentheses correspond to those in the drawings. In the names of the variables, L refers to length, W to width, and p, m, c and d to, respectively, the proximal, middle, central and distal parts of the bone fragment.

| | | males | | | | | females | | | | | males + females | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Variable | T | *n* | mean | SD | min | max | *n* | mean | SD | min | max | *n* | mean | SD | min | max | $P_D$ |
| TWeight | | 32 | 24.37 | 5.03 | 15.14 | 34.45 | 17.0 | 30.73 | 5.62 | 19.91 | 37.51 | 49 | 26.57 | 6.02 | 15.14 | 37.51 | 0.600 |
| SVL | | 32 | 62.97 | 4.32 | 54.00 | 71.00 | 17.0 | 68.53 | 3.76 | 63.00 | 75.00 | 49 | 64.90 | 4.89 | 54.00 | 75.00 | 0.861 |
| Lparas (01) | L | 32 | 11.49 | 0.81 | 9.97 | 12.88 | 16.0 | 12.22 | 0.84 | 10.83 | 13.91 | 48 | 11.73 | 0.88 | 9.97 | 13.91 | 0.383 |
| Wtparas (02) | W | 32 | 9.94 | 0.70 | 8.56 | 11.20 | 16.0 | 10.63 | 0.69 | 9.20 | 11.91 | 48 | 10.17 | 0.76 | 8.56 | 11.91 | 0.541 |
| Wcparas (03) | W | 32 | 2.45 | 0.25 | 2.03 | 2.99 | 16.0 | 2.59 | 0.22 | 2.24 | 2.97 | 48 | 2.50 | 0.25 | 2.03 | 2.99 | 0.190 |
| Wmparas (04) | Z | 32 | 2.10 | 0.27 | 1.63 | 2.61 | 16.0 | 2.14 | 0.24 | 1.62 | 2.47 | 48 | 2.11 | 0.26 | 1.62 | 2.61 | 0.512 |
| Wcorac (05) | L | 32 | 6.23 | 0.48 | 5.38 | 7.22 | 17.0 | 6.61 | 0.62 | 5.55 | 7.38 | 49 | 6.36 | 0.56 | 5.38 | 7.38 | 0.116 |
| Lpcorac (06) | W | 32 | 3.10 | 0.26 | 2.66 | 3.56 | 17.0 | 2.95 | 0.25 | 2.49 | 3.40 | 49 | 3.05 | 0.26 | 2.49 | 3.56 | <0.01 |
| Lmcorac (07) | Z | 32 | 1.44 | 0.17 | 1.03 | 1.79 | 17.0 | 1.40 | 0.15 | 1.08 | 1.56 | 49 | 1.43 | 0.16 | 1.03 | 1.79 | 0.116 |
| Ldcorac (08) | W | 32 | 4.81 | 0.36 | 4.08 | 5.46 | 17.0 | 4.64 | 0.47 | 3.98 | 5.54 | 49 | 4.75 | 0.40 | 3.98 | 5.54 | <0.01 |
| Lradul (09) | L | 31 | 11.86 | 1.02 | 10.37 | 14.03 | 17.0 | 10.83 | 0.98 | 8.94 | 12.53 | 48 | 11.49 | 1.11 | 8.94 | 14.03 | <0.01 |
| Wpradul (10) | W | 31 | 3.23 | 0.29 | 2.69 | 3.78 | 17.0 | 2.97 | 0.25 | 2.55 | 3.35 | 48 | 3.13 | 0.30 | 2.55 | 3.78 | <0.01 |
| Wcradul (11) | Z | 31 | 1.67 | 0.19 | 1.36 | 2.04 | 17.0 | 1.39 | 0.13 | 1.16 | 1.64 | 48 | 1.57 | 0.22 | 1.16 | 2.04 | <0.01 |
| Wdradul (12) | W | 31 | 3.66 | 0.35 | 3.14 | 4.45 | 17.0 | 3.61 | 0.27 | 3.11 | 4.16 | 48 | 3.64 | 0.32 | 3.11 | 4.45 | 0.032 |
| Lhumer (13) | L | 21 | 16.66 | 1.09 | 14.30 | 19.18 | 6.0 | 15.03 | 1.15 | 13.43 | 16.44 | 27 | 16.30 | 1.28 | 13.43 | 19.18 | 0.028 |
| Whumer (14) | W | 21 | 3.75 | 0.36 | 3.18 | 4.49 | 6.0 | 3.25 | 0.22 | 2.99 | 3.54 | 27 | 3.64 | 0.39 | 2.99 | 4.49 | 0.028 |
| Lcondyle (15) | Z | 21 | 2.50 | 0.26 | 2.07 | 3.02 | 6.0 | 2.14 | 0.26 | 1.82 | 2.48 | 27 | 2.42 | 0.30 | 1.82 | 3.02 | 0.028 |
| Acetab (16) | Z | 30 | 3.33 | 0.32 | 2.79 | 4.01 | 17.0 | 3.37 | 0.24 | 2.89 | 3.77 | 47 | 3.35 | 0.29 | 2.79 | 4.01 | 0.116 |
| Hilia (17) | W | 30 | 2.08 | 0.23 | 1.70 | 2.60 | 17.0 | 1.99 | 0.22 | 1.68 | 2.51 | 47 | 2.05 | 0.23 | 1.68 | 2.60 | 0.274 |
| Lfemur (18) | L | 32 | 27.62 | 2.32 | 23.53 | 32.25 | 16.0 | 27.93 | 2.16 | 23.81 | 31.15 | 48 | 27.73 | 2.25 | 23.53 | 32.25 | 0.029 |
| Wdfemur (19) | W | 32 | 2.84 | 0.22 | 2.37 | 3.34 | 16.0 | 3.06 | 0.18 | 2.83 | 3.34 | 48 | 2.91 | 0.23 | 2.37 | 3.34 | 0.512 |
| Wpfemur (20) | W | 32 | 2.13 | 0.21 | 1.72 | 2.59 | 16.0 | 2.30 | 0.18 | 1.95 | 2.57 | 48 | 2.19 | 0.21 | 1.72 | 2.59 | 0.541 |
| Lsacrum (21) | L | 30 | 3.22 | 0.32 | 2.66 | 3.85 | 11.0 | 3.32 | 0.32 | 2.80 | 3.74 | 41 | 3.25 | 0.32 | 2.66 | 3.85 | 0.019 |
| Wsacrum (22) | W | 30 | 9.26 | 0.87 | 7.07 | 11.13 | 11.0 | 9.67 | 1.06 | 8.28 | 11.34 | 41 | 9.37 | 0.93 | 7.07 | 11.34 | 0.049 |
| Wdsacrum (23) | Z | 30 | 2.83 | 0.22 | 2.40 | 3.34 | 11.0 | 2.90 | 0.19 | 2.61 | 3.25 | 41 | 2.85 | 0.21 | 2.40 | 3.34 | 0.339 |
| Lischium (24) | L | 32 | 3.15 | 0.34 | 2.50 | 3.99 | 17.0 | 3.24 | 0.31 | 2.80 | 3.67 | 49 | 3.18 | 0.33 | 2.50 | 3.99 | <0.01 |
| Hischium (25) | W | 32 | 5.52 | 0.57 | 4.38 | 6.50 | 17.0 | 5.69 | 0.55 | 4.62 | 6.52 | 49 | 5.58 | 0.56 | 4.38 | 6.52 | <0.01 |
| Hcischium (26) | Z | 32 | 3.19 | 0.37 | 2.47 | 3.85 | 17.0 | 3.22 | 0.24 | 2.72 | 3.69 | 49 | 3.20 | 0.33 | 2.47 | 3.85 | 0.040 |

TABLE 2. Equations for the estimation of size (SVL=$Y$) based on measurements on skeletal fragments. Linear regression, $Y = A + BX$, being (A: intercept, B: slope, SE: standard error of the estimate). Power function model, $Y = aX^b$, being Ln a: intercept in natural logarithms, b: slope, SE: standard error of the estimate). $R$: coefficient of determination.

| | | males | | | | | | | males + females | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Variable | | *R* | A | B | SE | Ln a | b | SE | *R* | A | B | SE | Ln a | b | SE |
| Tweight | | 0.92 | 42.86 | 0.82 | 1.223 | 3.12 | 0.32 | 0.017 | | | | | | | |
| Lparas | (01) | 0.76 | 9.50 | 4.65 | 2.125 | 2.06 | 0.85 | 0.033 | 0.76 | 8.19 | 4.83 | 2.494 | 1.99 | 0.89 | 0.038 |
| Wtparas | (02) | 0.53 | 18.28 | 4.49 | 3.011 | 2.50 | 0.72 | 0.047 | 0.62 | 13.11 | 5.09 | 3.084 | 2.30 | 0.80 | 0.047 |
| Wcparas | (03) | 0.42 | 35.51 | 11.19 | 3.318 | 3.74 | 0.45 | 0.051 | 0.45 | 31.44 | 13.40 | 3.690 | 3.69 | 0.53 | 0.056 |
| Wmparas | (04) | 0.18 | 49.08 | 6.62 | 3.994 | 3.98 | 0.21 | 0.064 | 0.18 | 47.81 | 8.10 | 4.521 | 3.98 | 0.26 | 0.070 |
| Wcorac | (05) | 0.74 | 14.05 | 7.85 | 2.211 | 2.71 | 0.78 | 0.035 | 0.72 | 17.27 | 7.48 | 2.598 | 2.82 | 0.73 | 0.041 |
| Lpcorac | (06) | 0.62 | 22.01 | 13.22 | 2.716 | 3.42 | 0.64 | 0.044 | | | | | | | |
| Lmcorac | (07) | 0.53 | 35.67 | 18.93 | 3.007 | 3.99 | 0.43 | 0.048 | 0.27 | 42.24 | 15.88 | 4.221 | 4.05 | 0.35 | 0.065 |
| Ldcorac | (08) | 0.64 | 16.22 | 9.71 | 2.626 | 3.00 | 0.73 | 0.042 | | | | | | | |
| Lradul | (09) | 0.71 | 20.07 | 3.62 | 2.402 | 2.42 | 0.70 | 0.038 | | | | | | | |
| Wpradul | (10) | 0.64 | 23.73 | 12.17 | 2.668 | 3.41 | 0.62 | 0.041 | | | | | | | |
| Wcradul | (11) | 0.50 | 35.18 | 16.65 | 3.135 | 3.91 | 0.45 | 0.048 | | | | | | | |
| Wdradul | (12) | 0.56 | 28.79 | 9.35 | 2.933 | 3.40 | 0.57 | 0.045 | | | | | | | |
| Lhumer | (13) | 0.76 | 5.42 | 3.37 | 2.150 | 1.56 | 0.91 | 0.034 | | | | | | | |
| Whumer | (14) | 0.88 | 20.11 | 11.05 | 1.515 | 3.23 | 0.68 | 0.025 | | | | | | | |
| Lcondyle | (15) | 0.79 | 26.03 | 14.23 | 1.953 | 3.60 | 0.57 | 0.032 | | | | | | | |
| Acetab | (16) | 0.49 | 32.60 | 9.20 | 3.106 | 3.54 | 0.50 | 0.049 | 0.40 | 30.99 | 10.21 | 3.775 | 3.52 | 0.55 | 0.057 |
| Hilia | (17) | 0.53 | 35.34 | 13.40 | 2.942 | 3.83 | 0.43 | 0.048 | 0.15 | 48.70 | 8.03 | 4.471 | 3.99 | 0.25 | 0.069 |
| Lfemur | (18) | 0.79 | 17.13 | 1.66 | 1.985 | 1.68 | 0.74 | 0.031 | | | | | | | |
| Wdfemur | (19) | 0.52 | 22.58 | 14.24 | 3.064 | 3.47 | 0.65 | 0.048 | 0.46 | 22.79 | 14.43 | 3.614 | 3.46 | 0.66 | 0.055 |
| Wpfemur | (20) | 0.30 | 39.43 | 11.03 | 3.677 | 3.85 | 0.39 | 0.058 | 0.44 | 32.08 | 14.95 | 3.714 | 3.77 | 0.50 | 0.057 |
| Lsacrum | (21) | 0.55 | 31.00 | 9.95 | 3.023 | 3.54 | 0.52 | 0.047 | | | | | | | |
| Wsacrum | (22) | 0.79 | 21.31 | 4.51 | 2.044 | 2.69 | 0.65 | 0.033 | | | | | | | |
| Wdsacrum | (23) | 0.38 | 28.00 | 12.38 | 3.492 | 3.55 | 0.57 | 0.054 | 0.40 | 22.43 | 14.76 | 3.892 | 3.47 | 0.67 | 0.060 |
| Lischium | (24) | 0.64 | 31.20 | 10.08 | 2.647 | 3.56 | 0.51 | 0.041 | | | | | | | |
| Hischium | (25) | 0.69 | 28.16 | 6.31 | 2.425 | 3.20 | 0.55 | 0.038 | | | | | | | |
| Hcischium | (26) | 0.77 | 29.89 | 10.36 | 2.107 | 3.53 | 0.52 | 0.033 | | | | | | | |

TABLE 3. Equations for the estimation of the total weight (TWeight=*Y*) based on measurements on skeletal fragments. Abbreviations as in Table 2.

| | | males | | | | | | | males + females | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Variable | | *R* | A | B | SE | Ln *a* | *b* | SE | *R* | A | B | SE | Ln *a* | *b* | SE |
| SVL | | 0.92 | -46.03 | 1.12 | 1.424 | -8.91 | 2.92 | 0.052 | | | | | | | |
| Lparas | (01) | 0.77 | -38.28 | 5.45 | 2.419 | -3.16 | 2.60 | 0.097 | 0.76 | -43.56 | 5.98 | 2.995 | -3.41 | 2.71 | 0.114 |
| Wtparas | (02) | 0.61 | -31.34 | 5.60 | 3.201 | -2.17 | 2.33 | 0.127 | 0.71 | -41.10 | 6.66 | 3.356 | -2.76 | 2.60 | 0.127 |
| Wcparas | (03) | 0.46 | -8.71 | 13.48 | 3.757 | 1.90 | 1.42 | 0.147 | 0.52 | -17.47 | 17.65 | 4.240 | 1.68 | 1.73 | 0.157 |
| Wmparas | (04) | 0.24 | 5.46 | 9.01 | 4.466 | 2.62 | 0.76 | 0.184 | 0.22 | 3.46 | 10.97 | 5.419 | 2.62 | 0.86 | 0.209 |
| Wcorac | (05) | 0.71 | -31.30 | 8.93 | 2.737 | -1.07 | 2.32 | 0.110 | 0.76 | -33.40 | 9.42 | 2.994 | -0.98 | 2.29 | 0.115 |
| Lpcorac | (06) | 0.58 | -21.90 | 14.94 | 3.306 | 1.06 | 1.88 | 0.138 | | | | | | | |
| Lmcorac | (07) | 0.55 | -7.75 | 22.27 | 3.456 | 2.70 | 1.32 | 0.139 | 0.31 | -3.47 | 21.05 | 5.038 | 2.84 | 1.18 | 0.188 |
| Ldcorac | (08) | 0.64 | -29.77 | 11.25 | 3.083 | -0.30 | 2.21 | 0.124 | | | | | | | |
| Lradul | (09) | 0.79 | -28.49 | 4.46 | 2.335 | -2.24 | 2.19 | 0.099 | | | | | | | |
| Wpradul | (10) | 0.66 | -21.69 | 14.29 | 3.050 | 0.93 | 1.92 | 0.120 | | | | | | | |
| Wcradul | (11) | 0.50 | -7.88 | 19.33 | 3.652 | 2.47 | 1.39 | 0.143 | | | | | | | |
| Wdradul | (12) | 0.64 | -17.65 | 11.50 | 3.136 | 0.83 | 1.82 | 0.123 | | | | | | | |
| Lhumer | (13) | 0.83 | -47.16 | 4.20 | 2.195 | -5.12 | 2.93 | 0.089 | | | | | | | |
| Whumer | (14) | 0.86 | -26.42 | 13.12 | 1.890 | 0.36 | 2.08 | 0.078 | | | | | | | |
| Lcondyle | (15) | 0.81 | -20.18 | 17.22 | 2.213 | 1.47 | 1.80 | 0.088 | | | | | | | |
| Acetab | (16) | 0.62 | -16.55 | 12.37 | 3.114 | 1.14 | 1.71 | 0.130 | 0.48 | -20.04 | 14.01 | 4.371 | 1.05 | 1.84 | 0.164 |
| Hilia | (17) | 0.52 | -7.70 | 15.54 | 3.553 | 2.23 | 1.31 | 0.148 | 0.17 | 4.94 | 10.70 | 5.506 | 2.65 | 0.86 | 0.209 |
| Lfemur | (18) | 0.86 | -31.10 | 2.01 | 1.913 | -4.49 | 2.31 | 0.078 | | | | | | | |
| Wdfemur | (19) | 0.50 | -21.97 | 16.34 | 3.619 | 1.17 | 1.93 | 0.146 | 0.36 | -19.01 | 15.60 | 4.787 | 1.31 | 1.82 | 0.178 |
| Wpfemur | (20) | 0.35 | -5.06 | 13.79 | 4.136 | 2.23 | 1.26 | 0.167 | 0.40 | -11.93 | 17.51 | 4.650 | 2.09 | 1.49 | 0.176 |
| Lsacrum | (21) | 0.61 | -14.67 | 12.18 | 3.267 | 1.28 | 1.63 | 0.130 | | | | | | | |
| Wsacrum | (22) | 0.79 | -24.05 | 5.25 | 2.339 | -1.24 | 1.99 | 0.093 | | | | | | | |
| Wdsacrum | (23) | 0.50 | -21.77 | 16.37 | 3.648 | 1.18 | 1.92 | 0.149 | 0.48 | -28.24 | 19.06 | 4.321 | 1.01 | 2.13 | 0.166 |
| Lischium | (24) | 0.69 | -14.18 | 12.23 | 2.836 | 1.32 | 1.62 | 0.111 | | | | | | | |
| Hischium | (25) | 0.74 | -17.32 | 7.55 | 2.628 | 0.24 | 1.72 | 0.106 | | | | | | | |
| Hcischium | (26) | 0.77 | -14.37 | 12.13 | 2.403 | 1.33 | 1.60 | 0.097 | | | | | | | |

The use of one subsample of the same age is here merely restricted to the determination of which variables should be analysed jointly or separately by sexes. Having determined the dimorphic status of the variables, all the available material is incorporated in the regressions, regardless of their age.

The parameters for the linear ($Y = A + BX$) and power ($Y = aX^b$) estimated regressions (Tables 2 and 3), and their standard errors, are given for males in all the variables and for the whole population (males + females) in the 11 variables that showed no sexual dimorphism. The complete female sample ($N = 17$) is not large enough to provide adequate estimations by itself. Dependent variables are total length or weight in all cases. Adequacy of the model to be chosen depends on the context of the study and the further use of the inference in particular cases. Nevertheless, the power function models obtained here, with related allometric slopes close to isometry (in the corresponding equations where size is the independent variable instead of the dependent one; e.g. Gould, 1966), give similar results to the linear one when applied to this rather homogeneous group of adults.

In a general way, lengths over the main axis of bones (usually proximo-distal lengths) are better predictors of size or mass than transverse measurements (widths). This result can be verified through the comparison of the correlation coefficients of both groups, which are significantly different ($P<0.05$ in the Mann-Whitney $U$ test). This result has been described in mammals (Alberdi, Prado & Ortiz-Jaureguizar, in press) and probably derives from mechanisms of growth control, not only from a bias in measurement errors. Lengths are probably less environmentally affected than widths during growth. If a range of skeletal material is available from the same specimen, the most appropriate measurements to estimate its size or weight can be selected, based on the coefficients of determination (Tables 2 and 3).

## DISCUSSION

The composition of the sample imposes several limitations to the results. In the first place, the sample incorporates only adult frogs that hibernated for up to three winters. These cohorts correspond to the most frequent ages in the populations from which the frogs were sampled (Augert & Joly, 1993). Froglets are not included and our regressions should not be used to predict juvenile sizes. For similar reasons, values obtained by extrapolation to larger sizes should be considered merely as tentative, and not to be used in other statistical calculations.

Another possible limitation of the data derives from the taxonomic differentiation of the species. It is presently unknown, but it could be expected that the other described subspecies of *Rana temporaria*, namely *R. t. parvipalmata* (northwest Iberia), *R. t. canigonensis* (Pyrenees) and *R. t. honnorati* (Alps) could have ontogenetic and growth trajectories different from the one represented by our sample. This distorting effect is more likely to occur in the case of *R. t. parvipalmata*, genetically well differentiated and approaching full species status (Arano, Esteban & Herrero, 1993) than in the other subspecies, whose validity in open to question (Dubois, 1982, 1983).

Both limitations mentioned above apply to the fossil *Rana mehelyi*, a rather common but controversial Pleistocene taxon in central Europe. This fossil has been considered as an extinct species, closely related to the living common grass frog (Dely, 1955), or merely as an extreme large-sized morphotype of *R. temporaria* (Rage, 1972; Bailón & Rage, 1992). Extreme caution should be taken for inferences in this context, as well as in other Quaternary cases characterized by the very large size of the fossil remains (Böhme, 1982).

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