

# Field body temperatures and heating rates in a montane frog population: the importance of black dorsal pattern for thermoregulation

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Thermoregulation is particularly important for amphibians under heterothermic high-altitude conditions, but remains largely unstudied in montane frogs. Field body temperatures (7.2–26.5 °C) in a Pyrenean population of the common frog (*Rana temporaria*) at 2100 m altitude were significantly higher than environmental temperatures (air, substrate, water) during the day. At night, the highest body temperatures were observed in individuals in the pond, which acted as a temperature buffer during the nocturnal drop in air temperature. Our results indicate active thermoregulation in these frogs, which was also verified by the observational data on basking individuals. No influence of the amount of black dorsal pattern on body temperatures was found in the field data, but body temperatures of individuals exposed experimentally to the sun were higher in dark than in lighter individuals. These trends were similar to those found in melanistic snakes, and support the hypothesis that the black pattern in montane *Rana temporaria* may provide benefits in terms of time allocation by enabling frogs to attain their preferred body temperatures more quickly.



**Fig. 1.** *Rana temporaria* individuals from the study pond (Ibón de las Ranas) without (left; coded as 1) and with extended black dorsal pattern (right; coded as 6).

## Introduction

Body temperature has an important influence on physiological and behavioural performance of ectothermic animals. These effects are well documented in reptiles (e.g., Huey 1982, Lillywhite 1987, Huey & Kingsolver 1989), as are their means of attaining optimum body temperatures by thermoregulation (Avery 1982, Hertz *et al.* 1993, Bauwens *et al.* 1996, Díaz *et al.* 1996, Castilla *et al.* 1999). In contrast, surprisingly few studies have investigated thermoregulatory behaviour of amphibians (but see Brattstrom 1979), with the exception of studies performed with species living in extreme xeric environments (e.g., Lillywhite *et al.* 1998, Shoemaker *et al.* 1987, 1989).

The common frog, *Rana temporaria*, is widely distributed in Europe and occurs over a wide array of different habitat types. Life history patterns of this species are known to vary along altitudinal and latitudinal gradients (Miaud *et al.* 1999, Merilä *et al.* 2000). Behavioural patterns also vary among populations: *Rana temporaria* is largely nocturnal at low altitudes but shows strong diurnal activity above 2000 m elevation in the Pyrenees (Vences *et al.* 2000). Furthermore these frogs are much more aquatic than lowland populations, most probably to avoid low nocturnal air temperatures (Vences *et al.* 2000). Individuals that can effectively buffer themselves against variations in the thermal environment might have substantial advantages under the heterothermic conditions at high alti-

tudes (Wollmuth *et al.* 1987).

A further characteristic of montane *Rana temporaria* is a dorsal pattern of deep black markings (Fig. 1) that expands ontogenetically, and can cover almost the complete dorsal surface in large adults (Riobó *et al.* 2000). Colours differ in reflectance, thereby influencing the rate at which solar radiation is converted into body heat; animals may, therefore, vary in the capacity to thermoregulate or in the efficiency of thermoregulation, depending on their colouration (Peterson *et al.* 1993). In snakes, melanistic individuals are known to heat faster and attain slightly higher temperatures than their lighter conspecifics (Gibson & Falls 1979, Forsman 1995), which may improve their performance in cold environments (e.g., Luiselli 1992, 1993).

Frogs are known to be declining globally, which may in part be related to increased UV-B exposure of eggs and embryos (Blaustein *et al.* 1994, Lizana & Pedraza 1998). Declines seem to affect especially montane frog populations (Blaustein & Wake 1995, La Marca & Lötters 1997). Diurnal activity and thermoregulation of montane frogs may be necessary to complete their life cycles in the limited periods of favourable climatic conditions. However, it also implies increased exposure to UV-B radiation. Dark markings in montane common frogs may be therefore be valuable to attain faster heating rates or higher body temperatures, and thereby performance benefits, or as protection against dangerous UV-B radiation.

We studied the thermal ecology of black-

patterned and normal-coloured common frogs. We analysed body temperatures in free-ranging Pyrenean *Rana temporaria* under different climatic conditions and in different microhabitats, and compared heating rates of individuals with extended black patterning to those of more lightly coloured individuals. We addressed three questions that are potentially informative with respect to the significance of the black pattern: (a) Do common frogs in montane environments actively select their microhabitat in order to attain higher temperatures than the surrounding environment? (b) Do free-ranging black-patterned individuals have higher body temperatures than light individuals? (c) Do heating rates and maximum body temperatures vary between dark-patterned and light individuals?

## Materials and methods

### Study area

Fieldwork was carried out around Ibón de las Ranas, a glacial lake in the Circo de Piedrafita area (2150 m), in the Central Pyrenees (Aragon region, Spain). The area and its *Rana temporaria* population have been described in more detail in Vences *et al.* (1999, 2000), Riobó *et al.* (2000) and Piqué *et al.* (2000).

### Field body temperatures

Individuals were captured and their body temperatures immediately measured by inserting a OF450/MD3037 probe, connected to a quick-reading Greisinger GTH 1200A digital thermometer (precision: 0.1 °C), 2–3 cm into the cloaca. For each individual, we recorded snout-vent length (SVL) to the nearest mm with a calliper, body mass to the nearest 0.1 g with a digital balance, and estimated the amount of black dorsal pattern (Fig. 1) according to the categories ranging from 1 (no or almost no black pattern) to 6 (dorsum almost completely covered by black pattern) as defined in Riobó *et al.* (2000). In addition, we recorded the distance of the individual from the pond shore, and measured air, substrate and water temperatures

at the capture site. For individuals found in the water, we measured substrate temperature at the nearest locality on the shore that was not directly in contact with the water of the pond. For individuals on the shore or on land we measured water temperature at the point nearest to the pond.

Considering previous knowledge on activity cycles and behavioural responses to different climatic conditions (Vences *et al.* 2000), we performed separate analyses depending on time and weather according to four criteria: individuals captured (1) during the day with sunshine, (2) during the day with rain, (3) during the night with clear sky, and (4) during the night with rain. Within each of these categories, the recorded data were further grouped depending on whether individuals were captured (a) in the water or in direct contact to water, (b) on the shore (up to 1 m from the water), or (c) far from the water (> 1 m distance). For simplicity, these habitat categories will be termed water, shore and land, respectively.

Using SPSS for Windows 10, we compared temperatures **among** these subdivisions using non-parametric Mann-Whitney *U*-tests. We calculated regressions of body temperatures on air, substrate and water temperature. To obtain a measure of which of the environmental temperatures exercises the most important influence on body temperature, we carried out analyses of covariance (ANCOVA), defining values of *y* (body temperatures) as the dependent variable, values of *x* (the environmental temperatures) as the covariate, and the different categories of environmental temperature (water, substrate, air) as factors. No regression analyses for data under rainy conditions were carried out due to small sample size.

In the largest data set (individuals captured during the day with sunshine), we further performed an ANCOVA with body mass as a covariate to test for a possible influence of the amount of black pattern on body temperature.

### Experimental body temperatures

To test for body temperature differences **among** colour morphs under experimental conditions,

we selected individuals (males only) of either very light colouration or with a large extension of black dorsal pattern. Individuals were first submerged for at least 10 min into the pond water, which had temperatures of 13–16 °C, and then each pair placed simultaneously in plastic containers covered with nylon nets and exposed to the sun. After 10 minutes their body temperatures were recorded. Using a binomial test, we compared the frequency of cases with the black patterned individual attaining a higher temperature than the light individual, expecting a random distribution as null hypothesis. Additionally we entered the differences between starting body temperature and final body temperature of each individual in an ANCOVA, to test simultaneously for influences of body mass, weather conditions and black pattern.

Since we expected an effect of individuals' body mass on their final body temperatures (due to a slower heating rate of heavier individuals), we matched them as closely as possible with respect to body mass. The average body mass over all experiments was  $24.9 \pm 4.8$  g (15.1–35.8 g) in the dark individuals and  $23.4 \pm 4.6$  g (13.5–38.7 g) in the light individuals. We followed a conservative approach in selecting mostly a dark individual with slightly higher body mass (and thus lower expected heating rate) than the light individual. In the “bright sun” category, the body masses were identical (to the nearest 0.1 g) in three experiments, the lighter individual was heavier in 28 experiments, and the dark individual was heavier in 94 experiments. The respective numbers in the “cloud/wind” category were 0, 30 and 104.

A total of 260 experiments of 10 minutes duration were carried out under natural conditions close to the shore of the study pond. Two categories of experiments were analyzed

separately: (1) those carried out at the time of maximum solar radiation (11–17 h), under clear skies and without wind (125 experiments; category “bright sun”), and (2) those carried out either before 11 h or after 17 h, or with partially cloudy skies or light to moderate wind (134 experiments; category “clouds/wind”).

### Heating rates and maximum body temperatures

To assess heating rates of different colour morphs we sacrificed two pairs of frogs (including one light coloured and one black patterned individual each) of similar body mass. The individuals were cooled down to similar temperatures (18 °C), and pairs were simultaneously exposed to the sun between 1100–1700 hrs when solar radiation was most intense. Using two digital thermometers, we recorded the time elapsed between each 1 °C temperature increase in both individuals. The experiments (eight repetitions per pair) were continued until no further increase of body temperature was observed.

## Results

### Field body temperatures

We measured field body temperatures in 422 individuals. Of these, 415 were males, and only seven were females (Table 1). The observed body temperatures ranged between 7.2 and 26.5 °C. An ANCOVA with body mass as a covariate revealed a significant difference among the four time/weather classes ( $F_{3,418} = 92.1$ ,  $P < 0.001$ ) and the three habitat classes ( $F_{2,419} = 4.3$ ,  $P < 0.05$ ), while no significant influence of the covariate

**Table 1.** Mean  $\pm$  S.D. (minimum and maximum) field body temperatures of *Rana temporaria* individuals around the Ibón de las Ranas, as measured in July 2000. Minimum and maximum values in parentheses.

	Day/sun ( $n = 272$ )	Day/rain ( $n = 45$ )	Night/clear sky ( $n = 80$ )	Night/rain ( $n = 25$ )
Individuals in water	17.7 $\pm$ 2.5 (12.8–25.1)	11.4 $\pm$ 1.6 (9.9–13.0)	14.2 $\pm$ 1.7 (9.8–17.3)	13.3 $\pm$ 1.8 (11.7–15.3)
Individuals on shore	19.4 $\pm$ 3.2 (10.2–26.5)	13.3 $\pm$ 2.7 (9.1–20.2)	11.8 $\pm$ 1.8 (8.5–14.3)	10.1 $\pm$ 2.6 (7.3–14.2)
Individuals on land	16.6 $\pm$ 3.5 (9.6–23.6)	13.9 $\pm$ 3.0 (9.6–20.2)	10.1 $\pm$ 1.8 (7.2–12.8)	9.1 $\pm$ 1.9 (7.3–12.8)
Total	18.6 $\pm$ 3.3 (9.6–26.5)	13.4 $\pm$ 2.7 (9.1–20.2)	13.0 $\pm$ 2.4 (7.2–17.3)	10.2 $\pm$ 2.6 (7.3–15.3)

was detected ( $P = 0.86$ ). Tukey's *post hoc* tests revealed highly significant ( $P < 0.001$ ) body temperature differences between all climatic/temporal and environmental categories except in the day/rain vs. the night/clear sky comparison.

In the diurnal observations, the highest mean temperatures corresponded to specimens outside of the water, and the mean body temperatures were usually higher than the respective environmental temperatures (Tables 1 and 2, Fig. 3). The strongest influences on body temperatures were exerted by substrate (individuals on shore and on land) and air temperatures (individuals in water) (Fig. 2). However, all values of  $r^2$  were low (Table 3), and between-regression differences (as revealed by ANCOVAs) were not significant in individuals in the water, but highly so in individuals on shore ( $P < 0.001$ ) and on land ( $P < 0.01$ ).

At night, the highest body temperatures corresponded to individuals captured in the water (Table 1), and the mean body temperatures at night were usually lower than the respective environmental temperatures (Table 2 and Fig. 3). The strongest influence on body temperature was exerted by water (individuals in water and on the shore) and substrate temperatures (individuals on land) (Fig. 2 and Table 3). Between-regression differences (as revealed by ANCOVAs) were not significant in individuals on shore, but were significant in individuals on land ( $P < 0.01$ ) and in water ( $P < 0.001$ ).

Body temperature of individuals with a substantial amount of black pattern was not significantly higher than that of individuals with lower amounts of black pattern (Table 4). An ANCOVA analysis with body mass as the covariate revealed significant support for the influence of habitat category ( $F_{2,269} = 7.9$ ,  $P < 0.001$ )

but not of body mass ( $P = 0.88$ ) or the amount of black dorsal pattern ( $F_{5,265} = 2.0$ ,  $P = 0.98$ ).

### Experimental body temperatures

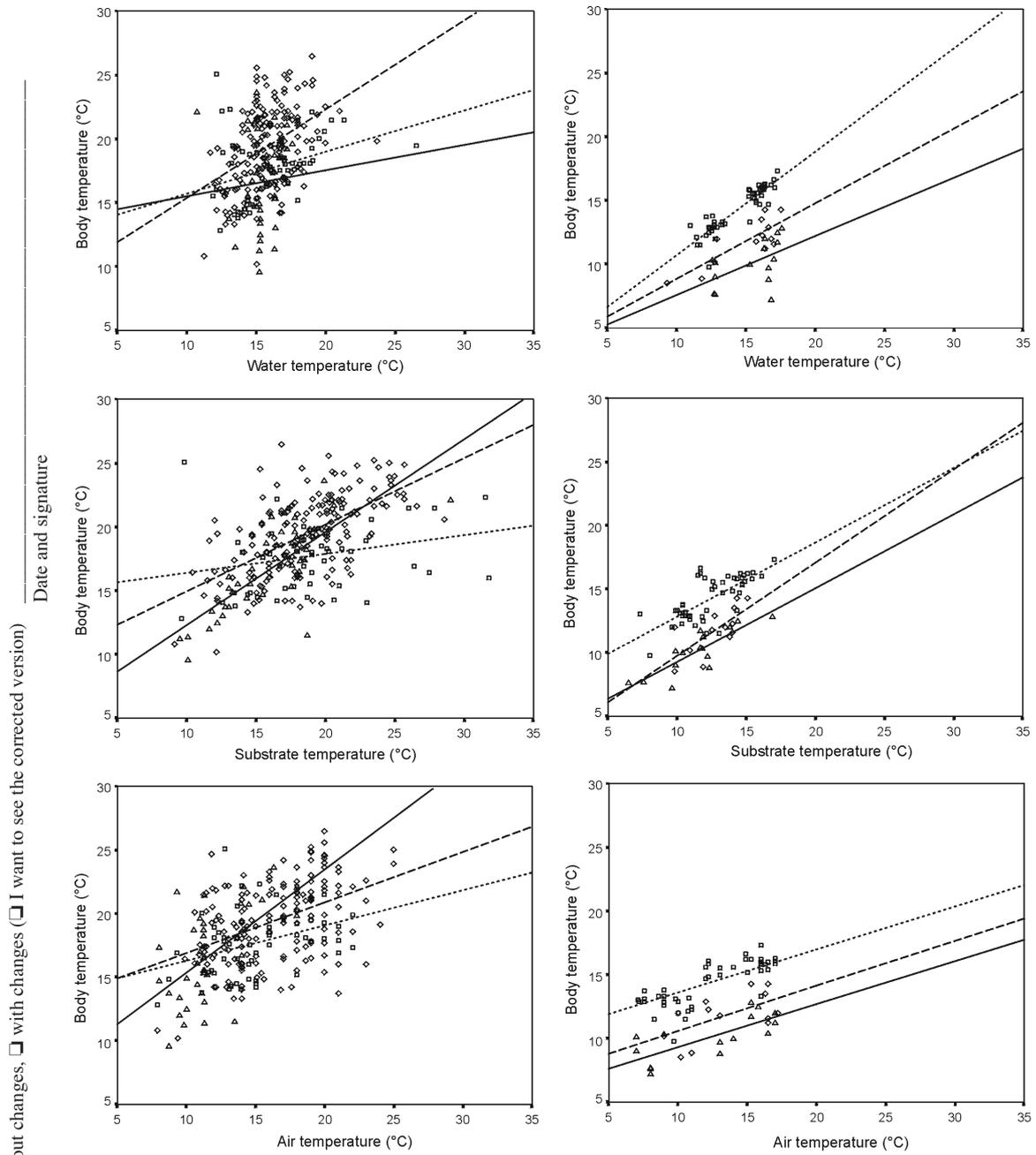
Neither in light nor in dark individuals did we find a significant correlation between the difference of starting and final body temperatures and body mass (Spearman rank correlation;  $P > 0.3$ ). In the "bright sun" category, the dark and the light individual had the same final body temperature in 10 cases, the light individual had a higher final body temperature in 39 cases, and the dark individual had a higher final body temperature in 76 cases (Fig. 4). The null hypothesis of a random (50%) distribution of final body temperatures was rejected (binomial test after exclusion of cases with equal temperatures;  $P < 0.001$ ). Final body temperatures were  $22.7 \pm 1.6$  °C (17.9–27.1 °C) in dark, and  $22.3 \pm 1.5$  °C (17.7–26.1 °C) in light individuals (Mann-Whitney *U*-test;  $P < 0.05$ ). The temperature increase (calculated by subtracting the starting body temperature from the final body temperature) was  $7.77 \pm 2.32$  °C (1.3–11.6 °C) in the dark individuals and  $7.40 \pm 2.14$  °C (1.1–11.1 °C) in the light individuals. This difference was not statistically significant.

In the "cloud/wind" category, the dark and the light individual had the same final body temperatures in three cases, the light individual had a higher final body temperature in 52 cases, and the dark individual had a higher final body temperature in 79 cases (Fig. 4); this difference was significant (binomial test;  $P < 0.05$ ). Final body temperatures were  $20.3 \pm 2.5$  °C (13.6–24.9 °C) in dark and  $20.1 \pm 2.6$  °C (13.9–25.3 °C) in light individuals (difference not

**Table 2.** Numbers and percentages of *Rana temporaria* individuals having field body temperatures higher than the respective environmental temperatures (air, water, substrate). The last column gives the goodness of fit statistics from a general loglinear analysis of differences between time/weather categories.

	Day/sun	Day/rain	Night/clear sky	Night/rain	Significance
$T_{\text{individual}} > T_{\text{air}}$	220 (81%)	43 (96%)	48 (60%)	21 (84%)	***
$T_{\text{individual}} > T_{\text{water}}$	222 (82%)	21 (47%)	22 (28%)	1 (4%)	***
$T_{\text{individual}} > T_{\text{substrate}}$	167 (61%)	35 (78%)	53 (66%)	9 (36%)	**

\*\*  $P < 0.01$ , \*\*\*  $P < 0.001$



**Fig. 2.** Scatterplots of field body temperatures of *Rana temporaria* captured around the study pond vs. environmental temperatures (water, substrate and air). The left row of graphs is based on measurements during the day under sunshine conditions, the right row on measurements at night (clear sky). Data and regression lines are given separately for individuals captured on land (triangular symbols; continuous line), on the shore (rhomboid symbols; dashed line) and in the water (square symbols; dotted line). Measurements under rainy conditions were not analyzed due to low sample sizes.

significant;  $P > 0.4$ ). The temperature increase was  $4.97 \pm 2.76$  °C ( $-1.9$ – $10.2$  °C) in the dark individuals,  $4.77 \pm 2.78$  °C ( $-1.6$ – $10.1$  °C) in the light individuals (difference not significant). Negative values (temperature decreases) were only obtained in a few experiments with the influence of wind.

An ANCOVA with body mass as a covariate gave highly significant evidence for the influence of the amount of black dorsal pattern ( $F_{6,511} = 22.8$ ,  $P < 0.001$ ) and of the weather (“bright sun” versus “cloud/wind”;  $F_{1,516} = 30.8$ ,  $P < 0.001$ ) on the difference between starting and final body temperature of the individuals; in contrast, the influence of body mass was not significant ( $P > 0.7$ ).

### Experimental heating rates

The maximum temperatures attained under “bright sun” conditions (see previous section) by the dark individuals in the 16 separate experiments were  $24$ – $35$  °C ( $31.1 \pm 2.8$  °C), while those of the light individuals were  $25$ – $33$ °C ( $29.6 \pm 2.1$  °C; Mann-Whitney  $U$ -test;  $U_{16,16} = 72.5$ ,  $P = 0.06$ ). The maximum temperatures were attained after  $1020$ – $2549$  s ( $1585 \pm 421$

s) and  $1020$ – $2284$  s ( $1602 \pm 414$  s) for dark and light individuals, respectively (Mann-Whitney  $U$ -test;  $U_{16,16} = 95.0$ ,  $P > 0.3$ ). The time intervals that elapsed between each heating step of  $1$ °C differed between the two groups (Mann-Whitney  $U$ -test;  $U_{195,172} = 14313.5$ ,  $P < 0.05$ ), the dark individuals needing a shorter period of time to heat up. The time needed for temperature increments of  $1$  °C increased with temperature, but this tendency was more pronounced for the light individuals (between-regression differences; ANCOVA;  $F_{1,33} = 18.2$ ,  $P < 0.001$ ) than for the dark ones (Fig. 5).

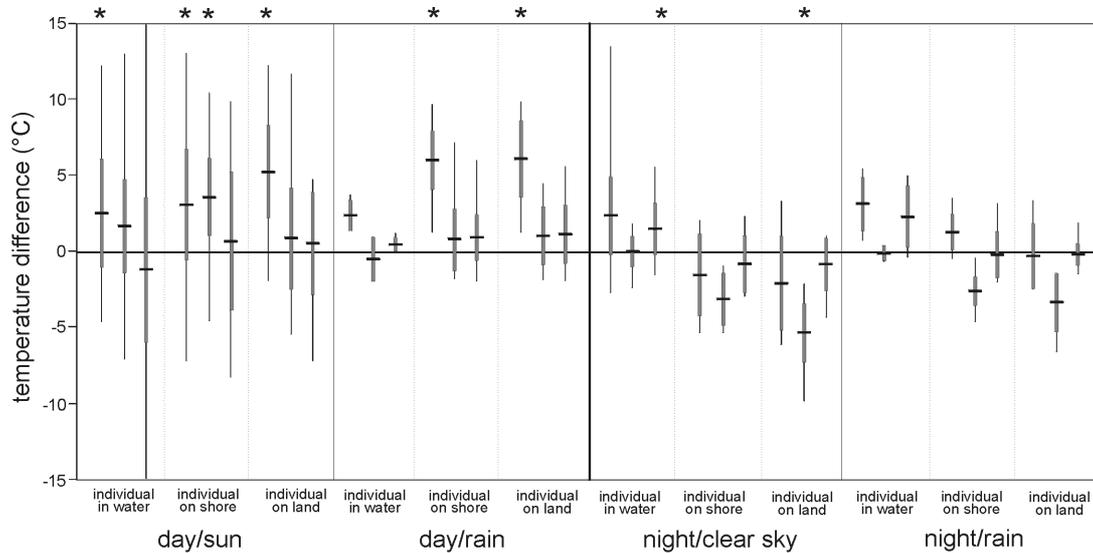
### Discussion

Our data provide strong evidence for active thermoregulatory behaviour of *Rana temporaria* in the Circo de Piedrafita area. During the day, individuals’ body temperatures were generally higher than environmental temperatures. These differences were significant especially under sunshine conditions, indicating that basking, which was often observed around the study pond, accounts for much of the increase in body temperature. In contrast, at night (especially under clear skies), the highest body temperatures were

**Table 3.** Values of  $r^2$  and slopes ( $\pm$  S.E.) of regressions of body temperature of *Rana temporaria* individuals against environmental temperatures.

	Day/sun		Night/clear sky	
	$r^2$	$B \pm$ S.E.	$r^2$	$B \pm$ S.E.
Individuals in water	$n = 58$		$n = 51$	
$T_{\text{air}}$	0.123	$0.325 \pm 0.118$ **	0.497	$0.810 \pm 0.052$ ***
$T_{\text{water}}$	0.103	$0.147 \pm 0.076$ **	0.829	$0.584 \pm 0.078$ ***
$T_{\text{substrate}}$	0.065	$0.277 \pm 0.092$	0.543	$0.337 \pm 0.048$ ***
Individuals on shore	$n = 170$		$n = 13$	
$T_{\text{air}}$	0.185	$0.695 \pm 0.114$ ***	0.339	$0.588 \pm 0.125$ *
$T_{\text{water}}$	0.181	$0.521 \pm 0.054$ ***	0.667	$0.732 \pm 0.223$ **
$T_{\text{substrate}}$	0.353	$0.397 \pm 0.065$ ***	0.494	$0.355 \pm 0.149$ **
Individuals on land	$n = 39$		$n = 15$	
$T_{\text{air}}$	0.280	$0.201 \pm 0.447$ **	0.569	$0.460 \pm 0.208$ **
$T_{\text{water}}$	0.005	$0.728 \pm 0.104$	0.273	$0.580 \pm 0.100$ *
$T_{\text{substrate}}$	0.571	$0.811 \pm 0.214$ ***	0.720	$0.339 \pm 0.082$ ***

\*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$



**Fig. 3.** Boxplots of temperature difference (environmental temperature – environmental temperature) from the field body temperatures of *Rana temporaria* individuals around the Ibón de las Ranas. Plots show mean (horizontal line), standard error (grey box) and minimum and range (vertical line). Each triplet of plots marks values after subtraction of air, water and substrate temperatures, respectively. Asterisks mark significant differences ( $P < 0.05$ ) in *U*-test comparisons between body temperatures and environmental temperatures, after Bonferroni correction over all 36 comparisons.

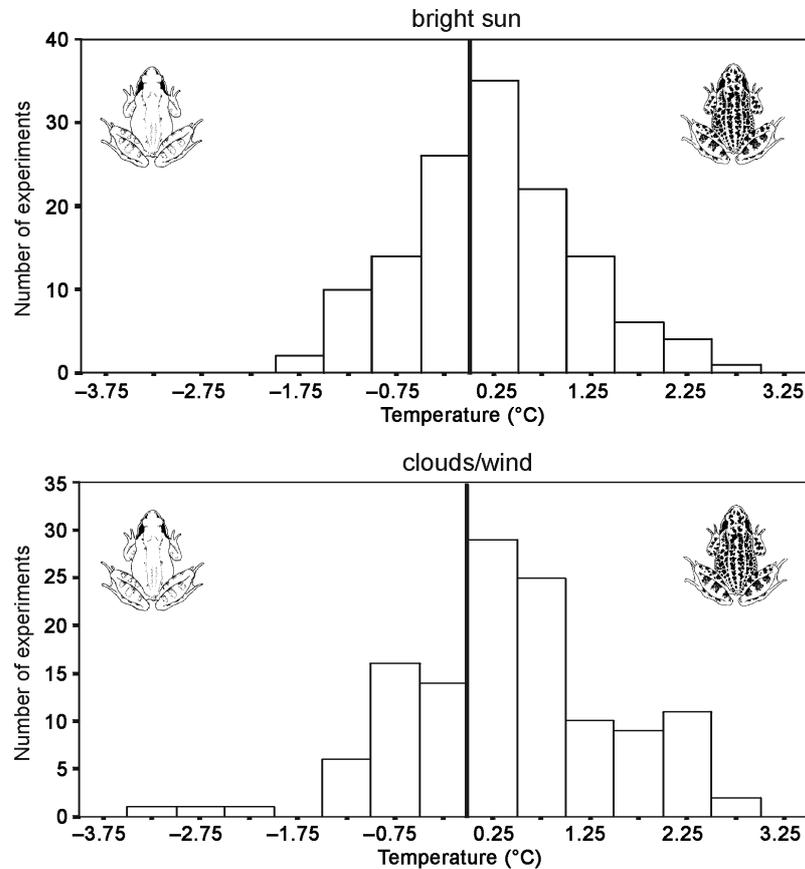
found in the individuals captured in the water, while the individuals captured outside the water were significantly colder than the water. This corresponds well to the aquatic habits of most individuals in the study pond at night (Vences et al. 2000), which correlate with decreasing air temperatures. Hence, the water of the pond acts as a thermoregulatory buffer at night, when air and substrate temperatures can drop to below 0 °C in these montane environments (Vences et al. 2000).

Maximum field body temperatures measured in free-ranging individuals (26.5 °C) were lower

than those obtained by exposing individuals experimentally 10 minutes to the sun (27.1 °C), and much lower than the maximum temperatures reached by sacrificed individuals after an exposure of 20–30 minutes to the sun (35 °C). This indicates that thermoregulatory behaviour of *Rana temporaria* may also include the active avoidance of body temperatures higher than 27 °C, since these could easily be obtained by basking in the bright sun for 20–30 minutes. This behaviour may also be a by-product of the need for water loss avoidance during long-term basking. However, even toads of the genus

**Table 4.** Comparison of field body temperatures (mean  $\pm$  S.D.; minimum and maximum values in parentheses) of *Rana temporaria* individuals with extended black dorsal pattern (dark individuals; classes 4–6) and individuals with few dark spots (light individuals; classes 0–3). *P*-values refer to pairwise comparisons for each habitat type by *U*-tests. Only diurnal measurements under sunshine conditions were considered.

	Dark individuals	Light individuals	<i>n</i>	<i>P</i>
Individuals in water	17.7 $\pm$ 2.6 (13.8–25.1)	17.8 $\pm$ 2.5 (12.8–22.1)	43/15	0.89
Individuals on shore	19.2 $\pm$ 2.9 (13.3–25.2)	19.9 $\pm$ 3.7 (10.2–26.5)	125/42	0.29
Individuals on land	16.9 $\pm$ 3.6 (11.2–23.6)	15.5 $\pm$ 3.2 (9.6–19.6)	31/8	0.32



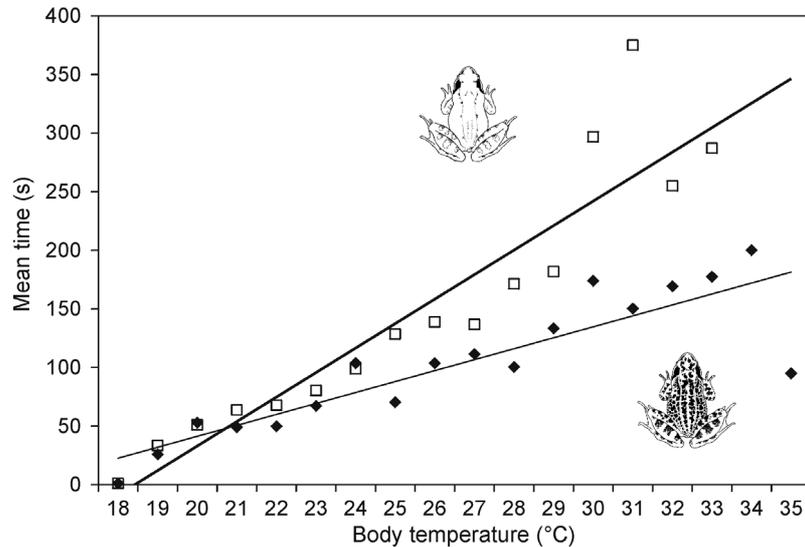
**Fig. 4.** Histograms of the distribution of the difference in temperature increase (in °C) between a dark and a light individual of *Rana temporaria*, respectively, submitted to a parallel heating experiment (10 min exposure to sun). Axis shows values resulting from the subtraction of the temperature increase of the light individual from that of the black individual. The upper histogram gives results under conditions of strong solar radiation, the lower shows the results under conditions of partly cloudy skies or incidence of wind. The bold lines marks the point of equal heating of the dark and the light individual. Both histograms are distinctly right-skewed, indicating a stronger heating of the dark individuals in most experiments (significant under binomial tests;  $P < 0.001$ ).

*Bufo*, which are better protected against water loss by a largely dry skin, selected relatively low temperatures (24.3–27.7 °C) under experimental conditions (Sievert 1991), and had low field body temperatures (Denton & Beebee 1994).

The experimental body temperatures of the dark and light individuals were slightly different under bright sun conditions, although the dark individuals attained higher temperatures significantly more often than the light individuals in pairwise comparisons both under bright sun and cloud/wind conditions. The experimental heating rates revealed differences between the

dark and light individuals at high temperatures (25–35 °C) that were only seldom observed in free-ranging individuals (Fig. 5). This may explain why we did not find differences of field body temperatures between dark and light individuals. The potential benefit of the dark colouration may be that it allows a shift in time allocation due to faster heating, but this effect certainly is small under the conditions prevailing at the study pond.

We did not perform experiments that could provide evidence for the primary function of the dark pattern, which may involve thermal ecology,



**Fig. 5.** Scatterplot of body temperatures of dead *Rana temporaria* individuals exposed to bright sun conditions, and mean time elapsed for each 1 °C temperature increase. Regressions were calculated separately for black pattered (black rhomboids;  $r^2 = 0.7739$ ) and light coloured individuals (white squares;  $r^2 = 0.8662$ ). Values are means across 16 heating experiments using one black pattered and one light individual. Two pairs of individuals matched by body mass were used (eight repetitions each). Since in this analysis we regarded separately the duration of 1°C temperature increases at different body temperatures, time was the dependent variable in the regression.

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UV protection, or mimesis. A comparison of available data indicates that the same trends seem to govern in melanic snakes and frogs: low but measurable differences in experimental heating rates between dark and light individuals but no differences between free-ranging individuals (Forsman 1995). This concordance is conspicuous because the squamate skin is covered with scales and is thereby protected against water loss. In contrast, evaporation is an important physiological challenge for amphibians and is used to regulate body temperatures (Brattstrom 1979, Shoemaker *et al.* 1989, Lillywhite *et al.* 1998), a fact that could lead to the *a priori* assumption of different thermoregulatory trends among these.

A major point that remains to be clarified regards the genetic or ontogenetic basis of the dark patterns. Such dark pigmentation is completely absent in juveniles, while the incidence of black patterns in adults correlates with body size, and therefore probably with age (Riobó *et al.* 2000). More work is necessary to determine if the pattern is genetically determined and established by selection in high-altitude

populations, or if it is an ontogenetic suntanning effect that occurs exceptionally among lower vertebrates (Lowe & Goodman-Lowe 1996).

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