Analysis of the displacement of five iberian anuran species in stress conditions

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Abstract

This study describes the movement paths —in situation of stress— of five anuran species (*Alytes obstetricans, Pelobates cultripes, Bufo bufo, Bufo calamita* and *Bufo viridis balearicus*) by trajectometric analysis. Different experimental treatments (artificial vs. natural) and seasonal variations were studied. The path structure reflects specific (phyogenetic) constraints. Each species showed a characteristic pattern of locomotion for different experimental situations and seasons.

Key words: Anurans, Behaviour, Stress, Trajectometry.

Resum. *Trajectometria en anurs*

L'estudi descriu els desplaçaments —en situació d'estrès— de cinc espècies d'anurs (*Alytes obstetricans, Pelobates cultripes, Bufo bufo, Bufo calamita* i *Bufo viridis balearicus*) mitjançant una anàlisi trajectomètric. Es van estudiar en diferents situacions experimentals (artificials i naturals) i en diferents èpoques de l'any. L'estructura del desplaçament reflecteix les pressions adaptatives específiques (filogenètiques). Cada espècie mostra un patró de locomoció característic i dependent de la situació experimental i de l'època de l'any.

Paraules clau: anurs, comportament, estrès, trajectometria.

Introduction

The amphibians, show strong constraints in relation to dampness (dehydration —Shoemaker et al., 1992— and reproduction- Pough et al., 1992), gravidity (locomotion), and air (respiration Boutilier et al., 1992). Anurans have in the order of amphibians, a greater autonomy regarding those constraints, and within them, there is also a diversification in species relatively dependent on aquatic media and others that can be qualified as animals of terrestrial habits.

Any behavioural description requires precise measures of its components (Huntingford, 1984). The paths followed by different anuran species in different experimental regimes have been quantified to compare their displacements.

Buytendijk (1918) was a pioneer in studying the locomotive behaviour in several species of Anura; he defined several variables to characterize quantitatively the paths that are currently used. In spite of many works concerning to the orientation, migratory paths and movement variation during the reproductive season in several *Bufo* species (Able, 1981; Adler, 1982; Bider, 1968; Moore, 1954; Oldham, 1966), have been done, no data are available on the detailed structure of movement paths. The studies made by Sinsch (1987a, 1987b, 1988, 1990a, 1990b, 1991) on comparative locomotory behaviour among toad species were performed especially under the scope of migratory behaviour.

There are few works that study the structure of the displacements in vertebrates, usually related to search for food (Bovet and Benhamou, 1988; Benhamou and Bovet, 1989; Krebs and Davies, 1981; Pyke, 1984; Smith, 1974a, 1974b; Sanuy and Bovet, 1997).

The locomotion type is a behaviour which can reflect different levels of adaptation to the terrestrial environment (Dingle, 1980; Pough et al., 1992). Therefore, different species can be expected to show distinct movement patterns. Also, it is known that habitat fluctuations throughout the year can bear upon the expression of the behaviour (Eibl-Eibesfeldt, 1974). Our aim in this work is to consider the influence of specific and ecological conditions on the structure of the locomotive paths of different anura; we address the following questions: a) Are there locomotory specific differences among species? (phylogenetic component); b) Are there differences due to distinct experimental situations, in time and space? (ecological component).

Materials and methods

The paths of 1449 specimens belonging to five species of Anurans were monitored (Table 1). The individuals of each species were from the same population. The

Table 1. Species studied, number of animals, species size and geographical and ecological procedence.

Specie	No. subjects	Specie size (mm)	Origin locality	Ecological site
Alytes obstetricans	237	40-50	Pyrenees	*Caricion nigrae* and *Adenostylo-Valerianetum-pyrenaicae*
Pelobates cultripes	276	70-100	Monegros*	*Agropyro-lygeion*
Bufo bufo	430	70-110	Pyrenees	*Quercetum rotundifoliae*
Bufo calamita	285	50-90	Pyrenees	*Buxo-Queretum Pubescens*
Bufo viridis ssp. *balearicus*	221	70-90	Majorca	*Apietum nodiflori*

*Sited in Aragón (north Spain).

observations were performed few days after collecting the animals. In the laboratory, the animals were kept in captivity in individual cages with high humidity and fed with alive prey. After testing, animals were released at their originals biotopes. The tests monitored the path of each animal after its release from the centre of test arena. The study was performed during two hours after sunrise and two hours before the sunset; the duration for each observation was 30 minutes. A grid contributed to locate the animal and made possible to transfer the path observed onto a sketch; along with the performed path, other features that allowed to identify and define each of the movements were noted. The observer remained hidden or if it was not possible, at a long distance in order not to disturb the animals. The path of the studied species was a succession of movements and stops. Each stop duration was measured; these were not always in places where the animal could stay hidden (vegetation, stones…). The visual horizon for the experimental animals was assumed to be diverse, with multiple shapes and intensities of light and dark.

The «itinerary» or path includes all aspects of an animal's trip from its release until its exit from the test arena or during the 30 minutes trial period. We considered a «stop» when the animal was still for more than two seconds. Different variables quantify the pattern of activity and non-activity of each itinerary.

— Initial time (IT). Elapsed time (seconds) from an animal's release in the centre of the arena until the first movement.
— Traject time (DT). The total (seconds) time of actual movement, excluding IT and the stops between successive movement phases.
— Number of movement phases (NS). Number of portions of the itinerary delimited by stops. Stops did not coincide with shelters and were rather typical of the path structure of these animals.
— Length (L). Whole distance travelled (cm) in an itinerary.
— Velocity or Distance for traject time or (V = L/DT). This variable, reported on the total speed of movement, including the time of permanence in each stop.
— Mean duration of movement phases (DT/NS). The average time of permanence in each of the stops performed by the animal. Actually, the animal spent almost 90 % of the time quiet in one of these stops. Thus this variable informed about the time the animal keeps still along the trip.
— Straightness (S). Distance in a straight line from the initial to the final point divided into the total length. (Batschelet, 1981; Sinsch, 1988; Bovet, 1983). The straightness was not compared between experiment because path lengths differ owing to different sizes of test arenas.
— Number of movement phases for unit length (NS/L). It defines the average length of the movement phases.
— Jumping (J). Number of stretches in which some jump were performed divided into the total number of stretches.

The experimental areas were located near Jaca (Huesca, Spain) and in protected areas belonging to the Pyrenean Centre of Ecology (CSIC). The tests were carried out in three experimental situations, considering 12-16 replicates for each type of experiment and time:

— Experiment 1 (ST-1). Closed Room. The tests were carried out in a 60-square-meters room. A 9-square-meters grid was drawn on the floor. The animals moved throughout this surface. A test ended either when the animal went beyond the marked space or when time exceeded 30 minutes. The environmental conditions were stable during the whole period of tests. Tests were performed during reproduction period. During the observation, the researcher remained hidden at a distance of 4 meters. The experiments were carried out at night, under dim red light (0.03 lux at ground level) —see Sanuy and Bovet 1997.
— Experiment 2 (ST-2). Bushes. Tests were performed in an open area —abandoned tennis court, with ground surface— of 1500 square meters close to a building; tests were done in spring and at the beginning of summer. Vegetation consisted of herbaceous bushes (mainly composites and leguminosae) and grasses, which did not allow animals to shelter. The animal was placed in the centre of a grid (30 x 50 m); the movement was observed either for 30 minutes or until the animal went over the field limits.
— Experiment 3 (ST-3). Meadow. Observations were performed in a meadow belonging to the domain of the *Quercion robori-pyrenaicae*, at 800 m of altitude; the herbaceous and shrub-like vegetation was very abundant. The size of vegetation allowed the animals to shelter. The space was signalled with stakes and the observer noted the movement of the animal from a distance of 6-8 meters. In this experimental situation, tests were performed in three different times of the year: before (ST-3A), during (ST-3B) and after (ST-3C) the period of setting and this for each of the species. ST-3A also includes the period of migrations towards the place of spawning, and ST-3C tests were carried out in summer. The temporal limit was the only one considered to finish the test in this experimental situation. There are not enough tests or data for *Alytes obstetricans* in ST-3C and for *Bufo viridis* in ST-3A. The number of paths for each species and experimental situation is specified in table 3.

Statistical analysis: The data were tested with an analysis of variance (Rouanet and Lépine, 1970, 1977) for each of the variables. This analysis includes a post-hoc Tukey test and logarithmic transformation of data when they were not normally distributed. Straightness was arcsine transformed. To study the influence of the environment (field vs. laboratory) a design of 5 species x 3 experimental situations (ST-1, ST-2, ST-3B) was performed; the tests were all performed during the spawning season of the species. To emphasize the influence of the time of the year, a design of 3 species (*Pelobates cultripes, Bufo bufo* and *Bufo calamita*) x 3 times of the year (ST-3A, ST-3B, ST-3C) was performed.

Similarities among data from ST-3B (natural habitat) were assessed with a cluster analysis (CSS-Statistica, 1991) on mean values (standarised data) using Euclidean distances and the single linkage method.

Results

Table 2 shows the values of the means and standard deviation for each species and experimental situation. Tables 3 and 5 show the result of the analysis of variance for the variables used and for both experimental designs. Relevant comparisons among experimental situations for each species and among species for each experimental situation were performed within each of the analyses. Figure 1 shows a graphical summary of the degree of similarity of each species for the different indexes or variables of table 2, and for the experimental situation ST-3B.

Table 2. Mean values and standard deviation for each species and experimental situation. IT: Initial time; S: Straightness; V: Velocity; DT/NS: Mean duration of stop; NS/L: Number of movement phases for unit length; J: Jumping (see text for variable definition and units). nº: sample size. AO: *Alytes obstetricans*; PC: *Pelobates cultripes;* BB: *Bufo bufo*; BC: *Bufo calamita;* BV: *Bufo viridis balearicus.*

		IT		**S**		**V**		**DT/NS**		**NS/L**		**J**		**No.**
		$\bar{X}$	sd	$\bar{X}$	sd	$\bar{X}$	sd	$\bar{X}$	sd	$\bar{X}$	sd	$\bar{X}$	sd	
AO	ST-1	498	321	0.54	0.29	0.94	0.54	29.07	21.71	12.12	7.24	0.58	0.33	81
	ST-2	372	250	0.75	0.35	0.70	0.47	24.48	17.67	5.53	3.28	0.37	0.21	57
	ST-3A	302	201	0.70	0.35	1.49	1.05	34.23	24.43	4.16	1.63	0.90	0.42	49
	ST-3B	133	79	0.65	0.30	1.89	1.26	25.78	17.27	3.75	1.35	0.83	0.41	50
PC	ST-1	426	307	0.45	0.21	0.98	0.64	85.29	45.43	4.72	1.98	0.15	0.07	50
	ST-2	151	72	0.81	0.51	1.41	1.17	79.92	47.25	3.18	1.61	0.25	0.11	77
	ST-3A	322	160	0.64	0.31	1.77	1.23	57.48	35.83	2.19	1.13	0.45	0.27	50
	ST-3B	129	92	0.61	0.27	2.39	1.71	42.34	27.38	2.16	0.95	0.67	0.39	49
	ST-3C	172	121	0.59	0.48	1.82	1.24	25.02	17.18	2.87	1.57	0.57	0.31	50
BB	ST-1	815	621	0.57	0.25	0.71	0.47	98.54	62.92	6.30	3.23	0.00	–	54
	ST-2	399	279	0.77	0.31	1.65	1.21	86.83	55.47	4.24	1.92	0.28	3.20	210
	ST-3A	505	394	0.69	0.27	2.47	2.11	83.44	51.73	0.76	0.28	0.00	–	50
	ST-3B	163	75	0.68	0.29	6.01	5.08	63.52	27.34	0.39	0.15	0.00	–	48
	ST-3C	173	140	0.62	0.33	2.61	1.69	64.54	25.54	1.09	0.75	0.18	6.06	68
BC	ST-1	271	150	0.75	0.39	2.82	2.06	23.65	12.27	5.40	3.34	0.00	–	74
	ST-2	200	110	0.57	0.21	2.55	1.56	31.92	16.60	5.71	3.12	0.00	–	62
	ST-3A	755	521	0.68	0.31	1.82	0.93	61.29	29.36	1.87	0.96	0.00	–	49
	ST-3B	128	96	0.67	0.29	3.08	2.36	50.13	21.19	1.52	1.16	0.00	–	50
	ST-3C	175	125	0.64	0.21	2.62	1.22	43.40	17.35	1.76	1.24	0.00	–	50
BV	ST-1	19	8	0.78	0.45	4.26	3.48	11.98	6.51	4.84	2.30	0.67	0.31	48
	ST-2	51	19	0.84	0.61	4.49	4.19	9.60	6.03	2.50	1.65	0.47	0.24	75
	ST-3B	70	27	0.66	0.52	5.34	4.77	10.04	6.21	2.72	1.19	0.96	0.46	49
	ST-3C	22	11	0.68	0.49	3.70	3.24	11.51	8.14	3.27	2.08	0.75	0.38	49

Table 3. Analysis of variance. p<0.05 in all tests. F: Values of F. dl: degrees of freedom. Design analyzed: five (5) species and three (3) experimental situations (ST-1, ST-2 and ST-3B, see text). IT: Initial time; V: Velocity; DT/NS: Mean duration of stop ; NS/L: Number of movement phases for unit length; J: Jumping (see text for variable definition and units).

Source		**IT**	**V**	**DT/NS**	**NS/L**	**J**
Species	F	25.9	88.9	15.7	107.2	92.6
	dl	(40, 1015)	(4, 961)	(4, 961)	(4, 961)	(4, 961)
Exp, Sit,	F	26.9	42.6	0.9	284.5	21.9
	dl	(2, 1015)	(2, 961)	(2, 961)	(2, 961)	(2, 961)
Interaction	F	18.1	43.5	7.3	121.5	32.9
	dl	(14, 1015)	(14, 961)	(14, 961)	(14, 961)	(14, 961)

Table 4. Statistical significance (+: p<0.05) of differences between species for ST3-B. IT: Initial time; S: Straightness; V: Velocity; DT/NS: Mean duration of stop; NS/L: Number of movement phases for unit length; J: Jumping (see text for variable definition and units). AO: *Alytes obstetricans*; PC: *Pelobates cultripes*; BB: *Bufo bufo*; BC: *Bufo calamita*; BV: *Bufo viridis balearicus*.

	IT	**V**	**DT/NS**	**NS/L**	**J**
BV-AO	+	+	+	+	–
BV-PC	+	+	+	+	+
BV-BB	+	+	+	+	+
BV-BC	+	+	+	+	+
AO-PC	–	+	+	+	+
AO-BC	–	+	+	+	+
AO-BB	–	+	+	+	+
PC-BC	–	+	–	+	+
PC-BB	–	+	–	+	+
BC-BB	–	+	–	+	–

Table 5. Analysis of variance. p<0.05 in all tests. F: Values of F. df: degrees of freedom. Design analyzed: three (3) species (*Pelobates cultripes*, *Bufo bufo* and *Bufo calamita*) and three (3) experimental situations (ST-3A, ST-3B and ST-3C see text). IT: Initial time; S: Straightness; L/DT: Distance for traject time; DT/NS: Mean duration of stop; NS/L: Number of movement phases for unit length; J: Jumping (see text for variable definition and units).

Source		**IT**	**S**	**V**	**DT/NS**	**NS/L**	**J**
Species	F	30.7	13.1	37.3	3.8	136.5	13.0
	dl	(4, 972)	(4, 908)	(4, 908)	(4, 908)	(4, 908)	(4, 908)
Exp, Sit,	F	9.0	3.9	28.2	12.2	27.0	140.2
	dl	(14, 972)	(14, 908)	(14, 908)	(14, 908)	(14, 908)	(14, 908)
Interaction	F	13.8	16.3	22.3	4.1	54.6	30.6
	dl	(14, 972)	(14, 908)	(14, 908)	(14, 908)	(14, 908)	(14, 908)

A. *Comparisons for five species in three different experimental situations (Closed Room (ST-1), Bushes (ST-2) and Meadow (ST-3B)). Test effected during the spawning season.*

The analysis of variance confirmed that species were different and this happens to all the variables with the exception of DT/NS (see Table 3).

Bufo viridis was the species with the shortest initial time (IT) and mean duration of the stretches (DT/NS) and accordingly moved at the highest velocity. Furthermore it was the species with the greater number of jumps (J) and the most straight paths.

Alytes obstetricans. The rate of stretches (NS/L) performed by this species is the highest in each experimental situation. It was the second species that jumped the most after *Bufo viridis*. This species needed a long time to leave the release point and on many occasions in ST-2 and ST-3 it did not move during the trial period (IT>30 minutes). Besides, it appears as the slower species. This was mainly due to the high number of stops and the time of permanence in each of them.

Bufo bufo. The initial time (IT) is very high in ST-1 because of high number of immobility scores (IT>30 minutes). This species makes few stops but it remains a substantial time in each of them. It carried out the paths at the highest speed after *Bufo viridis*, but the rate of stretches in a unit of length (NS/L) is the smallest.

Bufo calamita. Due to the characteristics of its trajectories, this species was somewhat similar to *Bufo bufo* and *Pelobates cultripes*. Like *Bufo bufo*, this species was characterised by the small number of jumps (only in a 0.6 % of the analysed stretches), but it moved quicker and spending less time in the stops than *Bufo bufo*.

Pelobates cultripes shows mean values that can be considered intermediate among *Bufo bufo, Bufo calamita* and other species.

Table 4 shows that all species are different according to some variables, from two *(Bufo calamita - Bufo bufo*) to five (*Bufo viridis -Pelobates cultri-*

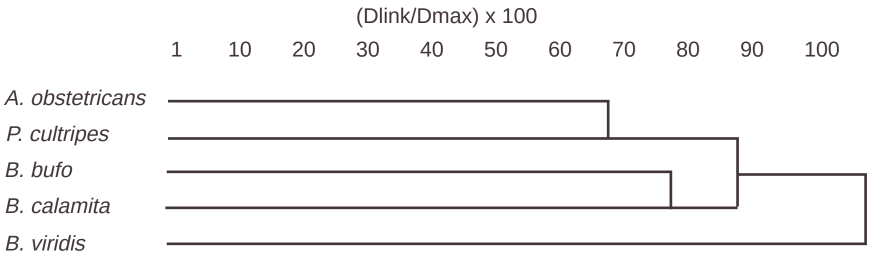

Figure 1. Single linkage cluster dendrogram of similarities between the five Anuran species (data from table 3, standarized). Only values from the natural experimental situation (ST-3B) were used.

pes, and *Bufo bufo - Bufo calamita*). Velocity (V) and the average length of stretches (NS/L) are useful to characterise and differentiate each species in the most natural experimental situation.

B. *Influence of season (effected in Meadow: before (ST-3A), during (ST-3B) and after ST-3C). Test realised by Pelobates cultripes, Bufo bufo and Bufo calamita.*

Analysis were done with the aim of testing possible differences in the displacements among three species (*Pelobates cultripes*, *Bufo bufo* and *Bufo calamita*) at different seasons. Results of the variance analysis (Tables 5 and 6) shows that the season has a marked influence on the path structure. During the season preceding the onset of reproduction (ST-3A) all species took considerably more time to start movement when placed on the initial point of the path. They spent also more time on intermediate stops and their speed of the movement was lower. During reproduction (ST-3B) all three species showed a marked increase in speed and the initial time and step number for total length was the smallest of the three seasons.

In summer (ST-3C), when vegetation drying-up and the animals were out of the reproductive season (migration and spawning), the time to initiate the movement is slightly higher that in ST-3B, the speed decreases and the number of stretches increases; this, for all of the species. *Pelobates cultripes* made a small number of jumps in this situation; this was also observed with the other two species, though with a level of significance of $p < 0.1$.

From table 2 it can be seen that variation in the distinct variables for the species PC, BC and BB, when considering the effect of season (ST-3A, ST-3B and ST-3C), shows persistent differences among species and that they show similar tendencies along the time of season.

Discussion

Path structure was analysed in five species of toads in different environments and/or in different seasons in the same biotope. The species studied showed a different path structure that is consistent in each of the experimental situation (Table 6); This

Table 6. Statistical significance (+: $p<0.05$) of differences between experimental situations, for five (5) species and three (3) experimental situations. IT: Initial time; S: Straightness; V: Velocity; DT/NS: Mean stop duration; NS/L: Step number/total length; J: Jumping (see text for variable definition and units).

	IT	S	V	DT/NS	NS/L	J
ST-3A/ST-3B	+	+	–	–	–	–
ST-3A/ST-3C	+	+	+	–	+	+
ST-3B/ST-3C	–	+	+	–	+	–

may be interpreted as a phylogenetic component in the locomotive behaviour. It can be noted specially that movement features of *Bufo viridis balearicus* differ strongly from the other species in all the situations studied. This is not surprising as this subspecies has marked aquatic habits (Vives et al., 1987) and even has morphological features (interdigital membrane, long legs: Vives et al., 1987, Pough and Magnusson, 1992; body proportions: Dobrowolska, 1973 and Emerson 1988) closer to other aquatic Anurans. Among the species studied, this species can be considered as the least terrestrial, concerning the path structure. The higher proportion of jumps clearly separates *Bufo viridis* from other representatives of the genus *Bufo*. It is worth mentioning that *Bufo calamita* is morphologically and phylogenetically the closest species to *Bufo viridis* out of the ones studied (Duellman and Trueb, 1986). Zug, 1972a, 1972b and Emerson 1988, suggested that jumps do not bring so many advantages to a terrestrial animal, but they do to one of aquatic habits.

The movements performed by *Alytes obstetricans* (short stretches, sinuous path, small velocity) may be related to the smaller size of this species. During the tests, it was observed that the individuals of this species used shelters (small bushes, holes between stones, etc.) that were not used by other species.

Pelobates cultripes is a highly specialised species living on soft and sandy soils. This imposes strict limits to its distribution (Vives et al., 1987 and Llorente et al., 1996). A marked tendency to bury itself was observed (and not to hide itself near vegetation or stones).

This study shows that each species behaves differently in each of the experimental situations. This could be expected for ST-1 due to the absolute artificiality (absence of vegetation hard substrate) and spatial limits imposed on the animals. The itineraries performed in ST-2 show intermediate values between ST-1 and ST-3B, but are more similar to the former. This could be due to the absence of vegetation for ST-1, the almost absence —only short grasses— for ST-2, and the spatial limits that truncated the paths.

The tests performed in ST-3 were done in different seasons (ST-3A, ST-3B and ST-3C) for three species. Before the spawning season the vegetation was rather poorly developed but the temperature and dampness were optimal for the three species. This could explain the long time needed to initiate the movement and spend on each stop in spite of the absence of refuges and references. The movement paths of these animals are strongly influenced by the presence of vegetation and its vegetative state. Scrubs and bushes provide shelters and protection against climatic factors. Paths in this season are more rectilinear. The smaller volume of vegetation, with the consequent reduction of shelters, and the climatic constraints, may be the cause. This is in agreement with Sinsch (1988) who suggested the straightness of the paths for *Bufo bufo* steadily decreases throughout the year, being smaller in summer.

The difference within phyllogenetically close species viz. *Bufo calamita* and *Bufo viridis* (Llorente et al., 1996), shows that ecological component are more influential than phylogenetic components in the design of a path.

Physiological factors (hormonal balance with the migration and/or reproduction phase) cannot be ruled out and could be also involved in the expression of the movements of the toads. This point is specially observed in the straightness of the path. The physiological conditions of the animal during the reproduction or migration and its wandering movements of exploration out the migrating season appear as mutually influencing each other in the shape of the path.

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