Intraspecific variability of the patterns of the locomotory behaviour in terrestrial iberian anurans

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Abstract

The variability in the locomotory behaviour between different species of anurans —the first vertebrates that are adapted to terrestrial environment— show the adaptive capacity of the different forms shaped by evolution. Each species adapts to the environment in a specific fashion. One uses the locomotory behaviour for measuring the variability of the patterns. The paths of the species effected in the different experimental situations —naturals and in the laboratory— were quantified, obtaining several parameters that define the path. The Coefficient of Variation of the mean of each variable is utilise for measuring the variability. The work shows the difference between variables, as a consequence of the specific locomotory behaviour and its adaptation of the environment. We also show, the different adaptability that exists when the experimental conditions change, and each species adapts itself in a different way. The variability of the pattern is an instrument to know this different adaptability.

Key words: anurans, natural vs artificial experiences, paths, trajectometry, variability.

Resum. *Variabilitat intraespecífica dels patrons del comportament locomotor en anurs terrestres ibèrics*

La variabilitat en el comportament locomotor entre distintes espècies d'anurs —els primers vertebrats que es van adaptar al medi terrestre— denota la capacitat adaptativa de les diferents formes que modela l'evolució. Cada espècie s'adapta al medi d'una manera que la diferencia de les altres. S'empra el comportament locomotor per mesurar la variabilitat de les pautes de conducta. Els comportaments locomotors de les espècies en diferents situacions experimentals —naturals i en un laboratori— es varen quantificar, es van obtenir una sèrie de variables que defineixen el recorregut i es va utilitzar el coeficient de variació de les mitjanes de cada una de les variables. Aquesta estadística s'empra per mesurar la variabilitat. Es mostren les diferències existents entre les variables, com a conseqüència del comportament locomotor específic i de la seva adaptació al medi. També es posa de relleu en el treball, la diferent adaptabilitat que existeix quan es canvien les condicions ambientals d'experimentació, i com cada una de les espècies s'hi adapta de manera diferent.

Paraules clau: anurs, experiments naturals o artificials, trajectometria, variabilitat.

Introduction

The interest for the variability has always been present in the ethological studies. Witham was a pioneer with his studies on different aspects of specific behaviour patterns in several species. Heinroth suggested that behavioural characters could be used as taxonomic tools and Lorenz (1965) postulated that these characters could be as valuable as morphological and anatomic ones for comparative studies.

The problem of measuring the behavioural phenotype requires a morphological description of the behaviour and its variability; variability is measured by many authors (see Schleidt, 1974; Barlow, 1977; Bekoff, 1977) with the statistic Coefficient of Variation (CV).

Variability is the substrate where natural selection operates; therefore it is interesting to know how evolution modulates the locomotory behaviour, eventually leading to a behavioural characterisation of species. We have chosen a group that is one of the first vertebrates in colonising the terrestrial environment. The species studied use walking and, to some extent, jumping.

There are few studies about variability of the locomotory patterns, and in fact we do not know of any work about trajectometry. Differences and comparisons among the parameters that measure the locomotory behaviour can be found in Sanuy and Martínez-Rica (1982) and Sanuy (1992). Here I am interested in finding out if there are differences, among different anouran Iberian species. The phylogenetic relationships are considered by Duellman and Trueb (1986). Specifically, if the behavioural patterns are fixed; if not, which is this range of variation. Two experimental situations (artificial vs. natural) were compared. In the natural condition, the path structure before, during and after reproduction was also compared.

Material and Methods

Animals

The locomotory paths of 5 anurans species were studied —*Alytes obstetricans* (144), *Pelobates cultripes* (146), *Bufo bufo* (153), *Bufo calamita* (134) and *Bufo viridis* (148)—. We used a number of 725 specimens. Animals were observed 2 or 3 days after their capture. The animals were housed in individual terrariums, and fed with alive preys. The animals were caught at 25 km of the experimental place in different sites, biotopes and several periods of the year.

Experimental situations

Tests were done in two different experimental sites (Sanuy 1992): one was inside a laboratory (ST-1), where the ground was divided in squares of 3 x 3 m; the second site (ST-2) was an field owned by the Instituto Pirenaico de Ecología (CSIC) near Jaca (Huesca, Spain). The place is a meadow from the association *Quercion robori-pyrenaica*, at 800 m altitude. The field where the tests where done was nearly flat. This space was squared with little pegs each 2.5 m, to help in animal localisation. Observations were done from 8-10 m far from the subjects.

The test was as follows: the animal was let free at the centre of the experimental reticule; the displacement was sketched and the locomotor movements annotated. After being free the toads stopped for a variable period of time in the initial point; then, they began to move to a fixed direction till they stopped, after this they started another movement to the same or different direction and so on. The test lasted for 30' or when the toads went beyond the marked limits. in any case an individual provided more than three paths and always with a minimum lapse of 24^h. The visual horizon for the experimental animals is assumed to be diverse, with multiple shapes and intensities of light and dark. The experiment were done for the two hours after sunrise and for the two hours before sunset.

The movements and path of an animal is defined as the trajectory done by the animal from the point where it was let free —initial point of departure— until the point where the experiment is finished.

The variables we use to define and quantify the movement are the following:

— Initial Time (IT). Time (seconds) the animal began the movement after it was liberated in the centre of the experimental space.
— Displacement Time (DT). It was the actual time used to perform the movement. The initial time (IT) was not considered for the calculus of this variable. Therefore, it included the time used for the movement plus the one of permanence in each of the stops of the path.
— Number of Stretches (NS). Number of stops (equivalent to stretches) performed throughout the itinerary. These stops do not have to coincide with a shelter and are typical of the abridged movement of theses animals.
— Jumping (ST). Number of stretches in which jumps were performed divided into the total number of stretches.
— Length (L). Total distance travelled (Cm) in a path.
— Straightness (R). Distance in a straight line from the initial to the final point divided into the total length. (Batschelet, 1981; Sinsch, 1988). The straightness was not compared among experiments because path lengths differ owing to different sizes of test arenas.
— Distance for path Time (during itinerary) (S). It is the speed medium during the path. The total time of actual movement (DT), excluding the «initial time» and the stops among succesive movement phases. It is a speed medium.
— Mean Duration of movement phases (MD). The average time of permanence in each of the stretches performed by the animal. The animal spent almost 90% of the time motionless in one of these stops. This variable informed about the time the animal keeps still throughout the path.
— Number of Stretches for unit Length (SL). It defines the average length of the stretches. It reports on the abridgement of the paths.

To study eventual differences of locomotory behaviour in distinct seasons, tests were done in coincidence with the respective times of reproduction or migration: before (ST-2A), during (ST-2B) and after (ST-2C) the reproduction. We have to note that tests at ST-1 belong to experimental situations in time after reproductive period.

Statistics

The Coefficient of Variation (CV) is used as in Bekoff (1977) and statistical differences between the CV vere assessed following Dawkins & Dawkins (1973).

Results

The values of CV by each species and in the four experimentl situation (ST-1, ST-2A, ST-2B and ST-2C), are presented in Table 1.

Comparisons of seasons in the natural site (ST-2A, ST-2B and ST-2C), the results show a gradual decreasing to the values of ST-2C (after the breeding period).

Comparing each variable of experimental situation ST-1 with the tests in the ST-2C (both accomplished in the same period), there is a significant difference among the variables: Initial time, Distance for path medium, and Mean duration of the stretch (See Table 2).

Table 1. Coefficient of Variation (CV) of the variables for the different species and different experimental situations. See test for the variables definition.

	IT	ST	R	S	MD	SL
Alytes obstetricans						
ST1	48.40	29.15	22.46	73.77	55.68	37.64
ST2A	61.53	7.53	61.14	37.87	88.42	50.87
ST2B	51.73	8.12	8.20	31.49	58.14	30.70
ST2C	44.10	6.79	6.07	23.50	60.67	27.10
Pelobates cultripes						
ST1	67.05	47.93	20.17	36.61	117.40	25.73
ST2A	64.05	35.23	15.17	35.15	55.11	38.56
ST2B	33.85	29.99	12.36	36.09	61.45	20.08
ST2C	83.17	17.57	14.23	22.09	26.74	11.70
Bufo bufo						
ST1	37.29		27.04	91.44	48.95	30.78
ST2A	59.62		11.18	25.72	35.05	30.11
ST2B	60.65		5.27	19.35	37.61	26.58
ST2C	56.08		10.58	28.40	38.26	25.13
Bufo calamita						
ST1	45.50		15.11	60.34	70.74	28.78
ST2A	57.76		4.82	35.43	35.39	48.68
ST2B	67.64		7.51	22.67	40.47	37.40
ST2C	21.96		9.09	26.22	30.11	36.85
Bufo viridis						
ST1	40.31	19.53	10.15	37.47	68.33	15.72
ST2A	44.26	15.82	7.72	27.69	36.45	13.51
ST2B	41.77	15.43	7.54	22.90	36.18	13.49
ST2C	37.70	15.12	4.97	20.61	25.66	13.37

For ST-1 and ST-2 the variable IT is very high; time variables are usually high and also their CV; compound variables in which time intervenes usually have very high CV as well.

Jumping is not calculable for *Bufo calamita,* and the results in *Bufo bufo* are haphazard, since it is a species which seldom jumps and this fact increases in its degree of variability.

The variable Straightenss presents the least variability and in comparison, it is different compared with other variables (See Table 3).

Table 2. Significative differences (S) and non significative (NS) for $p < 0.05$, according Dawkins & Dawkins test. On compare the experimental situations for the more representative variables. See text for the definition of variables.

Variables	ST1/ST2C	ST2A/ST2B	ST2A/ST2C	ST2B/ST2C
Initial Time (IT)	S	NS	NS	NS
Jumping (ST)	NS	NS	NS	NS
Straightness (R)	S	NS	NS	NS
During itinerary (S)	S	NS	NS	NS
Mean Duration (MD)	S	NS	NS	NS
Stretches for unit Length (SL)	S	NS	NS	NS

Table 3. Significative differences (S) and non significatives (NS) for $p < 0.05$, according Dawkins & Dawkins test. Interspecific comparison for each experimental situation. A.o. = *Alytes obstetricans;* P.c. = *Pelobates cultripes;* B.b. = *Bufo, bufo;* B.c. = *Bufo calamita;* B.v. = *Bufo viridis.* See text for the definition of variables.

		IT/R	IT/S	IT/MD	IT/SL	R/S	R/MD	R/SL	S/MD	S/SL	MD/SL
A.o.	ST1	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
	ST2A	S	S	NS	S	S	S	NS	NS	S	NS
	ST2B	S	NS	NS	NS	S	S	NS	NS	NS	NS
	ST2C	S	NS	NS	NS	S	S	NS	NS	NS	NS
P.c.	ST1	NS	NS	NS	NS	NS	S	NS	NS	NS	S
	ST2A	S	S	NS	NS	S	S	NS	NS	NS	NS
	ST2B	NS	NS	NS	NS	S	S	NS	NS	NS	NS
	ST2C	S	S	NS	S	S	NS	NS	NS	NS	NS
B.b.	ST1	S	NS	NS	NS	S	NS	NS	NS	S	NS
	ST2A	S	S	NS	NS	S	NS	NS	NS	NS	NS
	ST2B	S	S	NS	NS	S	S	NS	NS	NS	NS
	ST2C	S	S	NS	NS	S	NS	NS	NS	NS	NS
B.c.	ST1	S	NS	NS	NS	NS	NS	NS	NS	NS	NS
	ST2A	S	NS	NS	NS	S	S	S	NS	NS	NS
	ST2B	S	S	NS	NS	S	S	S	NS	NS	NS
	ST2C	NS	NS	NS	NS	S	NS	S	NS	NS	NS
B.v.	ST1	S	NS	NS	NS	NS	NS	NS	NS	NS	NS
	ST2A	S	NS	NS	NS	S	NS	NS	NS	NS	NS
	ST2B	S	NS	NS	NS	S	NS	NS	NS	NS	NS
	ST2C	S	S	NS	S	S	S	NS	NS	NS	NS

Bufo viridis is the species which shows the smallest CV except in the situation ST-1. Besides, the CV of variables are similar enough among them. The rest of species show similar values, at least, minor in the most natural situations ST-2.

The phylogenetic relationship among the studied species (see Duellman and Trueb, 1986) does not correspond with the similarities between the values of C.V.

Discussion

As Hazlett (1972) points out you cannot talk about a fixed behaviour pattern if its CV is found to be above 18%. This value is only found in the Straightness variable in the test made in ST-2 (A, B and C) —natural conditions—. This seems to indicate that path structure in the species studied is extremely variable.

In the laboratory tests the variability is globally less than in the other tests, done in more natural conditions, and it is so as a consequence of being in a place with no possibilities of protection. This rigidity is apparent in the temporal variables, in order to escape from the place where situated to start the test (IT).

After the reproductive period (ST-2C) the animals display a locomotive behaviour whith smaller variability than in the rest of natural conditions ($p < 0.05$). It is during this time when the animals stop their reproductive migrations and make shorter and more numerous trips around their nests; this movement already responds mostly to an alimentary —not reproductive— impulse (Sanuy, 1992).

The animals of the species most linked to the aquatic ecosystems (*Bufo viridis*) is the one presenting a higher fixing of his locomotory behaviour; we suggest that this kind of behaviour is due to the kind of habitat where the behaviours can be more rigid: in a dangerous situation they only need to escape towards water and take refuge in it. This kind of habitat allows for less elaborate behaviours than those necessary in more terrestrial habitats where behaviour must be most variable.

The variables where the time component intervenes in a specific action are the ones presenting a larger variability. Thereby they must be used cautiously when doing comparative studies on the type of locomotive behaviour.

Methodologically it does not seem proper to combine variables if we wish to diminish the value of the CV significantly, because the effect obstained may be even the reverse.

The animals underwent the test in the same experimental space and their route was modulated by the space situation of small shrubs and bushes that were in the most chosen direction (see Sanuy, 1992; Sanuy & Martínez-Rica, 1982). This implies that the values of straightness show a range of narrow variation.

This variable becomes a good index for comparative studies of trajectometry. In fact, this variable is widely used by many authors as description of a route or trajectory (Bovet, 1983; Benhamou & Bovet, 1989).

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