acta ethol (2002) 4:81–84
DOI 10.1007/s10211-001-0052-z

ORIGINAL ARTICLE

J.I. Robalo · V.C. Almada

Some features of the behaviour of the marbled newt *Triturus marmoratus* (Latreille, 1800) in captivity

Received: 23 October 2000 / Received in revised form: 31 May 2001 / Accepted: 20 July 2001 / Published online: 14 December 2001

Abstract The behaviour in groups of both sexes of marbled newts (*Triturus marmoratus*) from Sintra, Portugal, kept for a few weeks in a large aquarium, is described. Behaviour patterns described for this species and for other species in this genus were recognised. The following behaviours are described for the first time: Walk-over, Land-over, Stand-on, Show, Erect-body, Yawn, Circle, and Dig. Females seem to have a more active role in courtship than is usually considered. The behaviour frequencies for each sex were analysed using simulation statistics. Some elements usually classified as male sexual behaviours occur in both sexes and are likely to play other social roles.

Keywords *Triturus marmoratus pymaeus* · Newts · Social behaviour · Courtship

Introduction

There is a considerable body of literature concerning the behaviour of newts of the genus *Triturus*, especially of males (*T. vulgaris*, Halliday 1974; *T. marmoratus marmoratus*, Horta 1983; *T. montandoni*, Pecio and Rafinski 1985; *T. m. marmoratus* and *T. cristatus*, Sparreboom 1986; Zuiderwijk 1986, 1990; *T. cristatus*, Green 1989; Sparreboom and Teunis 1990; *T. boscai*, Faria 1993, 1995; *T. alpestris alpestris* and *T. a. cyreni*, Denoel 1996). Additionally, some comparisons have been made with other genera (*Paramesotriton*, Sparreboom 1983; *Cynops*, Sparreboom and Faria 1997). This was probably due to the diversity and conspicuousness of male newt displays and stereotyped behaviour patterns and the interest of several of the pioneer researchers of newt behaviour in the use of these ethological characters in phylogenetic studies.

As a consequence of this research tradition, many studies used standardised procedures, in which one or two breeding males were placed for a short period in a small tank and one or two females or other males were added and the behavioural sequences that occurred soon after the individuals were put in contact were recorded (e.g. Halliday 1974; Sparreboom 1986; Faria 1993; Denoel 1996). This means that, on one hand, the attention was focussed on the behaviour of the males, leaving the behaviour of females to be known in much less detail. On the other hand, much less information is available on the social behaviour of newts in more natural contexts (but see Zuiderwijk 1986 and Faria 1995 for examples of direct field observations on the behaviour of this genus), namely those in which both sexes live together for longer periods of weeks or months.

Despite this interest in comparative study, the behaviour of some species is still poorly known. In the case of *T. marmoratus*, few behavioural descriptions are available and some have not discriminated in detail between the behaviour of *T. marmoratus* and *T. cristatus*, which were studied together (Sparreboom 1986; Zuiderwijk 1986, 1990). For the subspecies *T. m. pymaeus*, which occurs from the centre of Portugal to the extreme south of the Iberian Peninsula (Garcia-Paris et al. 1993), there are no published ethological data (except for a brief study about oviposition behaviour, Diaz-Paniagua 1989), despite the fact that recent taxonomic and phylogenetic works (Garcia-Paris et al. 1993; Griffiths 1996) pose the question of whether *T. m. pygmaeus* should be assigned specific status.

In this article we present some results on the behaviour of a population of *T. marmoratus* from Sintra, Portugal (near Lisbon) that has been considered to belong to the *pygmaeus* subspecies, or species (Garcia-Paris et al. 1993). Our results are based on observations of two captive groups of newts of both sexes, maintained in captivity for several weeks. This option was chosen because we wanted to capture the diversity of interactions, both

Communicated by P. Gama Mota

J.I. Robalo (✉) · V.C. Almada
Unidade de Investigação em Eco-Etologia,
Instituto Superior de Psicologia Aplicada,
Rua Jardim do Tabaco 44, 1100 Lisbon, Portugal
e-mail: joanarobalo@netc.pt

within and between the sexes, so we avoided the standard test situations so frequently used to describe sexual interactions.

The study had two aims: (1) to describe as exhaustively as possible the behaviour patterns of this subspecies, and (2) to assess to what extent behaviour patterns that had been described in the context of male sexual behaviour occur more generally, namely, in males when not engaged in strictly sexual behaviour and in females. In other words, we considered the hypothesis that the interpretation of some behaviour patterns as belonging strictly to sexual behaviour could be an artefact of the traditional strategy commonly used to study newt behaviour. The failure to observe such patterns in females may result from a lower level of activity in that sex than in males, combined with a more reduced effort to observe newts outside of the typical male–female sexual interactions.

Methods

The newts were collected by hand net from artificial ponds at Serra de Sintra, near Lisbon, in the months of November and December 1997, after the onset of the breeding season. Only individuals with external signs of maturity (well developed crest and protuberant genital papillae in males and swollen abdomen in females) were used.

Two groups of newts (four males and four females and three males and five females, respectively) were kept for about 8 weeks in an aquaterrarium (100×60×70 cm; water depth 30 cm). The tank was provided with large stones and water plants. The newts were fed with chironomid larvae and chopped earthworms. The temperature ranged from 14 to 18.5°C with a natural photoperiod.

To describe behaviour patterns about 80 h of ad libitum observations were made. A list of the behaviour patterns observed was used as the basis for a series of focal observations (sensu Martin and Bateson 1993), using a minute as the smallest time unit. Each observation period lasted for 30 min and a total of 32 h of focal observations were made, with roughly the same amount of time allocated to each individual (mean observation time for males was 128.6 min and mean observation time for females was 113.3 min). This variation was due to the fact that if the focal animal moved out of the water, that period was not considered in the subsequent analysis. The newts were observed around dusk, with the help of a weak light. It was found that the behavioural list presented by previous authors for *T. m. marmoratus* and *T. cristatus* (Green 1989; Sparreboom and Teunis 1990; Zuiderwijk 1986, 1990) was applicable with minor additions that will be presented in the Results section.

To avoid the problems raised by the analysis of contingency tables with many empty cells and cells with low expected frequencies (e.g. Glantz 1992), we used a simulation statistical test written by one of us (TESTMAT, V.C. Almada). This test is equivalent to the software ACTUS (Estabrook and Estabrook 1989), but for larger tables. These simulation procedures have the double advantage of assessing the significance of a contingency table without the restrictions imposed by the use of the χ^2 distribution while allowing simultaneous assessment of the significance of the deviations between expected and observed frequencies of individual cells.

An activity level was computed for each individual as the number of behavioural transitions per minute of observation of that individual. The Mann–Whitney test was applied to assess the activity rates between the sexes. This test was performed using the software package STATISTICA (StatSoft 1995), version 5, for Windows.

Results

Behaviour patterns

The patterns of behaviour considered in this article and their absolute frequencies of occurrence in each sex are presented in Table 1. The behaviour patterns observed in the present study fall into three categories: (1) those that had been described for *T. m. marmoratus* and *T. cristatus* and are now reported for *T. m. pymaeus* (Approach, Move-to-the-front, Fan, Wave, Whip, Lean-in, Cat-buckle, Rocking, Guffing, Push, Handstand, Breathe, Static, Lay egg, Walk, Alert, and Sniff, although Wave, Alert, and Sniff suffered some minor changes in their operational description); (2) those that had been described for other species of the genus *Triturus* but not for *T. m. marmoratus* or *T. cristatus* (Rub); and (3) those that, as far as we know, are described for the first time in this article (Walk-over, Land-over, Stand-on, Show, Erect-body, Yawn, Circle, and Dig). Their operational descriptions are as follows:

- *Walk-over*. A newt walks over the body of another newt.
- *Land-over*. An individual that was swimming lands over the body of another newt.
- *Stand-on*. An individual stays for a while, sometimes for a few minutes, with its body pressing over parts of the body of another conspecific.
- *Show*. A newt orients its flanks or more frequently the cloaca towards the snout of another newt. This is frequently achieved when the animal is supported only by the front feet. The tail may vary in orientation, being sometimes raised.
- *Erect-body*. The animal assumes a bipedal posture with body raised and supported only by the hind feet and tail. This is often a posture that precedes swimming or some other kind of movement.
- *Yawn*. Outside of any obvious agonistic context, the animal fully opens the mouth, slowly closing it afterwards. The entire process may take a few seconds. The rest of the body may be in a variety of positions.
- *Circle*. The newt curls his body perpendicularly to the substrate, completing a circle, touching with his nose in the cloaca region or in the beginning of the tail.
- *Dig*. The individual digs the substrate, making some burrows. If they last for some time the newts may occupy them.

All these patterns were observed in both sexes except for Circle, which was only seen in males.

Behaviour frequencies

The frequencies of the various behaviour patterns in both sexes are presented in Table 1, where inspection reveals that the absolute number of behavioural acts performed

Table 1 Absolute frequencies of each behaviour pattern in males and females and the cases in which they are significantly higher or lower than expected by chance (TESTMAT, see text). *M+* behaviours significantly more frequent in males; *F+* behaviours significantly more frequent in females; *M–* behaviours significantly less frequent in males; *F–* behaviours significantly less frequent in females. *Sniff I* sniffing other newts; *Sniff E* sniffing other materials in the environment

Behaviour	Males		Females	
	Significance	Absolute frequencies	Significance	Absolute frequencies
Move-to-the-front	M+ ($P<0.05$)	26	F– ($P<0.001$)	0
Whip	M+ ($P<0.01$)	37	F– ($P<0.001$)	0
Fan		17	F– ($P<0.05$)	2
Wave	M– ($P<0.01$)	15	F+ ($P<0.01$)	37
Alert	M+ ($P<0.001$)	205	F– ($P<0.001$)	61
Sniff I	M+ ($P<0.001$)	132	F– ($P<0.001$)	23
Sniff E	M– ($P<0.001$)	11	F+ ($P<0.001$)	48
Lean-in	M+ ($P<0.05$)	29	F– ($P<0.001$)	2
Rub		16		4
Breathe		97	F– ($P<0.05$)	38
Approach	M+ ($P<0.01$)	302	F– ($P<0.01$)	135
Cat-buckle		15	F– ($P<0.05$)	1
Rocking		5		0
Handstand		10	F– ($P<0.05$)	0
Guffing		3		1
Static	M– ($P<0.01$)	192	F+ ($P<0.01$)	192
Swim	M– ($P<0.001$)	83	F+ ($P<0.001$)	131
Lay egg		0		16
Walk	M– ($P<0.01$)	52	F+ ($P<0.01$)	71
Walk-over	M– ($P<0.01$)	8	F+ ($P<0.01$)	26
Move-away		245		190
Land-over		14	F+ ($P<0.05$)	21
Erect-body		20		8
Stand-on		10		3
Dig		8		5
Circle		5		0
Show	M– ($P<0.01$)	7	F+ ($P<0.01$)	22
Yawn		1		4
Push		5		2

by females was clearly lower than that performed by males, despite the fact that the observation time allocated to each sex was approximately the same. Indeed, males performed 1,570 behavioural acts, whereas the corresponding value for females was only 1,043. The Mann–Whitney test revealed a higher activity level, expressed as the number of transitions/minute, for the males (males $n=7$, max.=2.69, min.=0.98, median=1.75; females $n=9$, max.=1.5, min.=0.28, median=1.02; $U=84$; $Z=2.6$; $P=0.009$). This means that a simple comparison of individual behaviour patterns between the sexes may be misleading, because a lower number of a given type of behaviour in females may not mean a lower relative frequency of that behaviour, being a mere reflection of an overall lower level of activity. Thus, a simulation test as described in the Methods section was applied for both sexes to the relative frequencies of all the behaviour patterns except for Creep, Bite, Eat, and Get-out, which were so rare that they were excluded from any statistical analysis.

The χ^2 obtained was 393.27 with $df=28$. The χ^2 value was never equalled or exceeded in 1,000 simulations, thus being significantly higher than could be expected by chance. The frequencies that were significantly higher or lower than expected by chance in each sex are presented in Table 1.

Inspection of Table 1 shows that, apart from Lay egg, there is a group of behaviour patterns (Rocking, Push, and Circle) that occurred only in one sex or nearly so but whose frequencies are very low; it seems premature to draw definitive conclusions on their distribution between the sexes, and they did not yield significant results in statistical analysis. The remaining behaviour patterns seem to be well represented in the repertoire of both sexes. This means that many behaviour patterns described as part of the male sexual behaviour repertoire are also expressed by females.

Discussion

Concerning the behaviour patterns described for the first time in this article, it could be argued that Walk-over, Land-over, and Stand-on could result by mere chance, as the animals move around the tank. Since the aquaterrarium was relatively large, we suspect that the movements and postures were not random and may have social meaning.

The analysis of the behaviour frequencies in both sexes confirms that behaviours like Move-to-the-front, Whip, Fan, Lean-in, Cat-buckle, Alert, and Handstand are more frequent in males and that females perform the following behaviours more often: Swim, Walk, Walk-over, Land-over, Show, Static, and Wave.

In the Sniff behaviour there is a marked difference between the sexes. Males tend to sniff mainly other newts (Sniff I), whereas females tend to sniff other materials of the environment (Sniff E). Could the newts, namely males, leave scent marks in the places where they move about?

Two other points are worth mentioning. First, the level of sexual behaviour recorded in all the observations was very low. It is likely that the much higher frequencies of sexual behaviour observed in standard encounters between the sexes is at least partly an artefact. Indeed, the values presented in this article agree with what was described for this species in natural conditions (Zuiderwijk 1990). Second, the activity level is not similar between the sexes, being higher in males, at least when the newts are in breeding condition as in our observations. Thus, simple comparisons of absolute frequencies of behavioural elements may lead to wrong interpretations. We suggest that the assessment of the relative frequencies of the different behaviour patterns, as attempted in this work, is a productive complement of this kind of analysis.

One feature of the approach followed in this article was that instead of assuming that some behaviour patterns are sex specific and belong to a given social motivational area (e.g. sexual or agonistic), we considered the possibility of occurrence of all behaviour patterns in both sexes, regardless of any previous interpretation of their motivational or functional context. In this respect, it is interesting to note that females performed behaviours like Alert, Fan, Lean-in, and Cat-buckle, and even Push. These behaviour patterns have been traditionally viewed as male specific and often interpreted as male sexual behaviour. Some authors have previously observed some of these behaviours in females for other species of the genus (e.g. Denoel 1996 for *T. alpestris alpestris* and *T. a. cyreni*) but considered them "pseudo-male" and "homosexual" behaviours, occurring in the absence of newts of the other sex. This was not the case, because both sexes were always together, and we suggest that further investigation is needed to test the hypothesis of a possible role of these elements either as part of the sexual repertoire of females or as actions with a role in agonistic interactions involving females.

Quantitative analysis of the contexts in which these behaviours occur, of the sequences in which they are integrated, and of the responses they elicit in other newts are clearly needed. Although the observations of groups of both sexes housed together for several weeks may yield a low number of strictly sexual interactions, they seem to be a fruitful ground for the identification of other features of the social behaviour of newts.

Acknowledgements We would like to acknowledge the following people and institutions: João Paulo Fonseca, Rui Edgar Guerreiro, Teresa Bento, Parque Natural Sintra-Cascais. This work was partially supported by the Fundação para a Ciência e Tecnologia through the Programa Plurianual de Apoio às Unidades de Investigação. We thank the reviewers for their careful reading of our manuscript and for their constructive suggestions. All experiments complied with the current laws of Portugal.

References

Denoel M (1996) Etude comparée du comportement de cour de *Triturus alpestris alpestris* (Laurenti, 1768) et *Triturus alpestris cyreni* (Wolterstorff, 1932) (Amphibia, Caudata): approche évolutive. Cah Ethol 16:133–258

Diaz-Paniagua C (1989) Oviposition behavior of *T. marmoratus pymaeus*. J Herpetol 23:159–163

Estabrook CB, Estabrook GF (1989) ACTUS: a solution to the problem of small samples in the analysis of two-way contingency tables. Hist Methods 22:5–8

Faria MM (1993) Sexual behaviour of Bosca's newt, *T. boscai*. Amphibia-Reptilia 14:169–185

Faria MM (1995) A field study of reproductive interaction in Bosca's newt, *T. boscai*. Amphibia-Reptilia 16:357–374

Garcia-Paris M, Herrero P, Martin C, Dorda J, Esteban M, Arano B (1993) Morphological characterization, cytogenetic analysis, and geographical distribution of the pygmy marbled Newt *Triturus marmoratus pygmaeus* (Wolterstorff, 1905) (Caudata: Salamandridae). Bijd Dierkd 63:3–14

Glantz SA (1992) Primer of biostatistics, 3rd edn. McGraw-Hill, New York

Green AJ (1989) The sexual behaviour of the great crested newt, *T. cristatus* (Amphibia: Salamandridae). Ethology 83:129–153

Griffiths RA (1996) Newts and salamanders of Europe. Poyser Natural History, London

Halliday TR (1974) Sexual behaviour of the smooth newt, *Triturus vulgaris* (Urodela, Salamandridae). J Herpetol 8:277–292

Horta N (1983) Notes sobre el comportamiento de *T. marmoratus marmoratus* (Latreille, 1800) (Amphibia, Caudata): conducta sexual. Bull Cat Ictiol Herpetol 3:5–9

Martin P, Bateson P (1993) Measuring behaviour, 2nd edn. Cambridge University Press, Cambridge

Pecio A, Rafinski J (1985) Sexual behaviour of the Montandon's newt, *Triturus montandoni* (Boulenger) (Caudata: Salamandridae). Amphibia-Reptilia 6:11–22

Sparreboom M (1983) On the sexual behaviour of *Paramesotriton caudopunctatus* (Liu & Hu) (Amphibia: Caudata: Salamandridae). Amphibia-Reptilia 4:25–33

Sparreboom M (1986) Note préliminaire sur le comportement sexuel du triton creté (*T. cristatus*) et du triton marbré (*T. marmoratus*) dans des conditions expérimentales. Bull Soc Herpetol Fr 40:36–42

Sparreboom M, Faria MM (1997) Sexual behaviour of the Chinese fire-bellied newt, *Cynops orientalis*. Amphibia-Reptilia 18: 27–38

Sparreboom M, Teunis B (1990) The courtship display of the marbled newt *Triturus marmoratus*. Amphibia-Reptilia 11:351–361

StatSoft, Inc. (1995) STATISTICA for Windows. (computer program manual) Tulsa, Okla.

Zuiderwijk A (1986) Interaction et accouplement du triton creté et du triton marbré (Urodela, Salamandridae). Méthodes d'observation. Bull Soc Herpetol Fr 40:28–35

Zuiderwijk A (1990) Sexual strategies in the newts *T. cristatus* and *T. marmoratus*. Bijd Dierkd 60:51–64