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ORIGINAL PAPER

Acoustic orientation in the palmate newt, *Lissotriton helveticus*

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Abstract Experiments reported here were carried out to investigate the use of acoustic cues by palmate newts (*Lissotriton helveticus*) for orientation and to study whether this behavior is learned, or whether two populations of palmate newts that cohabit with different frog species (Iberian green frog, *Rana perezi*, and European common brown frog, *Rana temporaria*) show different phonotactic preferences. The orientation tests consisted of presenting a control stimulus (white noise), a sympatric acoustic stimulus (calls of *R. perezi* or *R. temporaria*, depending on the origin of newts), or an allopatric stimulus (calls of natterjack toads, *Bufo calamita*, or *R. perezi*). Newts were released in a circular arena, while the acoustic stimuli were presented outside of the circular arena in four different compass orientation directions (0, 90, 180 and 270°). In this study, we show that *L. helveticus* performed positive phonotaxis toward the calls of *R. perezi* only when both species shared habitat, orienting randomly when *R. perezi* was absent from the newt's natal population. Newts from both populations oriented randomly when exposed to the allopatric and control acoustic stimuli. These results suggest, for the first time, that recognition of the sympatric heterospecific calls could be learned. However, newts sharing the breeding pond with a population of *R. temporaria* oriented randomly when exposed to the calls of this species. The fact that the breeding seasons of *R. temporaria* and *L. helveticus* do not overlap in time does not allow the use of *R. temporaria* calls as a guidance mechanism for migrating individuals of *L. helveticus*.

Keywords Acoustic orientation · Homing · Migration · Phonotaxis · Newt

Introduction

Homing ability has been documented in different species of newts (e.g., *Taricha rivularis*: Twitty et al. 1966; *Notophthalmus viridescens*: Phillips 1987; Phillips et al. 1995; *Triturus marmoratus*: Diego-Rasilla and Luengo 2002; *Mesotriton alpestris*: Joly and Miaud 1989; Diego-Rasilla 2003; Diego-Rasilla et al. 2005), and several cues have been shown to play a role in their homing orientation. Newts may be capable of homing using celestial (Landreth and Ferguson 1967; Diego-Rasilla and Luengo 2002) and magnetic cues (Phillips 1986; Fischer et al. 2001; Diego-Rasilla 2003, 2004; Diego-Rasilla et al. 2005). Also, it has been found that odors from ponds (Joly and Miaud 1993) and acoustic cues (Diego-Rasilla and Luengo 2004) may be stimuli involved in orientation responses, improving the accuracy of orientation during the final approach to the breeding pond.

The possible role of acoustic cues in orientation of newts has received little attention. However, although newts do not seem capable of acoustic communication (Wilczynski and Ryan 1988), a recent study has found that *T. marmoratus* shows heterospecific call recognition and positive phonotaxis when exposed to the advertisement

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calls of anurans with which they share a breeding pond (Diego-Rasilla and Luengo 2004).

Newts lack middle and external ears, but they have inner ears that can process sound (Hetherington 2001). Hetherington (2001) found that the lateral body wall and lungs of newts may function in sound reception, especially at relatively low frequencies (i.e., peak motion ranging from 1,600 to 2,500 Hz) in small newts, as is the case in palmate newts. Sound causes the newt's lungs to vibrate, and the vibrations are transmitted from the lungs to the newt's inner ear for processing.

Experiments reported here were carried out to characterize the use of acoustic cues by palmate newts (*Lissotriton helveticus*) for orientation, addressing some of the questions left open by our previous work (Diego-Rasilla and Luengo 2004), such as whether this behavior is learned, or whether two populations of the same species that cohabit with different frog species show different phonotactic preferences.

Specifically, we studied the orientation responses of palmate newts to the advertisement calls of natterjack toads (*Bufo calamita*), of European common brown frogs (*Rana temporaria*) and of Iberian green frogs (*Rana perezi*). We hypothesized that newts would recognize the signals of a sympatric species that would share habitat with them but not those of a species that would be absent from natal populations. Moreover, this capability might elicit positive phonotaxis.

Materials and methods

Subjects and study site

Two groups of adult palmate newts were collected in 2005; one group from a garden pond of 2 m^2, situated in Barros (Cantabria, northern Spain; 43°17′7″N, 4°4′41″W; 61 m a.s.l.), and another group collected from a pond situated in a mountainous area, at the Saja-Besaya Natural Park (Cantabria, northern Spain; 43°13′51″N, 4°09′50″W; 382 m a.s.l.). Newts were collected by dip netting from breeding ponds during the seasonal migratory periods. In the lowland area, palmate newts begin their migration to their breeding ponds in February, but large numbers of newts have not been found in the ponds until late March. However, in the mountainous area, their seasonal migratory period usually extends from late March to early May. Also, in both populations, the males are the first to arrive at the ponds (personal observation). During July or, even later, in August, the adult newts leave the water. Palmate newts typically hibernate in deep leaf litter in late September and no further than 150 m away from their spring reproductive area. The young newts have more terrestrial habits and show a high dispersal and colonization capacity, covering distances up to a few kilometers away from their birth area (Montori and Herrero 2004).

The two ponds were separated by 9.21 km. The garden pond was artificially created in 12 October 2001, and it was weekly monitored during the next 12 months to assess colonization by amphibians. This pond is situated 290 m away from the nearest aquatic habitat. The first amphibian species arriving at the pond was *R. perezi* (17 March 2002), followed by the appearance of *L. helveticus* 13 days later. No other species of amphibians have been found to date at the pond, although *Bufo bufo* and *Alytes obstetricans* have been observed in the study area. The pond at the Saja-Besaya Natural Park is used for breeding by three species of urodeles (*L. helveticus*, *Mesotriton alpestris* and *Salamandra salamandra*) and one anuran species (*R. temporaria*), which is found in Spain mainly in mountainous areas (Barbadillo et al. 1999).

Procedure

At the lowland site (Barros), 23 newts (9 adult males and 14 adult females) were captured in 2005 (6 May) between 1830 and 1900 hours (GMT). Sixteen newts (15 adult males and 1 adult female) were captured between 1530 and 1700 hours (GMT) in 2005 (30 March) at Saja-Besaya. Newts were placed in opaque plastic containers (54×35×21 cm) in which the water depth was 1 cm and taken to the indoor testing arena. Animals were tested between 2 and 9 h after being captured because they show the highest levels of activity during the first hours of the night, and their homing behavior takes place during the night (Montori and Herrero 2004). They were returned to their pond just after testing.

Testing protocols described by Diego-Rasilla and Luengo (2004) were basically used. Newts were tested indoors in an arena consisting of a circular plastic container (45 cm diameter, 25 cm high). The floor and arena walls were thoroughly wiped with a damp cloth between trials to eliminate directional olfactory cues (Fischer et al. 2001), and then, they were wiped dry using paper towels.

Just before their individual testing session, newts were kept individually, and acoustically isolated, for 5 min in opaque plastic containers (34×24×16 cm), containing water from the newt's home pond, in which the water depth was 1 cm. For testing, a newt was removed individually from its plastic container and put in the arena center in complete darkness beneath an opaque, cylindrical plastic container (9 cm diameter, 14.5 cm high) that served as a release device. Then, we presented the acoustic stimulus (see details below). Newts were held in the container for 1 min to overcome the effects of handling before the release device was lifted, allowing them to move freely about the arena. To minimize disturbance during the experiments, the observers moved away from the arena, leaving each animal undisturbed for 5 min. Individual trials were discontinued, if the newt remained motionless in the arena center for 5 min. The directional responses of each newt that left the central area was recorded by the moist trails that it left on the floor of the arena. In all cases, newts that left the central area moved directly from their initial position to the arena wall, tapped against the wall, and then clinging to the wall, proceeded to circle around the arena. Directional responses were recorded to 5° accuracy as the vector of the first point where an animal made contact with the wall.

We carried out two different experiments: (1) The first experiment was performed using newts collected from Saja-Besaya; in this experiment, the orientation tests consisted of presenting a control stimulus (white noise), a sympatric acoustic stimulus (the calls of *R. temporaria*), or an allopatric stimulus, the calls of *R. perezi*. (2) The second experiment was performed using newts collected from Barros; the orientation tests consisted of presenting a control stimulus (white noise), a sympatric acoustic stimulus (the calls of *R. perezi*), or an allopatric stimulus (the calls of *B. calamita*) that *L. helveticus* would not be expected to recognize. *L. helveticus* and *R. perezi* occur in sympatry in this lowland area, but *B. calamita* is not present in the study area. Thus, *B. calamita* occurs over most of the country, except the northern parts of the Iberian Peninsula where we carried out these experiments (Reques and Tejedo 2002). The nearest populations of *B. calamita* are ~30 km away from Barros and ~20 km away from Saja-Besaya (Reques and Tejedo 2002).

The calls of *R. perezi*, *R. temporaria* and *B. calamita* (Fig. 1; sample format 16-bit signed PCM [Pulse Code Modulation], sample rate 48,000 Hz) were obtained from Márquez and Mateu (1995) and were stored on a notebook computer (MITAC 5033). The length of time for playback sequences was 1 min, and they were played in continuous loop mode. The calls of *R. perezi* and *B. calamita* represent a small group of males (Fig. 1a,b), and the calls of *R. temporaria* were from a pair of males (Fig. 1c; Márquez

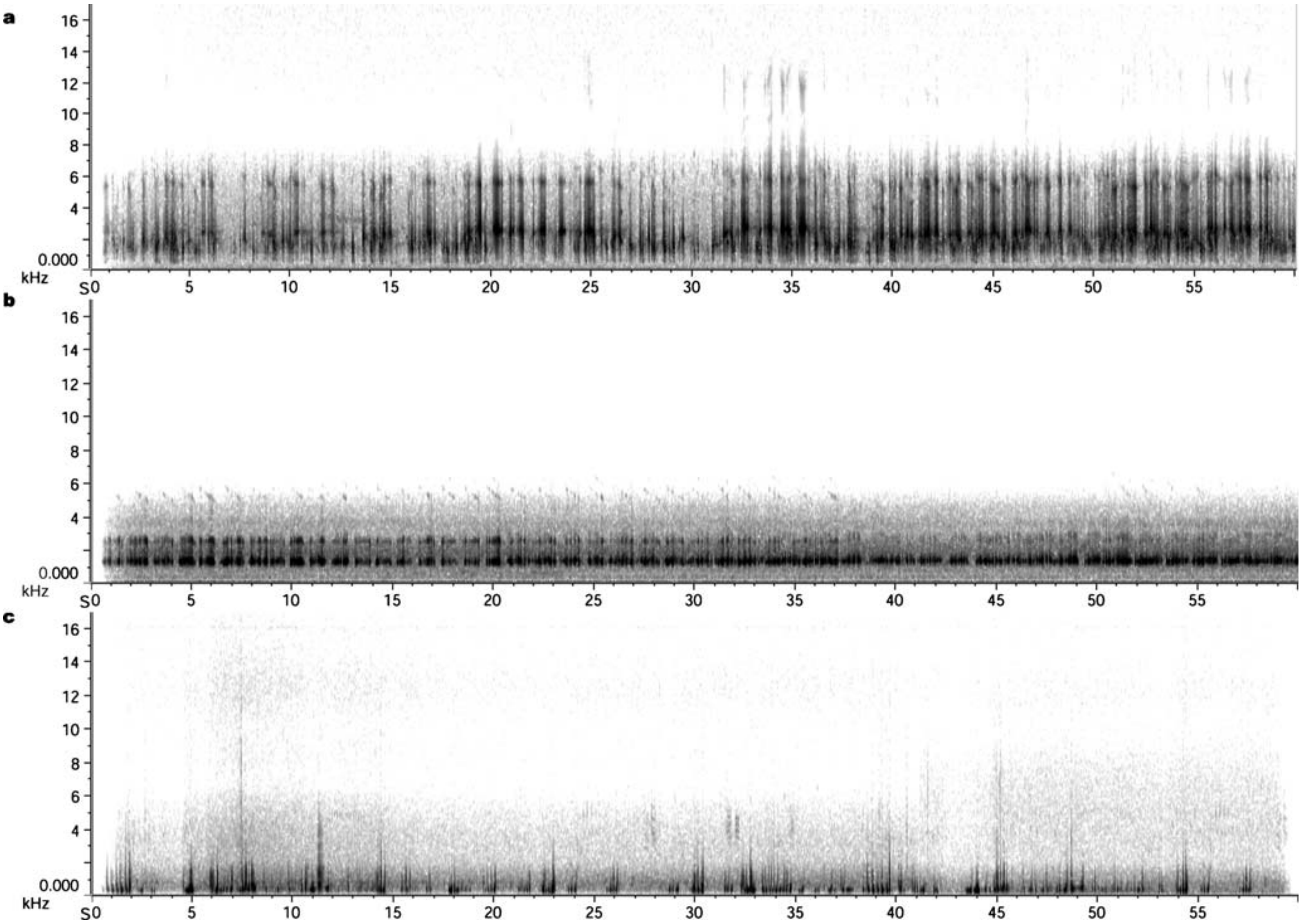

Fig. 1 Spectrogram views of acoustic signals. **a** Calls of *Rana perezi*, **b** calls of *Bufo calamita* and **c** calls of *Rana temporaria*. The spectrogram view represents time on the *horizontal axis*, frequency on the *vertical axis* in kHz and relative intensity at each time and frequency as a *grayscale value*. All three spectrograms have the same window type (Hann), window size (=512 samples, 10.7 ms), time grid spacing = 5.8 ms (frame overlap = 50%), frequency grid spacing = 93.8 Hz (FFT size = 512 samples) and 3-dB bandwidth (=135 Hz)

and Mateu 1995). The calls were broadcast to subjects using Tsunami EA-968 speakers (Tsunami, Guangdong, China) and Cool Edit 96 acoustics software (Syntrillium Software, Phoenix, USA). The overall absolute sound pressure level (dB SPL) of the calls, measured 20 cm from the speakers (i.e., the distance of the newt to the speakers) with a Digital Sound Level Meter (Electro Tools ET 9901, Guijarro Hermanos, Madrid, Spain), was 68 dB. This corresponds to the sound level of *R. perezi* calls 10–12 m from the breeding pond.

The acoustic stimuli were presented outside of the circular arena in four different compass orientation directions (0, 90, 180 and 270°), being the speakers positioned just below the lip of the arena. We randomized the order of the stimulus presentation for each individual in each experimental condition. In the first experiment, the first four newts were tested with the allopatric acoustic stimulus (i.e., the calls of *R. perezi*), followed by four fresh newts tested with the sympatric acoustic stimulus (i.e., the calls of *R. temporaria*) and four more newts tested with the control acoustic stimulus (i.e., white noise). In the second experiment, the first four newts were tested with the allopatric acoustic stimulus (i.e., the calls of *B. calamita*), followed by four fresh newts tested with the sympatric acoustic stimulus (i.e., the calls of *R. perezi*) and four more newts tested with the control acoustic stimulus (i.e., white noise). In both experiments, newts tested with the allopatric, sympatric and control acoustic stimuli were separately placed in opaque plastic containers (54×35×21 cm) in which the water depth was 1 cm. When all the newts had been tested in one of three acoustic conditions, newts previously tested with the allopatric acoustic stimulus were tested with the sympatric acoustic stimulus; those previously tested with the sympatric acoustic stimulus were tested with the control stimulus, and newts previously tested with the control acoustic stimulus were tested with the allopatric stimulus (this was again done in a random order). In all the experiments, these sequences were repeated until all the newts had been exposed once to the sympatric acoustic stimulus, once to the allopatric stimulus and once to the control stimulus. Also, in the first experiment, the first individual was tested with the acoustic stimulus from a 180° direction, the next individual was tested with the stimulus from 0°, followed by one tested with the stimulus from 90° and one tested with the stimulus from 270°. The order of the four acoustic stimuli directions was 270, 90, 180 and 0° in the second experiment. The order of the four acoustic stimuli directions was determined using a random number sequence. This sequence was repeated until the test had been completed. If a newt did not reach the orientation criterion within the appropriate time interval, the next individual was tested with the stimulus from the same direction. Accordingly, data pooled from an entire test series included roughly equal numbers of bearings from newts tested in each of the four symmetrical orientation directions of the acoustic stimuli. Data from the four conditions are combined by rotating the bearings so that the acoustic stimuli compass directions coincide at 0° (i.e., 90° is subtracted from the actual headings of newts tested with the acoustic stimuli from 90°, 180° from the headings of newts tested with acoustic stimuli from 180°, and 270° from the headings of newts tested with acoustic stimuli from 270°). Pooling the acoustic bearings from an approximately equal number of newts tested in each of the four acoustic stimuli directions made it possible to factor out any consistent non-acoustic bias (Diego-Rasilla and Luengo 2004).

Data were analyzed using standard circular statistics (Batschelet 1981; Fisher 1995). The mean vector bearing was calculated by vector addition and tested for significance using a modified Rayleigh test, the V test. This test was used to test closeness to expected orientation (i.e., the direction of the acoustic stimuli, 0°), and the Watson U^2 test was used to test for differences between distributions, providing a criteria to test whether two samples differ significantly from each other (Batschelet 1981; Mardia and Jupp 2000).

Results

Experiment 1 (Saja-Besaya/highland experiment)

Newts were randomly oriented with respect to sound in all of the three acoustic conditions: the calls of *R. temporaria* (i.e., the sympatric acoustic stimulus; 46±77°; V test with expected direction = 0° r=0.25, N=16, P=0.16; Fig. 2a), the calls of *R. perezi* (i.e., the allopatric acoustic stimulus; 49±73°; V test with expected direction = 0° r=0.32, N=15, P=0.123; Fig. 2b) and the white noise (195±99°; V test with expected direction = 0° r=0.23, N=11, P=0.845; Fig. 2c). The distributions of the orientation data under the three treatments are not significantly different (Watson U^2 test: NS in all cases; Fig. 2).

Experiment 2 (Barros/lowland experiment)

Newts tested with the sympatric acoustic stimulus (i.e., the calls of *R. perezi*) were oriented towards the sound source (34±42°; V test with expected direction = 0° r=0.41, N= 19, P=0.017; Fig. 3a), whereas both the distribution of bearings in the presence of the allopatric acoustic stimulus (i.e., the calls of *B. calamita*; 14°; V test with expected direction = 0° r=0.15, N=15, P=0.213; Fig. 3b), and the distribution of headings in the presence of the control acoustic stimulus (i.e., white noise; 78±168°; V test with

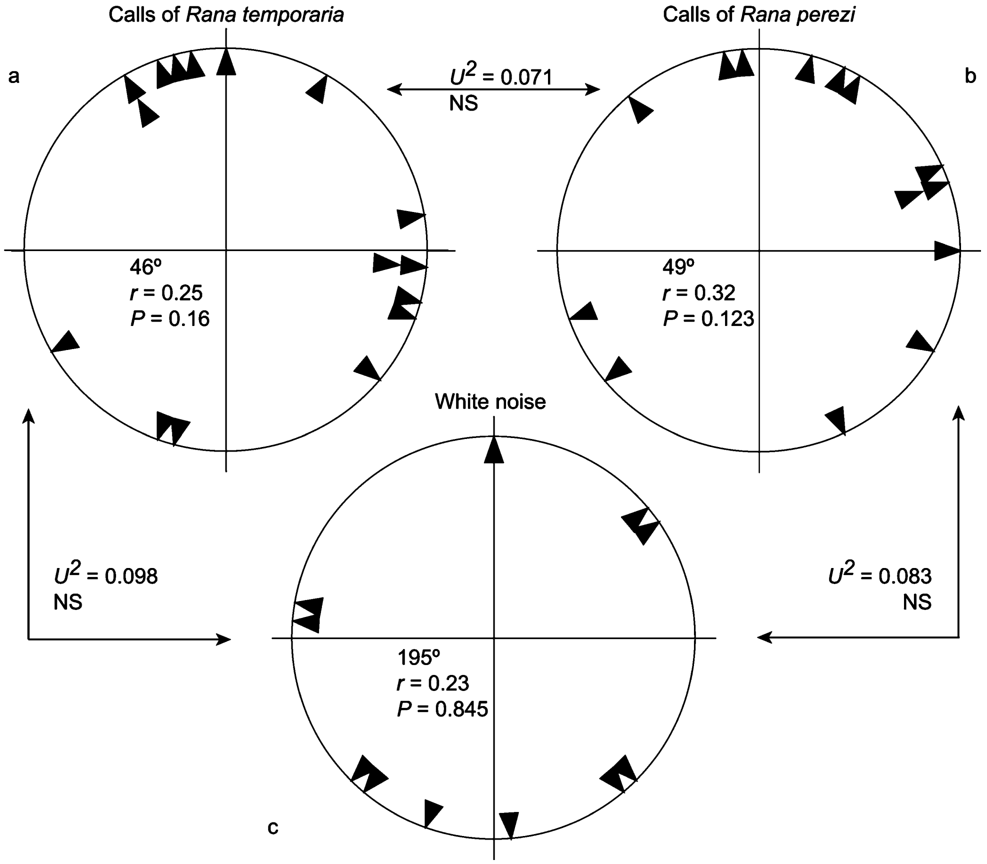

Fig. 2 Orientation responses of the palmate newts from the mountainous area (i.e., experiment 1) **a** to the sympatric acoustic stimulus (i.e., the calls of European common brown frogs), **b** to the allopatric acoustic stimulus (i.e., the calls of Iberian green frogs) and **c** to the white noise. *Symbols* indicate the direction of movement of each individual newt tested only once in one of four symmetrical acoustic stimuli orientation directions (i.e., 0, 90, 180 and 270°). The location of speakers broadcasting the calls is referenced at 0°. The *arrow at the center* of the diagram indicates the mean direction of orientation; the *length of the arrow* is proportional to the mean vector length (*r*). *Dashed lines* indicate the 95% confidence intervals for the mean vector length; the radius of each diagram corresponds to *r*=1

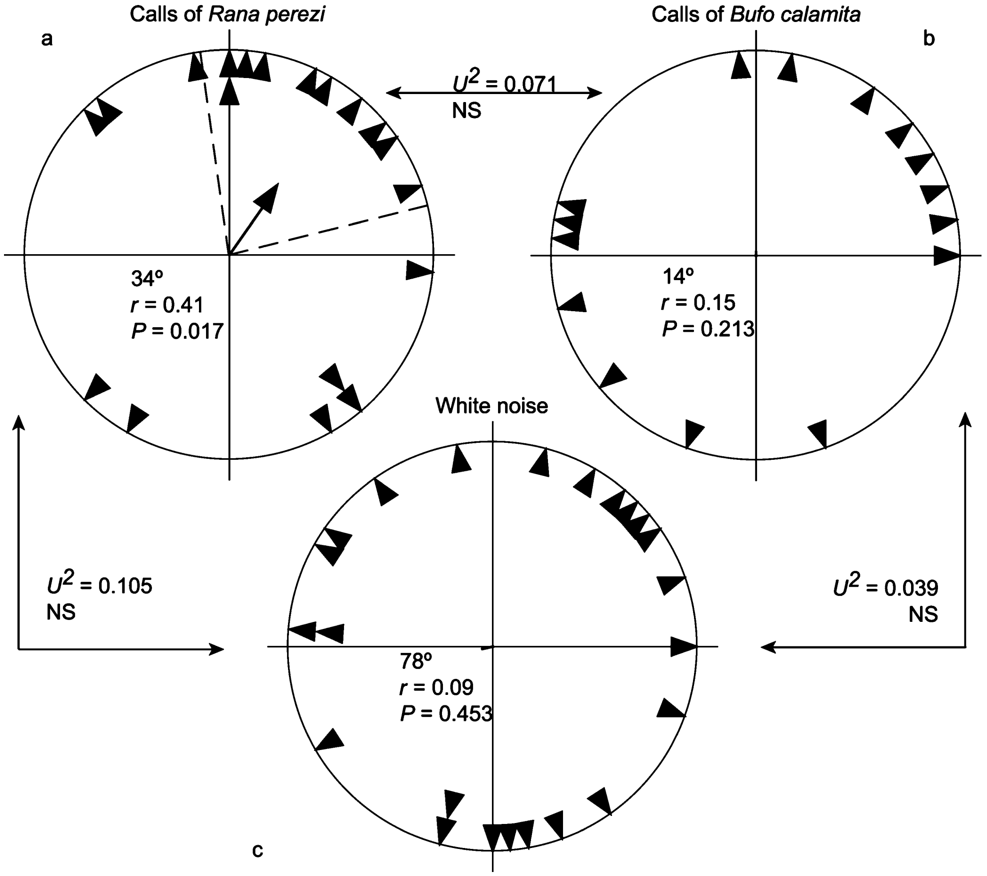

Fig. 3 Orientation responses of the palmate newts breeding in Barros (i.e., experiment 2) **a** to the sympatric acoustic stimulus (i.e., the calls of Iberian green frogs), **b** to the allopatric stimulus (i.e., the calls of natterjack toads) and **c** to the white noise. *Symbols* are the same as in Fig. 2

expected direction = 0° r=0.09, N=23, P=0.453; Fig. 3c) were indistinguishable from random. The distributions of the orientation data under the three treatments are not significantly different (Watson U^2 test: NS in all cases; Fig. 3).

Discussion

The present findings provide more evidence of heterospecific call recognition and positive phonotactic response in urodeles and show the role of acoustic cues as reference cues for orientation by *L. helveticus*, as previously described in *T. marmoratus* (Diego-Rasilla and Luengo 2004).

Palmate newts performed positive phonotaxis toward the calls of the Iberian green frogs only when both species shared habitat (i.e., lowland population), orienting randomly when the Iberian green frogs were absent from the newt's natal population (i.e., the population of the mountainous area). Also, newts from both populations oriented randomly when exposed to the allopatric and control acoustic stimuli. These findings support the hypothesis that the newts are capable of recognizing the advertisement calls of anurans with which they share a breeding pond (Diego-Rasilla and Luengo 2004), although palmate newts sharing the breeding pond with a population of European common brown frogs (i.e., newts from the mountainous area) did not show any orientation response when exposed to the calls of this anuran species.

Breeding phenology by *R. temporaria* could explain why their breeding calls did not elicit any orientation response. This species is an explosive pond breeder (i.e., reproduces in a very short time frame), and the breeding period is much shorter in this species than in other species of frogs (Elmberg 1990; Barbadillo et al. 1999; Nieto-Román et al. 2004). Also, R. temporaria usually breeds in our study area in early February, although we have found some floating clutches in early January (personal observation). However, in this mountainous area, palmate newts usually begin their migration to their breeding pond in late March, although large numbers of newts have not been found in the ponds until early May (personal observation). In reality, palmate newts co-occur in the pond with tadpoles of *R. temporaria* but not with adult frogs. Therefore, the fact that the breeding seasons of *R. temporaria* and *L. helveticus* do not overlap in time makes impossible the use of calls of *R. temporaria* as a guidance mechanism for migrating individuals of *L. helveticus*. Consequently, newts breeding in the same pond as European common brown frogs did not recognize their calls and oriented randomly when exposed to the calls of frogs.

In *L. helveticus* and *T. marmoratus* (Diego-Rasilla and Luengo 2004), we have found a lack of response to frog breeding calls broadcast in regions uninhabited by the frog species. The same breeding calls of natterjack toads were recognized and elicited positive phonotaxis by marbled newts (Diego-Rasilla and Luengo 2004), whereas palmate newts were unable to use them for orientation because natterjack toads are completely absent from our study area (Reques and Tejedo 2002), and the palmate newts had never heard the calls of this toad species. Our results suggest that this orientation behavior seems to be a plastic behavior pattern that can be adjusted to local conditions and community composition. Thus, the same species, *L. helveticus*, might use acoustic cues from different species or no cue at all depending upon the location of their breeding pond.

In some anuran species, like *B. calamita* (Sinsch 1990a, 1992a) and *Bufo fowleri* (Ferguson and Landreth 1966), conspecific calls are useful for orientation but not indispensable. Amphibians rely on a variety of orientation cues to find their way around their home ranges or to locate breeding ponds (Sinsch 1991, 1992b, 2006), and experimental studies in which these cues were manipulated suggest that the absence of one type of cue can reduce orientation ability, but no single cue is absolutely essential for the animals to locate breeding sites (Sinsch 1990a,b). Available information suggest that magnetic and celestial cues are primary cues involved in newt's homing orientation (Landreth and Ferguson 1967; Phillips 1986, 1987; Phillips and Borland 1994; Phillips et al. 1995; Diego-Rasilla and Luengo 2002; Diego-Rasilla 2003; Diego-Rasilla et al. 2005), whereas other orientation cues, such as odor cues from breeding ponds or acoustic cues, will be reliable over relatively short distances (Joly and Miaud 1993; Diego-Rasilla and Luengo 2004) and are unlikely to account for the long-distance homing exhibited by newts, although these cues might improve accuracy of orientation during the final approach to the breeding pond and should increase colonization of ponds near currently used ponds.

The results suggest that it is possible that the individuals from the lowland population may perform positive phonotaxis to the sympatric anuran calls because they have learned to associate these calls with the pond location and, thus, are able to distinguish the calls from other types of sound signals. In fact, the population showing the positive phonotactic response came from a man-made pond less than 4 years old. However, although this hypothesis is suggestive, it is not entirely conclusive because it may be possible that a genetically based recognition system could also function here, if the frogs and newts co-occur often enough that the presence of heterospecific signals is part of the "expected environment." The advantages of the demonstrated system are clear, so it is theoretically possible that the distinct behavioral types could arise through selection, if the newt and frog populations overlapped for a sufficient amount of time. Therefore, although feasible, learning is not a default conclusion for population differences in behavior.

Our results confirm that migrating newts can use the calls of anurans as a guidance mechanism. However, more research is needed to determine the types of sensory cues involved in the orientation behavior of *L. helveticus*, and a detailed study is now in progress. Furthermore, although our results support the acoustic orientation hypothesis, future work should be focused on testing the heterospecific attraction hypothesis (Mönkkönen et al. 1999). Because the palmate newts arrived at the garden pond after the Iberian green frogs, presumably colonizing newts might use the presence of resident species (Iberian green frogs) as a cue for profitable aquatic breeding sites. Thus, movements apparently in response to calls may favor dispersal in newts (Ferguson and Landreth 1966). Hence, later-arriving individuals might use the presence of earlier established species as a cue to profitable breeding sites (i.e., heterospecific attraction; Mönkkönen et al. 1999).

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References

Barbadillo LJ, Lacomba JI, Pérez-Mellado V, Sancho V, López-Jurado LF (1999) Anfibios y Reptiles de la Península Ibérica, Baleares y Canarias. Editorial GeoPlaneta, Barcelona

Batschelet E (1981) Circular statistics in biology. Academic, London

Diego-Rasilla FJ (2003) Homing ability and sensitivity to the geomagnetic field in the alpine newt, *Triturus alpestris*. Ethol Ecol Evol 15:251–259

Diego-Rasilla FJ (2004) El sentido magnético y su uso en la orientación de los animales. In: Pereira D, Bárcena MA, Rubio I, Sesma J (eds) Aproximación a las Ciencias Planetarias. Aquilafuente 74. Ediciones Universidad de Salamanca, Salamanca, pp 269–297

Diego-Rasilla FJ, Luengo RM (2002) Celestial orientation in the marbled newt (*Triturus marmoratus*). J Ethol 20:137–141 DOI 10.1007/s10164-002-0066-7

Diego-Rasilla FJ, Luengo RM (2004) Heterospecific call recognition and phonotaxis in the orientation behavior of the marbled newt, *Triturus marmoratus*. Behav Ecol Sociobiol 55:556–560 DOI 10.1007/s00265-003-0740-y

Diego-Rasilla FJ, Luengo RM, Phillips JB (2005) Magnetic compass mediates nocturnal homing by the alpine newt, *Triturus alpestris*. Behav Ecol Sociobiol 58:361–365 DOI 10.1007/s00265-005-0951-5

Elmberg J (1990) Long-term survival, length of breeding season, and operational sex ratio in a boreal population of common frogs, *Rana temporaria* L. Can J Zool 68:121–127

Ferguson DE, Landreth HF (1966) Celestial orientation of the fowler's toad *Bufo fowleri*. Behaviour 26:105–123

Fischer JH, Freake MJ, Borland SC, Phillips JB (2001) Evidence for the use of magnetic map information by an amphibian. Anim Behav 62:1–10 DOI 10.1006/anbe.2000.1722

Fisher NI (1995) Statistical analysis of circular data. Cambridge University Press, Cambridge

Hetherington T (2001) Laser vibrometric studies of sound-induced motion of the body walls and lungs of salamanders and lizards: implications for lung-based hearing. J Comp Physiol [A] 187:499–507

Joly P, Miaud C (1989) Fidelity to the breeding site in the alpine newt *Triturus alpestris*. Behav Processes 19:47–56

Joly P, Miaud C (1993) How does a newt find its pond? The role of chemical cues in migrating newts (*Triturus alpestris*). Ethol Ecol Evol 5:447–455

Landreth HF, Ferguson DE (1967) Newts: sun-compass orientation. Science 158:1459–1461

Mardia KV, Jupp PE (2000) Directional statistics. Wiley, New York

Márquez R, Mateu E (1995) Sounds of frogs and toads of Spain and Portugal. ALOSA, sonidos de la naturaleza, Barcelona

Mönkkönen M, Härdling R, Forsman JT, Tuomi J (1999) Evolution of heterospecific attraction: using other species as cues in habitat selection. Evol Ecol 13:93–106

Montori A, Herrero P (2004) *Lissotriton helveticus* (Rauzoumowsky, 1789). In: Ramos MA et al (eds), Amphibia, Lissamphibia. García-París M, Montori A, Herrero P, Fauna Ibérica, vol 24. Museo Nacional de Ciencias Naturales, CSIC, Madrid, pp 252–275

Nieto-Román S, Barluenga M, Palanca A, Vences M, Meyer A (2004) Post-mating clutch piracy in an amphibian. Nature 431:305–308 DOI 10.1038/nature02879

Phillips JB (1986) Two magnetoreception pathways in a migratory salamander. Science 233:765–767

Phillips JB (1987) Homing orientation in the eastern red-spotted newt (*Notophthalmus viridescens*). J Exp Biol 131:215–229

Phillips JB, Borland SC (1994) Use of a specialized magnetoreception system for homing by the eastern red-spotted newt *Notophthalmus viridescens*. J Exp Biol 188:275–291

Phillips JB, Adler K, Borland SC (1995) True navigation by an amphibian. Anim Behav 50:855–858

Reques R, Tejedo M (2002) *Bufo calamita*. In: Pleguezuelos JM, Márquez R, Lizana M (eds) Atlas y libro rojo de los anfibios y reptiles de España. Dirección General de Conservación de la Naturaleza-Asociación Herpetológica Española, Madrid, pp 107–109

Sinsch U (1990a) The orientation behaviour of three toad species (genus *Bufo*) displaced from the breeding site. In: Hanke W (ed) Fortschritte der Zoologie, vol 38, Biology and physiology of amphibians. Gustav Fischer Verlag, Stuttgart, pp 73–83

Sinsch U (1990b) Migration and orientation in anuran amphibians. Ethol Ecol Evol 2:65–79

Sinsch U (1991) The orientation behaviour of amphibians. Herpetol J 1:541–544

Sinsch U (1992a) Sex-biased site fidelity and orientation behaviour in reproductive natterjack toads (*Bufo calamita*). Ethol Ecol Evol 4:15–32

Sinsch U (1992b) Amphibians. In: Papi F (ed) Animal homing. Chapman and Hall, New York, pp 213–233

Sinsch U (2006) Orientation and navigation in Amphibia. Mar Freshw Behav Physiol 39:65–71

Twitty VC, Grant D, Anderson O (1966) Course and timing of the homing migration in the newt *Taricha rivularis*. Proc Natl Acad Sci USA 56:864–869

Wilczynski W, Ryan MJ (1988) The amphibian auditory system as a model for neurobiology, behavior, and evolution. In: Fritzsch B, Ryan MJ, Wilczynski W, Hetherington T, Walkowiak W (eds) The evolution of the amphibian auditory system. Wiley, New York, pp 3–12