and neighbour-joining resulted in identical topologies (see figure).

These results are significant for several reasons. First, the monophyly of the genus *Lynx* is strongly supported, a finding similar to that of Werdelin[2] but contrasting with some morphological accounts[4]. Second, relationships among the felid taxa are congruent with previous molecular data[5]. Third, the Iberian lynx is divergent from both the Eurasian lynx and Canadian species, and so can be considered an evolutionary unit (or valid phylogenetic species) in that from both a morphological and a genetic standpoint it is unique. The Iberian lynx revealed a lower level of nucleotide sequence divergence (0.006%) than the bobcat (0.61%) or Eurasian lynx (0.69%). It will be interesting to conduct a detailed study of the remaining isolated populations of Iberian lynx in an effort to learn more about the overall phylogeographical pattern and levels of genetic variation in this rapidly vanishing species.

Juan F. Beltrán
Estación Biológica de Doñana,
Consejo Superior de Investigaciones Científicas, Apartado 1056,
41080 Sevilla, Spain
John E. Rice
Rodney L. Honeycutt
Department of Wildlife and Fisheries Sciences,
Texas A&M University,
College Station, Texas 77843, USA

1. Werdelin, L. *Ann. Zool. Fenn.* **18,** 37–71 (1981).
2. Corbet, G. B. & Hill, J. E. *A World List of Mammalian Species* (Br. Mus. Nat. Hist., London, 1986).
3. Rodríguez, A. & Delibes, M. *Biol. Conserv.* **61,** 189–196 (1992).
4. Salles, L. O. *Am. Mus. Novit.* **3047,** 1–67 (1992).
5. Janczewski, D. N., Modi, W. S., Stephens, J. C. & O'Brien, S. J. *Molec. Biol. Evol.* **12,** 690–707 (1995).

Right-pawedness in toads

SIR—Preferential limb use, of which human handedness is the most clear example, is a prominent aspect of brain lateralization and has been reported in both birds and mammals[1]. There are reports of significant 'footedness' in avian species that use their feet to manipulate food and objects[2]; lateralized forelimb usage in large samples of inbred mice[3]; and in primates, recent assessments have revealed handedness in several species[4]. Neural lateralization for control of vocalizations has recently been reported in anurans[5], raising the possibility that preferences in limb use may exist in lower vertebrates, such as amphibians. Here we report the first evidence for behavioural asymmetry in forelimb usage at the population level in two species of anurans. Our findings suggest that pawedness has a long evolutionary history, dating back at least to early tetrapods.

We have examined the forepaw used by European toads (*Bufo bufo*) of natural populations during attempts to remove either a plastic balloon wrapped around the head (expt 1) or a strip of paper stuck onto the mouth/nose region (expt 2). In both experiments, toads showed a bias for right forepaw use at the population level (see table).

It is often assumed that laterality of limb use evolved only in those species that use their limbs for manipulative activities[6]. Domestic chickens (*Gallus gallus*), however, do not use their feet to pick up or manipulate objects, but they use their right foot preferentially during ground scratching[2]. Thus, it has been suggested that it is not manipulative ability alone which confers a population bias of footedness in avian species, but rather active use of the feet for feeding or searching for food[1,2]. *B. bufo* makes some use of the feet in feeding and also commonly wipes its head using one of its forepaws[7]. Active use of the forelimbs associated with feeding or grooming behaviour could thus produce asymmetrical forepaw usage in this species.

The South American cane toad (*Bufo marinus*) does not show asymmetry in the paper-strip test (see table; expt 3), but does have asymmetry in another behavioural test. We measured to which side *B. marinus* turned when positioned underwater, with the ventral surface of the toad uppermost (expt 4). From videotapes we determined that the toads pivoted preferentially to their left side. During the pivot, the left forepaw was released, and the right forepaw controlled rolling to the upright position.

Pawedness and motor asymmetries found in natural populations of toads could represent a precursor of handedness in higher vertebrates and thus contribute to our understanding of the evolution of brain lateralization.

Angelo Bisazza, Claudio Cantalupo
Dipartimento di Psicologia Generale, Università di Padova, 35131 Padova, Italy
Andrew Robins, Lesley J. Rogers
Department of Physiology, University of New England, Armidale, New South Wales 235, Australia
Giorgio Vallortigara*
Istituto di Filosofia, Pedagogia, Didattica delle Lingue Moderne, Università di Udine, 33100 Udine, Italy

EXPERIMENTS TO ASSESS PAWEDNESS

	Per cent 'right-pawed'	Student's *t*-test (two-tailed)	Probability	No. of animals showing preference 'Right-pawed'	'Left-pawed'	χ^2 test	Probability
Bufo bufo							
Expt 1							
(n=24)	59.2±3.9	2.325	<0.05	14	4	5.55	<0.02
Expt 2							
(n=46)	55.2±2.5	2.039	<0.05	26	10	7.11	<0.01
Bufo marinus							
Expt 3							
(n=18)	48.2±5.5	–0.330	>0.1				
Expt 4							
(n=18)	66.4±2.8	5.795	<0.001	15	2	9.940	0.002

Mature *B. bufo* were collected from natural populations (Valsanzibio, Colli Euganei, north Italy; expt 1: spring 1994; expt 2: spring 1995) and kept individually for at least 3 days before testing. Toads were placed in the middle of a circular tank (60 cm diameter) with a small plastic balloon wrapped around their head (expt 1), or a small wet piece of paper stuck on their mouth and nose (expt 2). They were given 10 successive trials; in each trial the first forepaw used in attempts to remove the annoyance was recorded. In expt 1 the animals were manipulated in turn by two experimenters (one right-handed and one left-handed); this produced no significant effect ($\chi^2(1)=2.28$). In expt 2 the animals were manipulated in turn by two right-handed experimenters, different from those of expt 1 and unaware of its results. In both experiments experimenters were alternated, one placing the annoyance and the other keeping and placing the toad in the arena. Mean percentages of right forepaw use (with s.e.m.) and number of animals showing predominant right or left forepaw use are shown. *B. marinus* were collected from north Queensland (expts 3 and 4: autumn 1995) and group-housed for at least 1 week before testing. Paper-strip tests (expt 3), followed by submersion–inversion tests (expt 4), were performed on each toad for 6 successive days. Expt 3: toads were placed in a circular tank, with a small strip of wet paper placed across their mouth and nose equidistant from the midline. One trial per day was performed for each toad, the first paw used in attempts to remove the strip being recorded. Expt 4: each toad was turned upside down and, still clasping the experimenter's fingers, immersed in a small tank of water. The side to which the toads turned when righting was recorded. Three trials per toad per day were performed. Every effort was made to randomize the direction of rotation of the toad when inverting and the orientation of the toad with respect to the experimenter. On day 1, nine toads were tested with the left hand and the remaining with the right hand for each trial. On day 2, they were tested alternately with left or right hand (random sequence of toads). From day 3 onwards each toad was tested (in random order) with R, L, R or L, R, L hands, for each of 3 trials. Results show mean % of right forepaw use and left side turning (with s.e.m.), and number of animals showing prevalent left or right turning over the 6 days.

1. Bradshaw J. L. & Rogers L. J. *The Evolution of Lateral Asymmetries, Language, Tool Use, and Intellect* (Academic, San Diego, 1993).
2. Rogers, L. J. & Workman, L. *Anim. Behav.* **45,** 409–411 (1993).
3. Waters, N. S. & Denenberg, V. H. *Behav. Brain Res.* **63,** 195–204 (1994).
4. Ward, J. P. & Hopkins, W. D. (eds) *Primate Laterality: Current Behavioural Evidence of Primate Asymmetries* (Springer, New York, 1993).
5. Bauer, R. H. *Psychobiology* **21,** 243–248 (1993).
6. Walker, S. F. *Br. J. Psychol.* **71,** 329–367 (1980).
7. Ewert, J. P. *Neuro-Ethology* (Springer, Berlin, 1980).

*To whom correspondence should be addressed.