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Short communication

First record of limb preferences in monotremes (*Zaglossus* spp.)

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Abstract. Lateralisation in forelimb use at the population and/or individual level has been found in a wide variety of vertebrate species. However, some large taxa have not yet been investigated and that limits a proper evolutionary interpretation of forelimb preferences. Among mammals lateralised use of the forelimbs has been shown for both placentals and marsupials, but nothing is known about behavioural lateralisation in monotremes. Here we examined lateral preferences in forelimb use in four long-beaked echidnas (male and female *Zaglossus bruijni*, and male and female *Z. bartoni*) in captivity. Three individuals showed significant forelimb preferences in unimanual behaviours associated with feeding. When stepping on an eminence with one forelimb first, the lateralisation at the individual level was found only in males of both species. During male–female interactions, the male *Z. bartoni* significantly preferred to put one of the forelimbs on the female's back. In both males, the direction of preferences was consistent across different types of behaviour. Our results confirm that manual lateralisation, at least at the individual level, is widespread among mammals. Further research is needed to investigate whether the monotremes display population-level lateralisation in forelimb use.

Additional keywords: feeding, hand preference, handedness, lateralisation, long-beaked echidna, manual laterality.

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Evidence for asymmetric limb use has been found in several vertebrate (reviewed in Ströckens *et al*. 2013; Versace and Vallortigara 2015) and some invertebrate species (Frasnelli *et al*. 2012; Romano *et al*. 2015). However, an understanding of the evolution of limb preferences remains limited because of the absence of data for several major taxa (Ströckens *et al*. 2013). In mammals manual lateralisation has been shown for both placentals and marsupials. For example, a recent study has found pronounced manual lateralisation in bipedal marsupials, comparable in strength with human handedness (Giljov *et al*. 2015). Quadrupedal species of marsupials, in contrast, do not show a population-wide lateralisation in forelimb use (Giljov *et al*. 2013, 2015). Monotremes (i.e. echidnas and platypus), however, have never been studied in terms of behavioural lateralisation. This mammalian taxon represents a lineage split very early from other mammals, and its members share several plesiomorphic and apomorphic features (Augee *et al*. 2006). Thus, the lack of data from monotremes represents a significant gap in our knowledge of phylogenetic continuity of lateralised limb use in mammalian evolution. Despite their having been considered as 'primitive' mammals in the past (Dawson 1973), monotreme species, such as echidnas, have a relative brain size similar to that of a placental carnivore (Nicol 2013). Furthermore, cognitive abilities (e.g. learning) and complexity of some types of behaviour (e.g. courtship) in echidnas is comparable with those of large-brained placentals (Miran and Miran 1987; Ashwell 2013; Nicol 2013). The complex brain and behaviour make the investigation of lateralisation in monotremes of special interest, taking into account the hypothesised link between the complexity of behaviour and the degree of lateralisation (Fagot and Vauclair 1991).

We studied four long-beaked echidnas of the genus *Zaglossus*, listed as critically endangered by the IUCN (Leary *et al*. 2008*a*, 2008*b*). To the best of our knowledge, the studied animals constitute 100% of the entire world captive population in this genus. Data on two individuals, a male and a female, of the western long-beaked echidna (*Z. bruijni*) were collected at Moscow Zoo, Russia (Fig. 1*a*). Data on another pair, also a male and a female, of the eastern long-beaked echidna (*Z. bartoni*), were collected at Taronga Zoo, Sydney, Australia (Fig. 1*b*). The two studied species are thought to be closely related (Nicol 2013).

The animals at the Moscow Zoo were housed in an indoor 17-m^2 enclosure with a floor covered with soil and wood chips (Zaharchuk *et al*. 1998). Animals were fed daily a diet mainly consisting of beef and liver (mashed or sliced into strips), live crickets, mealworms and earthworms. The food was placed in a bowl or on the floor in case of live invertebrates. At Taronga Zoo

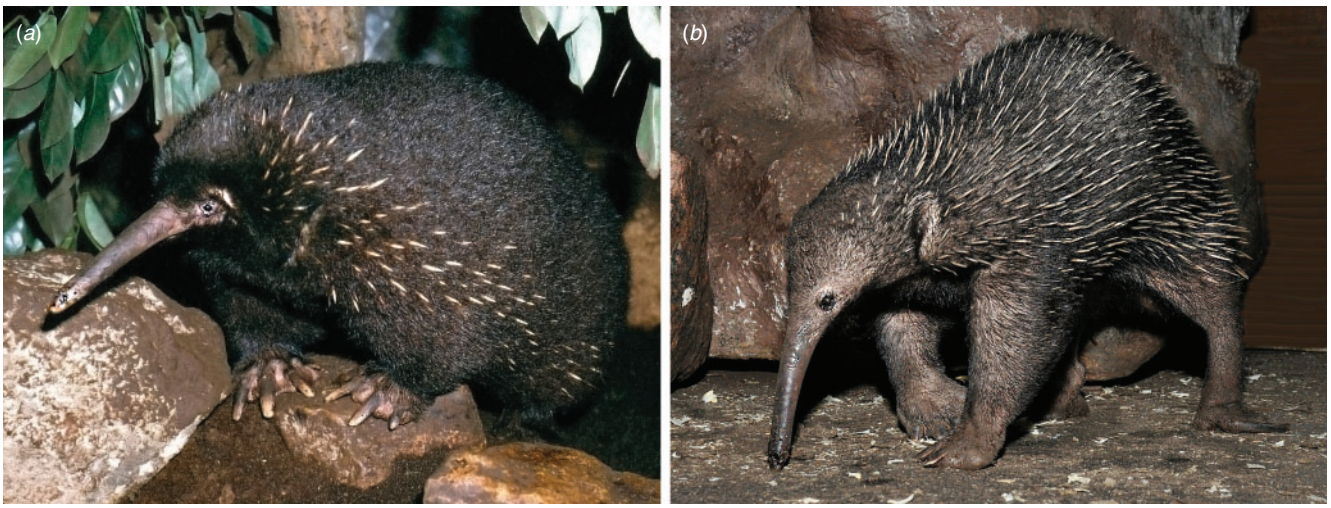

Fig. 1. The study subjects: (*a*) male eastern long-beaked echidna (*Zaglossus bartoni*), (*b*) male western long-beaked echidna (*Z. bruijni*).

the male long-beaked echidna was kept indoors (Nocturnal House, 15 m^2 enclosure) or in a naturalistic 16-m^2 outdoor pen (Grigg *et al*. 2003). The female was kept in 16-m^2 and 100-m^2 outside enclosures during the study. Enclosures had an earth or woodchip floor. The animals were fed daily a semiliquid food mixture based on minced meat, olive oil, eggs, and bran. A bowl with the mixture was placed into a round buried pipe feeder with a screw-top lid with a central hole.

We video-recorded the routine behaviour of the male *Z. bruijni* in March and August 2009. In total, 46 h of video-recordings were obtained for analysis. The data from the female *Z. bruijni* were scored from preexisting video-recordings (12 h) made by the staff of the Scientific Department of Moscow Zoo in December 1996 and June 1998. Direct observations and video-recording of the routine behaviour of the male *Z. bartoni* were carried out in July–August 2009, April 2011 and August 2013 (60 h 25 min in total). The behaviour of the female *Z. bartoni* was video-recorded in July–August 2009 and February 2010 (63 h in total). Since long-beaked echidnas are nocturnal, all observations and video-recordings were carried out during the dark phase of the light cycle, when the animals were active.

Three types of behaviour were studied: (1) feeding, when one forelimb was used to tread on a live invertebrate prey (cricket, mealworm or earthworm) in order to fix and squash it before swallowing (for echidnas at Moscow Zoo) (Fig. 2) (a video, which shows a male western long-beaked echidna treading on an insect with one forelimb, is available as Supplementary Material on the Journal's website), or when one foot was placed on the lid of the buried feeder, probably to facilitate reaching for food (for echidnas at Taronga Zoo); (2) stepping on an eminence, when one forelimb was used first to step on any elevation in the enclosure (earth hillocks, logs, rocks, edge of a pond, or water tub); (3) male–female interactions, when the male put one forelimb on the female's back, usually to push her away from the feeder (for the male at Taronga Zoo only: Fig. S1 in the Supplementary Material). To obtain discrete responses from the individual, only the first unimanual event in a bout was registered. The next event was scored only after the animal changed its location, i.e. made at least four steps. The unimanual actions performed from a biased position, for example, when the echidna's body was initially turned to one side, were discarded from the analysis.

From video recordings we scored the number of times a subject used the right or the left forelimb. A binomial *z* test was used to evaluate individual forelimb preferences separately for each type of behaviour. Significant individual forelimb preferences for feeding were found in three of the four echidnas. When stepping on an eminence the individual forelimb preferences were found in males only (Table 1). Males of both species had consistent preferences in feeding and stepping on an eminence: the male *Z. bruijni* preferred to use the left forelimb, while the male *Z. bartoni* preferred to use the right forelimb. During male–female interactions the male *Z. bartoni* significantly preferred to put his right forelimb on the female's back (26 of 33 acts, binomial $z = 3.13$, $P = 0.001$). Among females, only feeding by the female *Z. bruijni* was lateralised.

The present study showed that long-beaked echidnas display lateral forelimb preferences at the individual level. To our knowledge this is the first record of lateralised behaviour in monotreme mammals. Our finding is consistent with the general pattern in vertebrate lateralisation – most species studied in terms of lateralised limb use (~68%) show significant individual preferences in at least one task (Ströckens *et al*. 2013). Mounting empirical and theoretical evidence indicates that motor biases may reflect lateralised brain function (reviewed in Rogers 2009). We hypothesise that the forelimb preferences found in long-beaked echidnas are underpinned by hemispheric lateralisation. It has been previously assumed that echidnas have relatively symmetric brains without lateralisation of specific functions (Miran and Miran 1987). Our results do not support this assumption; however, a study with a larger sample size is required before any conclusions can be drawn.

Complex motor tasks (e.g. rapid and/or precise actions) have been found to enhance manual lateralisation in some placental mammals (Fagot and Vauclair 1991). For example, a recent study has shown that capuchins and squirrel monkeys display stronger hand preferences for catching live prey than for feeding on non-

Fig. 2. Male western long-beaked echidna, *Zaglossus bruijni*, treading on a live cricket with the left forelimb (photographed from different angles).

Table 1. Individual forelimb preferences in long-beaked echidnas

R, number of right-forelimb uses; L, number of left-forelimb uses. *z*, binomial *z* test: based on their scores, the subjects were categorised as having right-forelimb preference (Right, $z \geq 1.96$), left-forelimb preference (Left, $z \leq -1.96$) or ambipreferent (Ambi, $-1.96 < z < 1.96$) in each type of behaviour. Significant values ($P < 0.05$) are shown in bold

Zoo	Age (years)[A]	Sex	Feeding					Stepping on eminence				
			R	L	*z*	*P*	Pref.	R	L	*z*	*P*	Pref.
Moscow Zoo (*Z. bruijni*)	14	Male	12	54	**–5.05**	**<0.001**	Left	9	25	**–2.57**	**0.009**	Left
	2	Female	2	19	**–3.49**	**<0.001**	Left	10	17	–1.15	0.248	Ambi
Taronga Zoo (*Z. bartoni*)	40	Male	35	10	**3.58**	**<0.001**	Right	43	16	**3.38**	**<0.001**	Right
	46	Female	10	7	0.49	0.629	Ambi	10	7	0.49	0.629	Ambi

[A]The approximate age of the animals at the beginning of data collection.

living food (Pouydebat *et al*. 2014). The integration of visual information and fine motor movements has been suggested as a possible explanation of enhanced lateralised behaviour. In nocturnal long-beaked echidnas, electroreception is used to find invertebrate prey (Pettigrew 1999). We found significant forelimb preferences in both feeding on live invertebrate prey (in male and female *Z. bruijni*) and placing a forelimb on the buried feeder when feeding on semiliquid food mixture (in male *Z. bartoni*). The two types of unimanual actions seem to differ in the relative degree of complexity (e.g. in the degree of involvement of visuo-spatial attention). The same is true when comparing feeding and stepping on an eminence. In spite of this possible difference in the complexity of actions, both males showed similar preferences in both types of behaviour. Similarly, three species of marsupials showed no differences in manual lateralisation between feeding on non-living food and catching live prey (Giljov *et al*. 2012, 2013). Thus, the data on marsupials and monotremes suggest some inconsistency in the complexity effect on lateralisation between different groups of mammals.

Together with previous findings (reviewed in Ströckens *et al*. 2013), the results of the present study indicate that individual-level manual lateralisation is a common mammalian feature, which can be found in all major lineages of extant mammals: placentals (e.g. humans: Versace and Vallortigara 2015), marsupials (e.g. red kangaroos: Giljov *et al*. 2015) and monotremes (e.g. long-beaked echidnas). Notably, one of our subjects – the male *Z. bartoni* – showed consistent preferences for the use of the right forelimb in all three types of behaviour. According to the classification of kinds of manual behavioural lateralisation, forelimb preference consistent within a subject and across tasks is called ‘manual specialisation’, and is typical for several primate species (Marchant and McGrew 2013). Notably, the left forelimb preference for feeding in the male and female *Z. bruijni* is the opposite of the right-sided feeding biases found in different vertebrate classes (MacNeilage *et al*. 2009). Our sample size is insufficient to make conclusions about population-level forelimb preferences and further investigation of monotremes is needed to derive a proper evolutionary interpretation of manual lateralisation in mammals. The rarity of long-beaked echidnas in the wild is likely to preclude further studies on this genus. However, the striking neurological similarities with the long-beaked echidna (Ashwell *et al*. 2014) make the short-beaked echidna (*Tachyglossus aculeatus*) a promising model for future studies on lateralised forelimb use.

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