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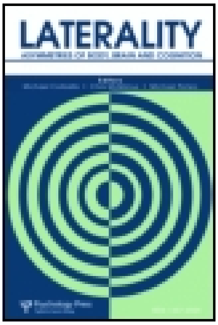

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Limb preferences in non-human vertebrates

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There is considerable debate about whether population-level asymmetries in limb preferences are uniquely human or are a common feature among vertebrates. In the present article the results of studies investigating limb preferences in all non-extinct vertebrate orders are systematically analysed by employing cladographic comparisons. These studies analysed 119 different species, with 61 (51.26%) showing evidence for population-level asymmetries, 20 (16.81%) showing evidence for individual-level asymmetries and 38 (31.93%) showing no evidence for asymmetry. The cladographic comparison revealed that research in several key taxa in particular (e.g., Chondrichtyes, Crocodylia, Atlantogenata and Palaeognathae) would have important implications for our understanding of the evolution of vertebrate limb preferences. Furthermore, the findings of the present study support the position that population-level asymmetries in limb preferences as such represent a common vertebrate feature. Looking into the details, however, some important differences from human handedness become visible: Non-human limb preferences typically show a less-skewed lateralisation pattern and there are larger numbers of individuals without a preference in most species compared to humans. Moreover, limb preferences in non-human animals are often less task-invariant than human handedness and are more frequently modulated by external factors and individual characteristics.

Keywords: Handedness; Footedness; Pawedness; Laterality; Lateralisation.

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We like to thank Jutta Peterburs for proofreading the manuscript. Figure 1B is reprinted from Giljov, A., Karenina, K., & Malashichev, Y. B. (2012). Limb preferences in a marsupial, *Macropus rufogriseus*: Evidence for postural effect. *Animal Behaviour, 83*(2), 525–534. Copyright (2012) with permission from Elsevier. We like to thank Dr Yegor B. Malashichev for providing this figure. We also like to thank Sharon McGavin for providing Figure 1C. Figure 1C is reprinted from McGavin, S. (2009) Footedness in North Island kaka (*Nestor meridionalis septentrionalis*). *Notornis*, 56, 139–143, with permisson from Notornis.

Within the subphylum Vertebrata several different forms of bilaterally symmetric limbs have evolved (e.g., arms, legs, wings, pectoral and ventral fins, flippers). While two paired limbs usually do not exhibit any pronounced anatomical asymmetries, there are several reports of functional limb preferences, i.e., one limb is more likely to be used to accomplish a specific task than the other (see Figure 1).

Essentially, three forms of limb preferences can be distinguished (see Figure 2; Palmer, 1996; Vallortigara, Rogers, & Bisazza, 1999):

(1) Absence of asymmetry: All members of the population prefer to use both the left and the right limb with equal probability.
(2) Individual-level asymmetry: Some individuals prefer to use the left limb, while others prefer to use the right limb, but there is no asymmetry at the population level.
(3) Population-level asymmetry: The majority of the population prefers to use either the left or the right limb.

Humans show clear population-level asymmetries for both their hands and their feet. About 90% of the human population prefer to use the right hand for

Figure 1. Examples of functional limb preferences in non-human animals. (A) A pigeon uses its foot to remove a piece of adhesive stripe from its beak (the so-called "snout-wiping task"). (B) Two red-necked wallabies feeding from a bipedal position. (C) A North Island kākā handling food. (D) A donkey showing a forelimb standing preference. Figure 1B is a reprint from Giljov, Karenina, & Malashichev (2009), used with permission of Yegor Malashichev and the publisher. Figure 1C is a reprint from McGavin (2009), used with permisson of Sharon McGavin and the publisher.

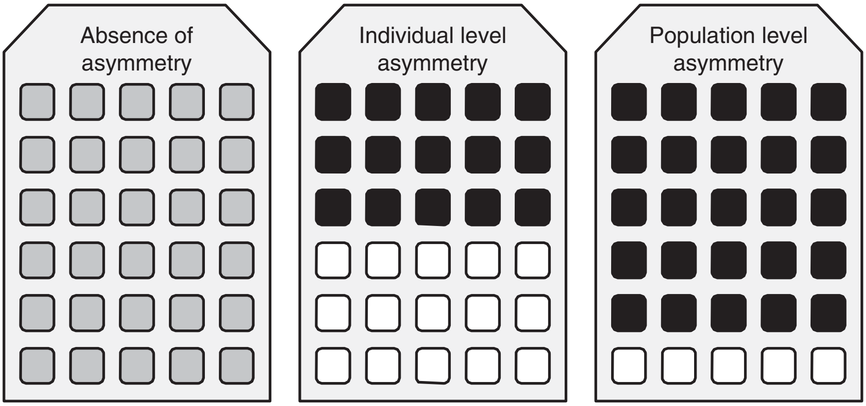


Figure 2. The three possible forms of limb preferences. Grey squares indicate individuals without a preference, black squares indicate individuals that prefer to use the right limb, and white squares indicate individuals that prefer to use left limb.

activities such as writing (Corballis, 2009), and about 75% to 80% prefer to use the right foot for activities such as kicking a ball (Carey et al., 2009). While some authors claim that these clear-cut population-level asymmetries are typically human and potentially constitute a turning point in human evolution (Crow, 2004), others argue that population-level asymmetries can also be observed in vertebrate species outside the *Homo* genus (Halpern, Güntürkün, Hopkins, & Rogers, 2005). Thus the question of whether or not population-level asymmetries are a common feature among vertebrates is far from being answered unequivocally. Moreover, it has recently been suggested that lateralisation per se may have been favoured during primate evolution, while the direction of the preference is modulated by developmental differences (Gil-da-Costa & Hauser, 2006), opening up a third possibility, which is that individual-level asymmetry is a common feature among vertebrates, while population-level asymmetry is not. Cladographic comparisons constitute a powerful tool to systematically investigate which of these three scenarios is the most likely one based on the currently available data for limb preferences (Ocklenburg, Ströckens, & Güntürkün, 2012). In the present article we therefore analyse the results of studies investigating limb preferences in vertebrates.

For a study to be included in the analysis, it had to comply with the following inclusion criteria:

1. Investigation of side preferences in bilaterally symmetric limbs (e.g., handedness, footedness, paw, fin, or flipper preferences).
2. The study had a minimum sample size of 5.
3. Sufficient information about the distribution of preferences was given (e.g., percentages).

By employing cladographic comparisons we identify those vertebrate orders in which evidence for absence of asymmetry, individual-level asymmetry or population-level asymmetry in limb use has been reported, and those orders in which further research is necessary. We then evaluate these findings in order to identify the phylogenetic origins of limb preferences, as far as this is possible.

AGNATHA

Since jawless fishes (e.g., hagfish and lampreys) lack paired fins, no research on limb preferences has been conducted in the Agnatha class.

CHONDRICHTHYES

To our knowledge, no research on fin preferences in cartilaginous fishes (e.g., rays and sharks) has been published yet.

OSTEICHTHYES

In bony fishes (e.g., mackerel and tuna) functional and structural asymmetries have been observed in several different species (Bisazza, Cantalupo, Capocchiano, & Vallortigara, 2000; Bisazza, Rogers, & Vallortigara, 1998). Research on fin preferences in this class started with a study by Fine et al. (1996), who investigated sound production in the channel catfish (*Ictalurus punctatus*). This species can generate communicative sounds using their fins, and out of 20 animals investigated by Fine et al. (1996), 9 (45%) showed a significant rightward preference, 1 (5%) showed a significant leftward preference, and 10 (50%) had no preference. It is, however, rather difficult to interpret these findings in the context of limb preferences, since they are likely to be influenced by the well-known left-hemispheric dominance for production of conspecific sounds in many vertebrates (Corballis, 2009; Ocklenburg, Güntürkün, & Beste, 2011; Ocklenburg et al., 2012).

More recently, an experimental protocol less likely to be influenced by hemispheric asymmetries for conspecific sound production was used by Bisazza, Lippolis, and Vallortigara (2001) to investigate fin preferences in the blue gourami (*Trichogaster trichopterus*). In two experiments these authors investigated the use of the ventral fins during initial exploration of novel plastic objects by the gouramis. In the first experiment 12 adult fishes were exposed to different inorganic plastic stimuli (e.g., a toy boat). Out of the 12 fishes, 4 (33.3%) showed a significant leftward preference, 3 (25%) showed a non-significant trend towards a leftward preference, 1 (8.3%) showed a significant rightward preference and 4 (33.3%) showed no preference. On the population level, a significant leftward population-level asymmetry was observed. In the second experiment 22 gouramis were tested with stimuli from three different categories (animals, plants, or minerals). Interestingly, the leftward population-level asymmetry observed in the first experiment was only replicated for the inorganic mineral category but not for the organic animal or plant categories, indicating that population-level asymmetry in gourami fin preference is stimulus-dependent to some extent.

AMPHIBIA

Anura

In anurans (e.g., frogs and toads) functional and structural asymmetries have been observed in several different species (Rogers, 2002).

Bisazza, Cantalupo, Robins, Rogers, and Vallortigara (1996, 1997) examined forepaw preferences of 70 European toads (*Bufo bufo*). In a first task animals had to remove a plastic balloon wrapped around their head. In a second task a paper strip attached to the mouth/nose region had to be removed (in the literature commonly referred to as the snout-wiping task). European toads showed a right paw preference in both tasks (59% and 55% respectively). In the same study 36 South American cane toads (*Bufo marinus*) where tested with the snout-wiping task in addition to another task in which the animals were submerged underwater in a supine position and had to right themselves using their forelimbs; 66% of the animals exhibited a right paw preference for turning their body, but no paw preference was observed in the snout-wiping task. European green toads (*Bufo viridis*), however, showed no limb preference in either task. A further study on forelimb preferences confirmed the data in South American cane toads (Robins & Rogers, 2002), reporting a 90% right limb preference for righting behaviour in 80 animals. Malashichev and Nikitina (2002) applied the snout-wiping task and the righting task as measures of behavioural laterality in 18 European green toads and 33 fire-bellied toads (*Bombina bombina*). In contrast to previous studies they found a bias towards use of the left forelimb (64%) and a tendency for a left hindlimb preference at the population level for European green toads and individual-level asymmetry for limb usage in fire-bellied toads. Goree and Wassersug (2001) applied the snout-wiping task to 24 Oriental fire-bellied toads (*Bombina orientalis*) and did not find any significant forelimb preferences. Apart from those studies mainly focusing on forelimb preference, Robins, Lippolis, Bisazza, Vallortigara, and Rogers (1998) examined hindlimb righting behaviour in 20 overturned European toads, 26 South American cane toads, and 15 European green toads on 2 consecutive days. They found a preference for the right hindlimb (67%) on the second but not on the first day in European toads, a right preference

(64.6%) in South American cane toads on the first but not on the second day, and a left preference (74.7%) in European Green Toads on the second but not on the first day. The authors argued that the differences between test sessions might be related to arousal of the animals, which might modulate lateralisation. However, since it is not entirely clear what caused these differences between test sessions in this study, independent replication in larger samples would be necessary before any final conclusion about lateralisation in these species can be drawn.

The most recent study on limb preferences in anurans was conducted by Robins and Rogers (2006) who investigated forelimb preferences during climbing in the green tree frog (*Litoria caerulea*). Out of 15 frogs, 6 (40%) showed a significant preference for using the right forelimb as the leading limb when climbing, while no animal preferred the left forelimb and 9 animals (60%) had no preference. Overall these data resulted in a significant rightward population-level asymmetry. Taken together, these studies clearly show that toads and frogs exhibit limb preferences on a number of different tasks. Several studies report a rightward population-level asymmetry, while a few also report a leftward population-level asymmetry (e.g., Malashichev & Nikitina, 2002) or no asymmetry at all (e.g., Goree & Wassersug, 2001). Thus it can be concluded that limb preferences in anurans are at least lateralised on the individual level, with the occurrence and direction of asymmetries being task- and species-dependent to some extent.

Caudata

While there is evidence for lateralisation within the order Caudata (e.g., salamanders, newts, and olms; Giljov, Karenina, & Malashichev, 2009), no study investigating limb preferences has yet been published.

Apoda

In the smallest Amphibia order, Apoda, no research on limb preference has yet been conducted, obviously due to the fact that caecilians secondarily lost their fore- and hindlimbs during evolution.

REPTILIA

Testudines

In the order Testudines (turtles), limb preferences have been investigated in the leatherback turtle (*Dermochelys coriacea*). Sieg, Zandonà, Izzo, Paladino, and Spotila (2010) investigated flipperedness in this species by assessing spontaneous flipper use of nesting leatherback turtles during oviposition. Analysing 1889 observations of 361 individual leatherback turtles, Sieg et al. (2010) found a significant rightward population-level asymmetry for hindlimb flipper use to cover the egg chamber when laying eggs. The turtles preferred to use the right hindlimb flipper in 54% of the observed cases. While this asymmetry reached significance at the population level, the authors pointed out that the effect size was rather small (Cohen's $d = 0.24$), and that among animals that had been observed multiple times only very few turtles showed significant preferences at the individual level (after Bonferroni correction for multiple significance tests, only two turtles showed a significant individual preference). Thus further research in leatherback turtles and other species within the order Testudines is needed before any definite conclusion on limb preferences in turtles can be drawn.

Squamata

Within the order Squamata (e.g., lizards and snakes), limb preferences have been investigated in Duvaucels geckos (*Hoplodactylus duvaucelii*) by Seligmann (2002). Seligmann (2002) assessed which hindlimb the animals preferentially released off the ground first when moving, and found that out of 57 geckos, 54% preferred to release the left hindlimb first, while the other 46% preferred the right. These data did not result in a significant population-level asymmetry, but indicate that this behaviour in geckos could display an individual asymmetry. However, since only a single observation was obtained from each individual, it is not clear whether individual preferences are stable over time, or whether either limb is chosen randomly for each movement. Interestingly, there are also several studies reporting population-level asymmetries in the number of subdigital lamellae under the toes of different Squamata species (e.g., Werner, Rothenstein, & Sivan, 1991; Seligmann, 1998, 2000; Seligmann, Beiles, & Werner, 2003). Since this structural asymmetry may have an impact on behaviour, it seems to be a worthwhile approach to further investigate its impact on functional asymmetries.

Taken together, there is no clear evidence for population-level asymmetries in Squamata limb preferences, and the results regarding individual-level asymmetry are difficult to interpret, since repeated observations in single individuals are missing. Clearly, more research is needed before any firm conclusion can be drawn.

Crocodylia

No research on limb preferences in the order Crocodylia (e.g., crocodiles, caimans, and alligators) has been published at the present date.

AVES

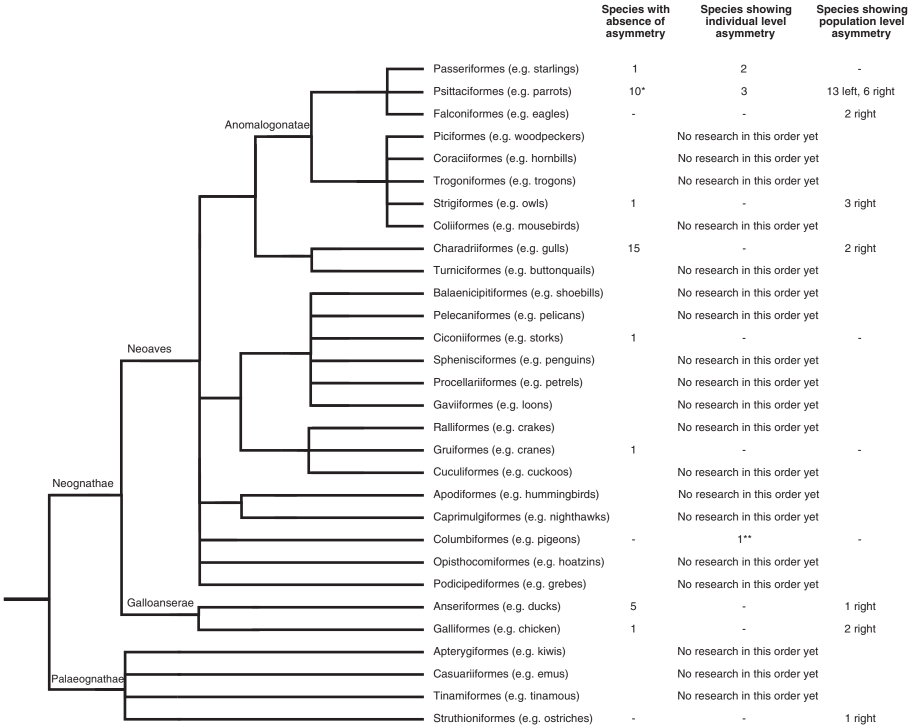
In contrast to the classes described above, extensive research on limb preference has been conducted in the Aves class (for an overview, see Figure 3). However, it should be kept in mind that, in contrast to mammals, all research on limb preference in birds is restricted to the hind limbs, since forelimbs have developed into wings which are normally not used for manipulating objects, a behaviour often used to assess limb preferences. Therefore one should be very careful when directly comparing foot preferences in birds to other tetrapod species.

Passeriformes

Although the majority of all birds are members of the Passeriformes order, only very few studies on foot preference have been performed in this order so far. In an early study (Vince, 1964), feeding behaviour of nine hand-reared great tits (*Parus major*) was observed. Great tits clamp food items like mealworms with one foot to the perch while pecking at it with their beak. Individual birds had a strong preference to use one foot to hold the food item, with about half of the animals being right-footed and the other half left-footed. Comparable results were obtained when the same animals had to perform a more complex string pulling task (Vince, 1964). Izawa, Kusayama, and Watanabe (2005) examined footedness in 15 hand-raised Japanese jungle crows (*Corvus macrorhynchos*) using a task in which the animals had to scratch away a rubber band attached to their beak. Out of 15 birds, 13 showed a clear foot preference for scratching behaviour, yet there was no preference at the population level. In a subsequent experiment 12 of the animals tested before were given a plastic bag with food items which they had to open with their beak while holding it with their foot. Ten animals showed a side preference for holding behaviour, with no bias in laterality at the population-level. Individual foot preference between the experiments was consistent. Berggren (2006) observed food searching behaviour in 14 wild North Island robins (*Petroica longipes*) which rapidly tremble one leg on the ground to stir up insects. He found no foot preference for this behaviour on flat ground, but a preference to use the upper leg while standing on a slope. Taken together, there is evidence for individual-level asymmetry within the Passeriformes order for two species (great tit and Japanese jungle crow) and evidence indicating absence of asymmetry in one species (North Islands robins).

Psittaciformes

Within the avian taxon, research on limb preference was first conducted in the Psittaciformes order. The first evidence for limb preferences in parrots



	Species with absence of asymmetry	Species showing individual level asymmetry	Species showing population level asymmetry
Passeriformes (e.g. starlings)	1	2	-
Psittaciformes (e.g. parrots)	10*	3	13 left, 6 right
Falconiformes (e.g. eagles)	-	-	2 right
Piciformes (e.g. woodpeckers)		No research in this order yet	
Coraciiformes (e.g. hornbills)		No research in this order yet	
Trogoniformes (e.g. trogons)		No research in this order yet	
Strigiformes (e.g. owls)	1	-	3 right
Coliiformes (e.g. mousebirds)		No research in this order yet	
Charadriiformes (e.g. gulls)	15	-	2 right
Turniciformes (e.g. buttonquails)		No research in this order yet	
Balaenicipitiformes (e.g. shoebills)		No research in this order yet	
Pelecaniformes (e.g. pelicans)		No research in this order yet	
Ciconiiformes (e.g. storks)	1	-	-
Sphenisciformes (e.g. penguins)		No research in this order yet	
Procellariiformes (e.g. petrels)		No research in this order yet	
Gaviiformes (e.g. loons)		No research in this order yet	
Ralliformes (e.g. crakes)		No research in this order yet	
Gruiformes (e.g. cranes)	1	-	-
Cuculiformes (e.g. cuckoos)		No research in this order yet	
Apodiformes (e.g. hummingbirds)		No research in this order yet	
Caprimulgiformes (e.g. nighthawks)		No research in this order yet	
Columbiformes (e.g. pigeons)	-	1**	-
Opisthocomiformes (e.g. hoatzins)		No research in this order yet	
Podicipediformes (e.g. grebes)		No research in this order yet	
Anseriformes (e.g. ducks)	5	-	1 right
Galliformes (e.g. chicken)	1	-	2 right
Apterygiformes (e.g. kiwis)		No research in this order yet	
Casuariiformes (e.g. emus)		No research in this order yet	
Tinamiformes (e.g. tinamous)		No research in this order yet	
Struthioniformes (e.g. ostriches)	-	-	1 right

Figure 3. Cladogram of the Aves class based on genetic sequences (modified after Hackett et al., 2008). Only non-extinct orders are included. The chart shows the number of species in a given order which exhibit no asymmetry, individual-level asymmetry, or population-level asymmetry with regard to their limb preferences. For population-level asymmetries the preferred side is given. *Galahs and ring-necked parakeets were counted as "species with absence of asymmetry" due to contradictory results in two studies for both species. **Contradictory results in studies for pigeons.

ranges back to the seventeenth century. At that time the English physician Thomas Browne reported that parrots express a preference to use their left foot more often. Further reports were given in the nineteenth century by William Ogle and David Livingstone who both found a preference in parrots for holding food items with their left foot (for a comprehensive review of historic research about footedness in parrots see Harris, 1989). In the 1930s Friedman and Davies (1938) tested 20 parrots of 17 different species (mainly *Amazona*, *Ara*, and *Brotogeris* genus) by placing a piece of apple or carrot on the bottom of the cages. The birds grabbed the apple with one foot and climbed back on their perch to eat their food still holding it in one claw. The authors found a preference for the left foot in around 75% of the parrots, with only one animal (*Tanygnathus megalorynchos*, great-billed parrot) being right-footed. Rogers (1980) reanalysed the data and found that only six animals were left-footed, and one bird right-footed, whereas the others showed no significant bias for one foot. However, due to the small sample size of animals from each of the species it is difficult to draw any conclusions about population-level asymmetries. In the same study Rogers (1980) investigated foot preference in nine Australian parrot species, and found that eight species (*Cacatua roseicapilla*, galah; *Cacatua galerita*, sulphur-crested cockatoo; *Cacatua sanguinea*, little corella; *Cacatua tenuirostris*, long-billed corella; *Cacatua leadbeateri*, pink cockatoo; *Calyptorhynchus funereus*, yellow-tailed black cockatoo; *Callocephalon fimbriatum*, gang-gang cockatoo; *Platycercus elegans flaveolus*, yellow rosella) showed a left foot preference, with only one being right-footed (*Platycercus elegans*, crimson rosella). The authors therefore concluded that Australian parrots are predominantly left-footed. In a more recent study Magat and Brown (2009) analysed 40 individuals of eight different parrot species (5 individuals each) by observing which foot was used first to manipulate food or to pull a string. They found that four species were left-footed (*Nymphicus hollandicus*, cockatiel; *Callocephalon fimbriatum*, gang-gang cockatoo; *Calyptorhynchus banksii*, red-tailed black cockatoo; *Cacatua galerita*, sulphur-crested Cockatoo), two were right-footed (*Alisterus scapularis*, Australian king parrot; *Polytelis swainsonii*, superb parrot) and two showed no foot preference (*Melopsittacus undulates*, budgerigar; *Eolophus roseicapilla*, galah). However, another study with a larger sample of budgerigars reported individual-level asymmetry for scratching a piece of tape off the beak in this species, while not observing population-level asymmetry (Rogers & Workman, 1993).

In an extensive follow-up study Brown and Magat (2011a) examined footedness in 23 wild and captive Australian parrot species during food grasping. Out of 23 species, 10 exhibited left footedness (*Cacatua galerita*, sulphur-crested cockatoo, $n = 20$, 96% left foot use; *Cacatua sanguinea*, little corella, $n = 20$, 90.5% left foot use; *Cacatua leadbeateri*, Major Mitchell's cockatoo, $n = 15$, 92% left foot use; *Callocephalon fimbriatum*, gang-gang cockatoo, $n = 12$, 100% left foot use; *Calyptorhynchus funereus*, yellow-tailed black cockatoo, $n = 20$, 96.5% left foot use; *Calyptorhynchus banksii*, red-tailed black cockatoo, $n = 20$, 93% left foot use; *Nyphicus hollandicus*, cockatiel, $n = 20$, 90% left foot use; *Probosciger aterrimus*, palm cockatoo, $n = 5$, 80% left foot use; *Purpureicephalus spurius*, red-capped parrot, $n = 5$, 72% left foot use; *Psephotus haematonotus*, red-rumped parrot, $n = 20$, 72% left foot use), 6 right footedness (*Eclectus roratus*, Eclectus parrot, $n = 20$, 74% right foot use; *Alisterus scapularis*, Australian king parrot, $n = 20$, *Aprosmictus erythropterus*, red-winged parrot, $n = 10$, 90% right foot use; 91.5% right foot use; *Polytelis swainsonii*, superb parrot, $n = 20$, 72.5% right foot use; *Platycercus elegans*, crimson rosella, $n = 12$, 82.5% right foot use; *Barnardius zonarius*, Australian ringneck, $n = 5$, 80% right foot use) and 7 species were unbiased at the population level (*Eolophus roseicapilla*, galah, $n = 20$; *Neophema pulchella*, turquoise parrot, $n = 10$; *Glossopsitta pusilla*, little lorikeet, $n = 15$; *Psitteuteles versicolor*, varied lorikeet, $n = 5$; *Trichoglossus haemadotus*, rainbow lorikeet, $n = 20$; *Melopsittacus undulates*, budgerigar, $n = 20$; *Neopsephotus bourkii*, Bourke's parrot, $n = 20$). Furthermore the authors analysed the phylogenic distribution of the observed footedness within the Psittaciformes order and found that all but one species in the Cacatuidae tribe showed left footedness, all species in the Psittaculini tribe showed right footedness and all species in the Loriinae tribe were unbiased, while the remaining species of the Platycercini tribe showed mixed results. Moreover, a correlation between body size and strength of lateralisation as well as a correlation between foraging mode and existence of footedness could be revealed. Bigger birds had an increased strength of their lateralisation than smaller ones while birds who fed from large seeds (which they tend to hold with one claw) were more likely to exhibit footedness than birds who fed on small grass seeds and blossoms (normally eaten without using a claw). The authors therefore concluded that foot preference is a highly conserved feature in parrot species with pattern and strength of this lateralisation being inherited from a common ancestor. The non-existence of footedness in the Loriinae tribe might be linked to a reduction in body size and a change in foraging mode during their evolutionary history (Brown & Magat, 2011a). Interestingly, Brown and Magat (2011b) also found a positive correlation between eye preference and foot preference in 15 out of 16 parrot species investigated. The authors suggested that footedness in parrots could be linked to visual lateralisation (e.g., a possible food item is usually grasped with the foot ipsilateral to the eye preferred for food examination) indicating a broader context of lateralised brain functions and ecological factors.

McNeil, Rodriguez, and Figuera (1971) analysed 56 individual brown-throated parakeets (*Aratinga pertinax*) during feeding, and found that 50%

of animals showed a preference for holding food with the right foot, while 50% preferred their left foot, indicating individual-level asymmetry. In a more recent study Randler, Braun, and Lintker (2011) investigated feeding behaviour, i.e., holding a fruit in one foot, in 184 wild-living ring-necked parakeets (*Psittacula krameri*), and only a small, insignificant difference in foot preference emerged. One alexandrine parakeet (*Psittacula eupatria*) that randomly showed up 14 times during the experiment used its left foot exclusively. In the same study 35 captive parakeets were monitored during feeding in an experimental set-up; 68.6% of the parakeets showed a preference for the left foot, while the remaining birds showed a preference for the right foot. The authors argued that, in contrast to captive animals, birds living in the wild are not always able to use their preferred foot due to unstable environmental conditions. McGavin (2009) observed 24 wild North Island kakas (*Nestor meridionalis septentrionalis*) eating food pellets from a feeder in a bird sanctuary. Like other Psittaciformes, kakas hold their food in one foot during feeding. A strong individual-level asymmetry, but no population-level asymmetry, was found. Taken together, research in the Psittaciformes delivered an extensive amount of data regarding limb preference. Of the species observed, 13 (sulphur-crested cockatoo, little corella, long-billed corella, pink cockatoo, yellow-tailed black cockatoo, gang-gang cockatoo, yellow rosella, cockatiel, red-tailed black cockatoo, Major Mitchell's cockatoo, palm cockatoo, red-capped parrot, red-rumped parrot) exhibit a left foot preference and six a right foot preference (Crimson rosella, Australian king parrot, superb parrot, eclectus parrot, red-winged parrot, Australian ringneck), while only 10 species (galah, ring-necked parakeet, budgerigar, turquoise parrot, little lorikeet, rainbow lorikeet, Bourke's parrot, brown-throated parakeets, north island kaka) have no foot preference at the population level. Furthermore three species showed individual-level asymmetry (budgerigar, brown-throated parakeet, north island kakas). However, it needs to be noted that the results for galahs and ring-necked parakeets are contradictory between two studies, with one study finding population-level asymmetry (Rogers, 1980) while the other study did not (Brown & Magat 2011a; Magat & Brown, 2009). The study by Friedman and Davies (1938) is not listed due to the extremely small sample sizes per species which do not allow meaningful conclusions.

Taken together, there is clear evidence for population-level asymmetry in many Psittaciformes species, but no consistent direction of preference across species. Despite frequent claims that parrots are left-footed, this does not hold true for all observed parrot species. For example Australian king parrots, crimson rosellas, and superb parrots show right foot preference, while brown-throated parakeets, wild living ring-necked parakeets, and wild North Island kakas exhibit no population-level asymmetry.

Falconiformes and Strigiformes

In an extensive study Csermely (2004) tested 223 birds of six species of the Falconiformes and Strigiformes order kept in a bird rehabilitation centre. In the two Falconiformes species, Eurasian buzzards (*Buteo buteo*) and common kestrels (*Falco tinnunculus*), he found a right foot preference for grasping prey from the ground. In three out of four Strigiformes species included in the study (barn owl, *Tyto alba*; northern long-eared owl, *Asio otus*; tawny owl *Strix aluco*), he also found a preference for prey grasping with the right foot, while the little owl (*Athene noctua*) did not show such a bias. Prey type, sex, and age had no influence on footedness. However, it should be noted that, in general, owls preferred to grasp their prey with both feet.

Other Anomalogonatae

In the remaining Anomalogonatae orders Piciformes (woodpeckers), Coraciiformes (hornbills), Trogoniformes (trogons), and Coliiformes (mousebirds), no research on limb preferences has been published yet.

Charadriiformes and Turniciformes

In large-scale study Randler (2007) observed roosting behaviour in 4646 seabirds of 25 different species including Charadriiformes. In this order Eurasian curlews (*Numenius arquata*) and pied avocets (*Recurvirostra avosetta*) show a right foot preference while roosting on the ground on one foot (55% and 57% right foot preference respectively). Eurasian oystercatchers (*Haematopus ostralegus*), common greenshanks (*Tringa nebularia*), golden plovers (*Pluvialis apricaria*), herring gulls (*Larus argentatus*), ringed plovers (*Charadrius hiaticula*), curlew sandpipers (*Calidris ferruginea*), common gulls (*Larus canus*), dunlins (*Calidris alpina*), northern papwings (*Vanellus vanellus*), black-tailed godwits (*Limosa limosa*), black-headed gulls (*Larus ridibundus*), common redshanks (*Tringa totanus*), grey plovers (*Pluvialis squatarola*), spotted redshanks (*Tringa erythropus*), and bar-tailed godwits (*Limosa lapponica*) exhibited no preference while roosting. Therefore, 2 out of 17 examined Charadriiformes species exhibited a rightward population asymmetry for roosting, while the remaining species were symmetric. No research on limb preference has yet been done in the Turniciformes order.

Ciconiiformes

In the study by Randler (2007) one species of the Ciconiiformes order was also observed. In 59 Eurasian spoonbills (*Platalea leucorodia*), no preference for one foot was found. The author did, however, argue that a possible left foot preference might be detectable within a larger sample.

Procellariiformes

In the seabird order Procellariiformes (e.g., petrels, albatrosses) there is no direct evidence for limb preferences.

Gruiformes

Within the Gruiformes order, limb preferences have been investigated in the Eurasian coot (*Fulica atra*). Randler (2007) observed one-footed roosting in 54 wild-living coots and found no significant differences in foot use (46% right, 54% left).

Ralliformes and Cuculiformes

For the Ralliformes and Cuculiformes, no research on footedness has been conducted yet.

Columbiformes

In an early study Fisher (1957) analysed lateralisation of landing behaviour in 11 pigeons (*Columba livia*) by measuring which foot touched the ground first. After analysing 7259 landings he found that seven birds had a preference for their right foot, three for the left foot, and one pigeon showed no particular preference for either foot. Furthermore, Fisher (1957) found that the right-sided preference was more distinct comparable to left foot preference, and that individual preferences were not stable over time and could change within 2 weeks. Fisher (1957) concluded that pigeons have an individual dominance for one foot. In contrast to this finding, Güntürkün, Kesch, and Delius (1988), who attached pieces of tape to the beaks of 50 pigeons, observed that the animals showed neither individual-level asymmetry nor population-level asymmetry for scratching the tape away. Therefore the authors concluded that pigeons show no asymmetry for limb usage. Davies and Green (1991) doubted the results of this study by arguing that the primary motor action involved in grooming the head is the head–neck system itself and not the usage of the feet. In order to rule out effects of other motor systems, these authors assessed foot preferences of 16 pigeons during landing and take-off, a method comparable to that applied by Fisher (1957). Out of 96 landings the animals preferred the right foot in 38 cases while the left foot was used in 28 cases; 38 landings were taken with both feet. Out of 72 take-offs the pigeons used their right foot as the leading foot 8 times, the left foot 12 times, and in 52 cases both feet simultaneously. Population-level asymmetry was present in neither landing nor take-off. However, an individual foot preference was evident during landing with 25% of the animals being strongly right-footed and 12.5% strongly left-footed, while for take-off no such effect could be found. The authors argued that foot preference in pigeons might be associated with fine visuomotor control instead of object manipulation (Davies & Green, 1991), which might explain the difference from the older beak-scratching study (Güntürkün et al., 1988). For the Columbiformes order, apparently at least pigeons show individual-level asymmetry in footedness, although this observation depends on the task with which footedness is assessed. Interestingly, the beak-scratching task which showed no lateralisation in pigeons is suitable to identify lateralisation in other bird orders (Psittaciformes, Galliformes).

Other Neoaves orders

For the remaining Neoaves orders Balaenicipitiformes (shoebills), Pelecaniformes (pelicans, gannets), Sphenisciformes (penguins), Apodiformes (hummingbirds), Caprimulgiformes (nighthawks), Opisthocomiformes (hoatzins), Podicipediformes (grebes) and Gaviiformes (loons), research on limb preference has yet to be published.

Galloanserae

Chicken (*Gallus gallus*) show a dominance of the right claw when scratching a piece of tape from their beak (Rogers & Workman, 1993). Out of 38 animals, 31 (81.6%) preferred to use their right foot. More evidence for a right limb preference in chicken was given by Casey and Martino (2000) and Casey (2005) who examined walking behaviour in three Galliformes species and found that 70% of the chickens observed in the study had a bias to use their right foot first when starting to walk, 9% had a left-sided bias, and 21% were unbiased. Such a right-sided bias was also found in 68% of observed bobwhite quails (*Colinus virginianus*), with 8% being left-biased and 24% unbiased, whereas Japanese quails (*Coturnix japonica*) did not show a leg preference for initialisation of walking. Disrupting the natural hatching behaviour, in which the animals turn inside the egg counterclockwise driven by the right leg, prevented formation of the right leg preference in chicken and bobwhite quails. The authors therefore suggested that prehatch motor activity might induce limb lateralisation in those animals. In a further study by Tommasi and Vallortigara (1999) limb preferences of chicken were tested in a ground-scratching task under monocular or binocular conditions. In the binocular condition chicken showed the same right-sided preference as reported by previous studies. In the monocular condition animals preferred to use the claw contralateral to the covered eye. It was argued that the active, not visually deprived hemisphere controls the leg for the more complex posture control, while the deprived hemisphere controls simple reflex-like scratching. This would make the right leg preference in chicken a secondary effect, resulting from a left side dominance for posture control.

Dharmaretnam, Vijitha, Priyadharshini, Jashini, and Vathany (2002) examined ground-scratching behaviour in 20 young chickens during the first 2 weeks after hatch. Starting from day five after hatch, 66.6% of chickens showed a preference for the right leg for initialising a scratching bout, subsequently decreasing to 55.5% on day seven. On day eight the bias switched to the left side with only 47.5% preference for the right leg, decreasing further to 37.4% on day ten. On day eleven a right-sided bias with 56.8% preference for the right leg was observed which increased to 70% on day eleven. Besides initialising a scratching bout, there was no preference during general scratching. Furthermore, tape removal from the beak was tested on day eight and day eleven after hatch in naïve animals and animals already trained to be used to handling and the testing side. There was a right-sided bias for tape removal in the trained group (73.6% right preference) but not in the naïve group. On day eleven the trained birds showed a left-sided bias (only 30% right leg preference) whereas the naïve birds showed a 75% right-sided bias. In conclusion, for the Galliformes there is a right-directed asymmetry in two species (chicken and bobwhite quail), and one species without any foot preference at the population level (Japanese quails). However it should be noted that individual foot preference has not yet been examined in Japanese quails. For chickens (and partly bobwhite quails) it could be shown that several factors, like hatching behaviour, eye use, or age can influence limb preference, a finding which so far has not been investigated in other bird orders.

In the Anseriformes order much less research has been done so far. Randler (2007) found that barnacle geese (*Branta leucopsis*), common shelducks (*Tadorna tadorna*), common teals (*Anas crecca*), greylag geese (*Anser anser*), and mallards (*Anas platyrhynchos*) all showed no detectable foot preference while roosting. Only northern shovellers (*Anas clypeata*) exhibit a preference for the right foot during this behaviour. Therefore only one out of six examined Anseriformes species show a population-level asymmetry.

Palaeognathae

Within the Struthioniformes order ostrich hatchlings (*Struthio camelus*) use the right leg to open the eggshell during hatching. Furthermore, ostriches initiate locomotion preferentially with their right foot and use mainly their right foot during resting posture (Baciadonna, Zucca, & Tommasi, 2010). Comparable to the hypothesis for chicken and quails (Casey, 2005;

Casey & Martino, 2000), the authors suggest that motor laterality observed during hatching might already be a precursor for lateralisation of leg use in adult ostriches. In the remaining Apterygiformes (kiwis), Casuariiformes (emus), and Tinamiformes (tinamous), no research on limb preference has yet been conducted.

MAMMALIA

Limb preferences have been investigated in several mammalian orders (see Figure 4 for an overview). In the following section we will review this evidence in detail.

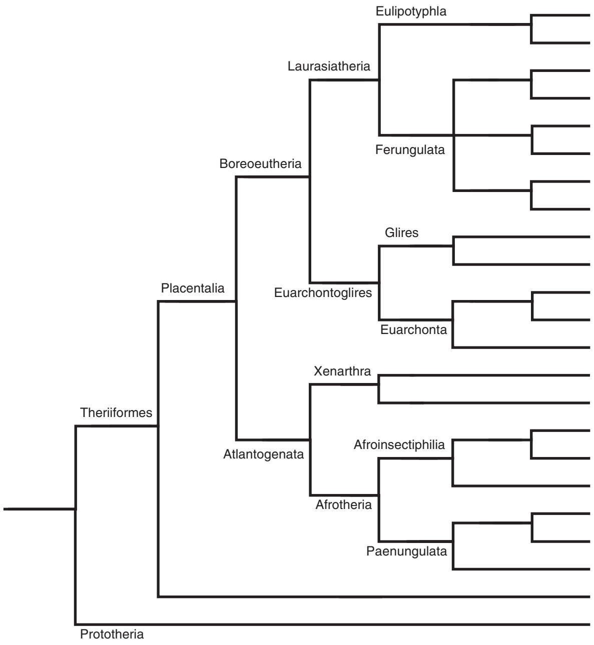
Subclass Prototheria

In Prototheria (e.g., echidnas and platypuses), no studies investigating limb preferences have been published at the present date.

Subclass Theria

Cohort Marsupialia. The first study investigating limb preference in marsupials (e.g., wombats or possums) was conducted by Megirian, Weller, Martin, and Watson (1977) in the brush-tailed possum *(Trichosurus vulpecula*) using a food-reaching task. Out of the 78 possums tested in this experiment, 40 (51%) preferred using the left forepaw, 35 (45%) preferred using the right forepaw, and 3 possums (4%) showed no forepaw preference when reaching for food. While the authors did not calculate any statistical test, the reported percentages strongly argue in favour of the existence of individual-level asymmetry, yet with no population-level asymmetry for this behaviour in brush-tailed possums. This finding is also somewhat supported by the findings of an earlier motor cortex lesion study in the same species: Rees and Hove (1970) reported that, in a sample of 18 adult brush-tailed possums, all individuals showed a preference for one particular forelimb when reaching for food prior to operation. Unfortunately no information on preference direction or the number of animals preferring the left or the right forearm is reported in the paper, rendering the interpretation of these results difficult.

Another marsupial species in which limb preferences have been investigated is the opossum (*Monodelphis domestica*). Ivanco, Pellis, and Whishaw (1996) reported that nearly all opossums in their sample showed strong individual preferences during skilled reaching. Most individuals (no exact number given in the paper) preferred the left limb to reach. However, due to the small sample size of this study (14 opossums) the authors did not calculate a statistical comparison to test whether a significant population-level



	Species with abscence of asymmetry	Species showing individual level asymmetry	Species showing population level asymmetry
Erinaceomorpha (e.g. hedgehogs)		No research in this order yet	
Soricomorpha (e.g. shrews)		No research in this order yet	
Cetacea (e.g. dolphins)	-	-	1 left - 1 right[1]
Artiodactyla (e.g. sheep)	1	-	1 left/right[2]
Perissodactyla (e.g. horses)	-	1	2 left - 1 right[2]
Chiroptera (e.g. bats)	-	-	1 right
Carnivora (e.g. dogs)	-	2[4]	3 right[3]
Pholidota (e.g. (scaly anteaters)		No research in this order yet	
Rodentia (e.g. mice)	-	1[2,3]	1 right[2]
Lagomorpha (e.g. rabbits)		No research in this order yet	
Scandentia (e.g. treeshrews)		No research in this order yet	
Dermoptera (e.g. culogos)		No research in this order yet	
Primates (e.g. apes)	1	6	7 left – 6 right[2,5,6]
Pilosa (e.g. anteaters)		No research in this order yet	
Cingulata (e.g. armadillos)		No research in this order yet	
Afrosoricida (e.g. tenrecs)		No research in this order yet	
Macroscelidea (e.g. elephant shrews)		No research in this order yet	
Tubulidentata (e.g. aardvarks)		No research in this order yet	
Sirenia (e.g. sea cows)		No research in this order yet	
Hyracoidea (e.g. hyraxes)		No research in this order yet	
Proboscidea (e.g. elephants)	-	1	-
Marsupialia (e.g. wombats)	-	2[2]	1 left[2]
Monotremata (e.g. platypuses)		No research in this order yet	

Figure 4. Cladogram of the mammalian phylum based on genetic sequences, modified after Murphy, Pringle, Crider, Springer, & Miller (2007). Only non-extinct orders are shown. Chart depicts numbers of species in a given order with no asymmetry, individual-level asymmetry, or population-level asymmetry in regard to limb preference. For population-level asymmetry the preferred side is also given. [1]No statistical analysis for humpback whales. [2]Dependent on experimental set-up or task, see text for further information. [3]Dependent on sex in cats. [4]Contradictory results in several studies for dogs. [5]Results from studies in which different species were pooled are counted as one species only. [6]Only a selection of primates with population-level asymmetries is listed.

asymmetry exists for this behaviour in opossums. Interestingly, in contrast to the pronounced individual-level asymmetry for food reaching, opossums showed no limb preferences at all when catching a cricket, making this behaviour symmetric. Thus in opossums the existence of individual-level asymmetry in limb preferences seems to be task-dependent.

The most recent study on limb preferences in marsupials has been conducted in the red-necked wallaby (*Macropus rufogriseus*). Giljov, Karenina, and Malashichev (2012) investigated lateralisation in forelimb use in 27 adult members of this species during their normal daily activities. When feeding from a bipedal position, 20 animals (74.1%) showed a left-hand preference, two (7.4%) a right hand preference and 5 (18.5%) no preference, resulting in a significant left-hand preference on population-level. However, a population-level asymmetry was not observed when the wallabies were feeding from a quadrupedal position. Here only 3 (11.1%) individuals showed a left-hand preference, while the other 24 (88.9%) animals showed no preference. The authors reported that significantly more animals were without than with preference, so that feeding from a quadrupedal position has to be categorised as a symmetric behaviour. Apart from the preferences of hand use when handling food, the authors also investigated the wallabies' individual forelimb preferences for supporting the body when in a tripedal stance. Here 3 animals (11.1%) showed a left-hand preference, 14 (51.9%) a right-hand preference, and 10 (37.0%) no preference, leading the authors to conclude that wallabies show a significant group-level bias for using the right forelimb for supporting their bodies

Taken together, there is evidence for individual-level asymmetry in several marsupial species, and also one study pointing towards population-level asymmetry for certain behavioural patterns in red-necked wallabies. However, since there are also some behavioural patterns that seem to be symmetric, the existence of lateralisation in marsupial limb preferences seems to be task-dependent to some extent.

Cohort Placentalia

Erinaceomorpha & Soricomorpha. No studies on limb preferences in Erinaceomorpha (hedgehogs and gymnures) and Soricomorpha (shrews and moles) have been published yet. There is, however, at least some evidence for lateralisation in the motor system of shrews, coming from a study investigating hunting behaviour in the Etruscan shrews (*Suncus etruscus*): Anjum, Turni, Mulder, van der Burg, and Brecht (2006) reported that these small nocturnal mammals show a rightward bias when attacking prey.

Cetacea. In Cetacea (dolphins, porpoises, and whales), limb preferences have been investigated in the Indo-Pacific bottlenose dolphin (*Tursiops* *aduncus*). Sakai, Hishii, Takeda, and Kohshima (2006) investigated flipper-to-body rubbing in this species, a social behaviour in which one dolphin rubs the body of another with its flipper. Overall this behaviour was conducted significantly more often with the left flipper than with the right flipper. On an individual level, 9 (45%) out of 20 dolphins showed a left-flipper bias, no dolphin showed a right-flipper bias, and 11 dolphins (55%) showed no preferences, resulting in a significant left-side population-level asymmetry for flipper use in a social context in this species.

A further study investigating flipper preferences in cetaceans was conducted by Clapham, Leimkuhler, Gray, and Mattila (1995) in humpback whales (*Megaptera novaeangliae*). These authors observed several types of active behaviour in humpback whales, one of them being flippering, the raise of one flipper into the air and subsequent slapping of the water surface with this flipper. Out of 34 observation periods, rightward lateralisation was observed in 17 (50%), leftward lateralisation in 5 (15%) and no preference in the remaining 12 (35%) periods. However, since no statistical tests for a population bias are reported in the paper, the interpretation of these finding is difficult.

Artiodactyla. In the even-toed ungulates (e.g., cattle, pigs, and sheep), limb preferences have been investigated in muskoxen (*Ovibos moschatus*). Schaeffer and Messier (1997) studied foreleg preferences while foraging in the winter. In contrast to what has been found in most other mammals, there was evidence for neither individual-level asymmetry nor population-level asymmetry. On the individual level, only 3 (7.5%) out of 40 animals showed a significant lateral bias, with no information on the directions given in the paper. Moreover, no population-level asymmetry was observed, with about 50% of the muskoxen preferring the right foreleg and the other 50% the left foreleg. These results clearly show the foraging behaviour in muskoxen is a symmetric behaviour. Besides muskoxen, limb preferences in Artiodactyla have also been investigated in the reindeer (also called caribou, *Rangifer tarandus*). Thing (1977) observed digging of feeding craters in 27 reindeers in Northwestern Alaska, and found that 15 (56%) of the animals preferred to use their right front leg for digging, resulting in a significant rightward bias at the population level. A population-level asymmetry for foreleg preference when digging feeding craters in reindeer was also reported in a more recent study by Espmark and Kinderas, (2002). Surprisingly, however, these authors reported a significant leftward bias at the population level with 21 (72%) out of 29 monitored reindeer preferring their left foreleg and only 8 (28%) preferring their right foreleg. Taken together, these results indicate that the occurrence of both individual-level asymmetry and population-level asymmetry in Artiodactyla seems to be species-dependent. Moreover, the reindeer data suggest that if population-level asymmetries exist in a species, their direction seems to be influenced by environmental factors to a large extent.

Perissodactyla. The first systematic investigation of limb preferences in odd-toed ungulates (e.g., horses, donkeys, and tapirs) was conducted by Grzimek (1949) who analysed four different behavioural patterns (pawing the ground, walking over an obstacle, leg preference when starting to walk, jumping over an obstacle) in 53 horses (*Equus ferus caballus*). He found that 77% of the horses showed a significant individual preference when pawing the ground. When only the animals that showed a significant preference were analysed, 58.6% preferred the right hoof to paw and 41.4% the left hoof. For walking over an obstacle only 9.5% of the horses showed a significant individual asymmetry (40% right and 60% left), while 66% of the animals significantly preferred to start with one leg (55% right and 45% left). Finally, when jumping over an obstacle 23% of the horses showed a significant preference (30% right and 70% left). While no statistical tests for population-level asymmetries were reported in the paper, the results suggest that horses show individual-level asymmetry exists for certain behaviours (pawing and starting to walk) while other behaviours are more likely to be symmetric (walking and jumping over an obstacle). More recently, McGreevy and Rogers (2005) reported that, out of 106 thoroughbred horses, 43 (41%) preferred to stand with the left forelimb advanced over the right, 10 (9%) preferred to stand with the right forelimb advanced over the left, and 53 (50%) had no significant preference. To further investigate this significant leftward population-level asymmetry, the sample used by McGreevy and Rogers (2005) was subsequently compared to two other populations of domestic horses; standardbreds and quarter horses (McGreevy & Thomson, 2006). For standardbreds McGreevy and Thomson (2006) also observed a significant leftward population-level asymmetry in foreleg standing preferences, with a left foreleg preferences in 16 (40%) out of 40 horses, a right foreleg preference in 5 (12.5%) individuals, and 19 (47.5%) horses exhibiting no preference. In quarter horses, however, 33 (82.5%) out of 40 animals did not have a significant foreleg preference, while 4 (10%) preferred the right foreleg and 3 (7.5%) the left foreleg. McGreevy and Thomson (2006) argue that these differences between the breeds are likely to be the result of training or selection effects. Interestingly there is also some evidence for foreleg preferences in quarter horses, coming from an earlier study by Deuel and Lawrence (1987). In contrast to McGreevy and Thomson (2006) who investigated foreleg standing preferences, these authors studied which foreleg was preferred as a lead when galloping in a rather small sample of four Quarter Horse fillies. All four horses preferred to gallop with the left foreleg leading, resulting in a significant population-level asymmetry.

In addition to studies in horses, limb preferences in odd-toed ungulates have also been investigated in the donkey (*Equus asinus*). Zucca, Cerri, Carluccio, and Baciadonna (2011) studied how space availability influences laterality in this species. In their study forelimb standing preferences in 19 adult domestic donkeys (two groups of 10 and 9 animals) were investigated in two conditions. In the baseline condition each group was housed in a large paddock (about 600 m^2), while in the experimental condition the groups were housed in smaller paddocks (about 300 m^2), resulting in less space being available for each individual animal. The results show that donkey foreleg standing preferences are modulated by space availability. In the baseline condition 79% of the donkeys showed a right foreleg preference, whereas only 21% of the donkeys showed a left foreleg preference, resulting in a statistically significant population-level asymmetry towards the right. In the experimental condition, however, no such asymmetry at the population level was observed, since 42% of the donkeys preferred the right foreleg, 53% preferred the left foreleg and 5% had no preference. The authors argue that this finding may be explained by increased stress in the experimental condition.

Taken together, there is evidence for a population-level asymmetry in limb preference in odd-toed ungulates, which however appears to be modulated by environmental factor (stress or training) to a much larger extent than human handedness. Additionally, the direction of this asymmetry seems to be species-dependent.

Chiroptera. In bats, limb preferences have been investigated in the echolocating Schreiber's Long-Fingered Bat (*Miniopterus schreibersii*). Zucca, Palladini, Baciadonna and Scaravelli (2010) investigated handedness in this species, and found a leftward population-level asymmetry. Out of 25 bats, 19 (76%) preferred the right hand and 6 (24%) the left hand when climbing the wall of a cylindrical arena.

Carnivora. Limb preferences in carnivorans have been investigated extensively, with several published studies for both suborders within this order (Feliformia and Caniformia). Within the Feliformia, limb preference has mainly been investigated in the domestic cat (*Felis silvestris catus*), starting with a study by Cole (1955). Using a food-reaching task, Cole (1955) found that 12 cats (20%) had a right-paw preference and 23 cats (38%) a left-paw preference, and 25 cats (42%) showed no clear paw preference. While Cole (1955) did not calculate a statistical test to determine whether population-level asymmetry exists for this behaviour, this has been done in later studies. For example, Pike and Maitland (1997) also investigated paw preference during food reaching in 48 cats (28 males and 20 females), reporting that 21 cats (44%) preferred that left paw, 22 cats (46%) preferred the right paw, and

5 cats (10%) had no preference. No statistically significant population-level asymmetry was observed, but the high number of lateralised animals clearly indicates individual-level asymmetry. Similar results (individual-level asymmetry, but no population-level asymmetry) have also been obtained by Tan and Kutlu (1991), Fabre-Thorpe, Fagot, Lorincz, Levesque, and Vauclair (1993) and Konerding, Hedrich, Bleich, and Zimmermann (2012).

Interestingly there are several studies reporting a larger number of right-pawed individuals among female than among male cats (Tan, 1993; Tan & Kutlu, 1991; Tan, Yaprak & Kutlu, 1990; Yetkin, 2002). For example, Tan and Kutlu (1991) tested 109 cats with a food-reaching task, and found that out of 63 female cats 34 individuals (54%) had a right-paw preference, 23 (36.5%) a left-paw preference, and 6 (9.5%) had no preference. Out of the 46 male cats only 20 (43.5%) had a right-paw preference, while 21 (45.7%) had a left-paw preference and 5 (10.9%) had no preference. These findings show that sex influences paw preferences in cats.

Besides the cat, limb preferences in Feliformia have been investigated in the lion (*Panthera leo*). Zucca, Baciadonna, Masci, and Mariscoli (2011) investigated forelimb preference in the quadrupedal standing position in 24 adult lions, and observed a significant rightward population-level asymmetry. Overall, 18 (75%) of the lions showed a right forelimb preference, while 5 (21%) showed a left forelimb preference and 1 animal (4%) showed no preference.

Besides the Feliformia, limb preferences in Carnivora have been investigated in several families within the suborder Caniformia. Paw preference in the dog (*Canis familiaris*, Canidae family) has been addressed in several research papers, the earliest being a study by Tan (1987). In this work the paw used to remove an adhesive plaster from the eye was determined in 28 dogs. Overall, 16 animals (57%) showed a right-paw preference, 5 animals (18%) a left-paw preference, and 7 animals (25%) had no preference, resulting in a statistically significant rightward population-level asymmetry. However, this initial finding was not replicated by several more recent studies. Using a very similar testing procedure as Tan (1987), Quaranta, Siniscalchi, Frate, and Vallortigara (2004) also observed population-level asymmetry in a sample of 80 dogs, but in opposite directions in male and female dogs. While male dogs significantly preferred their left paw to remove an adhesive strip, females preferred the right paw. Since Tan (1987) had 19 female but only 9 male dogs in his sample, the rightward asymmetry at the population level in this study might be an effect of over-representation of female animals in the sample. A strong influence of sex on the direction of dogs' paw preferences was also reported by Wells (2003), who tested 53 dogs (26 males, 27 females) with three different tasks (paw lifting, blanket removal, food retrieval). For all three tasks individual-level asymmetry but not population-level asymmetry was observed in the overall sample. In accordance with the results of Quaranta et al. (2004), separate analyses of male and female animals revealed that female animals showed a rightward population-level asymmetry, whereas male animals showed a leftward population-level asymmetry. While the findings of Quaranta et al. (2004) were in accordance with those of Wells (2003), a more recent study came to the conclusion that male and female dogs do not show different population-level asymmetries regarding their paw preferences (Poyser, Caldwell, & Cobb, 2006). In this study 79 dogs (36 females and 43 males) were tested with three behavioural tasks (manipulating food, removing an adhesive tape, manipulating a ball). For all three tasks neither population-level asymmetries nor sex differences were observed. Interestingly, male dogs showed a significant preference to use the left paw to manipulate the ball when only the first response was counted, but this preference disappeared when all paw uses were analysed. Thus Poyser et al. (2006) concluded that dogs' paw preferences are rather labile, unlike human handedness. Results indicating individual-level asymmetry rather than population-level asymmetry have also been reported by Branson and Rogers (2006), who used a food-reaching task. Out of 48 dogs (24 males and 24 females), 21 animals (44%) were significantly left-pawed, 16 (33%) significantly right-pawed, and 11 (23%) had no preference.

Apart from these findings in the Canidae family, Caniformia limb preferences have also been investigated in the Ursidae and the Odobenidae family. In the Ursidae family laterality of forepaw use during salmon hunting was assessed in the black bear (*Ursus americanus kermodei*). In an observational field study Reimchen and Spoljaric (2011) recorded 288 foraging and 186 scavenging events in a sample of approximately 15 different black bears. Of the foraging movements, 17% had a left-bias, 24% a right-bias, and 53% were unbiased (the missing 6% are not reported in the paper). Hence no significant population-level asymmetry was observed for this behaviour. The authors obtained repeated observations from six different identifiable bears, and found that two of these animals showed a significant individual leftward asymmetry, one a significant rightward asymmetry, and three no asymmetry. For scavenging, a significant rightward population-level asymmetry was observed, with the right paw being used for this behaviour in 68% of the cases.

In the Odobenidae family laterality during feeding behaviour of the walrus (*Odobenus rosmarus*) has been assessed by Levermann, Galatius, Ehlme, Rysgaard, and Born (2003). These authors analysed 12 underwater recordings of foraging walruses. Out of the 12 recordings, 6 (50%) indicated a preference for right flipper, none indicated a preference for the left flipper, 4 (33.3%) indicated no clear preference, and in 2 recordings (16.7%) the animal did not use its flippers. However, due to the low number of observations no statistical test was performed. Importantly, analysing only those observations in which the flippers were actually used, the walruses used their right flipper 89% of the time, hinting at the possibility of a population-level asymmetry in this species. However, more research in larger samples is needed before any conclusions can be drawn about Odobenidae limb preferences.

Taken together, the findings in Carnivora clearly show that individual-level asymmetry exists in this order. There are also several studies indicating population-level asymmetries in limb use, but they seem to be less stable than human handedness and also species-, task-, and especially sex-dependent.

Pholidota. In scaly anteaters, no research on limb preferences has been conducted yet.

Rodentia. Investigating limb preferences in rodents has a long history in laterality research. As early as the 1930s Tsai and Maurer (1930) investigated paw preferences in 105 "normal rats" (no Latin name given, but probably *Rattus norvegicus*) while reaching for food stored in a small glass bottle. In male rats 59% showed a right-paw preference, 26% a left-paw preference, and 15% no preference. In female rats 43% showed a right-paw preference, 37% a left-paw preference, and 20% no preference. Since no statistical tests were reported, no conclusion about population-level asymmetry can be drawn from this paper, but the percentages suggest that rats' paw preferences are probably at least asymmetric on an individual level. This conclusion is also supported by a conditioning study in which rats' paw preferences when pressing a lever to obtain food were recorded. Glick, Cox, and Greenstein (1975) reported that, out of 12 rats, 3 (25%) preferred the right paw, 5 (42%) the left paw, and 4 (33%) had no preference. As in the Tsai and Maurer (1930) study no statistical tests were reported, preventing any conclusion about population-level asymmetry. More recently, Güven, Elalmiş, Binokay, and Tan (2003) tested 198 rats with a food-reaching task, and observed a significant population-level asymmetry, with 144 rats (72.7%) showing a right-paw preference, 29 rats (19.7%) showing a left-paw preference, and 15 (7.6%) showing no preference. Similarly, Tang and Verstynen (2002) also observed a significant rightward population-level asymmetry in the untreated control group of a study investigating the effects of early environmental modulation on paw preferences. In the experimental group, which was exposed to a novel environment for 3 minutes on each of the first 21 days of their lives, this rightward bias was significantly reduced. Taken together, most studies indicate that rats show a rightward population-level asymmetry for paw preferences. This population-level asymmetry is, however, modulated by environmental factors (such as exposure to a novel environment). Moreover, there was one study (Glick et al., 1975) which actually reported that more animals preferred the left than the right paw.

Besides *Rattus norvegicus*, limb preferences in Rodentia have been extensively investigated in the mouse (*Mus musculus*), starting with a series of classic studies by Collins (1968, 1969, 1975). Collins (1968) tested 370 mice with a food-reaching task, and found that almost exactly one half of the mice preferred the left and the other half the right paw. While Collins (1968) could show that individual preferences were consistent over time, a later study (Collins, 1975) revealed that when the experimental apparatus favoured the use of either the left or the right paw, 90% of the mice showed paw preferences in accordance with the environmental bias, while only 10% preferred to use the other paw. Thus the direction of paw preference in mice is modulated by environmental biases to a much larger extent than the direction of human handedness. The initial finding of Collins (1968) that approximately half of the mice are left- and the other half right-pawed in an unbiased environment has subsequently been replicated by several studies (Betancur, Neveu, & Le Moal, 1991; Bulman-Fleming, Bryden, & Rogers, 1997; Manhães, Schmidt, & Filgueiras, 2005; Signore, Chaoui, Nosten-Bertrand, Perez-Diaz & Marchaland, 1991; Signore, Nosten-Bertrand, et al., 1991; Waters & Denenberg, 1991). A single study (Waters & Denenberg, 1994) also reported a significant leftward population-level asymmetry using the same test as Collins (1975), with 54.4% of the mice being left-pawed. Interestingly, Waters and Denenberg (1994) observed a significant rightward population-level asymmetry (61% of the animals were right-pawed) using the lateral paw preference test, a different task in which mice have to press either a left or a right hopper to obtain food. These results show that the testing protocol seems to have an influence on paw preferences in mice, an assumption that was also supported by the findings of Bulman-Fleming et al. (1997). In addition to testing protocol, sex (Betancur et al., 1991) and strain differences (Biddle & Eales, 1996; Cassells, Collins, & Wahlsten, 1990; Signore, Chaoui, et al., 1991) also have an impact on the distribution and degree of paw preferences. One paper (Takeda & Endo, 1993) reported that mice from the BALB/cA and JcI:ICR strains were largely ambidextrous and failed to show significant individual-level asymmetry regarding their paw preferences.

Taken together, the majority of findings clearly suggest that paw preferences in mice show individual-level asymmetry, but not population-level asymmetry. Moreover, several factor including environmental biases, sex, and strain seem to modulate the degree and direction of lateralisation in this species.

Lagomorpha. The only study that investigated limb preferences in Lagomorpha (e.g., rabbits) was conducted by Hackert, Maes, Herbin, Libourel, and Abourachid (2008) in the pica (*Ochotona rufescens*). While this study yielded preliminary evidence for individual-level asymmetry in limb preference in picas, it was not included in the cladographic analysis since it had a sample size of only four and therefore did not meet the inclusion criteria.

Primates. Phylogenetically, non-human primates are the closest living relatives of *Homo sapiens*, making it especially interesting to investigate handedness in this order. The Primates order can be divided into the suborders Strepsirrhini (e.g., lemurs and loris) and Haplorhini (humans, apes, monkeys, and tarsiers).

In Strepsirrhini several studies have investigated handedness in different lemur species. For example, Scheumann, Joly-Radko, Leliveld, and Zimmermann (2011) investigated food grasping in grey mouse lemurs (*Microcebus murinus*) and found evidence for individual-level asymmetry but no statistically significant population-level asymmetry. The same pattern of results was also reported by two other studies in the same species (Leliveld, Scheumann, & Zimmermann, 2008; Scheumann & Zimmermann, 2008), as well as by studies investigating handedness in Goodman's mouse lemurs (*Microcebus lehilahytsara*; Leliveld et al., 2008), aye-ayes (*Daubentonia madagascariensis*; Feistner, Price, & Milliken, 1994), and ring-tailed lemurs (*Lemur catta*; Mertl-Millhollen, 2007). In contrast to these findings, a large study investigating handedness in a sample of 194 animals of six lemur species (*Lemur catta*, *Lemur coronatus*, *Lemur Fulvus*, *Lemur macaco*, *Lemur mongoz*, *Lemur rubriventer*) found a significant leftward population-level asymmetry, with 91 animals (46.9%) preferring the left hand, 65 animals (33.5%) preferring the right hand, and 38 animals (19.6%) having no preference (Ward, Milliken, Dodson, Stafford, & Wallace, 1990). A leftward asymmetry at the population-level was also reported for ruffed lemurs (*Varecia variegata variegate*; Forsythe, Milliken, Stafford, & Ward, 1988; Nelson, O'Karma, Ruperti, & Novak, 2009) and black lemurs (Forsythe & Ward, 1988).

In Haplorhini it is undisputed that human handedness exhibits a highly significant population-level asymmetry (Corballis, 2009) while the situation is less clear for the non-human species within this suborder. Due to the very large number of studies investigating handedness in apes and monkeys it is not possible to review all of them within the present article. This is, fortunately, also not necessary since several other authors have written excellent reviews about this topic (e.g., Fagot & Vauclair, 1991; Hopkins & Cantalupo, 2005) or conducted meta-analyses (e.g., McGrew & Marchant, 1997).

Interestingly, the results of the analyses are not unequivocal. For example, while McGrew and Marchant (1997) concluded that non-human primates do not show population-level asymmetries, Hopkins and Cantalupo (2005) argue that chimpanzees show population-level asymmetries at least for some handedness measures. In great apes a recent large-scale study found evidence for population-level asymmetry in all three non-human genera of the Hominidae family (Pongus, Gorilla, and Pan). Hopkins et al. (2011) investigated handedness for coordinated bimanual actions in 47 orangutans (*Pongo pygmaeus*), 76 gorillas (*Gorilla gorilla*), 536 chimpanzees (*Pan troglodytes*), and 118 bonobos (*Pan paniscus*). While chimpanzees, bonobos, and gorillas showed a rightward population-level asymmetry, orangutans showed a leftward population-level asymmetry. Evidence for population-level asymmetries in handedness in great apes has also been reported by several other studies (e.g., Hopkins, 2006; Hopkins & Cantalupo, 2005; Hopkins, Russell, Cantalupo, Freeman, & Schapiro, 2005) but there are also a number of findings supporting the assumption that great apes do not show population-level asymmetry (e.g., Harrison & Nystrom, 2008; McGrew & Marchant, 2001, Palmer, 2002). These contradictory results suggest that, while population-level asymmetries exist in great apes, they are modulated by several external and internal factors including the complexity of the assessed form of behaviour and possible copying of the right-handedness of human caretakers (Güntürkün, 2009).

In old-world monkeys, limb preferences have been investigated in, for example, rhesus macaques (*Macaca mulatta*). Lehman (1978) tested limb preferences during food reaching in this species and found that out of 171 animals, 80 were right-handed (46.8%) and 91 left-handed (53.2%), with the number of left-handed monkeys not being significantly larger than the number of right-handed monkeys. Individual-level asymmetry, but not population-level asymmetry, for food reaching in rhesus macaques was also observed by an earlier study in this species (Warren, 1953). Interestingly, a more recent study by Westergaard, Kuhn, and Suomi (1998) found that rhesus macaques show individual-level asymmetry when reaching from a bipedal position, but a leftward population-level asymmetry when reaching from a quadrupedal position, indicating that posture influences limb preferences in rhesus macaques.

Limb preferences during food reaching were also investigated in two other macaque species. Itani, Tokuda, Furuya, Kano, and Shin (1963) reported a significant leftward population-level asymmetries in Japanese macaques (*Macaca fuscata*), with 149 (37.8%) out of 394 monkeys being left-handed, 118 (29.9%) being right-handed, and 127 (32.3%) having no clear preference. For the bonnet macaque (*Macaca radiata*), Brooker, Lehman, Heimbuch, and Kidd (1981) reported that out of 67 animals, 22 (33%) monkeys were right-handed, 21 (31%) monkeys were left-handed, and the remaining 24 (36%) monkeys had no significant preference. While no statistical test for population-level asymmetry was reported, the percentages suggest that individual-level asymmetry but not population-level asymmetry exists for food reaching in this species. Outside of the Macaca genus, limb preferences in old-world monkeys have also been extensively investigated in the Papio genus (baboons). In this genus two studies (Meguerditchian, Molesti, & Vauclair, 2011; Meguerditchian & Vauclair, 2006) reported a strong rightward population-level asymmetry for communicative gestures in the olive baboon (*Papio anubis*), a finding that may be linked to the left-hemispheric dominance for production and perception of conspecific communication. Interestingly, a study investigating unimanual and bimanual reaching for food in olive baboons (Vauclair, Meguerditchian & Hopkins, 2005) found a rightward population-level asymmetry for the complex bimanual task, but nor for the easier unimanual task. This shows that rightward population-level asymmetries in this species can also occur for non-communicative behaviours, but are modulated by task complexity. Population-level asymmetries for a complex task, but not for a simple task, were also reported by Fagot and Vauclair (1988) who investigated hand preferences in the Guinea baboon (*Papio papio*). However, in contrast to olive baboons, Guinea baboons showed a leftward population-level asymmetry.

Besides handedness, footedness has also been investigated in Old World monkeys. Zhao, Li, and Watanabe (2008) assessed foot preferences during quadrupedal and bipedal walking in the golden snub-nosed monkey (*Rhinopithecus roxellana*) and found that while all individuals showed significant individual-level preferences, no asymmetry at the population level existed for the two forms of walking in golden snub-nosed monkeys.

In New World monkeys limb preferences have been investigated in, for example, the common marmoset (*Callithrix jacchus*), starting with a study by Rothe (1973) who found that handedness during food reaching in this species fluctuated considerably over different test sessions and was completely reversed on several occasions. Moreover, the emotional status and environmental variables influenced the animals' preferences, leading Rothe (1973) to the conclusion that hand preferences in marmosets are mostly symmetric. This assumption was subsequently supported by a study by Box (1977) who found that, while most animals in his study showed significant individual preferences when reaching for food or holding it, five other behaviours (e.g., climbing and walking) were symmetric. Besides marmosets, handedness in New World monkeys was also investigated in several other species. For example, spider monkeys (*Ateles geoffroyi*) show a leftward population-level asymmetry for food reaching (Laska, 1996), while cotton-top tamarin (*Saguinus oedipus*) show a rightward population-level asymmetry for this behaviour, but no population-level asymmetry for four other manual behaviours (e.g., one arm vertical suspensions; King, 1995). Posture seems to influence hand preferences in New World monkeys as tufted capuchin monkeys (*Cebus apella*) show a rightward population-level asymmetry for bimanual food reaching and unimanual food reaching from an upright, but not from a quadrupedal posture (Spinozzi, Castorina, & Truppa, 1998). Also, there are species that show no population-level asymmetries over several different types of manual behaviour (including food reaching) like white-faced sakis (*Pithecia pithecia*; Smith & Thompson, 2011).

While it is not possible to discuss all studies investigating handedness in monkeys in the present article (see Table 1 in Smith & Thompson, 2011, for an overview of studies investigating handedness in New World monkeys) the presented studies show that there is compelling evidence for the existence of individual-level asymmetry in monkeys. Population-level asymmetries can also be observed, but their occurrence and direction seem to be modulated by external and internal factors to an even greater extent than in great apes, with especially posture and task complexity being highly influential (Fagot & Vauclair, 1991).

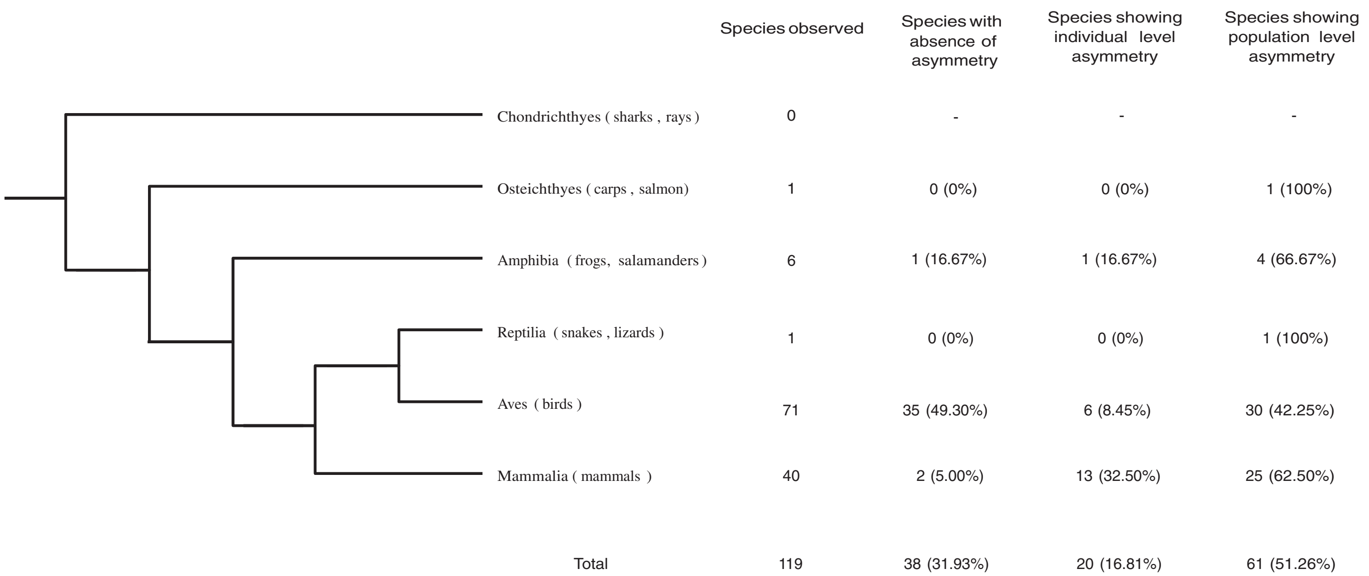
Taken together, there is clear evidence for the existence of population-level asymmetries within the non-human member of the order Primates, especially within the great apes, but there are also several primate species that show individual-level asymmetry, but not population-level asymmetry. Also, some primate species show rightward population-level asymmetries for handedness, while others show leftward population-level asymmetries. Thus the occurrence and direction of population-level asymmetries in primates seems to be species- as well as task-dependent.

Orders Dermoptera & Scandentia. Limb preferences have not yet been investigated in the orders Dermoptera (culogos) and Scandentia (threeshrews).

Magnorder Atlantogenata. Within the Magnorder Atlantogenata, including the orders Pilosa (anteaters and sloths), Cingulata (armadillos), Afrosoricida (golden moles and tenrecs), Macroscelidea (elephant shrews), Tubulidentata (aardvarks), Sirenia (sea cows), Hyracoidea (hyraxes), and Proboscidea (elephants), no studies about behavioural preferences in bilateral symmetric limbs have yet been published.

SUMMARY AND CONCLUSION

The aim of the present study was to identify all vertebrate orders for which evidence for absence of asymmetry, individual-level asymmetry, or population-level asymmetry in limb use has been reported, in order to clarify which theoretical position regarding the background of human handedness in vertebrate evolution is supported by the currently available data. Overall, 119 different species were included in the present cladographic analysis (see Figure 5 for numbers and percentages of species showing different forms of asymmetry for all classes). About half of them (51.26%) had population-level asymmetries with significant individual preferences in at least one conducted test; 20 species (16.81%) evinced a pattern of individual-level asymmetry. In 38 species (31.93%) no limb asymmetry at the group level could be revealed.



	Species observed	Species with absence of asymmetry	Species showing individual level asymmetry	Species showing population level asymmetry
Chondrichthyes (sharks , rays)	0	-	-	-
Osteichthyes (carps , salmon)	1	0 (0%)	0 (0%)	1 (100%)
Amphibia (frogs, salamanders)	6	1 (16.67%)	1 (16.67%)	4 (66.67%)
Reptilia (snakes , lizards)	1	0 (0%)	0 (0%)	1 (100%)
Aves (birds)	71	35 (49.30%)	6 (8.45%)	30 (42.25%)
Mammalia (mammals)	40	2 (5.00%)	13 (32.50%)	25 (62.50%)
Total	119	38 (31.93%)	20 (16.81%)	61 (51.26%)

Figure 5. Cladographic overview of the vertebrate clade. Agnatha (jawless fish) and extinct orders are not shown. The chart shows the total number of species per class in which limb preferences have been investigated. Numbers and percentages of species which exhibit no asymmetry, individual-level asymmetry, or population-level asymmetry with regard to their limb preferences are given.

In 3 of these 38 species this absence of asymmetry was also demonstrated to be true at the individual level. We will first discuss these data with regard to clade patterns before interpreting them in comparison to handedness in humans.

Clade patterns

To derive a proper evolutionary interpretation of limb preferences in vertebrates, studies in Agnatha and Chondrichtyes would be important. Unfortunately Agnatha have no paired fins and no studies on fin preferences have been published in Chondrichthyes. Additionally, only two such studies were conducted in Osteichthyes. Thus the first conclusion of our analysis is that studies in Chondrichtyes in particular could have important implications for our understanding of the early evolution of limb preferences in vertebrates. Furthermore, studies on coelacanths and lungfishes resided in the Osteichthyes class could be of some relevance since these species represent the closest non-extinct relatives of tetrapods (Shan & Gras, 2011).

In the Amphibia class considerable evidence for the existence of limb preferences has been published for the Anura order, while data for the Caudata and Apoda are not available at present. In the Reptilia class there is also some evidence indicating the existence of limb preferences, but the order of Crocodylia has not been investigated yet. This is unfortunate, since Crocodylia are the closest living relatives of birds and thus represent the closest non-extinct link between birds and mammals (Gower, 2001). Thus the lack of asymmetry studies in Crocodylia hampers a proper interpretation of the evolutionary scenario leading to limb preferences in the classes of Aves and Mammalia. So the second conclusion of our analysis is that studies on limb preferences in Crocodylia would be necessary for an evolutionary understanding of asymmetries in amniotes.

Most research on limb preferences has been conducted in the Aves and Mammalia classes. In birds 30 different non-extinct taxonomic groups were analysed (see Figure 2). Published studies investigating limb preferences were identified for 11 orders (37%), while for the remaining 19 orders (63%) no data were available at present. Looking at the bird cladograms (Figure 3) it is evident that especially studies on Palaeognathae (kiwis, emus, tinamous, ostriches) are needed to understand the evolutionary emerge of avian limb preferences.

In addition to birds, mammals were also intensively studied. Here 23 different non-extinct taxonomic groups were analysed (see Figure 4) and published studies investigating limb preferences were identified for 9 orders (39%), while no data were available for the remaining 14 orders (61%). Looking at Figure 4 it is evident that studies of Monotremata (e.g., platypus) and Atlantogenata (superorders Xenarthra and Afrotheria) in particular are lacking. Data on limb preferences in Xenarthra and Afrotheria would be particularly interesting, since the diversification of Placentalia into four superorders (Laurasiatheria, Euarchontoglires, Xenarthra, and Afrotheria) took place an estimated 64 to 104 million years ago (Murphy et al., 2001). Thus the occurrence of limb preferences in different Atlantogenata species would make a strong argument for an evolutionary early base of human handedness and should therefore definitively be investigated, for example by using observational techniques in the natural habitat of a species (e.g., videotaping of naturally occurring behaviour; see Reimchen & Spoljaric, 2011).

When future research has filled some of these gaps in the limb preference data, application of phylogenetic comparative methods could prove very valuable to identify shifts in the direction and/or strength of limb preferences during evolution (see for example Brown & Magat, 2011a). At the present moment, however, the application of such techniques is not possible due to the lack of data for several orders.

Comparison with human handedness

The result of the present analysis contradicts the idea that population-level asymmetries are unique for *Homo sapiens* (Crow, 2004). In only 38 of 119 analysed non-human species were no limb preferences observed. Obviously a publication bias in the data used for the cladographic analyses has to be considered (Jennions & Møller, 2002). But the number of species with reported limb preferences still testifies that motor asymmetries are very likely widespread within vertebrates and the case of Homo is far less exceptional than once thought (Halpern et al., 2005).

Although humans are certainly not exceptional with regard to a principal presence of limb preferences, this does not imply that human handedness is directly comparable to the motor asymmetries reviewed in this paper. First, limb asymmetries as observed in non-human animals can involve activities that are different from human manual activities, like the trailing limb when running or the foot that touches the ground first when landing from flight. Second, the distribution of left- to right-handers in humans is typically around 10/90 (Corballis, 2009), while in most other vertebrates the pattern is much less skewed (notable exceptions being the finding that 90% of South American cane toads showed a right-sided limb preference for righting behaviour; Robins & Rogers, 2002; and the food-grasping behaviour in several parrot species with limb preference ranging up to 100%; Brown & Magat, 2011a). Third, there is a considerably larger number of individuals without a preference in most non-human vertebrate species compared to humans. Fourth, while human handedness is mostly task-invariant, this is not necessarily the case in other species. Fifth, while strength and especially the direction of human handedness is highly stable over time, population-level asymmetries in most non-human vertebrates seem to be considerably more variant, with limb preferences in several species being modulated by external factors (e.g., environmental biases in mice, stress due to space limitations in donkeys, experimental paradigm in rats) and/or individual characteristics (e.g., sex in cats and dogs). Thus the findings of the present study support the position that population-level asymmetries in limb preferences per se are a common feature among vertebrates, while the strong and consistent rightward population-level asymmetry observed for human handedness is not.

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