Laterality

Asymmetries of Brain, Behaviour, and Cognition

ISSN: 1357-650X (Print) 1464-0678 (Online) Journal homepage: www.tandfonline.com/journals/plat20

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To cite this article: Felix Ströckens, Maike Schwalvenberg, Yasmin El Basbasse, Katrin Amunts, Onur Güntürkün & Sebastian Ocklenburg (20 May 2025): Limb preferences in non-human vertebrates: A new decade, Laterality, DOI: 10.1080/1357650X.2025.2499049

To link to this article: https://doi.org/10.1080/1357650X.2025.2499049

LATERALITY: ASYMMETRIES OF BRAIN, BEHAVIOUR, AND COGNITION
https://doi.org/10.1080/1357650X.2025.2499049

Routledge
Taylor & Francis Group

Limb preferences in non-human vertebrates: A new decade

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ABSTRACT
Over a decade ago, we demonstrated that population-level asymmetries in limb preferences are not uniquely human but occur in various species of non-human animals (Ströckens, F., Güntürkün, O., & Ocklenburg, S. (2013). Limb preferences in non-human vertebrates. *Laterality*, *18*(5), 536–575). While back then, vertebrate limb preference data were too scarce to reconstruct the evolutionary basis of human handedness or apply phylogenetic comparative methods, many voids were filled in the meantime. It is therefore high time to update the last analysis on limb preferences in all non-extinct vertebrate orders in the present article. We show that the robustness of empirical evidence for limb preference in non-human vertebrates increased in the last decade due to (1) more studies, (2) larger sample sizes, and (3) an increased number of meta-analyses integrating findings from various species (e.g., cats, dogs, rats, mice). Similar to the previous publication, we used cladographic comparisons to systematically assess limb preferences in non-extinct vertebrate orders. The identified studies analyzed 172 different species. Overall, 39.53% of species showed evidence for population-level asymmetries, 32.56% showed individual-level asymmetries, and 27.91% showed no asymmetry. These findings not only further support the notion that asymmetries are a widespread feature of vertebrate motor organization, but they also identify crucial gaps that should be filled by future investigations.

ARTICLE HISTORY Received 12 February 2025; Accepted 23 April 2025

KEYWORDS Handedness; footedness; pawedness; laterality; asymmetry

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Supplemental data for this article can be accessed online at https://doi.org/10.1080/1357650X.2025.2499049.

Introduction

About 10.6% of humans are left-handed, while 89.4% are right-handed, resulting in a strong rightward population-level asymmetry for handedness (Papadatou-Pastou et al., 2020). Handedness is not a uniquely human phenomenon. Comparative laterality research has identified a wide range of limb preferences, e.g., a preference to use one limb over the other for motor actions such as reaching for food (Ströckens et al., 2013). Some animals, like primates, show handedness; for other species, terms like "pawedness" or "flipperedness" have been used to describe limb preferences. Limb preferences have been linked to cerebral asymmetries in brain function in both humans and animals (Rogers, 2009), with the right motor cortex controlling left-sided limbs and the left motor cortex right-sided limbs. Due to the link between the right hemisphere and the processing of negative emotions, it has been suggested that knowledge about limb preferences could contribute to animal welfare (Rogers, 2023).

In 2013, we systematically assessed published studies on limb preferences in non-human animal species to clarify the question, whether similar population-level asymmetries for limb preferences can also be found in non-human species (Ströckens et al., 2013). We identified 119 different vertebrate species in which studies on limb preferences had been published. Overall, 61 species (51.26%) showed evidence for population-level asymmetries, 20 species (16.81%) showed evidence for individual-level asymmetries, and 38 species (31.93%) did not show any evidence for asymmetry. Interestingly, the findings of the 2013 paper showed that research on limb preferences was focused on some key taxa, while others were almost completely missing. Specifically, we highlighted that more research on limb preferences in *Chondrichtyes*, *Crocodylia*, *Atlantogenata,* and *Palaeognathae* would have important implications for our understanding of the evolution of vertebrate limb preferences. These clades represent sister groups in which limb preferences have been studied in at least one species. Therefore, the data from these clades could help identify a potential common ancestry for limb asymmetries across these groups. In the more than ten years that have passed since the publication of the 2013 paper, an astonishing amount of research has been published on limb preferences in non-human vertebrates (see below). Integrating these new findings in an updated cladographic framework comparable to the one used in the 2013 study has the potential to yield new insights into the neurobiology and evolution of behavioural preferences in vertebrates.

Aim of the present study

Therefore, the present study aimed to update the results of the 2013 publication on limb preferences in non-human animals (Ströckens et al., 2013). To this end, we conducted an updated search based on the methods of the previous article (see Methods section). Similar to the previous study, we aimed to determine for as many species as possible whether they showed individual-level asymmetry, population-level asymmetry, or no asymmetry for limb preferences.

Methods

Search strategy

While the 2013 article was a narrative review without a methods section, here we included a short method section to make the search strategy more transparent and replicable. To identify relevant studies that were not included in our 2013 review article, the following search strategy was used: Search for articles took place from March 2022 to April 2024. Three databases were used for literature search (PubMed, Google Scholar, and ScienceDirect). Additionally, the reference lists of identified articles were screened to identify further relevant articles. Two authors (YEB and MS) performed the literature search. We set the timeframe for the search to 2013 or later. Note that sometimes we also included studies that were published earlier if the search of reference lists of published articles identified relevant earlier articles that were not covered in our first limb preference paper. Search terms included “handedness”, “pawedness”, and “limb preferences” in combination with “animal” as well as with all clade names (see below).

Exclusion and inclusion criteria

The following inclusion criteria were used for inclusion of a study in the recent cladograms:

- The study was not included in the previous paper on limb preferences (Ströckens et al., 2013).
- The study reported on an investigation of limb preferences in a form of bilaterally symmetric limbs (e.g., handedness, footedness, pawedness, fin, or flipper preferences).
- The reported data on limb preferences in a non-human vertebrate species allowed for identification of whether the species showed population-level asymmetries, individual-level asymmetries, or no asymmetries. This typically required a form of statistical test.
- The study had a minimum sample size of five animals.
- The study was written in English.

The following exclusion criteria were used:

- All studies not reporting data on limb preferences in non-human vertebrates were excluded. We focused exclusively on limb preferences, so that studies focused on turning bias, jump direction, biting bias, escape direction, and other motor asymmetries unrelated to limb use were not considered.

- All studies focused exclusively on humans were excluded.
- All reviews, comments, and other forms of evidence synthesis apart from meta-analyses were excluded. Sometimes we refer the reader to relevant review articles for further information on specific topics.
- All studies that reported that animals were included based on their limb preferences (e.g., 10 left-handed and 10 right-handed chimpanzees were chosen from a larger group) were excluded since they did not allow any conclusions about the distributions of limb preferences.
- Studies that used the term “handedness” to describe something else than a motor limb preference were excluded (e.g., bodily asymmetries).

Decision strategy

The study aimed to determine for as many species as possible whether they showed population-level asymmetries, individual-level asymmetries, or no asymmetries. The following decision pathway was used to determine which form of asymmetry was present in species.

- If only one publication on limb preferences in a species was identified, that publication was used to make the decision which form of asymmetry is present in this species
- If several publications were identified in a species, it was first determined whether one or more of these publications were meta-analyses.
- If one or more publications for a given species were meta-analyses, the meta-analysis with the largest overall sample size was used to make the decision which form of asymmetry is present in this species
- If no meta-analysis existed for a given species, the largest empirical study was used to make this decision.
- If only one test was used in an empirical study to determine limb preferences, the results from this test were used
- If more than one test was used in an empirical study to determine limb preferences, the results from the test most closely resembling food reaching were used (as food reaching is likely the most widely used test to assess limb preferences in non-human animals)

Construction of cladograms

To help identify possible phylogenetic relationships in the occurrence of limb preferences, we conducted a cladographic comparison based on three cladograms. A vertebrate cladogram, summarizing the results of *Agnatha*, *Chondrichthyes, Osteichthyes, Amphibia* and (non-avian) *Reptilia* species and separate cladograms for *Aves* and *Mammalia* species with an order level resolution. Advances in genomic sequencing techniques over the last decade have generated genome-scale sequence data for hundreds of different species within all vertebrate clades. These data allowed the creation of phylogenetic trees, which are more precise than previous trees based on fossil data alone. The cladograms presented in this article are derived from recent phylogenetic trees based on molecular clock analyses (Álvarez-Carretero et al., 2022; Ezcurra et al., 2014; San Mauro, 2010; Stiller et al., 2024) and do differ considerably from our 2013 publication. Aside from introducing phylogenetic distance, position and number of orders have changed, with the avian cladogram now containing 44 orders compared to 30 in the 2013 version. In other cases, orders present in our 2013 publication have lost their order status and are now integrated into other orders. Most notable here is the former mammalian order *Cetacea*, which is now part of the order *Artiodactyla* (Álvarez-Carretero et al., 2022). If the order assignment for a given species has changed since our original publication, we will notify the reader at the beginning of the relevant paragraph.

Results

Over the last decade, dozens of additional studies investigating limb preferences in many vertebrate orders, including orders that were void of data in our 2013 publication, have been conducted. To avoid redundancies and keep the already long text of this publication within a reasonable length, we have concentrated our report on those studies not mentioned in our original publication. However, to give the reader quick access to all data used to create the cladograms, we have compiled a table listing all the literature we have screened for both publications. The table contains a list of all species, in which limb preferences have been investigated so far, including some which have not been used for our analyses due to the exclusion criteria mentioned above (e.g., low number). Further, the table separates the results for studies in which different behaviours have been observed since asymmetries in limb usage can be task-dependent (see also results below and discussion). Thus, the numbers in the table differ from those in the cladograms, as we did not distinguish between different behaviours here for clarity. Instead, cladograms were created using the criteria mentioned in the methods section above.

Agnatha *(e.g., hagfish and lampreys)*

During the Cambrian period, approximately 540–520 million years ago, a remarkable diversification of life forms took place, known as the Cambrian explosion. Around 530 million years ago, a new group of aquatic species emerged, characterized by the presence of a skull and a dorsal nerve cord supported by rudimentary cartilaginous vertebrae. These early vertebrates lacked jaws and were classified as *Agnatha*, meaning "jawless fish." Although the original *Agnatha* species eventually went extinct, their modern descendants, lampreys and hagfish, continue to thrive today, representing the most ancient lineage of contemporary vertebrates (Shimeld & Donoghue, 2012). However, due to their lack of true fins and any bilaterally organized limbs, limb preferences are not present in *Agnatha*. It is, however, worth mentioning that one study in Pacific hagfish (*Eptatretus stoutii*) reported that out of n = 40 hagfish 29 individuals showed a significant preference to coil in one direction (Miyashita & Palmer, 2014). No significant difference between clockwise and counterclockwise coiling hagfish was found, suggesting individual-level asymmetries for coiling in these limbless fish. This indicates that hagfish do show functional asymmetries. Since this study did not provide information on actual limb preferences and therefore did not meet our inclusion criteria, it was excluded from our analysis.

Chondrichthyes *(e.g., rays, sharks)*

About 440 million years ago, the descendants of early *Agnatha* developed jaws, leading to the emergence of the *Gnathostomata* clade, which includes all current vertebrates except *Agnatha*. These early *Gnathostomata* featured paired lateral fins with an internal skeleton, a key development for limb preferences (see Bayramov et al., 2024 for a review on fin evolution). Most of the original *Gnathostomata* clades disappeared during significant extinction events, with only two groups surviving to the present: *Chondrichthyes*, which includes cartilaginous fish like rays and sharks, and *Osteichthyes*, which encompasses bony fish such as mackerels and tunas. The latter group eventually gave rise to modern land-dwelling tetrapods (see below). While *Chondrichthyes* possess paired fins and may exhibit some lateralization in fin use, we could not find any relevant studies on limb preferences in this group. Of note, one study on behavioural laterality in Port Jackson sharks (*Heterodontus portusjacksoni*) was published in 2014, showing that these species showed considerable variation in turning bias in a T-maze (Byrnes et al., 2016). This indicates that sharks do show functional asymmetries. Once again, the study was excluded from our analysis because it did not provide findings on actual limb preferences.

Osteichthyes *(e.g., mackerels, tunas)*

We did not identify any relevant studies on limb preferences in bony fish in addition to those reported by our previous study on limb preferences in non-human vertebrates. An updated review on brain and behavioural asymmetry in fish was published in 2020 and gives an overview of the many findings on laterality in fish (Miletto Petrazzini et al., 2020).

Amphibia

Around 360 million years ago, predecessors of the *Amphibia* class began to colonize land on a larger scale, driving the evolution of robust limbs capable of withstanding increased gravity and supporting locomotion (Long & Gordon, 2004). These adaptations not only facilitated more efficient walking but also allowed for more flexible limb usage, creating the opportunity for the development of more complex limb preferences. As a result, amphibians became one of the first groups studied when systematic phylogenetic research on limb preferences began, providing crucial evidence of limb asymmetries that likely evolved before the emergence of the reptilian, avian, and mammalian classes (Bisazza et al., 1996).

Anura *(e.g., frogs, toads)*

Within the class *Amphia*, *Anura* was the order with the most papers on limb preferences discussed in our 2013 article. Limb preferences in toads and frogs remained an active research field in the years after 2013.

One study from 2023 assessed forelimb preferences in 19 anuran species using a task in which the animal had to remove a piece of cloth from their eyes (Rojas-Montoya & Vargas-Salinas, 2023). Evidence suggested that four species showed statistically significant population-level asymmetries. Cauca poison frogs *(Andinobates bombetes*), and small-headed tree frogs (*Dendropsophus microcephalus)* showed a significant rightward bias, while stripe-throated rocket frogs (*Leucostethus brachistriatus*) and Santa Marta harlequin toads (*Atelopus laetissimus*) showed a significant leftward bias. Since each animal was only tested once and they could use either the left or the right forelimb, it was difficult to assess the difference between the absence of asymmetry and individual-level asymmetry for the other 15 anuran species reported in the study. While the reported data suggest individual-level asymmetries in all remaining species, it was impossible in this design to find an absence of asymmetry. We therefore did not include these 15 species in the cladogram, since it was unclear what their results were. A study on forelimb preferences in n = 15 Rocky Mountain tailed frogs (*Ascaphus montanus*) reported that there was no statistical evidence for a population-level asymmetry during the righting response. To assess the righting response, the animal is placed upside-down. Then it is recorded whether the animal uprights itself to its left or right side. Only 3 animals showed significant individual-level asymmetry

(Sullivan, 2018). Thus, there seems to be an absence of asymmetry for the righting response in this species.

More recently, the preferences during the righting response were assessed in the cane toad (R*hinella marina*) in two groups of n = 38 and n = 25 animals. The authors reported a strong and significant rightward population-level asymmetry in this species (Robins & Rogers, 2022).

Moreover, we identified some studies published before 2013 that were not included in our previous article. One study from 2006 used the object wiping task and the righting task in five anuran species (Malashichev, 2006). The species included the green tree frog (*Litoria caerulea*), the European common frog (*Rana temporaria*), the pool frog (*Rana lessonae*), the common spadefoot toad (*Pelobates fuscus*), and the Argentine horned frog (*Ceratophrys ornate*). While no food-reaching task was performed, we focused on the results of the object wiping task, as this involves object manipulation and therefore is closer to food reaching than the righting task. The green tree frog showed a significant population-level rightward asymmetry. The pool frog, the common spadefoot toad, the Argentine horned frog, and the European common frog showed an absence of asymmetry. Furthermore, a 2007 study on limb preferences during feeding in European green toads (*Bufo viridis*) reported a significant leftward population-level asymmetry in this species (Sovrano, 2007).

Caudata *(e.g., salamanders and newts)*

We did not identify any study fulfilling the inclusion criteria in this order. One study investigated motor and visual lateralization in the Mexican axolotl (*Ambystoma mexicanum*) but did not report on limb preferences (Izvekov et al., 2018).

Gymnophiona *(e.g., caecilians)*

Since all extant *Gymnophiona* species are limbless, no studies in this order could be identified.

Reptilia

Research on limb preferences in non-avian reptiles is scarce. In our previous publication, we identified only two studies: one on foot use in Duvaucel's geckos (*Hoplodactylus duvaucelii*), showing no asymmetry, and another on leatherback turtles, indicating right-sided population-level asymmetry (Seligmann, 2002; Sieg et al., 2010). Although a few additional studies on reptilian limb usage have emerged in the past decade (see below), the reptilian class, encompassing roughly 12,000 species, remains largely uncharted.

Testudines *(e.g., turtles)*

Several studies on limb preferences in turtles have been published in the last 12 years, and we also identified an earlier study that was not covered in our 2013 publication.

Two studies focused on limb preferences in the tortoise (*Testudo hermanni*). A 2006 study that was not included in our 2013 paper and therefore is discussed here investigated the righting response in n = 34 tortoises (Stancher et al., 2006). A significant rightward population-level asymmetry was observed. A more recent study in the same species (Sovrano et al., 2018) focused on visual laterality, but also observed foot preferences when starting to walk. In a first experiment with n = 11 animals in which two mirrors were in the test chamber, a significant rightward population-level asymmetry was observed. However, in a second experiment with n = 8 animals, no such bias was observed.

Asymmetry of the righting response assessed in tortoises was also assessed in two species of sea turtles, the green turtle (*Chelonia mydas*) and the olive ridley turtle (*Lepidochelys olivacea*) (Malashichev, 2016). In n = 50 green turtles, a significant rightward population-level preference was found for the righting response. In n = 50 olive ridley turtles, there was a significant leftward population-level asymmetry.

In Aldabra giant tortoises (*Aldabrachelys gigantea*), a study in n = 67 animals assessed the preference for which front limb and hind limb were placed forward during sleep-like behaviour (Spiezio et al., 2022). For forelimbs, 88% of animals had a preference, with 52% preferring the left forelimb and 36% the right forelimb. There were significantly more lateralized animals than non-lateralized animals, indicating individual-level asymmetries. However, the comparison between animals with left and right preferences did not reach significance, suggesting that no population-level asymmetry was present in this species. Similar results were found for hind limb position preference.

Squamata *(e.g., lizards and snakes)*

In *Squamata*, a study focused on foot preferences in the gecko (*Ptyodactylus guttatus*) in n = 48 animals (Sion, 2018). Overall, most animals showed a preference on the individual level, but there was no population-level asymmetry. In female geckos, 50% of animals showed a rightward preference, 30% a leftward preference, and 20% no preference. In male geckos, 33% showed a rightward preference, 50% showed a leftward preference, and 16.7% showed no preference.

It has to be noted that due to the fact that the suborder *Serpentes* (e.g., snakes) is limbless, limb preferences are not a main focus in laterality research in *Squamata*. However, motor asymmetries have been investigated in other domains, such as coiling asymmetries in snakes (Roth, 2003), lateralized feeding behaviour (Reisz et al., 2020), lateralized escape behaviour (Bonati et al., 2010) and lateralized detouring behaviour (Csermely et al., 2010).

Crocodilia *(e.g., crocodiles and alligators)*

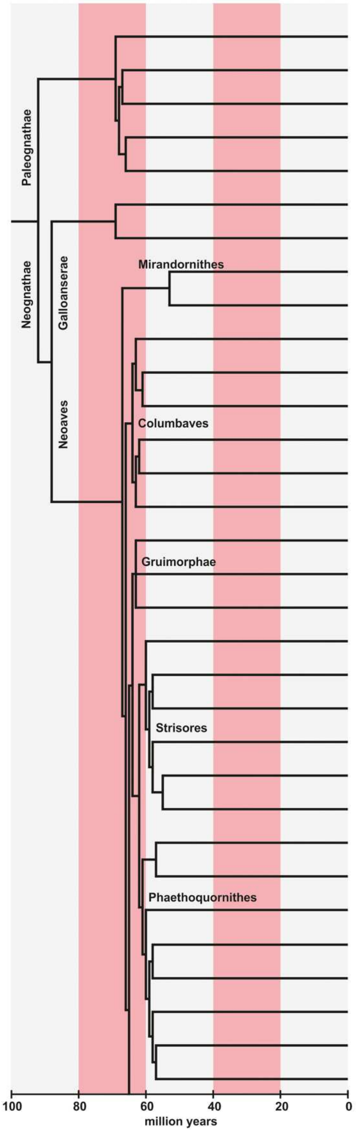
We did not identify any published study fulfilling the inclusion criteria in this order. Evidence for behavioural lateralization in crocodiles was provided by a study on bite side preferences in the American alligator (*Alligator mississippiensis*) (Honan & Murray, 2023), which found that bites were more often directed at targets positioned within the viewing field of the left eye. However, the study was not included into our analysis since it did not provide findings on actual limb preferences.

Aves

Research on limb preferences in avian species dates back to the nineteenth century, with studies on food handling preferences in several parrot species by Ogle (1871) and Dwight (1891) (reviewed by (Güntürkün et al., 2020)). Since then, bird species have turned into one of the prime models to study a variety of lateralized behaviours, including vocalization, eye use, and, not surprisingly, limb usage. Since the times of Ogle and Davies, dozens of studies on avian limb preferences have been published, revealing that asymmetries in limb usage are widespread in the *Aves* class. Figure 1 shows the updated cladogram for avian species. Compared to our previous cladogram, the last decade brought only a few additional studies on avian limb preferences, which are outlined below. Still, due to advances in the genetic sequencing techniques mentioned above, the avian phylogenetic tree has changed and now comprises a total of 44 orders, with several species having been moved to new orders or integrated into existing ones. This change affects our data pattern only slightly, since most of the changes made affected orders, in which no data on limb preference was available anyway. In the few cases where the changed cladogram pattern is relevant, we will mention this in the text. As we pointed out in our 2013 publication, it is important to note that limb preference studies in birds refer to their hind limbs, since avian forelimbs evolved into wings, rarely used for object manipulation. Thus, a one-to-one comparison with forelimb preferences in other vertebrates should be made with caution.

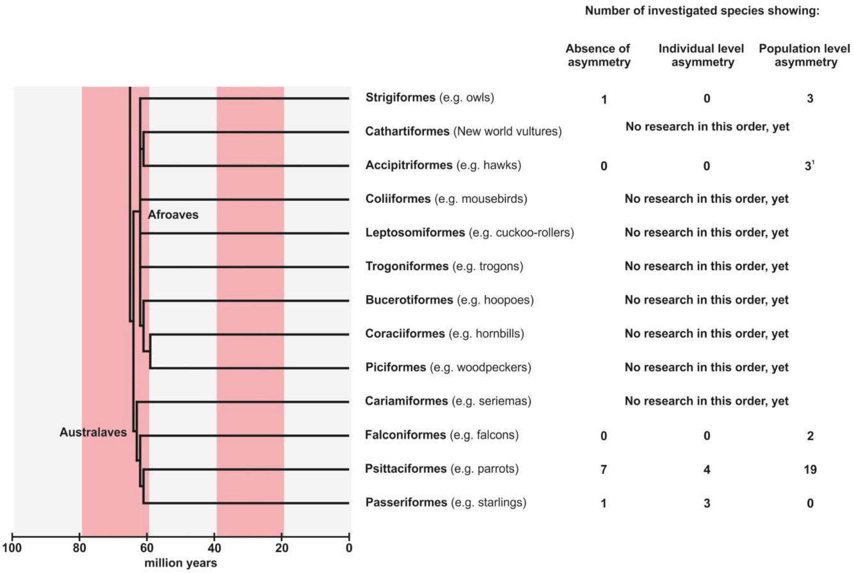
Palaeognathae *(e.g., ostriches)*

For the infraclass *Palaeognathae*, comprising five orders of evolutionary basal, flightless birds (*Struthioniformes, Casuariiformes, Apterygiformes, Rheiformes,*



	Number of investigated species showing:		
	Absence of asymmetry	Individual level asymmetry	Population level asymmetry
Struthioniformes (e.g. ostriches)	0	0	1
Casuariiformes (cassowaries & emus)	No research in this order, yet		
Apterygiformes (kiwis)	No research in this order, yet		
Rheiformes (rheas)	No research in this order, yet		
Tinamiformes (tinamous)	No research in this order, yet		
Galliformes (e.g. chicken)	1	0	3
Anseriformes (e.g. ducks)	5	0	1
Podicipediformes (e.g. grebes)	No research in this order, yet		
Phoenicopteriformes (e.g. flamingos)	1	0	2[1]
Columbiformes (e.g. pigeons)	0	1[1]	0
Mesitornithiformes (e.g. mesites)	No research in this order, yet		
Pterocliformes (e.g. sand grouse)	No research in this order, yet		
Cuculiformes (e.g. cuckoos)	No research in this order, yet		
Otidiformes (e.g. bustards)	No research in this order, yet		
Musophagiformes (turacos)	No research in this order, yet		
Opisthocomiformes (e.g. hoatzins)	No research in this order, yet		
Gruiformes (e.g. cranes)	1	1	0
Charadriiformes (e.g. gulls)	15	0	2
Caprimulgiformes (e.g. nighthawks)	No research in this order, yet		
Nyctibiiformes (potoos)	No research in this order, yet		
Steatornithiformes (oilbirds)	No research in this order, yet		
Podargiformes (frogmouths)	No research in this order, yet		
Aegotheliformes (owlet-nightjars)	No research in this order, yet		
Apodiformes (e.g. tree swifts)	No research in this order, yet		
Phaethontiformes (e.g. tropic birds)	No research in this order, yet		
Eurypygiformes (e.g. kagus)	No research in this order, yet		
Gaviiformes (e.g. loons)	No research in this order, yet		
Procellariiformes (e.g. petrels)	No research in this order, yet		
Sphenisciformes (e.g. penguins)	0	1[1]	0
Ciconiiformes (e.g. storks)	1	0	0
Suliformes (e.g. gannets)	No research in this order, yet		
Pelecaniformes (e.g. pelicans)	No research in this order, yet		

Figure 1. Cladistic overview of the *Aves* class, displaying the total number of species per class in which limb preferences have been studied. The chart displays the number of species within each order that exhibit no asymmetry, individual-level asymmetry, or population-level asymmetry in their limb preferences Phylogenetic tree is based on molecular clock data from (Stiller et al., 2024). Please note that some divergence points with a phylogenetic distance of less than 1 million years (Mya) have been merged for clarity. [1] Task dependent in greater flamingos (*Phoenicopteriformes*), rock pigeons (*Columbiformes*), Magellanic penguins (*Sphenisciformes*) and ospreys (*Accipitriformes*). [To view this figure in color, please see the online version of this journal.]



Number of investigated species showing:

	Absence of asymmetry	Individual level asymmetry	Population level asymmetry
Strigiformes (e.g. owls)	1	0	3
Cathartiformes (New world vultures)		No research in this order, yet	
Accipitriformes (e.g. hawks)	0	0	3^{1}
Coliiformes (e.g. mousebirds)		No research in this order, yet	
Leptosomiformes (e.g. cuckoo-rollers)		No research in this order, yet	
Trogoniformes (e.g. trogons)		No research in this order, yet	
Bucerotiformes (e.g. hoopoes)		No research in this order, yet	
Coraciiformes (e.g. hornbills)		No research in this order, yet	
Piciformes (e.g. woodpeckers)		No research in this order, yet	
Cariamiformes (e.g. seriemas)		No research in this order, yet	
Falconiformes (e.g. falcons)	0	0	2
Psittaciformes (e.g. parrots)	7	4	19
Passeriformes (e.g. starlings)	1	3	0

Figure 1 *Continued*

Tinamiformes), we could not find additional reports on limb preferences, aside from a study on common ostriches (*Struthio camelus,* order *Struthioniformes*) already included in our 2013 publication. Since *Palaeognathae* is the sister taxon to *Neognathae*, which includes all other extant bird species, and occupies a basal position in the avian phylogeny, further studies on limb preferences in this group could provide valuable insights into the evolutionary origins of limb preferences across all birds.

Galloanserae *(landfowl & waterfowl)*

The superorder *Galloanserae* comprises the orders *Galliformes* (landfowl like chickens, turkeys, and quails) and *Anseriformes* (waterfowl like ducks and geese). For the *Galliformes* order, in addition to studies reporting a right-sided population-level asymmetry in domestic chicken and Bobwhite quails already mentioned in our previous publication, two studies investigating foot preferences in common pheasants (*Phasianus colchicus*) have been published. Whiteside et al. observed, which foot 103 pheasants used to step over or on an obstacle and found a weak right-sided population-level asymmetry (Whiteside et al., 2018). In a follow-up study, Whiteside et al. tested another 135 common pheasants using the same setup and tried to correlate individual lateralization strength with cognitive performance in colour discrimination and spatial choice tasks (Whiteside et al., 2020). The authors reported a clear individual-level asymmetry of varying strength in the investigated pheasant group but did not conduct statistical analyses for potential population-level asymmetries. However, the data pattern indicates again a weak right-sided population bias. Further, the authors could not find a correlation between cognitive performance and individual lateralization strength in the stepping task. Still, these findings fit previous data on *Galliformes* species, reporting a population-level asymmetry for usage of the right foot (Casey, 2005).

For the *Anseriformes* order, we could not find additional studies aside from the ones already reported in our previous publication. It is noteworthy though, that in contrast to *Galliformes*, out of the six observed *Anseriformes* species, only one showed a right-sided population-level asymmetry, while the other five showed an absence of asymmetry (Randler, 2007). Whether this clade difference arises from variations in the observed behaviours – passive, one-leg roosting in *Anseriformes* versus active stepping/walking in *Galliformes* – or reflects an actual phylogenetic divergence between the two clades, remains to be investigated.

Mirandornithes *(grebes & flamingos)*

The clade *Mirandornithes* is a relatively recent addition to the avian phylogenetic tree and has been created due to molecular clock data indicating a close phylogenetic relation between *Podicipediformes* (e.g., grebes) and *Phoenicopteriformes* (e.g., flamingos). Thus, the position of the two orders within the phylogenetic tree has changed in comparison to our previous publication. More important however is, that there have been several studies on species of the *Phoenicopteriformes* order investigating limb preferences, which we did not report in our original work. Anderson & Williams investigated resting on one leg in 17 captive Caribbean flamingos (*Phoenicopterus ruber*) and found neither an individual nor a population-level asymmetry for this behaviour (Anderson & Williams, 2010). This finding was confirmed in a follow-up study (Anderson & Ialeggio, 2014). Interestingly, in another study performed by the same group on the same set of animals, one of the 17 individuals showed an individual-level asymmetry for roosting on one leg (Anderson & Robinson-Drummer, 2015). Still, given that the other studies could not provide evidence for individual-level asymmetry for this behaviour, we consider one-leg roosting in Caribbean flamingos to be not lateralized. Aside from roosting, the group also investigated head scratching with one leg in Caribbean flamingos. Again, no significant lateralization pattern, neither on the individual nor the population level could be identified (Peluso & Anderson, 2014). In contrast, a study with 29 Chilean flamingos (*Phoenicopterus chilensis*) could find a right-sided population level asymmetry for standing on one leg (Regaiolli, Spiezio, et al., 2021). The same study also investigated 41 greater flamingos (*Phoenicopterus roseus*) and could identify a right-sided population-level asymmetry for one-legged roosting in this species as well. However, a study by Vidal et al. examined a range of behaviours of wild greater flamingos for potential lateralization and found that the occurrence of an asymmetry in limb usage depends on the behaviour's complexity (Vidal et al., 2018). One-leg stand at rest in 91 individuals showed no asymmetry. For stamping for food, there was a right-sided population-level asymmetry, while for one out of five courtship behaviours, an individual-level asymmetry was observed. The other four courtship behaviours showed absence of asymmetry.

Taken together, data on limb preferences in *Phoenicopteriformes* is mixed, indicating that limb preferences in this order is dependent on species and behaviour. For the *Podicipediformes* order, we could not identify any study investigating lateralization in limb usage.

Columbaves *(e.g., pigeons and cuckoos)*

The *Columbaves* clade comprises the orders *Columbiformes* (e.g., pigeons), *Cuculiformes* (e.g., cuckoos), *Mesitornithiformes* (e.g., mesites), *Otidiformes* (e.g., bustards) and *Musophagiformes* (turacos). The latter three orders are rather recent additions to the avian phylogenetic tree discovered by genetic analyses. They consist of species, which were originally thought to be part of other orders, or to a suborder clade, which was raised to order level. While this affects the layout of the phylogenetic tree in comparison to our previous publication, the data pattern remains unaffected since the only published data on limb preferences in this clade stems from the order *Columbiformes,* and we could not find additional publications exceeding our previous report.

Opisthocomiformes (hoatzins)

There is still no study investigating limb preferences in the *Opisthocomiformes* order (hoatzins).

Gruimorphae *(e.g., cranes and gulls)*

The *Gruimorphae* clade includes the orders *Gruiformes* (e.g., cranes) and *Charadriiformes* (e.g., gulls). While no additional research on limb preferences has been published for the *Charadriiformes* order, one study investigated asymmetry in limb usage of a *Gruiformes* species. The pukeko (*Porphyrio p. melanotus*), also known as Australasian swamphen, showed no population-level asymmetry in limb usage during body/head scratching, food holding, or during pinning food items to the ground ($n = 359$). However, there was a strong individual-level limb preference for all observed behaviours (Rodgers & Cain, 2019). Thus, in contrast to our original publication, we can now report that at least individual-level asymmetry is present in the *Gruiformes* order.

Strisores *(nightbirds)*

No research on limb preferences has been so far conducted in the *Strisores* clade, comprising the orders *Caprimulgiformes* (e.g., nighthawks), *Nyctibiiformes* (potoos), *Steatornithiformes* (oilbirds), *Podargiformes* (frogmouths), *Aegotheliformes* (owlet-nightjars) and *Apodiformes* (e.g., tree swifts).

Phaethoquornithes *(e.g., penguins, storks and pelicans)*

Studies on limb preferences in the *Phaethoquornithes* clade, containing the orders *Phaethontiformes* (e.g., tropic birds), *Eurypygiformes* (e.g., kagus), *Gaviiformes* (e.g., loons), *Procellariiformes* (e.g., petrels), *Sphenisciformes* (e.g., penguins), *Ciconiiformes* (e.g., storks), *Suliforme*s (e.g., gannets) and *Pelecaniformes* (e.g., pelicans), are still rare. In addition to the non-lateralized, one-leg roosting in Eurasian spoonbills (*Platalea leucorodia*, order *Ciconiiformes*), already reported in our previous publication, we were only able to identify one study investigating limb preferences in the *Sphenisciformes* order. Stor et al. (Stor et al., 2019) analyzed different forms of limb usage in wild Magellanic penguins (*Spheniscus magellanicus*). For the first foot to step on an obstacle, 300 individuals showed a lack of asymmetry. For extending one leg for thermoregulation, the 121 observed individuals showed a right-sided population-level asymmetry. However, when the observation was repeated in the following year with 232 individuals, asymmetry was absent. The analysis of flipper usage, based on feather wear in 1217 individuals, revealed asymmetry at the individual level but not at the population level. The latter is noteworthy since it describes a forelimb lateralization, normally not present in avian species. Additionally, because the data were collected through observational means in the wild, each individual was scored only once, limiting the ability to draw meaningful conclusions about individual-level asymmetries for the first two behaviours.

Afroaves (e.g., owls, woodpeckers & buzzards)

The *Afroaves* clade is another recent addition to the avian phylogenetic tree, grouping the orders *Strigiformes* (e.g., owls), *Coliiformes* (e.g., mousebirds), *Trogoniformes* (e.g., trogons), *Coraciiformes* (e.g., hornbills) and *Piciformes* (e.g., woodpeckers) together. Further, it contains the newly defined orders *Cathartiformes* (New World vultures), *Bucerotiforme*s (e.g., hoopoes), *Leptosomiformes* (e.g., cuckoo-rollers), and *Accipitriformes* (e.g., hawks). In our original publication, we classified the Eurasian buzzard (*Buteo buteo*), which exhibits a right-sided population-level asymmetry in food grasping, under the order *Falconiformes*. However, as buzzards and hawks are now classified under the order *Accipitriformes*, we have updated the Eurasian buzzard data point accordingly. Further, we could identify two additional studies investigating limb preferences in *Accipitriformes* species. Allen et al. (Allen et al., 2018) gathered online images of ospreys (*Pandion haliaetus*) to analyze which foot was placed forward while standing, and whether there was a preference for holding food items during flight or nesting. They found a left-sided population-level asymmetry in the foot placed forward while standing, but no detectable asymmetry in the foot used to hold items, either in flight or while perching.

Also, in steppe buzzards (*Buteo vulpinus*), another species of the *Accipitriformes* order, limb preferences have been investigated. Yosef et al. examined which foot 367 steppe buzzards used to interact with a baited trap (Yosef et al., 2019). They found that 53.4% of the animals preferentially hit the trap with their right foot, indicating a weak right-sided population-level asymmetry. Apart from the data on *Strigiformes* reported in our previous publication, which demonstrated lateralized limb usage in several owl species, we found no additional studies investigating limb preferences in *Afroaves*. Thus, although research on limb preferences in *Afroaves* remains limited, there is at least some evidence of lateralization in limb usage, particularly in the *Accipitriformes* and *Strigiformes* orders.

Australaves *(e.g., parrots, falcons and songbirds)*

The sister clade to *Afroaves* is *Australaves*, which includes the orders *Falconiformes* (e.g., falcons), *Psittaciformes* (e.g., parrots), and *Passeriformes* (e.g., starlings), the latter being the largest avian order in terms of species diversity. In all three orders, new studies on the occurrence of limb preferences have been published during the last decade. Baciadonna et al. investigated which leg captive gyrfalcons (*Falco rusticolus*) preferentially stand on while sleeping, and which foot they use when grasping food. In a study of 50 individuals, they found a population-level left-leg lateralization during sleep, but only a trend toward a preference for grasping food with the left foot. This aligns with findings reported in our 2013 publication, which indicated population-level asymmetry in limb usage within *Falconiformes*.

Also, species from the *Psittaciformes* clade received further attention. Cussen and Mench observed 13 captive orange-winged amazon parrots (*Amazona amazonica*) while holding food items with one claw. They found an individual-level asymmetry but no asymmetry on the population level. While not presenting new data on limb preferences in Psittaciformes, a recent meta-analysis by Rogers & Kaplan is noteworthy (Kaplan & Rogers, 2021). Using data from their previous studies, the authors examined the correlation between foot preference strength, body weight, and brain size. They found that larger species exhibited stronger foot preferences and that species with larger brains also showed more pronounced lateralization in foot use.

In the *Passeriformes* order, research on limb preferences has been extended to one additional species. Yu et al. studied food holding and clamping behaviours in 36 yellow-bellied tits (*Pardaliparus venustulus*). Although no significant population-level asymmetry was found for these behaviours, a clear individual-level asymmetry was observed (Yu et al., 2020).

In summary, there is evidence of limb preferences across all *Australaves* orders, with research in *Psittaciformes* being the most extensive. This research has shown that both individual- and population-level asymmetries in limb usage are highly prevalent in parrot species. Whether this prevalence extends to the other two *Australaves* orders, where data are limited to only a few species, remains an open question for future studies.

Mammalia

Similar to the findings in birds, many new studies on limb preferences have been published since our first review. Figure 2 shows the updated cladogram for mammals that includes both the results of studies presented in the previous paper, as well as those newly identified for the present study. Note that orders may have changed compared to the corresponding figure in 2013. For example, *Cetacea* is now considered an infraorder of the order *Artiodactyla* and therefore not a category anymore.

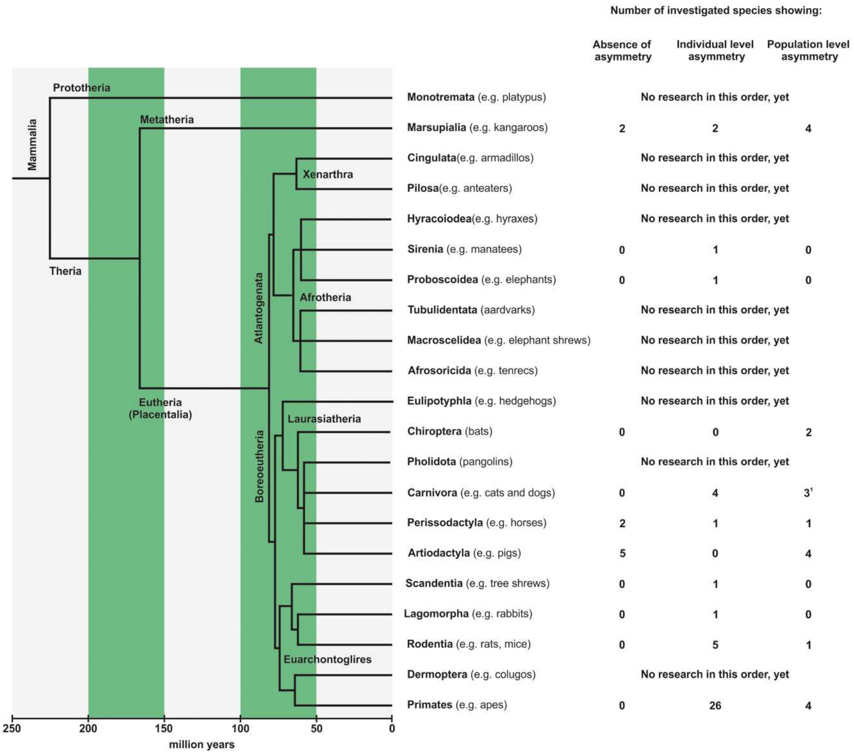
Monotremata *(e.g., platypuses)*

We did not identify any study fulfilling the inclusion criteria in this order. One published study investigated limb preferences in n = 4 long-beaked echidnas and found evidence for individual-level asymmetry (Giljov, Karenina, Hawkins, et al., 2015), but did not fulfil the inclusion criteria due to the small sample size.

Marsupiala *(e.g., kangaroos)*

Several papers on limb preferences in marsupials (e.g., kangaroos, wombats, or possums) and a book have been published (Giljov, Karenina, and Malashichev, 2017) in the past 11 years.

Interestingly, a study from 2015 included data on handedness from four *Macropodidae* species, including Goodfellow's tree-kangaroos (*Dendrolagus goodfellowi*), red-necked wallabies (*Macropus rufogriseus*), eastern grey kangaroos (*Macropus giganteus*), and red kangaroos (*Macropus rufus*) (Giljov, Karenina, Ingram, et al., 2015). In addition, the authors included data from other



Number of investigated species showing:

	Absence of asymmetry	Individual level asymmetry	Population level asymmetry
Monotremata (e.g. platypus)	No research in this order, yet		
Marsupialia (e.g. kangaroos)	2	2	4
Cingulata(e.g. armadillos)	No research in this order, yet		
Pilosa(e.g. anteaters)	No research in this order, yet		
Hyracoiodea(e.g. hyraxes)	No research in this order, yet		
Sirenia (e.g. manatees)	0	1	0
Proboscoidea (e.g. elephants)	0	1	0
Tubulidentata (aardvarks)	No research in this order, yet		
Macroscelidea (e.g. elephant shrews)	No research in this order, yet		
Afrosoricida (e.g. tenrecs)	No research in this order, yet		
Eulipotyphla (e.g. hedgehogs)	No research in this order, yet		
Chiroptera (bats)	0	0	2
Pholidota (pangolins)	No research in this order, yet		
Carnivora (e.g. cats and dogs)	0	4	3[1]
Perissodactyla (e.g. horses)	2	1	1
Artiodactyla (e.g. pigs)	5	0	4
Scandentia (e.g. tree shrews)	0	1	0
Lagomorpha (e.g. rabbits)	0	1	0
Rodentia (e.g. rats, mice)	0	5	1
Dermoptera (e.g. colugos)	No research in this order, yet		
Primates (e.g. apes)	0	26	4

Figure 2. Cladogram of the mammalian phylum, showing the number of species within each order that exhibit no asymmetry, individual-level asymmetry, or population-level asymmetry in limb preference. The phylogenetic tree is based on molecular clock data from (Álvarez-Carretero et al., 2022). Note that some divergence points with a phylogenetic distance of less than 5 million years (e.g., *Hyracoidea – Sirenia/Proboscidea*) have been merged for clarity. [1] Task dependent in black bears and Asian small clawed otters (*Carnivora*), domestic horses (*Perissodactyla*) and bottlenose dolphins (*Artiodactyla*) [2] Results taken from meta-analysis of (Soto et al., 2022). [To view this figure in color, please see the online version of this journal.]

marsupials that were published in previous studies, including the grey short-tailed opossum (*Monodelphis domestica*) (Giljov et al., 2013), the sugar glider (*Petaurus breviceps*) (Giljov et al., 2013) and the brush-tailed bettong (*Bettongia penicillata)* (Giljov et al., 2012). These data were analyzed using a cladographic analysis similar to that performed in our previous review article on limb preferences in non-human animals. The authors found that the sugar glider and the grey short-tailed opossum showed an absence of asymmetry. Goodfellow's tree-kangaroos showed individual-level asymmetry, and the remaining four species showed population-level asymmetry. After the publication of this article in 2015, further articles investigated limb preference in marsupials. In 2016, a small study in n = 10 red-necked wallabies reported that there was no population-level asymmetry for food reaching, and only two animals showed a significant individual-level asymmetry (Spiezio et al., 2016). A further study on limb preferences in n = 11 wild red-necked wallabies and n = 20 eastern grey kangaroos found a population-level leftward bias for both species for manipulating food objects in young animals (Giljov, Karenina, Ingram, et al., 2017).

Cingulata *(e.g., armadillos) and* Pilosa *(e.g., anteaters)*

We did not identify any published study fulfilling the inclusion criteria in these two xenarthran orders.

Hyracoiodea *(e.g., hyraxes)*

We did not identify any published study fulfilling the inclusion criteria in this order.

Sirenia *(e.g., manatees)*

An observational study investigated side preferences during flipper use in n = 123 wild and n = 16 captive Florida manatees (*Trichechus manatus latirostris*) (Tyler-Julian et al., 2016). Statistical analyses showed significant individual-level asymmetry, but no population-level asymmetry.

Proboscidea (e.g., elephants)

Side preferences in the forefoot movement of wild Asian elephants (*Elephas maximus*) were assessed by observing forefoot scuffing movements to uproot vegetation in a sample of n = 206 animals (Keerthipriya et al., 2015). Overall, 164 animals showed foot movements, and of those, 58% showed a significant preference for one foot. Statistical analysis revealed individual-level, but not population-level, asymmetries.

Tubulidentata *(e.g., aardvarks),* Macroscelidea *(e.g., elephant shrews) &* Afrosoricida *(e.g., tenrecs)*

We did not identify any published study fulfilling the inclusion criteria in these three *Afrotheria* orders.

Eulipotyphla *(e.g., hedgehogs)*

We did not identify any published study fulfilling the inclusion criteria in this order.

Chiroptera *(e.g., bats)*

In bats, a recent study assessed limb preferences in Great Himalayan leaf-nosed bats (*Hipposideros Armiger*) from three different populations (Zhang et al., 2023). The authors analyzed limb preferences in boxing displays during antagonistic interactions between bats. A statistically significant population-level asymmetry was observed with bats preferring the left forearm to attack opponents in an overall sample of 167 individual bats.

Pholidota *(e.g., pangolins)*

We did not identify any published study fulfilling the inclusion criteria in this order.

Carnivora *(e.g., cats and dogs)*

A substantial number of studies on forelimb preferences in carnivores have been published since the publication of our previous study on limb preferences. The most widely investigated species are cats (Isparta et al., 2020; McDowell et al., 2018; Wells & McDowell, 2019) and dogs (Barnard et al., 2017; Barnard et al., 2018; Gough & McGuire, 2015; Laverack et al., 2021; Marshall-Pescini et al., 2013; Schneider et al., 2013; Simon et al., 2022; Siniscalchi, Bertino, et al., 2014; Wells et al., 2016; Wells et al., 2017, 2018; Wells et al., 2019). In 2019, a meta-analysis on limb preferences in cats and dogs was published (Ocklenburg et al., 2019). The results indicated that overall, both species showed individual-level asymmetries, with 78% of cats and 68% of dogs showing a preference for one side. However, there was no evidence for population-level asymmetry. Interestingly, a sex difference was found in cats, with female cats having greater odds of being right-pawed than male cats.

In addition to cats and dogs, limb preferences have been investigated in several other carnivores. In wolves, a small study of n = 7 wolves (*Canis lupus*) reported individual-level asymmetry, but no significant population-level asymmetry during manipulation of food-related environmental enrichment devices (Regaiolli, Mancini, et al., 2021). A subsequent larger study in n = 93 wild wolves assessed the foot that was trapped in a foothold trap baited with food when the wolves were captured to recollar them (Barber-Meyer, 2022). Overall, there were 45 left-foot captures and 48 right-foot captures. Statistical analysis showed that there was no population-level asymmetry. However, since every wolf was only captured once (and data from any recaptures were excluded), the data from this study do not allow for an assessment of individual-level asymmetry. Taken together, the data from the two wolf studies clearly show that, comparable to dogs, there is no population-level asymmetry for paw preferences in wolves. The results from the smaller study suggest that wolves show individual-level asymmetries, but more research on wolves is needed to make any final conclusions due to the low sample size of this study.

Moreover, limb preferences in *Carnivora* were assessed in two small studies in Asian small-clawed otters (*Amblonyx cinerea*). One of these studies (n = 6) reported that Asian small-clawed otters show individual-level asymmetries during tool use (James, 2017). The second study in Asian small-clawed otters had a slightly larger sample size (n = 10) and assessed paw preferences in four different types of behaviour (food reaching, non-food reaching, reaching into a hole, carrying an object) (Manns et al., 2018). Otters showed individual-level asymmetry but not population-level asymmetry for food reaching and a population-level rightward bias for reaching into a hole.

In the Chinese red panda (*Ailurus styani*), limb preferences during food handling were assessed in a small sample of n = 5 (Lin et al., 2022). For handling fruit pieces, significant individual-level asymmetries were observed, but no significant asymmetries were observed for handling and eating bamboo. Since both of these tasks incorporate handling food, it is not possible to determine the type of asymmetry in Chinese red pandas. More research in larger samples is needed.

Moreover, one study was published in California sea lions (*Zalophus californianus*), but was excluded because of the small sample size of four animals (Le Ray et al., 2017).

Perissodactyla *(e.g., horses)*

The studies on limb preferences in *Perissodactyla* discussed in our 2013 paper focused on the horse (*Equus caballus*) and the donkey (*Equus asinus*). Both species were also investigated in further studies in the last 11 years.

In the donkey (*Equus asinus*), a study on limb preferences in n = 47 animals showed individual-level asymmetry, with 15 donkeys showing a significant leftward asymmetry, 18 a significant rightward asymmetry and 12 no preference (Díaz, Murray, and Rodway, 2021). Statistical analysis showed that there was no evidence for a population-level asymmetry.

In the horse (*Equus caballus*), a study in n = 14 Quarter horses assessed laterality in different motor tasks (Siniscalchi, Padalino, et al., 2014). A significant population-level asymmetry was found for forelimb use during truck loading and stepping off a step. No significant asymmetries were found for moving forward, stepping on a step and forelimb use during truck unloading. This shows that population-level asymmetries in forelimb use in horses are task-dependent, which is in line with earlier studies discussed in our previous review article on limb preference in non-human animals (Ströckens et al., 2013). Furthermore, a study in two groups of feral horses (Austin & Rogers,

2012) with sample sizes of n = 20 and n = 54 assessed the preference for placing one forelimb in front of the other. No significant population-level asymmetry was observed. Twelve out of 26 immature horses showed significant individual-level preferences, but only four out of 45 adult horses. As none of these studies were larger than those discussed in our previous study, we still rated horses as showing population-level asymmetries. Asymmetries in horses also seem to be task-dependent to some extent.

In the feral Przewalski horse (*Equus przewalskii*), forelimb placing preferences during grazing were assessed in n = 33 animals (Austin & Rogers, 2014). Statistical analysis revealed that there was no significant population-level asymmetry. Overall, 5 out of 31 horses showed significant individual-level asymmetries, so that the majority of animals showed no preference for this behaviour.

Artiodactyla *(e.g., pigs and whales)*

Please note that in contrast to our 2013 paper, cetaceans are not considered a separate order anymore by now, but are now considered to be an infraorder within the *Artiodactyla* order. Thus, we did not include a separate *Cetacea* section in this article anymore. Instead, *Cetacea* are listed in this section. Several new studies on limb preferences in terrestrial artiodactyls have been published in the last 11 years.

In the domestic pig (*Sus scrofa*), preferential foot use for entering or leaving an arena was assessed in n = 60 male animals (Goursot et al., 2018). For both behaviours, significantly more animals were ambilateral than lateralized and the laterality index had a peak at zero. This suggests absence of asymmetry for this motor behaviour in pigs.

In goats (*Capra hircus*), limb preferences for stepping off a wooden platform were assessed in n = 30 animals (Baruzzi et al., 2018). 11 out of 30 goats showed an individual-level preference for stepping off the platform. 20% of animals were right-lateralized, 16.6% left-lateralized, and the remaining animals did not show a clear preference. There was no statistical evidence for population-level or individual-level asymmetry.

In wild elk (*Cervus canadensis*), front-limb biases when accessing snow-covered grasses by digging through the snow were assessed in two populations in Banff and Jasper National Parks in Canada (Found & St Clair, 2017). The authors reported a significant herd-wide leftward bias in Banff in 2011 based on 6130 observations, but no significant bias in 2012 (based on 1292 observations). In Jasper, a significant rightward bias was observed based on 1469 observations. Since the 2011 observations in Banff had the highest statistical power, we rated elk as showing a leftward population bias.

In reindeer (*Rangifer tarandus tarandus*), forelimb preferences were assessed by observing n = 20 animals while digging through snow to reach food (Andersson, 2020). The results showed that there was no sign of population-level asymmetry. On the individual level, only 2 out of 20 animals showed significant individual-level asymmetries, while 18 showed absence of asymmetry. These findings are in contrast to two previous studies on reindeer discussed in our 2013 article. Both reported population-level asymmetries in reindeer. One article found a significant rightward bias in 27 reindeers (Thing, 1977), while another found a significant leftward bias in 29 reindeer (Espmark & Kinderås, 2002). Due to these conflicting results, we rated reindeer as having a leftward population-level asymmetry, as this is what the largest study reported.

Moreover, one study reported that in a sample of n = 4 male giraffes (*Giraffa camelopardalis reticulate*) all four animals showed a leftward preference (Svoke, 2017). However, this study was not included in the cladogram as the inclusion criterion of a minimum sample size of n = 5 was not fulfilled.

Comparable to the terrestrial artiodactyls, several new studies on limb preferences in aquatic artiodactyls have been published in the last 11 years. For example, one study investigated lateralized behaviour in Guiana dolphins (*Sotalia guianensis*) in Brazil (Casagrande et al., 2013). Flippering (e.g., the dolphin raises on flipper out of the water and then slaps the water surface) was rare (only 23 events) and there was no evidence for asymmetry.

In contrast, orcas (*Orcinus orca*) showed a significant rightward population-level asymmetry for flippering in a sample of n = 16 animals (Giljov et al., 2016). Overall, 15 animals used that right flipper, and only one animal the left flipper.

Moreover, limb preferences have been investigated in the bottlenose dolphins (*Tursiops truncatus*). An honours thesis (Poelma, 2013) and later publication (Winship et al., 2017) reported data on the preferred fin for pectoral fin contacts from a sample of 27 dolphins. The authors did not provide formal statistical analysis on whether the dolphins showed population-level asymmetries, but the mean handedness index was −0.02, so very close to zero. This suggests that bottlenose dolphins do not show population-level asymmetries. However, when age groups were analyzed separately, calves showed a significant right-fin handedness, while sub-adults and adults did not. The distribution of individual handedness index data suggests that individual-level asymmetries exist, with some animals having values higher than 0.50 or lower than −0.60 (on a scale of −1 to 1). A further study in dolphins assessed different lateralized behaviours in n = 26 animals, of which 25 were bottlenose dolphins (*Tursiops truncatus*) and one was an Atlantic spotted dolphin (*Stenella frontalis*). For flippering, a population laterality index of −0.10 was observed that did not reach statistical significance, indicating that no population-level asymmetries were observed for flippering for the animals in this study (Jaakkola et al., 2021). There was, however, a population-level rightward bias for contact and rubbing with inanimate objects (LI = 0.19).

Scandentia *(e.g., tree shrews)*

Two studies haven investigated limb preferences in the northern tree shrew (*Tupaia belangeri*). In the first one, n = 36 northern tree shrews were tested with a simple food grasping task (Joly et al., 2012). Independent of the posture of the animal, individual-level asymmetry but no population-level asymmetry was observed. Similar results were also obtained in a study with a food reaching task in n = 30 northern tree shrews (Maille et al., 2013). Independent of whether the food reaching tube was visible to the animals or not, they showed individual-level asymmetry but no population-level asymmetry.

Lagomorpha *(e.g., rabbits)*

We did not identify any published study fulfilling the inclusion criteria in this order beyond the 2008 study in the pica (Hackert et al., 2008) discussed in our 2013 article.

Rodentia *(e.g., rats and mice)*

The research on limb preferences in rodents has largely focused on rats and mice. Most studies published in the past 11 years also focused on rats (Cabrera & Ortega, 2018; Cunha et al., 2017; Volnova & Kurzina, 2013) or mice (Stieger et al., 2021). Given the substantial number of studies on limb preferences in rats and mice, a meta-analysis on these studies was performed in 2021 (Manns et al., 2021). The results demonstrated that both species show individual-level asymmetry but not population-level asymmetry for paw use. In mice, 81% of animals showed an individual-level preference for the left or right paw; in rats, it was 84%. Both analyses reached significance. However, all analyses for either leftward or rightward population-level asymmetries in both species failed to reach significance. In addition to rats and mice, rodent limb preferences have been investigated in the Talas tuco-tuco (*Ctenomys talarum*), a subterranean rodent endemic to Argentina (Schleich, 2016). The author assessed different aspects of feeding behaviour in a sample of n = 14 tuco-tucos. For the paw used by the tuco-tucos to catch food, an absence of asymmetry was observed, as well as for the paw used to rotate plant stems while removing superficial layers. However, for the paw used to take food to the mouth to eat (the behaviour that resembles the food-reaching tasks used in many other studies the most), 10 out of 14 animals showed a clear leftward preference, while the other 4 did not have a preference to either side. Statistical analysis revealed a significant leftward population-level asymmetry.

Moreover, paw preferences in rodents were assessed in the striped field mouse (*Apodemus agrarius*), the bank vole (*Clethrionomys glareolus*), and the northern red-backed vole (*Clethrionomys rutilus*) (Agulova et al., 2010; Agulova et al., 2012). The findings showed that these three species showed individual-level asymmetries in using one of their limbs to stand up with support against a wall. Since population-level varied according to gender, time point, and biotope, these species do not seem to show clear overarching population-level asymmetries in one direction.

Dermoptera *(e.g., colugos)*

We did not identify any published study fulfilling the inclusion criteria in this order.

Primates *(e.g., apes)*

Comparable to what was reported in our previous review on limb preferences in non-human animals, the largest number of studies on limb preferences in the last 11 years was published within the *Primates* order (Bailoo et al., 2019; Bardo et al., 2015; Batist & Mayhew, 2020; Becker et al., 2022; Boulinguez-Ambroise et al., 2022; Braccini, 2014; Crespo Mingueza, 2016; Cubí & Llorente, 2021; Díaz, Murray, Roberts, et al., 2021; Fan et al., 2017; Fu et al., 2019; Hopkins et al., 2009; Hopkins et al., 2019; Hopkins et al., 2021; Hopkins, Reamer, et al., 2015; Hopkins, Schaeffer, et al., 2015; Mangalam et al., 2014; Meguerditchian et al., 2015; Molesti et al., 2016; Morino et al., 2017; Motes Rodrigo et al., 2018; Moura, 2015; Nelson et al., 2015; Nelson & Boeving, 2015; Olsen & Sommer, 2014; Padrell et al., 2019; Poindexter et al., 2018; Pouydebat et al., 2014; Prieur et al., 2016, 2017, 2018; Prieur, Barbu, et al., 2017; Prieur, Pika, Blois-Heulin, et al., 2018; Regaiolli, Spiezio, and Hopkins, 2016; Regaiolli, Spiezio, and Vallortigara, 2016; Rogers, 2018; Salmi et al., 2016; Schnoell et al., 2014; Spoelstra, 2021; Stacherl, 2019; Tabiowo & Forrester, 2013; Tomassetti et al., 2019; Vaughan et al., 2019; Wang et al., 2022; Zhao et al., 2015; Zhao, Tian, et al., 2016; Zhao, Wang, et al., 2016). Since a recent systematic review and meta-analysis on hand preferences in coordinated bimanual tasks in non-human primates exists (Soto et al., 2022), we refrained from reviewing all these studies in detail, as the overlap with the Soto et al. (2022) would be extremely high. In the meta-analysis (Soto et al., 2022) data from n = 2891 subjects from 38 primate species obtained from 76 published articles were included. In the first set of meta-analyses, the presence of individual-level asymmetries in the tube task (food reaching) and other tasks was assessed (30 species included). The model reached significance, with 82% of individuals showing individual-level asymmetry across species and 12% showing the absence of asymmetry. However, there was significant heterogeneity, indicating differences between studies. For other bimanual tasks than the tube task, the model also reached significance. Here, 90% of animals showed individual-level asymmetry and 10% absence of asymmetry. A measure of between-study heterogeneity in meta-analysis was also significant, indicating differences between studies. Moderator analysis showed that species was an almost significant moderator for the tube task ($p = 0.053$), but not for the other bimanual task ($p = 0.738$). Thus, primates seem to show significant individual-level asymmetries irrespective of species. The authors of the meta-analysis then also performed a second set of meta-analyses to test for the existence of a population-level rightward asymmetry in primate handedness. For the tube task (30 species included), the model reached significance but indicated that there were significantly more non-right-lateralized individuals than right-handed animals. For other tasks than the tube task, the model failed to reach significance. This suggests an absence of population-level asymmetry for primates on average. However, heterogeneity between studies was high and heterogeneity tests reached significance for both models. Moderator analysis revealed that the model reached significance for four species for the tube task, indicating population-level rightward asymmetries in these species. They included the bonobo (*Pan paniscus*), the orangutan (*Pongo pygmaeus*), the golden snub-nosed monkey (*Rinopithecus roxellana*), and the Tonkean macaque (*Macaca tonkeana*). Thus, based on the results of this meta-analysis for the tube task, 26 primate species showed individual-level asymmetry and four showed population-level asymmetries.

Discussion

General distribution of asymmetry levels

The aim of the present study was to provide an update of the results of the 2013 publication on limb preferences in non-human animals (Ströckens et al., 2013). Similar to the previous study, we aimed to determine for as many species as possible whether they showed individual-level asymmetry, population-level asymmetries, or no asymmetries for limb preferences. Table 1 shows an overview of the data from our previous study compared with the present findings.

In the present update, the percentage of species showing absence of asymmetry stayed largely the same, with a small decrease of about 4 percentage points. A larger change was observed for individual-level asymmetries. Here, the percentage almost doubled, from 16.81% in 2013 to 32.56% in 2024. Interestingly, this effect seemed to be mostly driven by the larger number of meta-analyses and large-scale studies in the updated analysis. For example, individual-level asymmetries were observed in meta-analyses in cats, dogs, rats, and mice (Manns et al., 2021; Ocklenburg et al., 2019). In contrast to individual-level asymmetry, the percentage of population-level asymmetries decreased from 51.26% to 39.53%. This finding suggests an

Table 1. Numbers and percentages for absence of asymmetry, individual-level asymmetry and population-level asymmetry from our previous publications on limb preferences in non-human animals (Ströckens et al., 2013) and the present analysis.

	2013 analysis	2024 analysis
Absence of asymmetry	38 (31.93%)	48 (27.91%)
Individual-level asymmetry	20 (16.81%)	56 (32.56%)
Population-level asymmetry	61 (51.26%)	68 (39.53%)
Overall number	119	172

important role of statistical robustness in research on limb preferences and implies that some of the findings showing significant population-level asymmetries in studies with small sample sizes may have been spurious findings that may be difficult to replicate.

Clade patterns

In our previous publication, we reported data on limb preferences for 68 avian species with 32 (47.06%) exhibiting an absence of asymmetry, 6 (8.82%) individual-level asymmetry and 30 (44.12%) a population-level asymmetry.[1] Since then, studies investigated the occurrence of limb preferences in 11 further species, extending data for the orders *Accipitriformes, Falconiformes, Galliformes, Gruiformes, Passeriformes, Phoenicopteriformes and Psittaciformes.* Although these data points provide valuable insights, they only slightly alter the overall distribution pattern of lateralized limb usage. Specifically, we now can report that 33 species (41.77%) demonstrate no asymmetry, 10 species (12.66%) exhibit individual-level asymmetry, and 36 species (45.57%) show population-level asymmetry. From a phylogenetic perspective, the newly added data from the *Phoenicopteriformes* order (flamingos) provides valuable insights. *Phoenicopteriformes*, along with the *Podicipediformes* order (grebes), form the *Mirandornithes* clade, which is sister to all other extant Neoaves (see Figure 3). The observed population-level asymmetries in limb usage for at least some tasks within *Mirandornithes* support the hypothesis that limb preferences evolved before the emergence of the *Neoaves* clade and have been conserved across its branches. Further research on *Podicipediformes* species, as the sister clade to *Phoenicopteriformes*, would provide additional support for this hypothesis.

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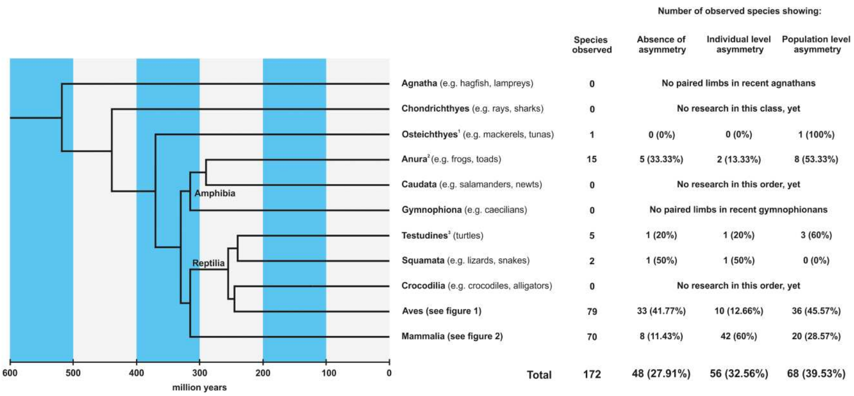
[1] In our 2013 publication, we presented data on limb preferences for 71 avian species. Our findings indicated that 35 species (49.30%) showed no asymmetry, 6 species (8.45%) exhibited individual-level asymmetry, and 30 species (42.25%) displayed population-level asymmetry. However, we mistakenly included 3 parrot species (budgerigar, brown-throated parakeet, north island kaka) in both the absence of asymmetry category and the individual-level asymmetry category. These species should only be counted in the individual-level asymmetry category. As a result, the corrected numbers provided above differ from those in our original publication.

Limb preferences in avian species, similar to other vertebrate classes, appear to be task-dependent and are not as stable as hand preferences in humans. A notable example is the study by Stor et al. (Stor et al., 2019), which found that Magellanic penguins exhibit no asymmetry in the leading foot during stepping, individual-level asymmetry in the flipper used for swimming and searching, and population-level asymmetry in the foot lifted for thermoregulation. Based on our inclusion criteria (see methods section), we classified Magellanic penguins under individual-level asymmetry. However, it is important to note that this does not suggest that all instances of limb usage follow the same pattern. Asymmetries can vary depending on the specific task and the limb involved (hindlimb for stepping/thermoregulation and forelimb for swimming/searching behaviour). Further, the population-level asymmetry found for foot lifting for thermoregulation was not consistent between years, indicating a stronger effect of local environmental factors compared to humans.

In our previous publication, we reported data on limb preferences for 40 mammalian species, with 2 (5%) exhibiting an absence of asymmetry, 13 (32.50%) individual-level asymmetry and 25 (62.50%) population-level asymmetry (Ströckens et al., 2013). After the update, data from 70 mammalian species were included, with 8 (11.43%) exhibiting an absence of asymmetry, 42 (60%) individual-level asymmetry and 20 (28.57%) population-level asymmetry. Despite the large increase in species included in the analysis, only two orders that were not included in the 2013 analysis were included (*Sirenia* and *Lagomorpha*, both showing evidence for individual-level asymmetry) (see Figure 3). Thus, most of the newly included publications covered research in orders that were already included in the 2013 analysis, and there are still many mammalian orders in which no research on limb preferences has been carried out. Nonetheless, the recent data from the *Sirenia* order, along with findings from cetaceans (a group within the *Artiodactyla* order), are highly significant. Both species groups consist exclusively of aquatic mammals, which diverged from their terrestrial ancestors around 50 million years ago (Coombs et al., 2022; Heritage & Seiffert, 2022). Over this time, they underwent profound anatomical adaptations to thrive in their aquatic environments, including the transformation of their forelimbs into flippers. Despite these substantial anatomical changes, the data suggest that both *Sirenia* and *Cetacea* have preserved lateralization in forelimb usage, even though their environments differ drastically from those of their terrestrial relatives.

The most notable finding in mammals was the clear decrease of population-level asymmetries from around 60% to around 30% and the increase of individual-level asymmetries from around 30% to 60%. This major shift in result patterns was mainly driven by the inclusion of meta-analytic data in primates, rodents and carnivores, which showed individual-level



	Species observed	Number of observed species showing: Absence of asymmetry	Individual level asymmetry	Population level asymmetry
Agnatha (e.g. hagfish, lampreys)	0	No paired limbs in recent agnathans		
Chondrichthyes (e.g. rays, sharks)	0	No research in this class, yet		
Osteichthyes[1] (e.g. mackerels, tunas)	1	0 (0%)	0 (0%)	1 (100%)
Anura[2] (e.g. frogs, toads)	15	5 (33.33%)	2 (13.33%)	8 (53.33%)
Caudata (e.g. salamanders, newts)	0	No research in this order, yet		
Gymnophiona (e.g. caecilians)	0	No paired limbs in recent gymnophionans		
Testudines[3] (turtles)	5	1 (20%)	1 (20%)	3 (60%)
Squamata (e.g. lizards, snakes)	2	1 (50%)	1 (50%)	0 (0%)
Crocodilia (e.g. crocodiles, alligators)	0	No research in this order, yet		
Aves (see figure 1)	79	33 (41.77%)	10 (12.66%)	36 (45.57%)
Mammalia (see figure 2)	70	8 (11.43%)	42 (60%)	20 (28.57%)
Total	172	48 (27.91%)	56 (32.56%)	68 (39.53%)

Figure 3. Cladistic overview of the vertebrate clade, displaying the total number of species per class in which limb preferences have been studied. The numbers and percentages of species showing no asymmetry, individual-level asymmetry, or population-level asymmetry in limb preferences are provided. The phylogenetic tree is based on data from (San Mauro, 2010) and (Ezcurra et al., 2014). [1]For the sake of clarity, we summarize recent, non-tetrapod bony fishes under the term *Osteichthyes*, including the classes *Actinopterygii*, *Actinistia* and *Dipnoi*. [2]Data on individual-level asymmetry by (Rojas-Montoya & Vargas-Salinas, 2023) are not included, since test design is unable to differentiate between absence of asymmetry and individual-level asymmetry. [3]Note that the positioning and divergence point of *Testudines* within the reptilian phylogenetic tree is still under debate, see e.g., (Gardner & van Vranken, 2020). [To view this figure in color, please see the online version of this journal.]

asymmetries in species that were classified as population-level asymmetry in the 2013 study. Comparable to findings in birds, limb preferences in non-human mammals were more task-dependent than human handedness. This was shown particularly by the task-dependency effects in the included primate meta-analysis (see discussion above).

Comparison with human handedness

There are two major ways to assess handedness in humans: Hand preference, which is typically assessed using preference questionnaires, and hand skill, which is typically assessed using motor skill tests (Ocklenburg, 2024).

Humans show a strong, population-level rightward hand preference, with only 10.6% of individuals being left-handed (Papadatou-Pastou et al., 2020). Some studies also include a third handedness category (mixed-handedness) in addition to left- and right-handedness (Mundorf et al., 2024). The interest in human handedness extends well beyond the motor domain, as handedness is associated with other lateralized brain functions such as language (Johnstone et al., 2021; Karlsson et al., 2023; Qin et al., 2024; Woodhead et al., 2021). Moreover, there is interest in human handedness from a clinical neuroscience perspective, as several neurodevelopmental disorders have been linked to a higher prevalence of left-handedness and mixed-handedness (Ocklenburg et al., 2024).

Comparing the asymmetry patterns observed in the present study with those in humans can yield important insights into the phylogenesis of human handedness (Frasnelli et al., 2012; Frasnelli & Vallortigara, 2018; Ocklenburg & Guo, 2024; Vallortigara & Rogers, 2020). Comparable to the findings of our 2013 study, we found that population-level asymmetries were common in non-human animals, clearly refuting the idea that they only emerge in humans. Interestingly, population-level asymmetries were not limited to mammals and, in fact, birds showed a higher percentage of population-level asymmetries than mammals. Moreover, turtles, toads and frogs, and bony fish also showed evidence for population-level asymmetries in some species, suggesting that they may have independently evolved several times.

Interestingly, a recent study on the evolution of hand preferences in anthropoid primates combined published data from the literature with original data to compare data on human handedness with that of 37 non-human primates (Caspar et al., 2022). The authors concluded that human handedness represents an extreme value in primate limb preferences and that population-level asymmetries were rare in non-human primate species. Using similar statistical integration approaches as Caspar et al. (2022) across all species reported in the present study may yield important insights into the evolution of motor lateralization, but may pose serious methodological challenges given the high heterogeneity of tasks used to assess limb preferences across species.

Similar to the findings of the 2013 analyses, we again found that limb preferences in non-human species may have a stronger task dependency than human handedness. Humans tend to have relatively stable handedness across different handedness tasks, with significant correlations between the results of different tasks (Mundorf et al., 2023). In both birds and mammals, however, different studies showed a high task dependency of pawedness classification, suggesting that environmental constraints affect limb preferences in non-human animals to a stronger extent than handedness in humans. Translational research investigating limb preferences in non-human animals and handedness in humans using several different tasks would be important to quantify the extent of this difference.

Moreover, we also again found that in general, there seems to be a higher amount of non-lateralized individuals in different animal species than in humans, as well as a less skewed distribution of left-to-right-preferent animals compared to humans. This suggests that the difference between humans and non-human species in terms of limb preference is one of degree, rather than a fundamentally different organization of motor behaviour.

Limb preferences outside the subphylum Vertebrata

Aside from the studies investigating limb preferences in vertebrates reviewed in this publication, the last decade has seen an astonishing increase in publications on functional and anatomical left-right differences in various invertebrate species (Buchanan et al., 2015; Frasnelli et al., 2014; Goulson et al., 2013; Jasmin & Devaux, 2015; Ong et al., 2017; Perez et al., 2015; Romano et al., 2016; Tina et al., 2015, 2016; Yosef et al., 2021). Importantly, several studies suggested the existence of individual-level limb preferences or even population-level limb preferences in insects. For example, in the order *Orthoptera* (grasshoppers, locusts, and crickets), it has been demonstrated that desert locusts (*Schistocerca gregaria*) show individual-level limb preferences during targeted forelimb placement when crossing a gap (Bell, 2016; Bell & Niven, 2014, 2016). In the order *Coleoptera* (beetles), a study in mating Khapra beetle pairs reported that females showed a leftward population-level asymmetry for post-copulatory kicks. In contrast, males showed a rightward population-level asymmetry for foreleg tapping (Benelli et al., 2017). In the order *Diptera* (flies), several studies showed population-level asymmetries for wing or leg use during aggressive behaviour, but the direction of the asymmetry was species-dependent (Benelli et al., 2015; Benelli et al., 2015a, 2015b; Romano et al., 2015). While a systematic integration of these findings was beyond the scope of the present article, the data strongly suggest that invertebrates, like vertebrates exhibit limb preferences. Future studies need to systematically investigate the implications of these findings for the evolutionary bases of vertebrate limb preferences.

Outlook

Most importantly, research on limb preferences is needed in orders that currently have zero entries in the cladogram. Such data would help to identify one or possibly several common ancestries of limb preferences. However, also in orders in which research has already been published, more research, particularly meta-analytical integration and large-scale empirical studies, is needed. Like in research on human handedness, meta-analyses are an important tool of evidence synthesis in research on limb preferences in non-human animals. Besides in non-human primates (Soto et al., 2022), meta-analyses on limb preferences have been performed in cats, dogs, rats and mice (Manns et al., 2021; Ocklenburg et al., 2019). Interestingly, all of these species showed individual-level but not population-level asymmetries. In contrast, studies that reported population-level asymmetries often had small sample sizes. Given that low statistical power due to small sample sizes is still occasionally an issue in research on limb preferences (e.g., we had to exclude a study because only four animals were tested), it would be important to conduct more similar meta-analyses to increase the robustness of findings. If the amount of published studies does not allow for a single-species meta-analysis, cross-species meta-analysis may be a solution (Ocklenburg et al., 2023; Soto et al., 2022) may be a meaningful methodological option. Given the number of studies published, this would likely be possible in several orders discussed in the present article (e.g., *Artiodactyla*).

An additional open question is to what extent limb preferences are affected by fluctuating asymmetries, e.g., random deviations from morphological symmetry due to environmental stress and developmental instability (Dongen, 2006). In general, the association between fluctuating asymmetries and functional asymmetries is not well understood and deserves more investigation.

As in our previous publication, we again encourage researchers to further investigate limb preferences in avian species. Despite being the best-studied vertebrate class in terms of species diversity, with 79 individual avian species investigated, the majority of studies are concentrated in just 13 of the 44 avian clades. This concentration limits the phylogenetic interpretation of the data. Notably, the *Phaethoquornithes* and *Strisores* clades remain under-researched, and any studies on species within these clades would be highly valuable. Additionally, while *Passeriformes* species have become key models for neuroscientists and behavioural researchers in recent decades, limb preferences have been studied in only four *Passeriformes* species. Given the extensive research on various finch and corvid species (Apostel et al., 2023; Moll et al., 2023) it should be relatively easy to gather limb preference data for these species, especially since many studies have utilized video recordings that could be reanalyzed to examine behaviours such as standing preferences (Manns et al., 2018).

A more urgent concern is the need for additional research on limb preferences in the *Palaeognathae* infraclass. While some studies have examined limb preferences in *Struthioniformes* species, no data have yet been collected for the other four orders – *Rheiformes*, *Tinamiformes*, *Apterygiformes*, and *Casuariiformes*. These orders, located at the base of the avian phylogenetic tree, typically consist of only a few species, many of which are considered vulnerable to extinction by the International Union for Conservation of Nature. For instance, the *Apterygiformes* order includes five species of kiwis, which are endemic to New Zealand. Of these five species, four are classified as vulnerable to extinction, and one is nearly threatened (IUCN, 2024). Without further research on limb preferences in these species, we risk losing the opportunity to gather valuable data altogether.

Apart from that, larger scale, preregistered studies with a high number of trials per individual animal are needed for most species in order to increase the robustness of the observed results.

Conclusion

In conclusion, the present, updated study largely confirms the results of our previous study, with some important changes. As in the previous study, population-level asymmetry was the most frequently observed category, challenging the idea that population-level asymmetries are unique for human handedness. However, by including more highly robust results from meta-analyses in our study than in the previous paper, the percentage of species with population-level asymmetry went down considerably, suggesting that some of the previously reported effects may have been due to spurious findings in small samples that are hard to replicate. As in the previous analyses, limb preferences in most animal species showed a less skewed pattern than the 89.4% to 10.6% distribution observed for human handedness (Papadatou-Pastou et al., 2020). Moreover, limb preferences in non-human animals are more task-dependent than handedness in humans.

Acknowledgments

The AI tool ChatGPT (v2, 2025, OpenAI, https://openai.com/chatgpt) was used for proofreading certain sections of the manuscript after it was written by the authors.

Disclosure statement

No potential conflict of interest was reported by the author(s).

Funding

The author(s) reported there is no funding associated with the work featured in this article.

Data availability statement

The authors confirm that the data supporting the findings of this study are available within the article and its supplementary materials.

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