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Paw preferences in cats and dogs: Meta-analysis

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ABSTRACT

Predator–prey relationships have been suggested to be one of the primary evolutionary factors driving the development of functional hemispheric asymmetries. However, lateralization in many predator species is not well understood and existing studies often are statistically underpowered due to small sample sizes and they moreover show conflicting results. Here, we statistically integrated findings on paw preferences in cats and dogs, two predator species within the *Carnivora* order that are commonly kept as pets in many societies around the globe. For both species, there were significantly more lateralized than non-lateralized animals. We found that 78% of cats and 68% of dogs showed either left- or right-sided paw preference. Unlike humans, neither dogs nor cats showed a rightward paw preference on the population level. For cats, but not dogs, we found a significant sex difference, with female animals having greater odds of being right-lateralized compared to male animals.

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KEYWORDS Handedness; limb preferences; hemispheric asymmetries; *Carnivora*; meta-analysis

Introduction

The most prominent feature of behavioural lateralization in humans, handedness, shows a 90:10 distribution of right- vs. left-handedness that is stable across time epochs and geographical regions (Faurie & Raymond, 2004; Raymond & Pontier, 2004). However, neither its ontogenesis, nor its phylogenesis are well understood (Brandler & Paracchini, 2014; Güntürkün & Ocklenburg, 2017; Ocklenburg, Beste, & Güntürkün, 2013; Schmitz, Metz, Güntürkün, & Ocklenburg, 2017). Systematic evaluation of limb preferences in non-human animals is one way to shed light on the phylogenesis of handedness (Ocklenburg & Güntürkün, 2012; Ströckens, Güntürkün, & Ocklenburg,

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2013). For example, it has been suggested that handedness is specific to humans relative to all other primates, which would imply that the phylogenetic bases of handedness are likely to be found among gene loci that originated at the time of origin of the hominid lineage (Crow, 2008). In contrast, if it could be shown that stable population-level asymmetries exist in other primate species or even non-primate orders, this would imply that genes conserved between different mammalian species might also be relevant for human behavioural asymmetries.

In order to understand the evolutionary bases of handedness, it is essential to determine limb preferences in a wide variety of vertebrate species and considerable progress has been made in this regard over the last decade (Cochet & Byrne, 2013; Fitch & Braccini, 2013; MacNeilage, 2013; MacNeilage, 2014; Ocklenburg & Güntürkün, 2012; Ocklenburg & Güntürkün, 2018). For example, Ströckens et al. (2013) systematically analysed studies investigating limb preferences in all non-extinct vertebrate orders using cladographic comparisons. Overall, the authors identified studies investigating limb preferences in 119 different species. Out of these, 61 species (51.26%) showed evidence for population-level asymmetries, 20 (16.81%) showed evidence for individual-level asymmetries, and 38 (31.93%) showed no evidence for asymmetry.

Due to their evolutionary closeness to humans, research on animal limb preferences has been overly focused on primates (Hopkins, 2006; Hopkins, 2013; Meguerditchian et al., 2015; O'malley & McGrew, 2006; Prieur, Barbu, Blois-Heulin, & Pika, 2017). In many other orders, sample sizes have been small, potentially leading to replication issues. Thus, in order to make reliable estimates about the evolution of human handedness, large sample sizes are needed in research on animal limb preferences. Alternatively, data from multiple studies with smaller sample sizes can be integrated statistically using meta-analytic techniques. This has been done multiple times to clarify questions in research on human handedness, for example, the relationship of handedness and IQ (Ntolka & Papadatou-Pastou, 2018; Papadatou-Pastou & Tomprou, 2015), handedness and autism (Markou, Ahtam, & Papadatou-Pastou, 2017; Preslar, Kushner, Marino, & Pearce, 2014), handedness and deafness (Papadatou-Pastou & Sáfár, 2016), or sex differences in handedness (Papadatou-Pastou, Martin, Munafò, & Jones, 2008). However, so far meta-analytic techniques have only been sparsely used in the investigation of limb preferences in non-human animals outside the primate order.

In non-primate mammals, a sizeable body of research has been conducted in the *Carnivora* order, for example in the lion (*Panthera leo*) (Zucca, Baciadonna, Masci, & Mariscoli, 2011), the black bear (*Ursus americanus kermodei*) (Reimchen & Spoljaric, 2011), the cat (*Felis silvestris catus*) (McDowell, Wells, Hepper, & Dempster, 2016), and the dog (*Canis lupus familiaris*) (Wells, Hepper, Milligan, & Barnard, 2017). A systematic integration of these studies would be particularly interesting as the vast majority of Mammalian apex

predators comes from the *Carnivora* order and predator–prey relationships have been shown to be a critical factor in the emergence of functional hemispheric asymmetries (Bisazza, de Santi, & Vallortigara, 1999; Ghirlanda, Frasnelli, & Vallortigara, 2009; Lippolis, Bisazza, Rogers, & Vallortigara, 2002; Lippolis, Joss, & Rogers, 2009; Vallortigara, 2006). Especially in cats and dogs, a larger number of independent, small-scale studies with often conflicting results have been published.

However, a comparison with the human data is often difficult. While in humans, sample sizes with tens of thousands of individuals, allowing for reliable estimates of population frequencies, have been published (e.g., Medland et al., 2009), the large majority of studies in non-human animals suffer from low statistical power. Moreover, there are considerable differences in the literature regarding direction and strength of pawedness. For example, some studies report a leftward and other studies a rightward overall paw preference in their samples. For lions, bears and other members of the *Carnivora* order unfortunately too few studies on pawedness have been published so far to allow for meaningful meta-analysis.

Investigating laterality in cats and dogs is also relevant for another reason. Cats and dogs are two of the main animal species that have been domesticated by humans and are kept as pets around the world. Domesticated animals have ontogenetic experiences that are similar to human ontogenetic experiences, for example living in a human society, in a human home, listening to human language, not having to hunt for food or to fight off competitors to mate (Johnston, McAuliffe, & Santos, 2015). Therefore, it has been argued that domesticated animals can be used to understand human cognition (Johnston, Holden, & Santos, 2017), and a similar argument could be made for behavioural preferences such as pawedness. However, the direction of this relationship is not well understood. On the one hand, it could be conceived that domesticated animals like pet cats and dogs do not have to hone their natural tendencies to hunt, as they get fed by their human owners. If it is assumed that pawedness develops in the context of food handling, for example, hunting and killing prey with the paws in cats, then domesticated animals will not develop pawedness as much as their wild relatives (e.g., wolves or wild cats). On the other hand, it could also be conceived that domesticated animals develop stronger pawedness, as they may imitate humans, a species that shows strong behavioural asymmetries. To differentiate between these assumptions, it is essential to reliably determine the existence and extent of population level paw preferences in domesticated cats and dogs, so future studies can compare these with paw preferences in wolves and wild cats.

In cats, the first studies on paw preferences were published by Graystyan and Molnar (Graystyan & Molnar, 1954a; Graystyan & Molnar, 1954b). Using a food reaching task, they found that out of 15 cats, 8 were right-pawed, 4

left-pawed, and 3 ambilateral. One year later, Cole (1955) found more cats to be left- than right-pawed using a similar food reaching task. Specifically, he reported that out of 60 cats, 23 were left-pawed and 12 were right-pawed. The remaining 25 animals were ambilateral. In the decades following these initial publications on paw preferences in cats, several authors have published papers supporting the idea that cats on average show a right-sided paw preference. However, there has also been a number of studies supporting the view that cats on average have a left-sided paw preference (e.g., Konerding, Hedrich, Bleich, & Zimmermann, 2012; Lorincz & Fabre-Thorpe, 1996). Moreover, there is evidence suggesting a sex difference in pawedness, for example, that more female cats show a preference for the right paw, while males have a greater preference to use their left paw (Wells & Millsopp, 2012). Other studies, however, did not find such a sex difference (Yetkin, 2002). Most likely, these diverging results are due to the typically low sample sizes (many studies tested less than 20 animals) in studies investigating paw preferences in cats and resulting statistical issues. However, they could also reflect true differences but to test these in a statistically robust way, larger sample sizes or statistical integration of smaller studies via meta-analysis is needed. Moreover, different tasks have been used to assess pawedness, for example, food reaching, toy reaching, or reaching for moving targets. As task complexity has been shown to affect paw preference (Wells & Millsopp, 2009), this might also affect individual study results.

For dogs, the results pattern of paw preferences is not much different from that found in cats. In 1974, Popova published a paper in which paw preferences in three dogs were investigated (Popova, 1974). The author noted that the animals showed a strong preference to use the right paw in a food reaching task, despite equal effectiveness of the left paw in obtaining the food. More than a decade later, Tan (1987) investigated paw preferences in dogs in a larger sample of 28 animals by having the animals remove an adhesive plaster from their eyes. He found that 57.1% of the animals showed a right-sided paw preference, 17.9% showed a left-sided paw preference, and 25% were ambilateral. However, later studies also presented data indicating leftward paw preference (Poyser, Caldwell, & Cobb, 2006; Schneider, Delfabbro, & Burns, 2012). Like in cats, there is also evidence for a potential sex difference in dogs' pawedness, for example, it has been shown that female dogs show on average a right-sided paw preference, but male dogs a left-sided paw preference (Wells, 2003). Thus, similar to the situation in cats, it is unclear whether dogs show a population-level asymmetry for paw preference and if they do, to which side it is. Taken together, while these studies have yielded important insights into paw preferences in cats and dogs, their sample sizes are typically small, as discussed above.

In order to evaluate the presence of laterality in paw preferences on the individual level as well as the direction of this putative asymmetry on the population level in these two species, the current study seeks to systematically analyse and statistically integrate studies investigating paw preferences in cats and dogs. To this end, two different sets of meta-analyses were performed, one for cats and one for dogs. In step 1 we assessed the presence of laterality regardless of direction, namely whether significantly more animals preferred one paw (either right or left) for actions that can be performed with one paw compared to the number of animals who did not show a preference. In step 2 we assessed the direction of laterality, for example, whether there was a significant left- or right-sided paw preference at the group level.

Materials and methods

Location of studies and inclusion criteria

The studies that were included in the meta-analyses were identified using the following procedure (see Figure 1). As a first step, the electronic databases PubMed (<https://www.ncbi.nlm.nih.gov/pubmed/>) and Web of Science (<http://apps.webofknowledge.com>) were searched using either the search term “cat” or “dog” and the search terms (pawedness OR handedness OR

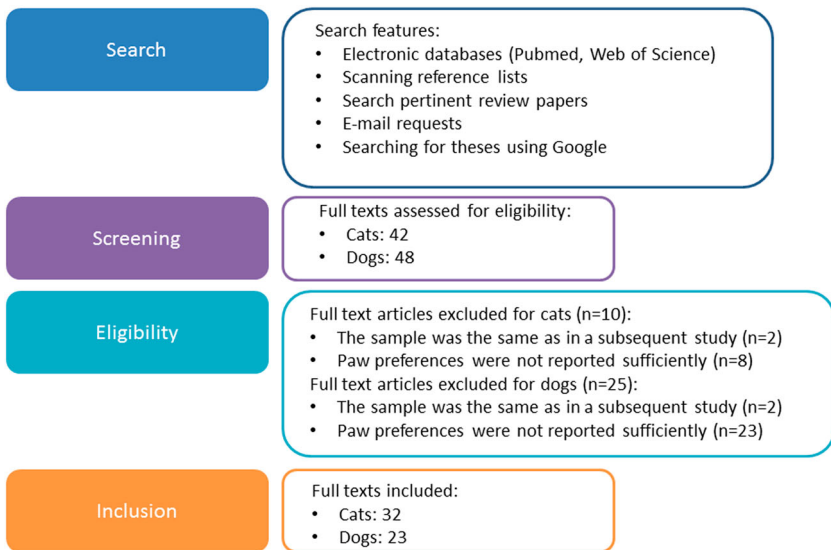


Figure 1. Flow diagram for the search and inclusion criteria for studies in the meta-analyses for paw preferences in cats and dogs. Adapted from Moher et al. (2009). To view this figure in colour, please see the online version of this journal.

“limb preference” OR laterality OR asymmetry). In addition, the reference lists of all articles eligible for inclusion were scanned for further relevant articles, and relevant review articles were searched (e.g., Ströckens et al., 2013). Moreover, Google was used to search for unpublished Bachelor, Master, or PhD theses. E-mail requests for both unpublished data and further information on published data were sent to the authors of eligible or potentially eligible articles (the e-mail addresses of these authors were retrieved in all but one case from the papers).

The following criteria were used for study inclusion:

- (1) Species: For the cat meta-analyses, the study had to report pawedness data in the domestic cat (*F. silvestris catus*). For the dog meta-analyses, the study had to report pawedness data in the domestic dog (*Canis lupus familiaris*). Data from all other species were excluded.
- (2) Study Language: Only reports written in English or German were included.
- (3) No selection of animals based on paw preferences: Studies in which animals were included in equal groups based on a pre-screening of paw preferences were excluded.
- (4) No use of split-brain animals: Studies in which the corpus callosum had been surgically removed in the animals were not included, as this might affect paw preferences.
- (5) Report of paw preferences: Only studies in which paw preferences were reported with a clear number or percentage of animals in each group (left and right or left, right, and ambilateral) or studies for which authors provided such information on request were included.

For cats, the number of full-text articles assessed for eligibility was 42. Thirty-two studies were included in the meta-analyses. For dogs, the number of full-text articles assessed for eligibility was 48. Twenty-three studies were included in the meta-analyses. Studies included in the analyses can be seen in [Tables 1](#) and [2](#). Data extraction was performed by Sevim Isparta and Sebastian Ocklenburg.

During the data extraction process, when multiple data points were reported for the same animals, the following rules were applied:

- If multiple pawedness tests were used in the same animals, we used the data for food reaching, as this was the most commonly used task in both cats and dogs and ensured the greatest comparability between studies. This happened for four studies (Forward, Warren, & Hara, 1962; Konerding et al., 2012; Villablanca, Hovda, Jackson, & Gayek, 1993; Wells & Millsopp, 2009).
- If the same animals were tested multiple times (e.g., at different years of age), we used the first testing point to avoid training effects (e.g., in the case of Wells & Millsopp, 2012).

Table 1. Studies included in the meta-analyses for cats.

Number	Study	Number of pawedness categories
1	Konerding et al. (2012)	3
2	Fabre-Thorpe et al. (1993)	2
3	Pike and Maitland (1997)	3
4	McDowell, Wells, and Hepper (2018)	3
5	Wells and Millsopp (2012)	3
6	McDowell et al. (2016)	3
7	Wells and Millsopp (2009)	3
8	Reiss and Reiss (1998)	3
9	Graystyan and Molnar (1954b)	3
10	Yetkin (2002)	2
11	Cole (1955)	3
12	Villablanca et al. (1993)	2
13	Lorincz and Fabre-Thorpe (1996)	3
14	Villablanca, Marcus, and Olmstead (1976)	2
15	Forward et al. (1962)	2
16	Webster (1981)	3
17	Burgess and Villablanca (1986)	2
18	Tan (1992)	2
19	Tan (1993b)	2
20	Tan and Kutlu (1992)	2
21	Tan (1993a)	2
22	Tan, Yaprak, and Kutlu (1990)	2
23	Dane and Tan (1992)	3
24	Tan and Kutlu (1993d)	3
25	Tan and Kutlu (1991)	3
26	Tan and Kutlu (1993a)	3
27	Calışkan and Tan (1990a)	2
28	Tan and Kutlu (1993c)	2
29	Tan and Kutlu (1993b)	2
30	Calışkan and Tan (1990b)	2
31	Tan, Kara, and Kutlu (1991)	2
32	Tan, Gepdiremen, Kutlu, and Cankaya (1992)	2

- If different criteria were used to score the data from the same test regarding paw preferences (e.g., an animal was considered right-pawed if it used the right paw on more than 50% of trials vs. more than 90% of trials), we used the data from the less strict criterion (e.g., in the case of Fabre-Thorpe, Fagot, Lorincz, Levesque, & Vauclair, 1993).

Any inconsistencies were resolved through discussion. Data collection ended in May 2018. Study selection and meta-analyses followed the guidelines established in the PRISMA statement (Moher, Liberati, Tetzlaff, & Altman, 2009). The data used in the present meta-analysis are available on OSF (<https://osf.io/sg2p9/>).

Statistical analyses

We determined the absolute number of left- and right-pawed cats and dogs for studies with two categories for pawedness, as well as the absolute number of left-pawed, right-pawed, and ambilateral animals for studies with three

Table 2. Studies included in the meta-analyses for dogs.

Number	Study	Number of categories
1	Schneider et al. (2012)	3
2	Wells (2003)	3
3	Marshall-Pescini et al. (2013)	3
4	Tomkins, Thomson, and McGreevy (2010)	3
5	Schneider, Delfabbro, and Burns (2013)	3
6	Siniscalchi et al. (2008)	3
7	Tomkins, Thomson, and McGreevy (2012)	3
8	Wells, Hepper, Milligan, and Barnard (2016)	3
9	van Alphen, Bosse, Jonker, and Koeman (2005)	2
10	Barnard, Wells, Hepper, and Milligan (2017)	3
11	Siniscalchi, d'Ingeo, Fornelli, and Quaranta (2016)	3
12	Poyser et al. (2006)	2
13	Wells et al. (2017)	3
14	Branson (2006)	3
15	Carleton-Prangnell (2012)	3
16	van Staaveren (2012)	3
17	McGreevy et al. (2010)	3
18	Aydinlioglu et al. (2000)	2
19	Aydinlioglu, Arslan, Cengiz, Ragbetli, and Erdogan (2006)	2
20	Wells, Hepper, Milligan, and Barnard (2018)	3
21	Plueckhahn, Schneider, and Delfabbro (2016)	3
22	Tan (1987)	3
23	Tan and Calişkan (1987)	3

categories for pawedness. We then calculated chi-square tests for equal distribution of the two categories (right-pawed: 50%, left-pawed: 50%), respectively for the three categories (right-pawed: 33.33%, left-pawed: 33.33%, ambilateral: 33.33%) to determine whether these categories had equal frequencies in the population or not.

However, it has to be noted that these were unweighted estimates (not weighted by study size), as the figures included in the chi-square analysis were simply the sum of the number of animals in all studies. This could lead to potential flaws, as non-weighted estimates are heavily dependent on the included studies' sample sizes, with larger studies driving the findings. Especially in this literature, where different studies have used different tasks to measure pawedness, possibly over- or under-estimating the true prevalence of paw preference, unweighted estimates cannot provide an accurate summary of findings.

Therefore, we also conducted meta-analyses to provide weighted estimates. Meta-analysis further allowed for the calculation of heterogeneity, and in case of heterogeneity the investigation of possible moderating effects. Moreover, it allowed for the estimation of publication bias. All meta-analyses were conducted using Comprehensive Meta-Analysis Version 2.2.064 (<https://www.meta-analysis.com/>) software.

Specifically, in a first step, we wanted to assess whether cats and dogs showed individual level asymmetries, and more specifically whether there were significantly more animals showing a left- or right-sided preference

than animals that were ambilateral. To this end, we only analysed studies that assessed pawedness as a variable with three possible outcomes (left, right, ambilateral). For each of these studies, we grouped animals into lateralized animals (left or right) and ambilateral animals. The number of “events” (lateralized animals) in comparison to the sample size of each study was then used to determine the event rate that was used for meta-analyses.

In a second step, we wanted to assess whether cats and dogs showed population-level asymmetries. To test this, we analysed all studies that were identified. For each study, we compared the right-lateralized animals to the total number of animals.

In addition to those core analyses, we also performed additional meta-analyses comparing male and female animals in order to test potential sex effects. As sex differences in pawedness have been reported for the direction, not the strength, of asymmetries in cats and dogs (Wells, 2003; Wells & Millsopp, 2012), we specifically performed meta-analysis for direction in order to assess sex differences. Since there was a substantial number of ambilateral animals within the cohorts that have been tested with three possible outcomes, including them with either the left- or the right-preference group would massively bias the outcome of the sex differences meta-analyses in one direction. We therefore excluded all ambilateral animals from this specific analysis. The number of animals with a rightward preference in relation to the overall number of animals with a leftward or rightward preference for each sex was coded as event for these meta-analyses. We then calculated male to female odds ratio for rightward preference and corresponding two-tailed 95% confidence intervals for each data set independently. Odds ratios have been used before to meta-analytically assess sex differences in left-handedness in humans (Papadatou-Pastou et al., 2008). We then combined these odds ratios using a conditionally random effects model to provide a pooled odds ratio and a test for the overall effect (Z statistic). Here, an odds ratio value of 1.0 corresponds to the null hypothesis of no sex differences. Moreover, values smaller than 1.0 indicate a larger proportion of female to male animals with a rightward preference. In contrast, values larger than 1.0 indicate a larger proportion of male to female animals with a rightward preference.

For all steps, the overall analysis followed a “conditionally random-effects” procedure (Hedges & Vevea, 1998) which started with an overall estimation using a fixed effects model. The Z statistic was used to test the statistical significance of the overall effect (whether it differs significantly from 0.50). The event rates obtained from this model were then tested to see if they came from a single population. Three different tests of heterogeneity were used: the Q statistic, the I^2 index, and the Tau^2 statistic. I^2 index levels could be classified into low (25%), moderate (50%), and high (75%) (Higgins, Thompson, Deeks, & Altman, 2003). If statistically significant heterogeneity was

detected, a random effects model was employed instead of the fixed effects model (Hedges & Vevea, 1998). Forest plots were used to visualize the data. Publication bias (also known as ascertainment bias) analysis was also conducted using the funnel plot graphical test and Egger's t statistical test. For the purposes of the moderator variables analysis, the average effect sizes in the groups of studies using two-way classifications (i.e., left vs. right) and three-way classifications (i.e., left vs. right vs. ambilateral) were compared by means of the Q statistic.

Results

Descriptive statistics and unweighted estimates

Cats

For cats, 16 out of 32 studies (50%) with an overall n of 636 cats reported pawedness as a dichotomous variable (right vs. left) with no ambilateral group. Out of these animals, 292 (46%) were left-pawed and 344 (54%) were right-pawed. A chi-square test against equal distribution of the two categories (right-pawed: 50%, left-pawed: 50%) indicated a significant population-level rightward paw preference in this sample ($\chi^2 = 4.25$; $p = .04$).

Furthermore, the remaining 16 out of 32 studies (50%, overall $n = 844$) assessed pawedness as a variable with three possible outcomes (left, right, ambilateral) (see Figure 2). Also in this group of studies, right-pawedness was the most common phenotype ($n = 325$; 39%), followed by left-pawedness ($n = 307$; 36%), and ambilaterality ($n = 212$; 25%). A chi-square test against equal distribution of the three categories (right-pawed: 33.33%, left-pawed: 33.33%, ambilateral: 33.33%) indicated that the three categories were not

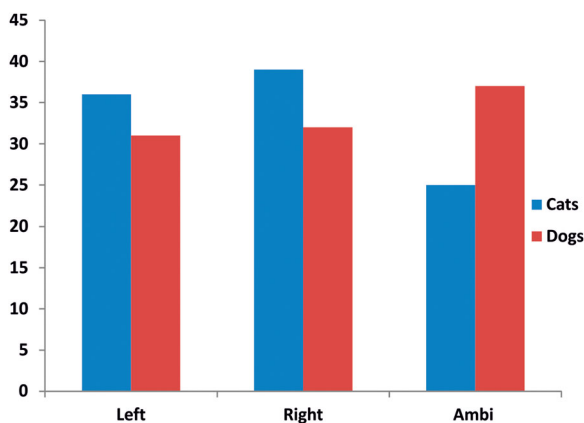


Figure 2. Percentage of left-pawed, right-pawed and ambilateral animals for cats and dogs, taken from studies using a 3-way classification. To view this figure in colour, please see the online version of this journal.

equally distributed ($\chi^2 = 26.21$; $p < .001$), presumably mainly because ambilaterality was less frequently observed than left- or right-pawedness. To determine whether right-pawedness was significantly more frequent than left-pawedness, we re-analysed the data in this sample after excluding all ambilateral animals. Here, the chi-square test against equal distribution failed to reach significance ($\chi^2 = 0.51$; $p = .47$), indicating that left- and right-pawedness had equal frequencies. However, both right-pawedness ($\chi^2 = 23.77$; $p < .001$) and left-pawedness ($\chi^2 = 17.89$; $p < .001$), were significantly more frequent than ambilaterality.

Dogs

For dogs, there were only four studies that reported pawedness as a dichotomous variable (right vs. left) with no ambilateral group. Out of these 216 animals, 114 (53%) showed a leftward paw preference and 102 (47%) showed a rightward preference. A chi-square test against equal distribution of the two categories (right-pawed: 50%, left-pawed: 50%) indicated no significant population-level preference in this sample ($\chi^2 = 0.67$; $p = .41$).

The remaining 19 studies had an overall n of 1132 animals and assessed pawedness as a variable with three possible outcomes (left, right, ambilateral) (see [Figure 2](#)). Here, 347 animals showed a leftward preference (31%), 367 animals showed a rightward preference (32%), and 418 animals were ambilateral (37%). A chi-square test against equal distribution of the three categories (right-pawed: 33.33%, left-pawed: 33.33%, ambilateral: 33.33%) indicated that the three categories did not have equal frequencies in the sample ($\chi^2 = 7.10$; $p = .03$). Further chi-square tests revealed that there were no significant effects for the left-pawedness vs. right-pawedness comparison ($\chi^2 = 0.56$; $p = .45$) and the right-pawedness vs. ambilaterality comparison ($\chi^2 = 3.13$; $p = .07$), although this comparison showed a non-significant trend towards ambilaterality being more frequent than right-pawedness. Additionally, ambilaterality was significantly more frequent than left-pawedness ($\chi^2 = 6.59$; $p = .01$).

Meta-analyses 1: presence of laterality

Presence of laterality in cats

Sixteen studies with an overall $n = 844$ assessed pawedness as a variable with three possible outcomes (left, right, ambilateral) and were included in this analysis. Overall, 75% of animals showed either leftward or rightward lateralization on the individual level, while 25% did not. In each of the 16 studies, there were more lateralized than non-lateralized animals in the sample. We first calculated an overall effect estimation using a fixed effects model. This model gave an event rate of 0.71 (95% Confidence Interval [CI] lower limit: 0.68, upper limit: 0.75). The model reached significance ($Z = 10.77$, $p < .001$). However, heterogeneity among data sets was found to be significant,

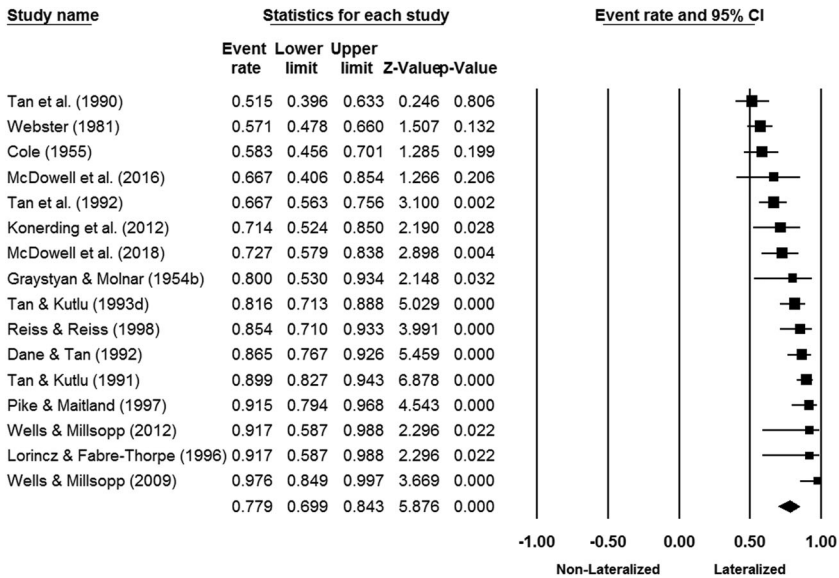


Figure 3. Forest plot for the lateralized vs. total comparison for cats. The 95% confidence interval for each study is represented by a horizontal line and the point estimate is represented by a square. The confidence intervals for overall mean effect is represented by the horizontal ends of the diamond shape at the bottom of the figure (this is also the case for all following Forest plots).

$Q(15) = 80.01$, $p < .001$, $\text{Tau}^2 = 0.52$, with strong inconsistency between studies ($I^2 = 81.25\%$). Therefore, we performed an effect re-estimation using a random effects model, which gave an event rate of 0.78 (95% CI lower limit: 0.70, upper limit: 0.84). Like the fixed effects model, this random effects model reached significance ($Z = 5.87$, $p < .001$), indicating that cats showed individual level lateralization as there were significantly more lateralized than ambilateral animals. Specifically, it indicated that the range of laterality prevalence in the distribution of populations studied is 70–84%. The results of the meta-analysis are shown in [Figure 3](#). Publication bias was detected using Egger's Test, $t(14) = 3.16$, $p = .007$. Visual inspection of the funnel plot graphical test indeed suggested that the left side of the funnel (representing a lesser prevalence of lateralized animals) is underrepresented (see [Figure 4](#)).

Presence of laterality in dogs

Nineteen studies with an overall n of 1132 animals were included in the analysis. Overall, 63% of animals showed individual level lateralization, while 37% did not. In all but two studies (Marshall-Pescini, Barnard, Branson, & Valsecchi, 2013; McGreevy, Brueckner, Thomson, & Branson, 2010), there were more lateralized than ambilateral animals.

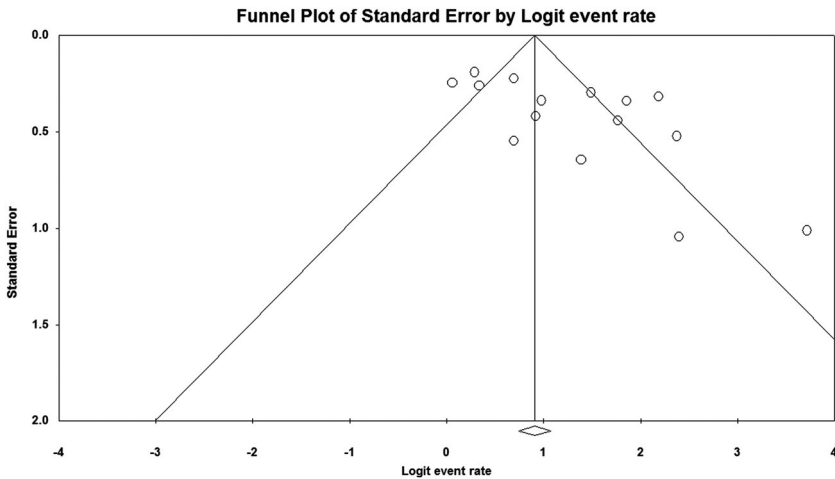


Figure 4. Funnel plot of standard error by logit even rate for the lateralized vs. total comparison for cats. White circles represent observed studies.

We first calculated an overall effect estimation using a fixed effects model. This model gave an event rate of 0.61 (95% CI lower limit: 0.57, upper limit: 0.64). This model reached significance ($Z = 6.38$, $p < .001$). However, heterogeneity among data sets was found to be significant, $Q(18) = 116.02$, $p < .001$, $\text{Tau}^2 = 0.50$, with strong inconsistency between studies ($I^2 = 84.49\%$). Therefore, we performed an effect re-estimation using a random effects model, which gave an event rate of 0.68 (95% CI lower limit: 0.60, upper limit: 0.76). Like the fixed effects model, this random effects model reached significance ($Z = 4.17$, $p < .001$), indicating that dogs showed individual level lateralization as there were significantly more lateralized than ambilateral animals. Specifically, it indicated that the range of laterality prevalence in the distribution of populations studied is 60–76%. The results of the meta-analysis are shown in [Figure 5](#). Publication bias was detected using Egger's Test, $t(17) = 4.23$, $p < .001$. Visual inspection of the funnel plot graphical test indeed suggested that the left side of the funnel (representing a lesser prevalence of lateralized animals) is underrepresented (see [Figure 6](#)).

Meta-analyses 2: direction of laterality

Direction of laterality in cats

Thirty-two studies with an overall n of 1,484 cats were included in the analysis. We first calculated an overall effect estimation using a fixed effects model. This model gave an event rate of 0.46 (95% CI lower limit: 0.43, upper limit: 0.48). The model reached significance with a negative Z -value ($Z = -3.25$, $p < .001$). However, heterogeneity among data sets was found to be significant, $Q(32) =$

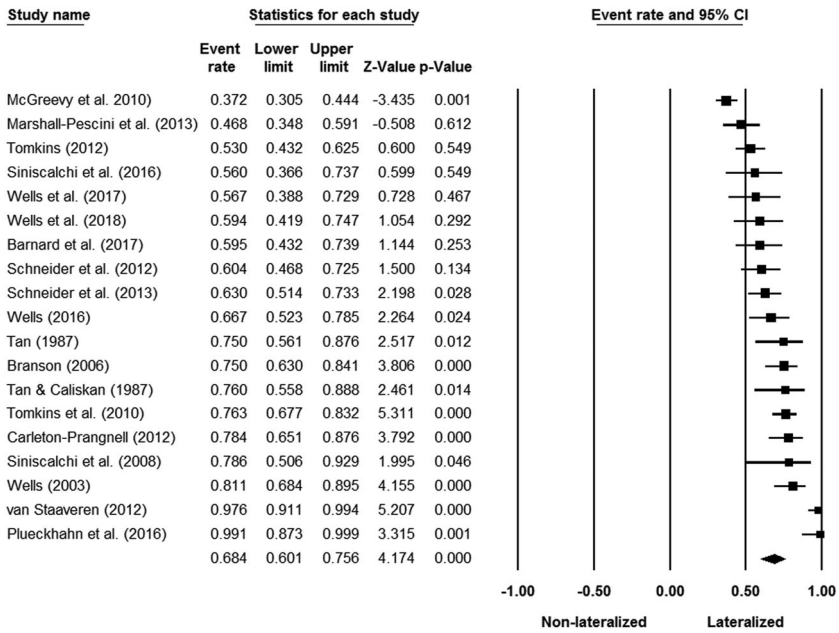


Figure 5. Forest plot for the lateralized vs. total comparison for dogs.

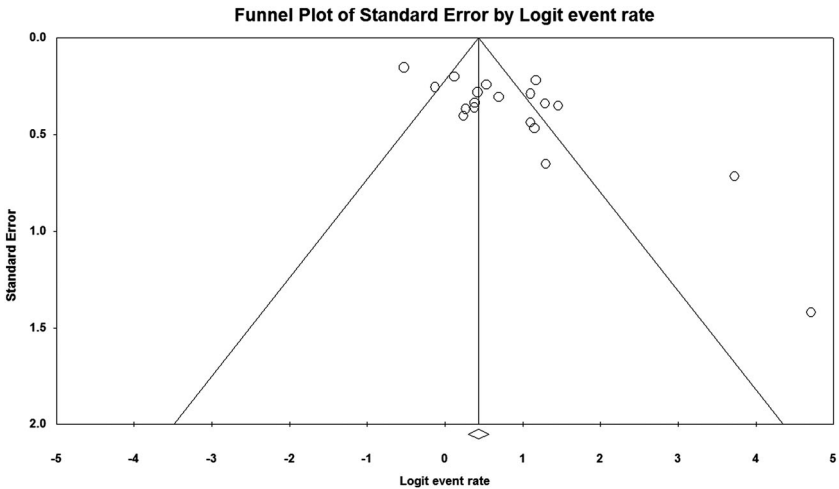


Figure 6. Funnel plot of standard error by logit even rate for the lateralized vs. total comparison for dogs. White circles represent observed studies.

86.19, $p < .001$, $\text{Tau}^2 = 0.17$, with rather strong inconsistency between studies ($I^2 = 62.87\%$). Therefore, we performed an effect re-estimation using a random effects model (see [Figure 7](#)), which gave an event rate of 0.46 (95% CI lower

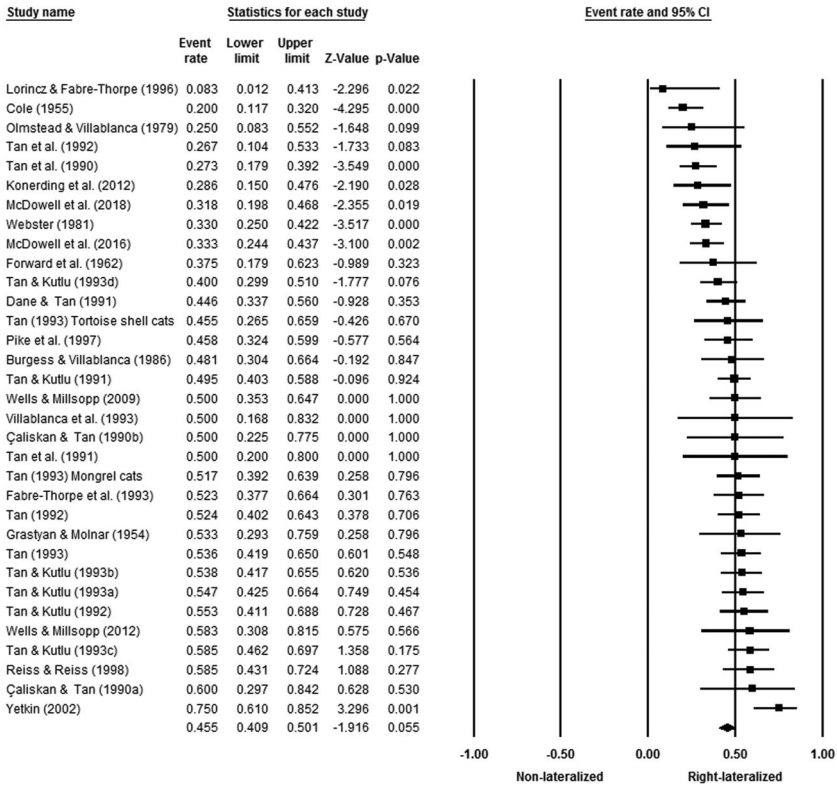


Figure 7. Forest plot for the right-lateralized vs. total comparison for cats.

limit: 0.41, upper limit: 0.50). In contrast to the fixed effects model, this random effects model did not reach significance ($Z = -1.92$, $p = .06$), although there was a clear trend. This indicated that cats showed a trend towards non-rightward asymmetry on the population level, but there was no significant difference between the frequencies of non-right-lateralized animals and right-lateralized animals. No publication bias was detected using Egger's Test, $t(31) = 0.42$, $p = .68$. Visual inspection of the funnel plot graphical test indeed suggested symmetry (see [Figure 8](#)).

Since the data sets included in this meta-analysis were found to be heterogeneous, we performed a moderator variables analysis to investigate if the different classifications of laterality (i.e., two-way vs. three-way classifications) might be causing this heterogeneity. The moderating effect of classification was found to be significant, $Q(1) = 15.00$, $p < .001$ (see [Figure 9](#)). Specifically, the prevalence of right-pawedness was found to be 0.53 (95% CI lower limit: 0.48, upper limit: 0.59), $Z = 1.22$, $p = .22$, for the two-way classification and 0.39 (95% CI: 0.34, 0.44), $Z = -4.33$, $p < .001$, for the three-way classification. Therefore, only when using a three-way classification is the non-

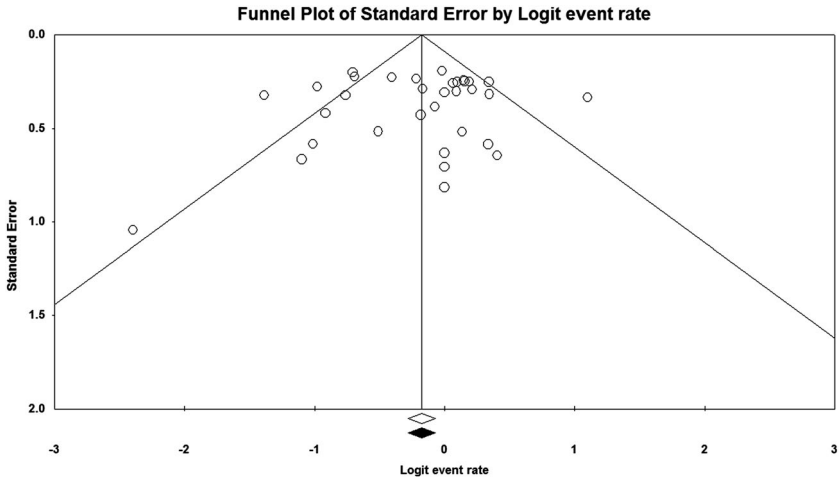


Figure 8. Funnel plot of standard error by logit even rate for right-lateralized vs. total comparison for cats. White circles represent observed studies.

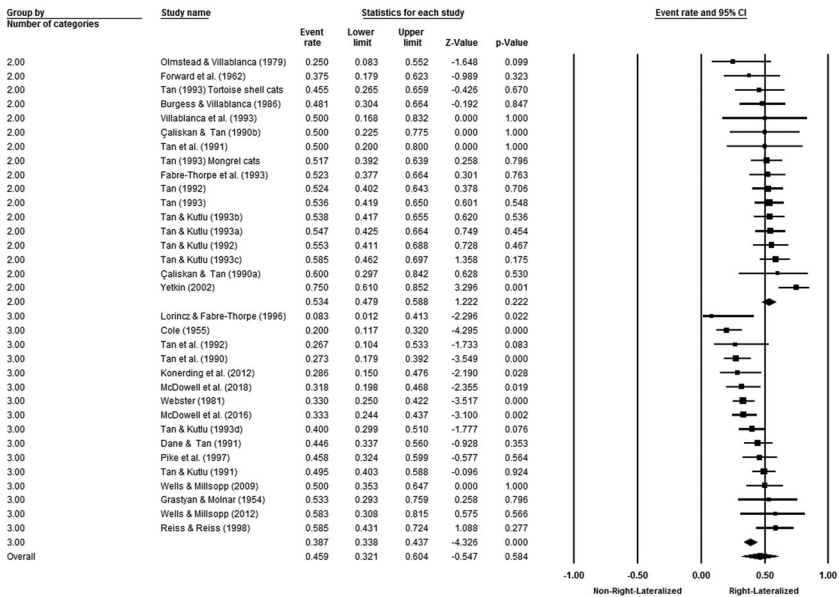


Figure 9. Forest plot depicting separately the studies using two-way and three-way classifications for cats.

right-pawedness prevalence significantly higher compared to right-pawedness. Heterogeneity was further examined and revealed significant heterogeneity only within the studies that used a three-way classification, $Q(15) = 40.04, p < .001, I^2 = 62.53\%$, but not within the studies that had used a two-

way classification, $Q(16) = 15.31$, $p = .50$, $I^2 = 0.00\%$. Possibly, three-way classifications use a variety of cut-off criteria to determine their ambilateral group, whereas two-way classifications generally just use an LQ of zero (or an equivalent of that) as the cut-off to determine left- and right-pawed animals.

Direction of laterality in dogs

Twenty-three studies with an overall n of 1,348 animals were included in the analysis (Figure 10). We first calculated an overall effect estimation using a fixed effects model. This model gave an event rate of 0.37 (95% CI lower limit: 0.34, upper limit: 0.40). The model reached significance with a negative Z -value ($Z = -9.23$, $p < .001$). However, heterogeneity among data sets was found to be significant, $Q(22) = 77.73$, $p < .001$, $\text{Tau}^2 = 0.20$, with rather strong inconsistency between studies ($I^2 = 71.70\%$). Therefore, we performed an effect re-estimation using a random effects model, which gave an event rate of 0.37 (95% CI lower limit: 0.32, upper limit: 0.42). Like the fixed effects model, this random effects model reached significance with a negative Z -value ($Z = -4.66$, $p < .001$), indicating that dogs did not show a significant rightward asymmetry on the population level, as there were significantly more non-right-lateralized animals than right-lateralized animals. No

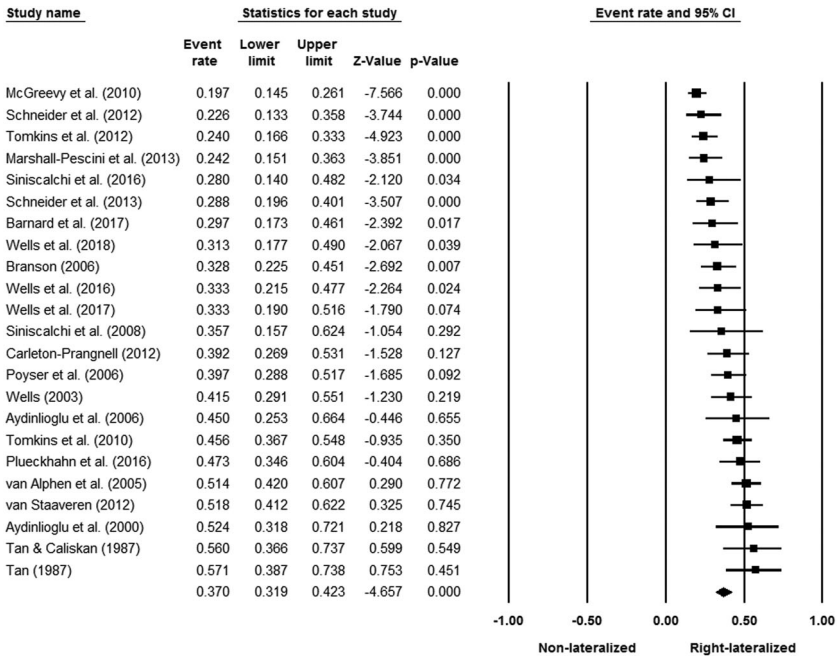


Figure 10. Forest plot for the right-lateralized vs. total comparison for dogs.

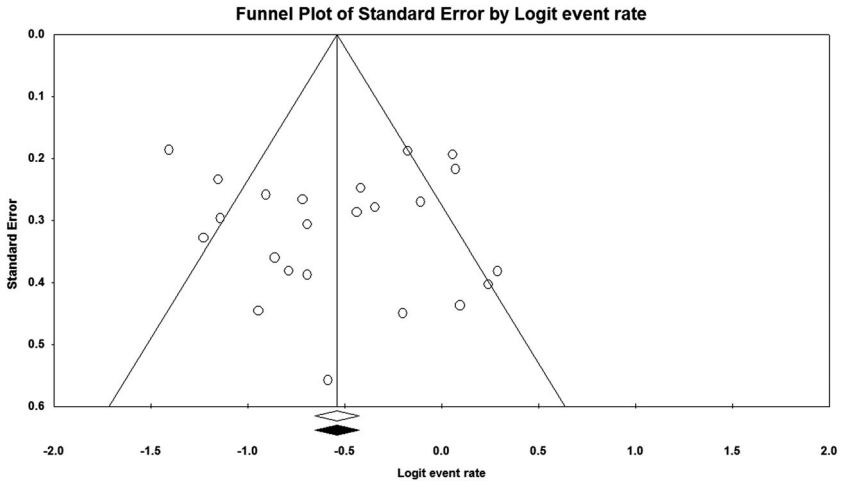


Figure 11. Funnel plot of standard error by logit even rate for the right-lateralized vs. total comparison for dogs. White circles represent observed studies.

publication bias was detected using Egger’s Test, $t(21) = 0.16, p = .88$. Visual inspection of the funnel plot graphical test indeed suggested symmetry (see Figure 11).

Since the data sets included in this meta-analysis were also found to be heterogeneous, we similarly performed a moderator variables analysis for type of classification of laterality (i.e., two-way vs. three-way classifications). The moderating effect of classification was not found to be significant, although there was a trend, $Q(1) = 2.92, p = .087$ (see Figure 12). Specifically,

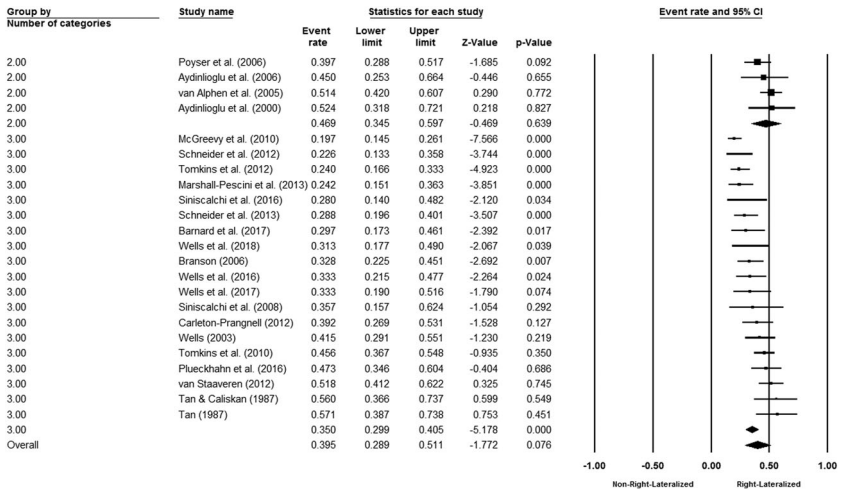


Figure 12. Forest plot depicting separately the studies using two-way and three-way classifications for dogs.

the prevalence of right-pawedness was found to be 0.47 (95% CI .35, 0.60), $Z = -0.47$, $p = .64$, for the two-way classification and 0.35 (95% CI lower limit: 0.30, upper limit: 0.41), $Z = -5.18$, $p < .001$, for the three-way classification. Therefore, only when using a three-way classification is the non-right-pawedness prevalence significantly higher than right- or left-pawedness. However, in this case, only four data sets had used the two-way classification, therefore the findings of these analysis must be read with caution. Heterogeneity was further examined and revealed significant heterogeneity only within the studies that used a three-way classification, $Q(18) = 63.07$, $p < .001$, $I^2 = 71.46\%$, but not within the studies that had used a two-way classification, $Q(3) = 2.54$, $p = .47$, $I^2 = 0\%$. Again, cut-off criteria might differ among studies and could be driving this heterogeneity.

Sex differences

Descriptive statistics and unweighted estimates

Cats. Out of the 16 studies that reported pawedness as a dichotomous variable, nine studies (overall $n = 475$ animals) reported separate data for male and female cats. Out of 178 male animals, 96 (54%) showed a left-sided preference and 82 (46%) showed a right-sided preference. Out of 297 female animals, 118 (40%) showed a left-sided preference and 179 (60%) showed a right-sided preference. Overall, there was a significant sex difference ($\chi^2 = 9.07$; $p < .01$), indicating that male and female cats differed regarding their paw preferences, with male cats showing a left-sided preference and female cats showing a right-sided preference. Separate analysis of male and female cats showed that this effect was mainly driven by the female animals, as this group shows a significant rightward preference on the population level ($\chi^2 = 12.53$; $p < .001$). In male animals, the effect failed to reach significance ($\chi^2 = 1.01$; $p = .29$), indicating no significant population-level asymmetries in this group. However, as the number of male cats was much smaller than that of female cats, these results have to be interpreted with caution.

Out of the 16 studies that reported pawedness as a variable with three different outcomes, 10 (overall $n = 562$) reported separate data for male and female cats. Out of the 260 male animals, 136 showed a left-sided preference, 80 showed a right-sided preference and 44 showed no preference. Out of the 302 female animals, 82 showed a left-sided preference, 157 showed a right-sided preference and 63 showed no preference. There was a significant sex difference ($U = 30,318$, $p < .001$), indicating a more leftward preference in male animals and a more rightward preference in female animals.

Dogs. Out of the four studies that reported pawedness as a dichotomous variable, three studies (overall $n = 195$ animals) reported separate data for male

and female cats. Both male and female dogs showed a small absolute preference to the right side (male: 52 dogs right and 47 dogs left; female: 52 dogs right and 44 dogs left), but there was no significant sex difference ($\chi^2 = 0.53$; $p = .89$). However, given the very small number of studies involved in this analysis, this result is hardly robust.

Out of the 19 studies that reported pawedness as a variable with three different outcomes in dogs, 8 (overall $n = 370$) reported separate data for male and female dogs. Here, the absolute data showed a leftward preference in male dogs (left: 68; right: 51; ambilateral: 67), but a rightward preference in female dogs (left: 46, right: 59; ambilateral: 79), with a substantial number of ambilateral animals present for both sexes. This sex difference failed to reach significance, but represented a trend ($U = 15,333$, $p = .066$).

Meta-analysis

Cats. Eighteen studies with an overall n of 930 animals were included in the analysis, one with two samples (Figure 13). We first calculated an overall effect estimation using a fixed effects model. The model reached significance with a negative Z -value ($Z = -5.16$, $p < .001$). However, heterogeneity among data sets was found to be significant, $Q(18) = 37.40$, $p < .005$, $\text{Tau}^2 = 0.43$, with moderate inconsistency between studies ($I^2 = 51.87\%$). Therefore, we performed an effect re-estimation using a random effects model. Like the fixed effects model, this random effects model reached significance with a negative Z -value ($Z = -3.87$, $p < .001$) and an odds ratio of 0.43 (95% Ci lower limit: 0.28, upper limit: 0.66), indicating that cats showed a significant sex difference, with female animals having greater odds of presenting with a rightward paw preference than male animals.

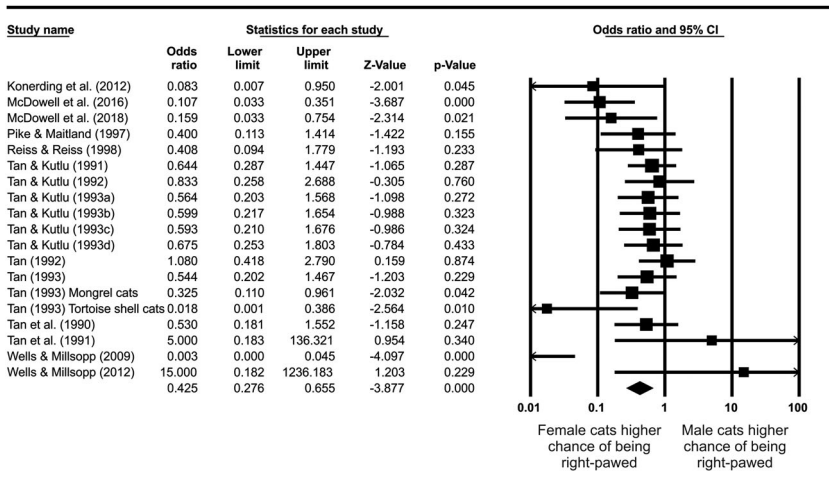


Figure 13. Forest plot for the male vs. female comparison in cats.

Dogs. Eleven studies with an overall n of 224 animals were included in the analysis. We first calculated an overall effect estimation using a fixed effects model. The model failed to reach significance ($Z = -1.16$, $p = .24$), but showed significant heterogeneity ($Q(10) = 19.34$, $p < .05$, $\text{Tau}^2 = 0.46$). Therefore we calculated a random effects model that also failed to reach significance ($Z = -0.85$, $p < .40$). Thus, no sex differences in pawedness can be shown for dogs at the present moment, but this result needs to be interpreted carefully, given the small number of studies and low overall n included in this meta-analysis.

Discussion

The aim of the present study was to statistically integrate studies on paw preferences in cats and dogs in order to determine the magnitude and direction of these paw preferences. To this end, several meta-analyses were performed.

As a first unweighted estimate we determined whether there was a larger number of lateralized (left- or right-sided paw preference combined) animals than non-lateralized animals. For cats, 75% of animals showed either leftward or rightward lateralization on the individual level, while 25% did not. In dogs, the unweighted estimate indicated that 63% of animals showed individual level lateralization, while 37% did not. Thus, in both species there were significantly more animals that showed lateralization than animals that did not in absolute terms, which was also supported by the chi-square test results. However, the absolute percentages were much lower than in humans, where it has been shown that only about 1% of the population is ambidextrous for writing (Rodriguez et al., 2010). However, for less trained activities higher prevalence of ambidexterity has been reported, for example, 24.4% of individuals use either hand when using a remote control (Fagard, Chapelain, & Bonnet, 2015).

However, as pointed out above, unweighted estimates are not an optimal way to estimate paw preferences in the population, as they are heavily dependent on the included studies' sample size, with larger studies driving the findings. Therefore, we also used weighted estimates in form of a meta-analytic approach to estimate pawedness in cats and dogs. In a first set of meta-analyses, we checked the presence of lateralization in cats and dogs by assessing studies that investigated pawedness as a variable with three outcomes (left-pawed, right-pawed, and ambilateral). We compared the number of lateralized animals (left or right) against the number of ambilateral animals. For both cats and dogs, the number of lateralized animals was higher than that of ambilateral animals and the effect reached significance. For cats, the random effects model indicated an average event rate of 78% lateralized animals, with a range between 70% and 84%. For dogs, the random effects model gave an event rate of 68%, with the range of laterality prevalence in

the distribution of populations studied being 60–76%. It has to be noted that for both cats and dogs the initially calculated fixed effects models were not informative, as significant study heterogeneity was detected.

From reading individual studies, several possible moderator variables could be identified. One factor that may play a role is the breed of animals. For example, McGreevy et al. (2010) assessed pawedness in four breeds of dogs selected for their morphological differences: greyhounds, whippets, pugs, and boxers. They found that for greyhounds 24% were left-pawed, 20% were right-pawed, and 56% did not show pawedness. For whippets, 21% were left-pawed, 21% were right-pawed, and 58% did not show pawedness. For pugs, 11% were left-pawed, 24% were right-pawed, and 65% did not show pawedness. For boxers, 13% were left-pawed, 13% were right-pawed, and 74% did not show pawedness. Thus, greyhounds on average had more left-pawed than right-pawed individuals, while this relation was reversed in pugs. Thus, depending on the breed that was used in different studies, this might have contributed to study heterogeneity. Unfortunately, almost all other studies do not report the breeds of the cats or dogs investigated, so a moderator variables analysis using breed as the moderator could not be performed.

Another variable that clearly affects paw preferences in cats is sex, as we found that female animals had greater odds of showing a rightward preference compared to male animals, which showed a leftward preference. This provides meta-analytical support for the idea that there might be two populations of paw preference in cats that cluster around sex (Wells & Millsopp, 2012).

A similar pattern has been suggested for dogs (Wells, 2003) but was not confirmed in our analysis. However, this might well be due to the small number of studies included in this analysis and future meta-analyses that include more empirical data are needed to make more firm conclusions. The idea that dogs also show a sex difference in paw preference is also supported by a study using an adhesive tape removal task repeatedly and calculating lateralization quotients for individual animals (Quaranta, Siniscalchi, Frate, & Vallortigara, 2004). Here, male animals showed a clear leftward preference, while female animals showed a trend towards a rightward preference.

Other potential moderator variables include the use of the standard food reaching task, vs. other tasks, as well as the animal's age. It would have been ideal to assess this heterogeneity statistically using moderator analysis. Unfortunately, only very few individual studies report each of these possible moderator variables, rendering a moderator analysis not feasible at the present time point. Therefore, future studies should include these variables in order to make it possible for future meta-analyses to investigate their moderating effects.

In a second set of meta-analysis, we aimed to determine whether cats and dogs show a population-level rightward bias for pawedness like humans show for handedness (Ocklenburg et al., 2013). Here, we included both studies with two categories for pawedness and three categories for pawedness and tested whether the number of right-pawed animals was larger than that of non-right-lateralized animals (e.g., left-pawed animals and ambilateral animals). As for the first set of meta-analyses, significant heterogeneity was detected so that the initially calculated fixed effect models could not be used and random effect models were applied instead.

For cats, the random effects model did not reach significance, indicating that there was no significant difference between the frequencies of non-right-lateralized animals (54%) and right-lateralized animals (46%) and therefore no population-level rightward pawedness in the overall set of studies. Since significant heterogeneity between studies was found, we investigated pawedness classification as a possible moderator variable. The moderating effect of classification was found to be significant, indicating that the prevalence of right-pawedness was found to be 53% for the two-way classification and 39% for the three-way classification. The event rate did not reach significance for the two-way classification. For the three-way classification, the effect reached significance, but as the event rate of right-pawedness was lower than 50% and the Z-value negative, this comparison indicated that non-right-pawedness was more common than right-pawedness. Thus, this analysis further confirms that there is no population-level rightward pawedness in cats. The difference in prevalence rates of right-pawedness between the two-way and three-way classifications is likely caused by the fact that the ambilateral group in studies with a three-way classification system would likely include some of the animals that would have been classified as right-pawed in the two-way classification system.

For dogs, the random effects model did reach significance with a negative Z-value, indicating that dogs did not show a significant rightward asymmetry on the population level, as there were significantly more non-right-lateralized animals (61%) than right-lateralized animals (39%). In contrast to cats, the moderating effect of classification was not significant.

Taken together, there was no evidence for population-level rightward pawedness in cats and dogs. As for cats, the model did not reach significance, indicating equal frequencies of right-pawedness and non-right-pawedness. For dogs, non-right-pawedness was actually more frequent than right-pawedness. Thus, there seems to be a somewhat higher incidence of right-pawedness in cats (46%) as compared to dogs (39%). We can only speculate why this difference exists, despite both species being members of the *Carnivora* order. Cats have sharp, retractable claws on their front toes to catch, hold and kill prey, and cat skeletons have been shown to reflect an adaptation for making leaps and striking at their prey with their paws (Gonyea, 1978;

Kleiman & Eisenberg, 1973; Landsberg, Hunthausen, & Ackerman, 2013; Murray, Boutin, O'Donoghue, & Nams, 1995). Thus, they are highly specialized to hunt and hold and manipulate their prey and other food with their paws.

Dogs, in contrast, are long-legged and adapted for running, but only very rarely strike and kill prey with their paws—instead they almost exclusively use their teeth (Landsberg et al., 2013). Moreover, the domestic cat investigated in our study is derived from the North African wildcat, which has been domesticated for a much shorter time period than the wolf from which the dog is derived and which is also a more specialized predator (Bradshaw, 2006). Since predator–prey relationships have been shown to be a critical factor in the emergence of functional hemispheric asymmetries (Bisazza et al., 1999), this higher relevance of the paws for hunting in cats could potentially explain why they show a slightly more rightward asymmetry than dogs, as cats might face a stronger evolutionary pressure to develop pawedness. However, empirical studies are needed to confirm this assumption. Importantly, limb preferences have been linked to a number of behavioural differences when reacting to the environment. For example, in marmosets (*Callithrix jacchus*) it has been shown that left- and right-handed animals show significant differences in exploratory, social, and vocal behaviour (Gordon & Rogers, 2010; Gordon & Rogers, 2015; Hook & Rogers, 2008). Further research on these links between limb preferences and behaviour in cats and dogs might also help to understand potential differential evolutionary pressures on the development of pawedness in the two species. Moreover, it has been shown in some species that even if they do not show a population-level asymmetry for limb preferences, they still might show population-level asymmetry for other measures of laterality, such as sensory or social laterality (Austin & Rogers, 2012; Hook-Costigan & Rogers, 1998). Thus, meta-analytic integration of other forms of laterality in cats and dogs would also be beneficial in order to get a better understanding of how hemispheric asymmetries are organized in these species.

Meta-analytic integration of laterality data in domesticated animals can also be crucial for informing discussions about animal welfare. It has been suggested that functional cerebral asymmetry measurements such as asymmetric tail wagging or face perception can be used to assess and understand emotional states of domesticated animals, so that emotional distress can be estimated (Artelle, Dumoulin, & Reimchen, 2011; Guo, Meints, Hall, Hall, & Mills, 2009; Racca, Guo, Meints, & Mills, 2012; Siniscalchi et al., 2011; Siniscalchi, Lusito, Vallortigara, & Quaranta, 2013). For example, it has been shown that dogs turn left to emotionally threatening stimuli, such as snakes or hearing the sounds of a thunderstorm, implicating that the right side of the brain is more responsive to threatening and alarming stimuli (Siniscalchi, Quaranta, & Rogers, 2008; Siniscalchi, Sasso, Pepe, Vallortigara, & Quaranta, 2010). For paw preferences, it has been shown that dogs without a significant paw preference

were significantly more reactive to threatening sounds like thunderstorms or fireworks than dogs with either a significant left- or right-paw preference (Branson & Rogers, 2006). Establishing a reliable baseline for population-level asymmetries in large samples of cats and dogs can therefore be critical to understanding the results of studies on stress in these animals correctly. Thus, beyond the present pawedness meta-analysis, further meta-analyses of laterality data in cats and dogs, for example, regarding emotional lateralization, are desirable.

In conclusion, our study shows that both cats and dogs show a significantly higher frequency of animals with a left or right paw preference as compared to non-lateralized animals. In contrast to humans, there is no population-level right-sided paw preference in these two species when both sexes were analysed together. However, sex seems to crucially affect paw preferences in cats, as female animals show a rightward preference and male animals a leftward preference.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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