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ISSN: (Print) (Online) Journal homepage: <https://www.tandfonline.com/loi/plat20>

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To cite this article: Barbara Regaiolli , Luca Mancini , Giorgio Vallortigara & Caterina Spiezio (2020): Paw preference in wolves (*Canis lupus*): A preliminary study using manipulative tasks, *Laterality*, DOI: [10.1080/1357650X.2020.1853763](https://doi.org/10.1080/1357650X.2020.1853763)

To link to this article: <https://doi.org/10.1080/1357650X.2020.1853763>



Published online: 03 Dec 2020.



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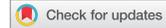
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Paw preference in wolves (*Canis lupus*): A preliminary study using manipulative tasks

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ABSTRACT

Behavioural and brain lateralization is widespread among non-human vertebrates. Motor lateralization has been investigated in the domestic dog, revealing that “pawedness” in this species seems to be sex and task related; however, few if any studies considered this asymmetry in wolves (*Canis lupus*). The aim of this study was to investigate the paw preference of seven wolves housed at Parco Natura Viva – Italy, during the interaction with food-related (FD) and olfactory (OLF) environmental enrichment devices. Eleven sessions were done (22 session in total) per condition (FD and OLF), and data about enrichment manipulation were collected. Most of the wolves manipulated the enrichment devices using one paw rather than both paws. At the individual level, all subjects were lateralized in paw use, six were right pawed, one was left pawed (the alpha male) regardless of the enrichment condition. The fact that one paw rather than both was frequently involved in manipulation could indicate a practical advantage for each individual in being lateralized in paw use. Despite the small sample size, our results provide interesting insights about lateralization in wolves, deserving further investigations. More studies are needed considering factors such as temperament, social rank and task complexity on canid motor lateralization.

ARTICLE HISTORY Received 2 October 2020; Accepted 17 November 2020

KEYWORDS Grey wolf; paw preference; feeding task; olfactory stimuli

Introduction

The study of motor lateralization in non-human animals can provide useful information on the evolution of handedness in humans (Ocklenburg & Güntürkün, 2012; Ocklenburg, Isparta, Peterburs, & Papadatou-Pastou, 2019; Stancher, Sovrano, & Vallortigara, 2018; Vallortigara & Rogers, 2020). Paw preference in dogs (*Canis familiaris*) has been investigated through several tasks, from the First-stepping Test, evaluating paw usage to start moving

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(Tomkins, Thomson, & McGreevy, 2010) to the Kong™ Test, a rubber cylinder dispensing food after manipulation (e.g.,; Marshall-Pescini, Barnard, Branson, & Valsecchi, 2013; McGreevy, Brueckner, Thomson, & Branson, 2010; Siniscalchi, Quaranta, & Rogers, 2008; Tomkins et al., 2010; Wells, Hepper, Milligan, & Barnard, 2016). In general, dogs have been found to be lateralized rather than ambi-preferent, showing preferential use of one paw (Aydinlioglu et al., 2000; 2006; Branson & Rogers, 2006; Hackert, Maes, Herbin, Libourel, & Abourachid, 2008; Ocklenburg et al., 2019; Siniscalchi et al., 2008), although no group-level bias in lateralization was found for either the right or the left (for review see Ocklenburg et al., 2019).

Based on a recent review of studies on paw preference by Ocklenburg et al. (2019), dogs seem to be characterized by an individual-level paw preference, with a greater number of individuals showing lateralization than non-lateralized animals. Factors such as sex and task seem to affect motor lateralization in the domestic dog. In particular, male and female dogs seem to be characterized by opposite lateralization, with males showing a leftward preference and females a rightward preference (Ocklenburg et al., 2019; Quaranta, Siniscalchi, Frate, & Vallortigara, 2004; Wells, 2003). Finally, the paw preference of domestic dogs seems to be influenced by the task used, as the frequency of right and left paw use seems to vary in food reaching tasks and other problem solving or motor tasks (Batt, Batt, Baguley, & McGreevy, 2008; Ocklenburg et al., 2019; Tomkins et al., 2010; Wells, Hepper, Milligan, & Barnard, 2018). Moreover, a strong relationship between visuospatial orienting attention bias and paw preference related to food detection has been recently reported (Siniscalchi, d'Ingeo, Fornelli, & Quaranta, 2016).

Despite several studies have been focusing on motor lateralization in the domestic dogs (for review see Ocklenburg et al., 2019), to our knowledge there are no reports of paw preferences in manipulative tasks in their wild counterpart, the wolf (*Canis lupus*). As the domestication process is known to affect several aspects of animal morphology, behaviour and sociality (e.g., Marshall-Pescini, Cafazzo, Virányi, & Range, 2017, 2018; Range, Marshall-Pescini, Kratz, & Virányi, 2019; Sánchez-Villagra, Geiger, & Schneider, 2016), studying motor lateralization in wolves might shed new light on the evolution and roles of hemispheric specialization and its correlates in animals.

In the current study, we investigated whether food-related and olfactory stimuli may differentially affect the paw preference of grey wolves, as they rely heavily on their sense of smell (Lord, 2013; Mech, 1970). Moreover, previous research suggested lateralization of processing of odours in both vertebrate and invertebrate species, highlighting a right-hemisphere involvement in the presence of different types of olfactory stimuli (McGreevy & Rogers, 2005; Rogers & Andrew, 2002; Rogers & Vallortigara, 2008; Royet & Plailly, 2004; Siniscalchi et al., 2011; Vallortigara & Andrew, 1994). In the domestic dog, the right nostril (right hemisphere) seems to be involved in the initial process of novel non-aversive

odour stimuli, whereas a consistent right-nostril bias was present in the case of arousal sniffing stimuli related to threatening or stressful situations (Siniscalchi et al., 2011; Siniscalchi, d'Ingeo, & Quaranta, 2016). However, there are no reports of lateralization during the process of odours in wolves.

The aim of this study was to investigate the forepaw use in captive grey wolves (*Canis lupus*) during the interaction with manipulative tasks, specifically olfactory and food-related environmental enrichment devices. If domestic dogs and wolves share the hemispheric specialization mechanisms and therefore show similar motor lateralization, based on previous literature on domestic dogs we would expect 1) a predominant use of one paw, either the right or the left one, rather than both paws simultaneously; 2) the preferential use of one paw at the individual level; 3) a more pronounced bias toward the left paw in the presence of olfactory stimuli, due to the activation of the right hemisphere for processing of novel odours reported in dogs and other vertebrate and invertebrate species.

Material & methods

Subjects & area

The study was carried out with a family pack of seven adult wolves, six males and one female, housed in Parco Natura Viva – Garda Zoological Park, Verona (Italy). All wolves were related, and parent reared. Subjects were housed in an open-topped woody enclosure of 4067.99 m², built on a slope and furnished with trees (mainly oaks), logs, branches, rocks, and several burrows. Wolves were fed once a day six out of seven days a week with meat or fish as well as fruits, vegetables, and croquettes. The feeding time was in the late afternoon, after the zoo closed to the public. Wolves were involved in an environmental enrichment programme and were provided daily with food-related, sensory, or manipulative items. Water was provided ad libitum. The study was carried out through the behavioural observation of the wolves, using non-invasive techniques. The study procedure was in accordance with the EU Directive 2010/63/EU and the Italian legislative decree 26/2,014 for Animal Research. No special permission to involve animals in the current ethological non-invasive study was required, as zoological gardens in Italy are expected to carry out behavioural observations of the individuals in their care, in order to guarantee animal welfare (D. Lgs.73/2005).

Enrichment devices

Food-based enrichment consists in the provision of novel food or providing food in new ways (e.g., hidden in boxes or scattered around in small pieces to promote foraging), as we did in the current study, to promote foraging/food

processing behaviours (Hosey, Melfi, & Pankhurst, 2013). Olfactory enrichment implies the introduction of odours such as spices, feces, perfums into the captive environment, to stimulate animals' senses and behaviours such as scent marking (Hosey et al., 2013; Swaisgood & Shepherdson, 2005).

Environmental enrichment devices filled with food or scents were used to investigate paw preference of the subjects (Figure 1). In particular, food-related devices (FD) consisted of paper bags (23 × 33 cm) filled with straw and one type of fruit (apple, pear) or one type of vegetable (zucchini, carrots, tomatoes) or other food items (different types of dog croquettes, dry bread), whereas olfactory devices (OLF) were paper bags filled with straw impregnated with herbivore scents (*e.g.*, faeces) or spices (*e.g.*, curry, paprika, cinnamon, garlic). The wolves were familiar with all the food items used in the study. Bags were sealed with adhesive tape and scattered around in the enclosure. To retrieve the food or to explore the devices, wolves had to manipulate the bag with one paw and/or break it up with the mouth, while the other paw provided postural support (Figure 1). To avoid competition between subjects, a minimum of two devices per wolf was provided.

Procedure and data collection

Wolves were tested in their social context and in their everyday enclosure. Data were collected by one experimenter through the live observation of



Figure 1. A grey wolf (*Canis lupus*) interacting with an environmental enrichment device. One paw and the mouth are used to manipulate the device while the other paw is supporting the body.

the pack during the interaction with the devices. A total of 22 sessions were done, 11 sessions with food-related devices, 11 with olfactory devices. Olfactory and food-related enrichment devices were provided on alternate days in the early afternoon. The use of the left (L) or right (R) forepaw or both forepaws together (B) to manipulate the device was recorded. Each session ended when one bout of manipulation per wolf was collected or when all devices were destroyed. Per wolf and per session, we collected the first bout of interaction (single-paw manipulation) with an enrichment device. A bout was defined as the first occurrence in a series of the same action (e.g., Hopkins et al., 2001; McGrew & Marchant, 1997; Regaiolli, Spiezio, & Hopkins, 2016; 2018).

Data analyses

To investigate individual-level paw preference for manipulating the enrichment device, the binomial z-score was used to classify the subjects as left pawed ($z < -1.96$), right pawed ($z > 1.96$) or ambi-preferent ($-1.96 < z < 1.96$) (Michel, Sheu & Brumley, 2002). In addition, for each wolf a Handedness Index score (HI) was calculated: $HI = (R - L)/(R + L)$ (R: bouts of right paw use; L: bouts of left paw use). The HI ranges between -1 (left bias) and 1 (right bias). The strength of the hand preference was assessed using the absolute values of the HI (ABS-HI) (Hopkins, 1999, 2013; Marshall-Pescini et al., 2013). Given that Shapiro–Wilk Goodness-of-Fit tests revealed that not all data were normally distributed, non-parametric statistical tests were used. The group-level analysis was done using a one-sample Wilcoxon test with the HI serving as dependent measures, to test the symmetry of the paw use distribution. Moreover, both the HI and ABS-HI were compared between conditions (FD and OLF) using paired-sample Wilcoxon-tests to evaluate whether different stimuli can influence direction and strength of paw preference in wolves. Statistical analysis was carried out in the R 3.5.0 environment. Significance level was set at $p < 0.05$, all tests were two-tailed.

Results

Overall paw preference

As not all wolves interacted with the devices in all sessions, the number of bouts collected ranged from 6 to 11. First, we investigated paw preference for manipulating the enrichment devices regardless of the condition (FD and OLF), considering all sessions together ($N = 22$). The median (IQR) number of bouts was 2 (2) for the left paw, 19 (6) for the right paw and 1 (1) for both paws. Thus, 95% of the manipulation bouts were performed

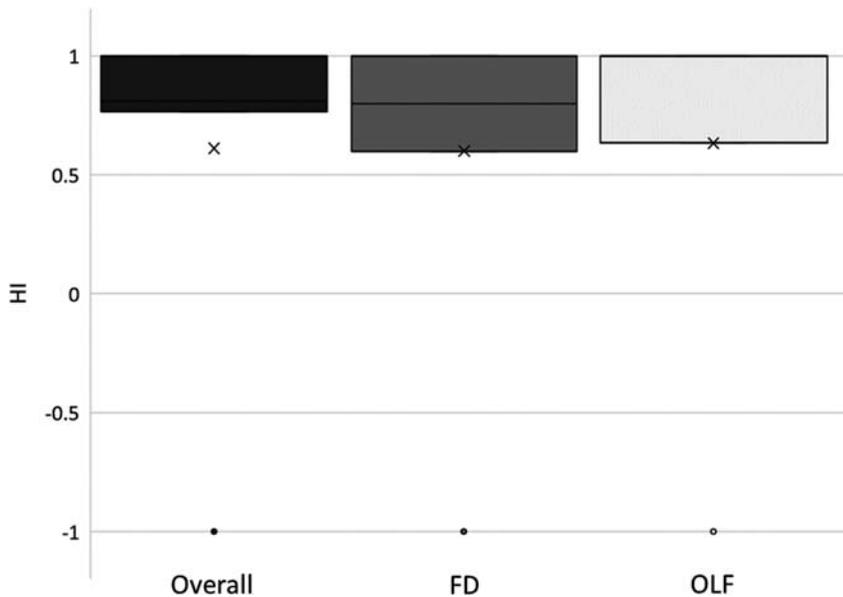


Figure 2. Paw preference (Handedness Index) in the grey wolf (*Canis lupus*) in different conditions (FD: food-related enrichments; OLF: olfactory enrichments; Overall: FD + OLF). The horizontal lines within the box indicate the medians, crosses indicate means, boundaries of the box indicate the first and third quartile. Values that are 1.5 times outside the interquartile range (IQR) are considered outliers and are drawn as points.

with either the right or the left paw, whereas 5% were performed with both paws. When considering bouts performed with only one paw, at the individual level, all subjects were significantly lateralized: six were right pawed, one (the alpha male, A) was left pawed (Table 1). At the group level, the median (IQR) HI was 0.81 (0.24) and the median (IQR) ABS-HI was 0.90 (0.20). One-sample Wilcoxon test revealed no bias in the HI distribution ($V=22$, $p=0.202$) (Figure 2).

Paw preference in different conditions

In the presence of food-related enrichment devices, only six subjects were included in the analysis as one of the wolves did not perform enough bouts for statistical testing. At the individual level, four wolves were significantly lateralized: four were right pawed, one (the alpha male, A) was left pawed whereas one subject was ambi-preferent (Table 1). At the group level, the median (IQR) HI was 0.80 (0.40) and the median (IQR) ABS-HI was 1.00 (0.20). One-sample Wilcoxon test revealed no bias in the HI distribution ($V=22.5$, $p=0.168$).

Table 1. Paw preference in the study wolves.

	Food-related			Olfactory			Overall					
	HI	N	z-score	p-value	HI	N	z-score	p-value	HI	N	z-score	p-value
A	-1.00	11	-3.02	0.001	-1.00	11	-3.02	0.001	-1.00	22	-4.48	< 0.001
B	1.00	10	2.85	0.002	1.00	11	3.02	0.001	1.00	21	4.36	< 0.001
C	0.60	10	1.58	0.109	1.00	11	3.02	0.001	0.81	21	3.49	< 0.001
D	1.00	10	2.85	0.002	1.00	11	3.02	0.001	1.00	21	4.36	< 0.001
E	0.80	10	2.21	0.022	0.80	10	2.21	0.022	0.80	20	2.2361	< 0.001
F	0.80	10	2.21	0.022	1.00	10	2.85	0.002	0.90	20	3.8	< 0.001
G	1.00	6	#	#	0.64	11	1.81	0.065	0.76	17	2.91	0.002

For each subject and for each condition (food-related enrichments, olfactory enrichments, overall: food-related + olfactory), the table reports the HI, the total number of bouts collected, the z-score and the p-value of the binomial tests between the bouts with the right and left paw.

Statistical analysis was not possible due to data deficiency.

In the presence of olfactory enrichment devices, at the individual level, six wolves were significantly lateralized: five were right pawed, one (the alpha male, A) was left pawed whereas one subject was ambi-preferent (Table 1). At the group level, the median (IQR) HI was 1.00 (0.36) (Figure 2) and the median (IQR) ABS-HI was 1.00 (0.20) (Figure 3). One-sample Wilcoxon test revealed no bias in the HI distribution ($V = 23$, $p = 0.136$).

Wilcoxon test revealed no significant differences between FD and OLF conditions considering both the HI ($V = 2$; $p = 0.789$) (Figure 2) and the ABS-HI ($V = 2$; $p = 0.789$) (Figure 3).

Discussion & conclusion

The main findings of this study are 1) that wolves interacted with the enrichment devices using preferentially one paw, either the right or the left one, showing individual-level lateralization rather than ambidexterity; 2) that the wolves were significantly right pawed, with the exception of the alpha male, that was left pawed; 3) no differences in paw preference in the presence of food-related and olfactory stimuli.

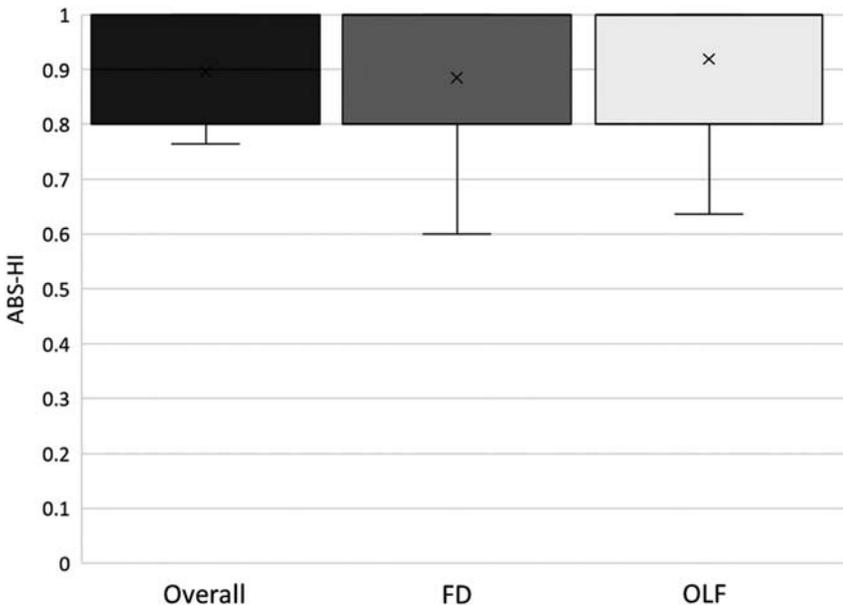


Figure 3. Strength of the paw preference (ABS-HI) in the grey wolf (*Canis lupus*) in different conditions (FD: food-related enrichments; OLF: olfactory enrichments; Overall: FD + OLF). The horizontal lines within the box indicate the medians, crosses within the indicate means, boundaries of the box indicate the first and third quartile. The whiskers extend down from the bottom of the box to the smallest data element that is larger than 1.5 times the interquartile range (IQR).

In the current study, 95% of the bouts were performed using one forepaw rather than both paws and wolves were significantly lateralized at the individual level. This finding is consistent with previous literature on domestic dogs, suggesting that individual-level lateralization is more likely than ambidexterity (Aydinlioglu et al., 2000, 2006; Branson & Rogers, 2006; Hackert et al., 2008; Ocklenburg et al., 2019; Siniscalchi et al., 2008), suggesting that being lateralized can be advantageous during problem-solving tasks (e.g., Magat & Brown, 2009; Rogers, Zucca, & Vallortigara, 2006) such as manipulating environmental enrichment devices.

At the individual level, six out of seven subjects showed a right-paw preference, whereas one wolf was left-pawed. The same pattern was reported also within each condition, in the presence of food-related (four subjects right pawed, one left pawed) and olfactory stimuli (five subjects right pawed, one left pawed). Interestingly, in all conditions, the only left-pawed subject was the alpha male of the pack (A), whereas all other subjects were right-pawed. The finding of a right-paw preference, even if only at the individual level, adds to previous literature on the domestic dog, reporting that approximately 60% of the study individuals showed a right-bias in paw lateralization (Tan, 1987), although more recent studies on this species have highlighted leftward paw preference (Poyser, Caldwell, & Cobb, 2006; Schneider, Delfabbro, & Burns, 2012) or no preference at the group level (Marshall-Pescini et al., 2013; Ocklenburg et al., 2019). When interacting with the enrichment devices, wolves used one paw for holding/manipulating the bag and the other one to provide postural support, as reported in the domestic dog (Wells et al., 2016). It is possible that the right-paw preference for manipulation reported in most of the study subjects resulted from a left-paw preference for postural support that has been extensively described in primates (Harrison & Nystrom, 2010; Hopkins, 2008; Hopkins & de Waal, 1995; Morcillo, Fernandez-Carriba, & Loeches, 2006; Regaiolli et al., 2016) and other vertebrate species (Giljov, Karenina, Ingram, & Malashichev, 2015; Malashichev, 2006; Tommasi & Vallortigara, 1999). If so, this finding would support the hypothesis by MacNeilage and colleagues suggesting a right-hemisphere/left-limb specialization for postural support, allowing the right limb to perform food-related and other activities, leading to the evolution of human right handedness (MacNeilage, 2007; MacNeilage, Rogers, & Vallortigara, 2009; MacNeilage, Studert-Kennedy, & Lindblom, 1987).

Motor lateralization has been found to be related to emotional functioning and temperament in different animal species (for review see Rogers, 2009; Rogers, Vallortigara, & Andrew, 2013). In humans, left-handedness has been associated to a greater involvement in fighting situations (Richardson & Gilman, 2019) and aggression (Faurie & Raymond, 2005), as well as to a greater risk investment (Kuderer & Kirchengast, 2016). These features

related to left-handedness in humans might also characterize the alpha wolf of the current study, explaining the left-paw preference during the interaction with the enrichment devices. Alternatively, we hypothesize that the left-paw preference for postural support in subordinate wolves may result from the activation of right hemisphere characterizing low-ranking individuals. In these subjects, aggressive responses, processing of conspecifics' faces or avoidance and withdrawal behaviours can activate the right side of the brain more than in high-ranking individuals, due to their higher stress level and social tension (Rogers et al., 2013; Vallortigara & Rogers, 2020). Using the left paw to support the body while interacting with the devices would allow a better processing of social stimuli and a quicker response in the case of social tensions or conspecifics' attack, situations involving emotive implications. However, the current study is preliminary and characterized by a very low sample size and scarce data set, thus caution is needed when speculating on our results. Future research on wolves or wild canids is needed to investigate the effect of temperament and sociality on motor lateralization in these species, as well as to understand the role of sex and age in the dog wild counterpart.

Previous research suggested a lateralization of processing of odours in both vertebrate and invertebrate species, suggesting a right-hemisphere involvement in the presence of olfactory stimuli (McGreevy & Rogers, 2005; Rogers & Andrew, 2002; Rogers & Vallortigara, 2008; Royet & Plailly, 2004; Siniscalchi et al., 2011; Siniscalchi, d'Ingeo, Fornelli, et al., 2016; Vallortigara & Andrew, 1994). In the current study, we found no significant differences in both direction and strength of paw preference in the interaction with food-related and olfactory enrichments, suggesting that task typology (manipulation) rather than the stimuli involved affected paw preference in wolves. This lack of differences might be due to the fact that wolves rely on their olfaction when processing and exploring both types of enrichments, involving similar mechanisms and therefore hemispheric activation. Given that the preferential use of a nostril has been shown to be related to the type of odour (Siniscalchi, d'Ingeo, Fornelli, et al., 2016), more studies are needed to investigate lateralization in odours' processing, focusing on different behaviours (e.g., nostril use) that can be biased in the presence of novel or relevant scents.

Finally, previous research on the domestic dog revealed that male and female showed paw preferences at the group level in opposite directions, with female dogs showing a right bias and males being more inclined to use their left paw (Ocklenburg et al., 2019; Quaranta et al., 2004; Wells, 2003). Our results seem not to support this finding in wolves, as all males of the study except for the alpha male were right pawed. However, a greater sample of wolves including both females and males is necessary to investigate the effect of sex on the lateralization in this species.

In conclusion, findings of this study underlined the presence of an individual-level lateralization in wolves, with most of the subjects showing a preference for the right paw when manipulating an object. Thus, being lateralized in paw use seems to be advantageous for wolves, at least during manipulative tasks. The prevalence of lateralized subjects underlined similarities in motor lateralization between domestic dogs and their wild counterparts. Despite the very low sample size of the study pack, these preliminary results seem to reveal traces of lateralization in captive wolves, highlighting a right-pawedness for manipulation in most of the study subjects. However, more studies are needed considering factors such as temperament, hierarchical rank and task complexity on motor lateralization, to shed new light on the evolution of this trait in canids and the effect of domestication.

Acknowledgements

We would like to thank Cesare Avesani Zaborra, Parco Natura Viva CEO and Camillo Sandri, General Curator, for allowing this study to take place at the zoo. We thank the two anonymous reviewers and the Editor for their comments and revisions that improved and clarified the manuscript.

Disclosure statement

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

References

- Aydinlioglu, A. A., Arslanirli, K. A., Cengiz, N., Ragbetli, M. C., & Riza Erdogan, M. A. (2006). The relationships of dog hippocampus to sex and paw preference. *The International Journal of Neuroscience*, 116, 77–88.
- Aydinlioglu, A. A., Arslanirli, K. A., Riza Erdogan, M. A., Ragbetli, M. C., Keleş, P., & Diyarbakirli, S. (2000). The relationship of callosal anatomy to paw preference in dogs. *European Journal of Morphology*, 38, 128–133.
- Batt, L., Batt, M., Baguley, J., & McGreevy, P. (2008). Stability of motor lateralisation in maturing dogs. *Laterality: Asymmetries of Body, Brain and Cognition*, 13, 468–479.
- Branson, N. J., & Rogers, L. J. (2006). Relationship between paw preference strength and noise phobia in *Canis familiaris*. *Journal of Comparative Psychology*, 120, 176–183.
- Faurie, C., & Raymond, M. (2005). Handedness, homicide and negative frequency-dependent selection. *Proceedings of the Royal Society B: Biological Sciences*, 272, 25–28. doi:10.1098/rspb.2004.2926
- Giljov, A., Karenina, K., Ingram, J., & Malashichev, Y. (2015). Parallel emergence of true handedness in the evolution of marsupials and placentals. *Current Biology*, 25, 1878–1884. doi:10.1016/j.cub.2015.05.043
- Hackert, R., Maes, L. D., Herbin, M., Libourel, P. A., & Abourachid, A. (2008). Limb preference in the gallop of dogs and the half-bound of pikas on flat ground. *Laterality: Asymmetries of Body, Brain and Cognition*, 13, 310–319.

- Harrison, R. M., & Nystrom, P. (2010). Handedness in captive gorillas (*Gorilla gorilla*). *Primates*, *51*, 251–261. doi:[10.1007/s10329-010-0191-9](https://doi.org/10.1007/s10329-010-0191-9)
- Hopkins, W. D. (1999). On the other hand: Statistical issues in the assessment and interpretation of hand preference data in nonhuman primates. *International Journal of Primatology*, *20*, 852–866.
- Hopkins, W. D. (2008). Brief communication: Locomotor limb preferences in captive chimpanzees (*Pan troglodytes*): implications for morphological asymmetries in limb bones. *American Journal of Physical Anthropology*, *137*, 113–118. doi:[10.1002/ajpa.20834](https://doi.org/10.1002/ajpa.20834)
- Hopkins, W. D. (2013). Independence of data points in the measurement of hand preferences in primates: statistical problem or urban myth? *American Journal of Physical Anthropology*, *151*, 151–157. doi:[10.1002/ajpa.22248](https://doi.org/10.1002/ajpa.22248)
- Hopkins, W. D., & de Waal, F. B. M. (1995). Behavioral laterality in captive bonobos (*Pan paniscus*): replication and extension. *International Journal of Primatology*, *16*, 261–276. doi:[10.1007/BF02735481](https://doi.org/10.1007/BF02735481)
- Hopkins, W. D., Wesley, M. J., Hostetter, A., Fernandez-Carriba, S., Pilcher, D., & Poss, S. (2001). The use of bouts and frequencies in the evaluation of hand preferences for a coordinated bimanual task in chimpanzees (*Pan troglodytes*): An empirical study comparing two different indices of laterality. *Journal of Comparative Psychology*, *115*, 294–299. doi:[10.1037/0735-7036.115.3.294](https://doi.org/10.1037/0735-7036.115.3.294)
- Hosey, G., Melfi, V., & Pankhurst, S. (2013). *Zoo animals: Behaviour, Management, & welfare* (2nd ed.). Oxford, UK: Oxford University Press.
- Kuderer, S., & Kirchengast, S. (2016). The association of hand preference and sensation seeking behavior. *Journal of Biological and Clinical Anthropology*, *73*, 187–194.
- Lord, K. (2013). A Comparison of the sensory Development of wolves (*Canis lupus lupus*) and dogs (*Canis lupus familiaris*). *Ethology*, *119*, 110–120. doi:[10.1111/eth.12044](https://doi.org/10.1111/eth.12044)
- MacNeillage, P. F. (2007). Present status of the postural origins theory. In W. D. Hopkins (Ed.), *The evolution of hemispheric specialization in primates* (pp. 59–91). Oxford, UK: American Society of Primatologists, Elsevier.
- MacNeillage, P. F., Rogers, L. J., & Vallortigara, G. (2009). Origins of the left and right brain. *Scientific American*, *301*, 60–67.
- MacNeillage, P. F., Studdert-Kennedy, M. G., & Lindblom, B. (1987). Primate handedness reconsidered. *Behavioral Brain Science*, *10*, 247–263. doi:[10.1017/S0140525X00047695](https://doi.org/10.1017/S0140525X00047695)
- Magat, M., & Brown, C. (2009). Laterality enhances cognition in Australian parrots. *Proceedings of the Royal Society B: Biological Sciences*, *276*, 4155–4162. doi:[10.1098/rspb.2009.1397](https://doi.org/10.1098/rspb.2009.1397)
- Malashichev, Y. B. (2006). One-sided limb preference is linked to alternating-limb locomotion in anuran amphibians. *Journal of Comparative Psychology*, *120*, 401–410. doi:[10.1037/0735-7036.120.4.401](https://doi.org/10.1037/0735-7036.120.4.401)
- Marshall-Pescini, S., Barnard, S., Branson, N. J., & Valsecchi, P. (2013). The effect of preferential paw usage on dogs' (*Canis familiaris*) performance in a manipulative problem-solving task. *Behavioural Processes*, *100*, 40–43.
- Marshall-Pescini, S., Basin, C., & Range, F. (2018). A task-experienced partner does not help dogs be as successful as wolves in a cooperative string-pulling task. *Scientific Reports*, *8*, 16049.
- Marshall-Pescini, S., Cafazzo, S., Virányi, Z., & Range, F. (2017). Integrating social ecology in explanations of wolf-dog behavioral differences. *Current Opinion in Behavioral Sciences*, 80–86.
- McGreevy, P. D., Brueckner, A., Thomson, P. C., & Branson, N. J. (2010). Motor laterality in 4 breeds of dog. *Journal of Veterinary Behavior: Clinical Applications and Research*, *5*, 318–323.

- McGreevy, P. D., & Rogers, L. J. (2005). Motor and sensory laterality in thoroughbred horses. *Applied Animal Behaviour Science*, *92*, 337–352.
- McGrew, W. C., & Marchant, L. F. (1997). On the other hand: Current issues in and meta-analysis of the behavioral laterality of hand function in nonhuman primates. *Yearbook of Physical Anthropology*, *40*, 201–232. doi:10.1002/(SICI)1096-8644(1997)25? \201:AID-AJPA8[3.0.CO;2-6
- Mech, L.D. (1970). *The wolf: The ecology and behavior of an endangered species*. (1st ed, p. 384). New York, NY: Natural History Press.
- Michel, G. F., Sheu, C., & Brumley, M. R. (2002). Evidence of a right-shift factor 682 affecting infant hand-use preference from 7 to 11 months of age as revealed by latent class analysis. *Developmental Psychobiology*, *40*, 1–13.
- Morcillo, A., Fernandez-Carriba, D., & Loeches, A. (2006). Asymmetries in postural control and locomotion in chimpanzees (*Pan troglodytes*). *American Journal of Primatology*, *68*, 802–811. doi:10.1002/ajp.20280
- Ocklenburg, S., & Güntürkün, O. (2012). Hemispheric asymmetries: The comparative view. *Frontiers in Psychology*, *3*, 5.
- Ocklenburg, S., Isparta, S., Peterburs, J., & Papadatou-Pastou, M. (2019). Paw preferences in cats. And dogs: Meta-analysis. *Laterality*, *10*, 1–31.
- Poyser, F., Caldwell, C., & Cobb, M. (2006). Dog paw preference shows lability and sex differences. *Behavioural Processes*, *73*, 216–221.
- Quaranta, A., Siniscalchi, M., Frate, A., & Vallortigara, G. (2004). Paw preference in dogs: Relations between lateralised behaviour and immunity. *Behavioural Brain Research*, *153*, 521–525.
- Range, F., Marshall-Pescini, S., Kratz, C., & Virányi, Z. (2019). Wolves lead and dogs follow, but they both cooperate with humans. *Scientific Reports*, *9*, 3796. doi:10.1038/s41598-019-40468-y
- Regaiolli, B., Spiezio, C., & Hopkins, W. D. (2016). Three actions, two groups: Looking for the origin of primate manual lateralization. *Journal of Comparative Psychology*, *130*, 259–268.
- Regaiolli, B., Spiezio, C., & Hopkins, W. D. (2018). Hand preference on unimanual and bimanual tasks in Barbary macaques (*Macaca sylvanus*). *American Journal of Primatology*, *80*, e22745.
- Richardson, T., & Gilman, R. T. (2019). Left-handedness is associated with greater fighting success in humans. *Scientific Reports*, *9*, 15402.
- Rogers, L. J., & Andrew, R. J. (2002). *Comparative vertebrate lateralization*. NY: Cambridge University Press.
- Rogers, L. J., & Vallortigara, G. (2008). From antenna to antenna: Lateral shift of olfactory memory recall by honeybees. *PLoS ONE*, *3*, e2340. doi:10.1371/journal.pone.0002340
- Rogers, L. J., Vallortigara, G., & Andrew, R. J. (2013). *Divided brains: The biology and behaviour of brain asymmetries*. Cambridge University Press.
- Rogers, L. J., Zucca, P., & Vallortigara, G. (2006). Advantages of having a lateralized brain. *Proceedings of the Royal Society B: Biological Sciences (Suppl.)*, *271*, S420–S422.
- Royet, J. P., & Plailly, J. (2004). Lateralization of olfactory processes. *Chemical Senses*, *29*, 731–745.
- Sánchez-Villagra, M. R., Geiger, M., & Schneider, R. A. (2016). The taming of the neural crest: A developmental perspective on the origins of morphological covariation in domesticated mammals. *Royal Society Open Science*, *3*, 160107.
- Schneider, L. A., Delfabbro, P. H., & Burns, N. R. (2012). The influence of cerebral lateralisation on the behaviour of the racing greyhound. *Applied Animal Behaviour Science*, *141*, 57–64.

- Siniscalchi, M., d'Ingeo, S., & Quaranta, A. (2016). The dog nose "KNOWS" fear: Asymmetric nostril use during sniffing at canine and human emotional stimuli. *Behavioural Brain Research*, *304*, 34–41.
- Siniscalchi, M., Quaranta, A., & Rogers, L. J. (2008). Hemispheric specialization in dogs for processing different acoustic stimuli. *PLoS One*, *3*, e3349.
- Siniscalchi, M., Sasso, R., Pepe, A. M., Dimatteo, S., Vallortigara, G., & Quaranta, A. (2011). Sniffing with the right nostril: Lateralization of response to odour stimuli by dogs. *Animal Behaviour*, *82*, 399–404.
- Siniscalchi, M., d'Ingeo, S., Fornelli, S., & Quaranta, A. (2016). Relationship between visuospatial attention and paw preference in dogs. *Scientific Reports*, *6*, 31682. doi:[10.1038/srep31682](https://doi.org/10.1038/srep31682)
- Stancher, G., Sovrano, V. A., & Vallortigara, G. (2018). Motor asymmetries in fishes, amphibians and reptiles. In: Cerebral lateralization and cognition: Evolutionary and Developmental investigations of behavioral Biases. *Progress in Brain Research*, *238*, 35–56.
- Swaigood, R. R., & Shepherdson, D. J. (2005). Scientific Approaches to enrichment and Stereotypies in Zoo animals: What's been done and Where should We Go Next? *Zoo Biology*, *24*, 499–518.
- Tan, U. (1987). Paw preferences in dogs. *The International Journal of Neuroscience*, *32*, 825–829.
- Tomkins, L. M., Thomson, P. C., & McGreevy, P. D. (2010). First-stepping test as a measure of motor laterality in dogs (*Canis familiaris*). *Journal of Veterinary Behavior: Clinical Applications and Research*, *5*, 247–255.
- Tommasi, L., & Vallortigara, G. (1999). Footedness in binocular and monocular chicks. *Laterality: Asymmetries of Body, Brain and Cognition*, *4*, 89–95.
- Vallortigara, G., & Andrew, R. J. (1994). Olfactory lateralization in the chick. *Neuropsychologia*, *32*, 417–423.
- Vallortigara, G., & Rogers, L. J. (2020). A function for the bicameral mind. *Cortex*, *124*, 274–285. doi:[10.1016/j.cortex.2019.11.018](https://doi.org/10.1016/j.cortex.2019.11.018)
- Wells, D. L. (2003). Lateralised behaviour in the domestic dog, *Canis familiaris*. *Behavioural Processes*, *61*, 27–35.
- Wells, D. L., Hepper, P. G., Milligan, A. D., & Barnard, S. (2016). Comparing lateral bias in dogs and humans using the Kong™ ball test. *Applied Animal Behaviour Science*, *176*, 70–76.
- Wells, D. L., Hepper, P. G., Milligan, A. D. S., & Barnard, S. (2018). Stability of motor bias in the domestic dog, *Canis familiaris*. *Behavioural Processes*, *149*, 1–7. doi:[10.1016/j.beproc.2018.01.012](https://doi.org/10.1016/j.beproc.2018.01.012)