



# No evidence for side preference or handedness in a New Zealand rail species with habitual foot-usage, the pukekeo



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## ABSTRACT

Many animals show evidence of cerebral lateralisation, i.e. morphological differences and functional specialisation in two separate hemispheres of the brain. Laterality in behaviour is commonly used as an indicator of cerebral lateralisation, as asymmetry in actions often mirrors asymmetry in the brain. It has been predicted that species that habitually use limbs to manipulate food or resources will develop strong limb preferences, and data in a limited set of taxa support this prediction. However, relatively few species have been studied, limiting our understanding of how taxonomically widespread such behavioural asymmetries might be, and thus how such preferences evolve. Here, we test for limb preference within a new taxon, the rails, using the pukekeo (*Porphyrio p. melanotus*), a species that frequently uses its feet while feeding. We quantified foot-use of 359 individual pukekeo and found that though some individuals show preferences, there was no overall side preference at the population level - roughly equal numbers of individuals showed a left preference, a right preference, or no preference, though we detected a weak preference in adults during long-use behaviours. We also found that the strength of side preference weakened with increased observations of foot-usage. Finally, though patterns were similar when looking at brief and longer foot uses, the within-individual relationships between preference in those contexts was only significant in birds that used their feet at least five times. Together these findings question whether habitual foot use will lead to side preference and suggest that the apparent wide-spread and prevalent nature of this pattern in current literature may be due to a publication bias rather than the general presence of a relationship. Studies that cover a great taxonomic spread are needed.

## 1. Introduction

Cerebral lateralisation, the segregation of the brain into two functionally differing halves is a well-defined characteristic in humans and is widespread through-out vertebrates and some invertebrate species (Rogers, 1997; Bisazza et al., 1998; Byrne et al., 2004; Vallortigara and Rogers, 2005; Jozet-Alves et al., 2012; Rogers et al., 2013; Karenina et al., 2017). When lateralised, the hemispheres of the brain share some functions, but each hemisphere also performs some specialised functions preferentially (Bisazza et al., 1998; Ventolini et al., 2005; Rogers et al., 2013). For example, with visual lateralisation, the right eye/left hemisphere is generally more involved with the processing and coordination of responses that require slower reactions and more consideration (discrimination), whereas the left eye/right hemisphere is more involved in the processing and coordination of responses requiring rapid responses (e.g. vigilance) (Rogers et al., 2004, 2013). The evolution of this lateralisation has allowed the division of labour and has increased neural efficiency and capacity of the brain, leading to

lateralisation of the body and its behaviours, which can alter species biology (Tommasi, 2009; Vallortigara and Rogers, 2005). For example, in many mammalian species mother-infant behaviours occur more often and are stronger on the left side of the body, suggesting that the right hemisphere has dominance in processing social interactions (Karenina et al., 2017). In parrots, strongly lateralised individuals perform better in cognitive tasks (Magat and Brown, 2009). Findings in parrots also indicates that lateralisation of foot use may be related to evolutionary features such as body size and foraging mode (Brown and Magat, 2011b). Additionally, studies have suggested that predator-identification is improved on most species' left side as this form of processing is dominant in the right hemisphere, and as a result, animals are slower to identify or respond to predators approaching on their right side (Rogers et al., 2004).

Brain lateralisation often results in varying kinds of behavioural asymmetries, where side preference can arise in behaviours where there is a choice. For example, when a preference arises in the side is used for an activity (e.g. left or right handed). Side preferences can be observed

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**Table 1**  
Summary of preference behaviours in various invertebrate and vertebrate species. Open circle represents preference present, closed circle represents no preference present. Note that this table is a representative sample of studies rather than a systematic review of all studies.

Class	Species name	Common name	Individual lateralisation	Population lateralisation	Population lateralisation	Reference(s)	Type of preference	Direction of preference	
Cephalopods	<i>Octopus vulgaris</i>	Octopus	○	○	●	Byrne et al., 2004	Visual	Left	
	<i>Sepia officinalis</i>	Cuttlefish	○	○	○	Jozet-Alves et al., 2012; Alves et al., 2007	Behavioural	Left	
Fishes	<i>Corydora aeneus</i>	Bronze corydoras	○	○	○	Bisazza et al., 2000	Behavioural	Right	
	<i>Girardinus falcatus</i>	Goldbelly topminnow	○	○	○	Bisazza et al., 2000	Behavioural	Right	
	<i>Lepomis gibbosus</i>	Pumpkinseed	○	○	○	Bisazza et al., 2000	Behavioural	Right	
	<i>Kribia punctatissima</i>	Italian spring goby	○	○	○	Bisazza et al., 2000	Behavioural	Right	
	<i>Padogobius martensi</i>	Gobies	○	○	○	Bisazza et al., 2000	Behavioural	Right	
	<i>Ancistrus sp.</i>	Common bristlenose catfish	○	○	○	Bisazza et al., 2000	Behavioural	Left	
	<i>Barbus conchomis</i>	Rosy barb	○	○	○	Bisazza et al., 2000	Behavioural	Left	
	<i>Trichogaster trichopterus</i>	Three spot gourami	○	○	○	Bisazza et al., 2000	Behavioural	Left	
	<i>Brachydanio rerio</i>	Zebrafish	○	○	○	Bisazza et al., 2000	Behavioural	Left	
	<i>Pterophyllum scalare</i>	Freshwater angelfish	○	○	○	Bisazza et al., 2000	Behavioural	Left	
	<i>Betta splendens</i>	Siamese fighting fish	○/●	○	●	Bisazza et al., 2000	Behavioural	N/A	
	<i>Channa obscura</i>	Obscure snakehead	○/●	○	●	Bisazza et al., 2000	Behavioural	N/A	
	<i>Gyrinocheilus aymonieri</i>	Siamese algae eater	○/●	○	●	Bisazza et al., 2000	Behavioural	N/A	
	<i>Jenynsia multidentata</i>	Onesided livebearer	○/●	○	●	Bisazza et al., 2000	Behavioural	N/A	
	<i>Syngnathus pulchellus</i>	Pipefish	○/●	○	●	Bisazza et al., 2000	Behavioural	N/A	
	<i>Xenotoca eiseni</i>	Redtail splitfin	○/●	○	●	Bisazza et al., 2000	Behavioural	N/A	
	<i>E. G. C. Aeneus, B. conchorius</i>	Shoaling fish species	○	○	○	Bisazza et al., 2000	Behavioural	All lateralised	
	<i>E. G. C. obscura, X. eiseni</i>	Non-shoaling fish species	○/●	○	○	Bisazza et al., 2000	Behavioural	40% lateralised	
	Amphibians	<i>Bufo viridis</i>	European green toad	●	●	●	Bisazza et al., 1997	Handedness	NA
	Reptiles	<i>Akistrodon piscivorus</i>	Cottonmouth (snake)	○/●	○/●	○/●	Roth, 2003	Coiling Direction	Varied by indiv. & popn. subset
Birds	<i>Neopsophonus bourkii</i>	Bourke's parrot	○	○	○	Brown and Magat, 2011a, b	Handedness	Left	
	<i>Melospitacus undulatus</i>	Budgerigar	○	○	○	Brown and Magat, 2011a, b	Handedness	Left	
	<i>Platyreus elegans</i>	Crimson rosella	○	○	○	Brown and Magat, 2011a, b	Handedness	Left	
	<i>Eclectus roratus</i>	Eclectus parrot	○	○	○	Brown and Magat, 2011a, b	Handedness	Left	
	<i>Eolophus roseicapilla</i>	Galah	○	○	○	Brown and Magat, 2011a, b	Handedness	Left	
	<i>Cacatua sanguinea</i>	Little corella	○	○	○	Brown and Magat, 2011a, b	Handedness	Left	
	<i>Glossopsitta pusilla</i>	Little lorikeet	○	○	○	Brown and Magat, 2011a, b	Handedness	Left	
	<i>Trichoglossus moluccanus</i>	Rainbow lorikeet	○	○	○	Brown and Magat, 2011a, b	Handedness	Left	
	<i>Psephotus haematotus</i>	Red-rumped parrot	○	○	○	Brown and Magat, 2011a, b	Handedness	Left	
	<i>Cacatua galerita</i>	Sulphur-crested cockatoo	○	○	○	Brown and Magat, 2011a, b	Handedness	Left	
	<i>Neophema pulchella</i>	Turquoise parrot	○	○	○	Brown and Magat, 2011a, b	Handedness	Left	
	<i>Alisterus scapularis</i>	Australian king parrot	○	○	○	Brown and Magat, 2011a, b	Handedness	Left	
	<i>Cacatua leadbeateri</i>	Major Mitchell's cockatoo	○	○	○	Brown and Magat, 2011a, b	Handedness	Left	
	<i>Calyptorhynchus banksii</i>	Red-tailed black cockatoo	○	○	○	Brown and Magat, 2011a, b	Handedness	Left	
	<i>Aprosmictus erythropterus</i>	Red-winged parrot	○	○	○	Brown and Magat, 2011a, b	Handedness	Left	
	<i>Polytelis swainsonii</i>	Superb parrot	○	○	○	Brown and Magat, 2011a, b	Handedness	Left	
	<i>Calyptorhynchus finereus</i>	Yellow-tailed black cockatoo	○	○	○	Brown and Magat, 2011a, b	Handedness	Left	
	<i>Nymphicalia hollandicus</i>	Cockatiel	○	○	○	Brown and Magat, 2011a, b	Handedness	Left	
	<i>Amazona amazone</i>	Orange-winged parrot	○	○	○	Friedman and Davis, 1938	Handedness	Left	
	<i>Amazona auripalliata</i>	Yellow-naped parrot	○	○	○	Friedman and Davis, 1938	Handedness	Left	
<i>Amazona oratrix</i>	Yellow-headed parrot	○	○	○	Friedman and Davis, 1938	Handedness	Left		
<i>Amazona festiva</i>	Festive parrot	○	○	○	Friedman and Davis, 1938	Handedness	Left		
<i>Amazona barbadensis</i>	Yellow-shouldered parrot	●	○	○	Friedman and Davis, 1938	Handedness	NA		
<i>Amazona albifrons</i>	Blue-fronted parrot	○	○	○	Friedman and Davis, 1938	Handedness	Left		
<i>Coracopsis nigra</i>	Black parrot	○	○	○	Friedman and Davis, 1938	Handedness	Left		
<i>Psittacula longicauda</i>	Long-tailed parakeet	○	○	○	Friedman and Davis, 1938	Handedness	Left		
<i>Ara severa</i>	Chest-fronted macaw	○	○	○	Friedman and Davis, 1938	Handedness	Left		
<i>Ara macroura</i>	Blue-winged macaw	○	○	○	Friedman and Davis, 1938	Handedness	Left		
<i>Ara macao</i>	Scarlet macaw	○	○	○	Friedman and Davis, 1938	Handedness	Left		
<i>Aratinga leucophthalmus</i>	White-eyed parakeet	○	○	○	Friedman and Davis, 1938	Handedness	Left		

(continued on next page)

Table 1 (continued)

Class	Species name	Common name	Individual lateralisation	Population lateralisation	Reference(s)	Type of preference	Direction of preference
Marsupial mammals	<i>Tanygnathus megalorhynchus</i>	Blue-naped parrot	○	○	Friedman and Davis, 1938	Handedness	Left
	<i>Brothergus jugularis</i>	Orange-chinned parakeet	○	○	Friedman and Davis, 1938	Handedness	Left
	<i>Gallus gallus domesticus</i>	Domestic chicken	○	○	Rogers and Workman, 1993; Tommasi, 1999	Handedness	Right
	<i>Gallus gallus domesticus</i>	Domestic chicken	○	○	Rogers and Anson, 1979	Functions	Varied by function
	<i>Columba livia</i>	Rock dove	○	○	Güntürkün et al., 2000	Visual	Right
	<i>Passer montanus</i>	Tree sparrow	○	○	Franklin and Lima, 2001	Visual	Left
	<i>Junco hyemalis</i>	Dark-eyed junco	○	○	Franklin and Lima, 2001	Visual	Right
	<i>Corvus moneduloides</i>	New Caledonian crow	○	○	Weir et al., 2004	Tool use	Varied by individual
	<i>Himantopus himantopus</i>	Black-winged Stilt	○	○	Ventolini et al., 2005	Multiple Behaviours	Varied by individual
	<i>Parus major</i>	Great tit	○	○	Vince, 1964	Handedness	Varied by individual
	<i>Phoenicopterus ruber</i>	American flamingo	○	○	Anderson et al., 2009, 2010	Neck-resting	Right
	<i>Porphyrio p. melanotus</i>	Pukeko	○	○	Rodgers and Cain, see results	Handedness	NA
	<i>Macropus giganteus</i>	Eastern Kangaroo (Bipedal)	○	○	Karenina et al., 2017; Giljov et al., 2015	Multiple Behaviours	Left
	<i>Macropus rufus</i>	Red Kangaroo (Bipedal)	○	○	Karenina et al., 2017; Giljov et al., 2015	Multiple Behaviours	Left
	<i>Macropus rufogriseus</i>	Red-necked wallaby (Bipedal)	○	○	Giljov et al., 2015	Handedness	Left
Dentalia	<i>Dendrolagus goodfellowi</i>	Goodfellows tree kangaroo	○	●	Giljov et al., 2015	Handedness	Varied by individual
	<i>Bettongia penicillata</i>	Brush-tailed bettong (Bipedal)	○	○	Giljov et al., 2015	Handedness	Left
Placental mammals	<i>Petaurus breviceps</i>	Sugar glider	●	●	Giljov et al., 2015	Handedness	NA
	<i>Monodelphis domestica</i>	Grey short-tailed opossum	●	●	Giljov et al., 2015	Handedness	NA
	<i>Homo sapien</i>	Humans	○	○	Karenina et al., 2017; Forrester et al., 2013	Handedness	Right
	<i>Pan troglodytes</i>	Chimpanzees	○	○	Llorente et al., 2011; Hopkins et al., 2003; Warren, 1980	Handedness	Right
	<i>Equus ferus caballus</i>	Horse	○	○	Karenina et al., 2017	Social Behaviour	Left
Placental mammals	<i>Ruagifer tarandus</i>	Reindeer	○	○	Karenina et al., 2017	Social Behaviour	Left
	<i>Saiga tatarica</i>	Saiga antelope	○	○	Karenina et al., 2017	Social Behaviour	Left
	<i>Ovibos moschatus</i>	Muskox	○	○	Karenina et al., 2017	Social Behaviour	Left
	<i>Ovis ammon</i>	Argali	○	○	Karenina et al., 2017	Social Behaviour	Left
	<i>Ovis aries</i>	Domestic sheep	○	○	Karenina et al., 2017	Social Behaviour	Left
	<i>Odobenus rosmarus</i>	Walrus	○	○	Karenina et al., 2017	Social Behaviour	Left
	<i>Eubalaena australis</i>	Southern right whale	○	○	Karenina et al., 2017	Social Behaviour	Left
	<i>Delphinapterus leucas</i>	Beluga whale	○	○	Karenina et al., 2017	Social Behaviour	Left
	<i>Orcinus orca</i>	Orca	○	○	Karenina et al., 2017	Social Behaviour	Left
	<i>Myotis capaccinii</i>	Long-fingered bat	○	○	Zucca et al., 2010	Handedness	Left

in many behaviours (Table 1), such as side-by-side interactions between mother and infant (Karenina et al., 2017), coiling directions in snakes (Roth, 2003), turn preference in fish (Bisazza et al., 2000), tool use and manufacture in corvids (Weir et al., 2004) and hand or foot preference in bird species, macropods, and primates (Elias et al., 1998; Hopkins et al., 2003; Byrne et al., 2004; Brown and Magat, 2011a, 2011; Gilijov et al., 2015). Limb preference or handedness is one possible product of cerebral lateralisation, and because it is easily observed, it is commonly used to test for evidence of brain lateralisation (McManus and Bryden, 1992). To date, in many species that show manipulative limb use, researchers have reported strong side preferences (Table 1). This led Walker (1980) to argue that extensive manipulative limb use, particularly in food tasks, favours the development of limb preference. However, few species in the animal kingdom use their limbs in manipulative actions, and some species studied show no strong preference (Table 1). Consequently, we have a limited understanding of how phylogenetically widespread handedness, and thus the potential for cerebral lateralisation, might be. This difference across species may be due to evolutionary history (phylogenetic constraints), ecological adaption, context specific costs of laterality, difference in predator risk, or a lack of selective pressure for specialised or manipulative limb use (Brown and Magat, 2011a; Gilijov et al., 2015), suggesting that tests in a variety of species is critical to greater understanding.

The bulk of evidence for handedness in birds stems from the Psittaciformes or parrots, an order known for their intelligence and learning. Within parrots, the majority of species examined show a strong bias when manipulating food objects, only a few species show no apparent side preference (Friedman and Davis, 1938; Rogers, 1980; Harris, 1989; Brown and Magat, 2011a). Few studies have been completed outside this group, with the notable exception of corvids, a group also noted for their intelligence and learning (Weir et al., 2004). The pukeko (*Porphyrio p. melanotus*) is a sub-species of the Australasian swamphen, a widely distributed, large, ground-feeding rail, and a member of the Galliformes, among the oldest order of birds, and quite distant from the parrots. Pukeko often use their feet while feeding, using their toes to manipulate food such as grass stalks and tubers (Pellis, 2011). They are an ideal species to investigate for presence of side preferences and behavioural lateralisation in a distinct order of vertebrates. Here, we observed free-foraging individuals and quantify their foot-usage. We then test for a population preference, individual preferences and age differences, and then explore the relationships between the number of observations of foot-usage, and the strength of the observed foot preference in different groups, to investigate the overall patterns in side preference or handedness within this pukeko population.

## 2. Methods

### 2.1. Field techniques

Data was collected from Tawharanui Regional Park (36.37°S, 174.83°E), a fenced sanctuary north of Auckland, New Zealand operating both recreationally and agriculturally. The area is free of invasive mammalian predators, consists of pastoral, forested and swamp areas, and has a high density of pukeko. Pukeko are highly territorial and sedentary birds (Craig, 1979). Data was collected by systematically moving through these territories and collecting data from each social group, one individual at a time. Because of the territorial and sedentary nature of pukeko, it is unlikely that any individual was sampled more than once.

To quantify potential side preference in foot usage, each individual bird was observed for 5 min. Every instance of foot-usage was noted, along with the type of usage: two types of food-to-beak behaviours, scratch (foot used to scratch face or body), or hold down (using foot to manipulate food item on the ground). During pilot studies we observed that birds displayed two types of foot-to-beak, either bringing food

quickly to the mouth and returning the foot to the ground or standing for a substantial amount of time holding and manipulating the food item. Therefore, food-to-beak was split into transitory (< 3 s) and long (> 3 s) categories. If a bird was out of sight or stopped feeding for longer than 30 s, timing was paused until feeding resumed. If the bird did not reappear, observation ceased, and data was discarded. All observations were made by R. Rodgers, using binoculars or a telescope. Observations ran from November 2016 to February 2017 (Austral summer) and were made between 9am and 5 pm. A general age classification (adult, juvenile or chick) based on basic physical characteristics in size, plumage development and colour of the red frontal shield (black in juveniles) was also identified for each individual (Marchant and Higgins, 1993; Heather and Robertson, 2005). Behavioural data was recorded for a total of 359 individuals; 314 adults, 38 juveniles, and 7 chicks.

### 2.2. Statistical analysis

We calculated total foot-use frequencies for each behavioural type. Because scratches and hold downs were infrequent overall (80 individuals scratched; 39 individuals used their feet to hold food down for manipulation), and almost always occurred only once during the observations period, we excluded these behaviours from further analyses. Few chicks were observed, and they rarely used their feet ( $n = 7$ ), so chick observations were excluded from all analyses. Food-to-beak was the most common observation, and we used each individuals foot-use frequencies to calculate a laterality index score (LI hereafter), the proportion of total uses by the left foot ( $LI = (L-R)/(L + R)$ ) (Richardson, 1976). The laterality index was scaled so that individuals with a pure right preference scored -1, and pure left preference scored +1; individuals showing no preference scored zero. We calculated a separate score for transitory and long use behaviour. Individuals that did not ever show transitory or long foot-to-beak use were excluded from each respective analysis. Birds were grouped for side preference using their laterality indices: right preference ( $R$ ) =  $-1.0:-0.25$ ; ambidextrous =  $-0.25:0.25$ ; left preference ( $L$ ) =  $0.25:1.0$ . These boundaries require a bird to use one foot at least 75% of the time to be considered lateralised (Friedman & David 1938; Weir et al., 2004). Once again, these groups were determined separately for transitory and long use. The degree of handedness (or strength of the preference) can be evaluated using the absolute value of the side preference while the sign indicates direction of preference. These groups are only used to test for differences in foot use frequency and for figures.

We tested for differences in total observed foot-usages according to age (adult / juvenile), and preference group (Right, Left, Ambidextrous), using separate Generalized Linear Models with a Poisson error distribution. To determine whether the number of foot-usages was related to the strength of the foot preference, we tested for a relationship between the total number of foot uses and absolute laterality index score (magnitude without regard for sign), and included laterality group, and the interaction absolute index and group. In this manner a strong left or right preference has the same score. These analyses were repeated for both transitory and long use indices. Finally, because animals may show different preferences when engaged in different activities, we then examined the relationships between transitory and long laterality indices. This model included only individuals that showed both types of behaviours at least once. Because we observed age effects that might alter results, and because number of foot uses was related to laterality index, we repeated all analyses after excluding juveniles and after excluding individuals that failed to use their feet at least 5 times during the observation period. For overall population laterality we also repeated this test using only individuals that engaged in foot-to-beak uses at least 10 times, though this results in a very limited dataset ( $N = 70$ ). All analyses were conducted in JMP 14 (SAS Institute). To visualise the relationships between frequency of foot-use and strength of foot preference we have used funnel plots. Funnel plots illustrate the dependence of apparent preference on the number of foot

**Table 2**  
Series of tests repeated for each of three datasets. Bold indicates significant relationships, italics indicate trends.

Question, test statistic	Full dataset n = 244 (excludes chicks, and adults that did not use feet at least once) Test statistic, p-value	Adult dataset n = 279 (Full dataset excluding juveniles) Test statistic, p-value	Five-use dataset n = 153 (Full dataset excluding individuals that did not use their feet at least 5x) Test statistic, p-value
a) Age difference in total number of foot uses GLM Poisson distribution.	Adult: n, mean $\pm$ SE; 223, 8.3 $\pm$ 0.42 Juveniles :n, mean $\pm$ SE; 21, 6.7 $\pm$ 1.38 <b>GLM X<sup>2</sup> = 6.8, Age B 0.11 <math>\pm</math> 0.04, P = 0.009</b>	NA	Adult: n, mean $\pm$ SE 141, 11.67 $\pm$ 0.50 Juveniles: n, mean $\pm$ SE 12, 9.9 $\pm$ 1.71 <i>GLM X<sup>2</sup> = 2.7, Age B 0.08 <math>\pm</math> 0.05, P = 0.10</i>
b) Age differences in <i>transitory</i> use laterality index GLM Normal distribution	Adult: n, mean $\pm$ SE 221, 0.03 $\pm$ 0.05 Juveniles: n, mean $\pm$ SE 23, 0.05 $\pm$ 0.15 GLM X <sup>2</sup> = 0.03 Age B -0.013 $\pm$ 0.08, P = 0.9	NA	Adult: n, mean $\pm$ SE, 119, 0.002 $\pm$ 0.06 Juveniles: n, mean $\pm$ SE, 10, -0.07 $\pm$ 0.19 GLM X <sup>2</sup> = 0.15 Age B 0.04 $\pm$ 0.10, P = 0.7
c) Age differences in <i>long</i> use laterality index GLM Normal distribution	Adult: n, mean $\pm$ SE 215, 0.09 $\pm$ 0.05 Juveniles: n, mean $\pm$ SE 18, -0.17 $\pm$ 0.17 GLM X <sup>2</sup> = 2.2 Age B 0.58 $\pm$ 0.4, P = 0.14	NA	Adult: n, mean $\pm$ SE, 122, 0.04 $\pm$ 0.05 Juveniles: n, mean $\pm$ SE, 11, -0.19 $\pm$ 0.17 GLM X <sup>2</sup> = 0.16 Age B 0.90 $\pm$ 0.64, P = 0.2
d) Population level side preference <i>Transitory</i> laterality (Percentages in groups and one-sample t-test on indices)	<i>Ambi</i> , n = 57, 23.4% Left, n = 94, 38.5% Right, n = 93, 38.1% laterality score $\pm$ SE, 0.031 $\pm$ 0.05 <i>t</i> <sub>244</sub> = 0.66, P = 0.5	<i>Ambi</i> , n = 51, 23.1% Left, n = 85, 38.5% Right, n = 85, 38.5% laterality score $\pm$ SE, 0.029 $\pm$ 0.05 <i>t</i> <sub>221</sub> = 0.58, P = 0.56	<i>Ambi</i> , n = 41, 28.3% Left, n = 45, 31.0% Right, n = 59, 40.7%; laterality score $\pm$ SE, -0.025 $\pm$ 0.05 <i>t</i> <sub>160</sub> = -0.48, P = 0.63
e) Population level side preference <i>Long</i> laterality (Percentages in groups and one-sample t-test on indices)	<i>Ambi</i> , n = 75, 32.1% Left, n = 94, 40.3% Right, n = 64, 27.5% laterality score $\pm$ SE, 0.07 $\pm$ 0.05 <i>t</i> <sub>215</sub> = 1.55, P = 0.12	<i>Ambi</i> , n = 65, 30.2% Left, n = 90, 41.9% Right, n = 60, 27.9% laterality score $\pm$ SE, 0.09 $\pm$ 0.05 <i>t</i> <sub>215</sub> = 1.93, P = 0.055	<i>Ambi</i> , n = 43, 28.9% Left, n = 50, 33.6% Right, n = 56, 37.6%; laterality score $\pm$ SE, 0.05 $\pm$ 0.06 <i>t</i> <sub>150</sub> = 0.95, P = 0.25
f) <i>Transitory</i> laterality group differences in total number of transitory food to beak actions GLM Poisson *denotes sig difference from <i>Ambi</i>	<i>Ambi</i> uses $\pm$ SE, 4.9 $\pm$ 0.4 Left uses $\pm$ SE, 2.7 $\pm$ 0.3*Right uses $\pm$ SE, 3.2 $\pm$ 0.6*GLM X <sup>2</sup> = 48.9, P < 0.0001	<i>Ambi</i> uses $\pm$ SE, 5.0 $\pm$ 0.4 Left uses $\pm$ SE, 2.8 $\pm$ 0.3*Right uses $\pm$ SE, 3.2 $\pm$ 0.3*GLM X <sup>2</sup> = 42.7, P < 0.0001	<i>Ambi</i> uses $\pm$ SE, 6.1 $\pm$ 0.6 Left uses $\pm$ SE, 4.3 $\pm$ 0.6*Right uses $\pm$ SE, 4.6 $\pm$ 0.6*GLM X <sup>2</sup> = 13.3, P = 0.001
g) <i>Long</i> laterality group differences in total number of long food to beak actions. GLM Poisson* denotes sig difference from <i>Ambi</i>	<i>Ambi</i> uses $\pm$ SE, 7.6 $\pm$ 0.5*Left uses $\pm$ SE, 4.4 $\pm$ 0.4*Right uses $\pm$ SE, 4.1 $\pm$ 0.5*GLM X <sup>2</sup> = 95.1, P < 0.0001	<i>Ambi</i> uses $\pm$ SE, 7.6 $\pm$ 0.5*Left uses $\pm$ SE, 4.54 $\pm$ 0.4*Right uses $\pm$ SE, 4.1 $\pm$ 0.5*GLM X <sup>2</sup> = 81.4, P < 0.0001	<i>Ambi</i> uses $\pm$ SE, 9.1 $\pm$ 0.6 Left uses $\pm$ SE, 9.5 $\pm$ 0.6 Right uses $\pm$ SE, 8.2 $\pm$ 0.6 GLM X <sup>2</sup> = 2.9, P = 0.2
h) Relationship between strength of foot preference in <i>transitory</i> uses (absolute index) and total number of transitory uses. GLM Normal	GLM X <sup>2</sup> = 329.5, P < 0.0001 Total uses X <sup>2</sup> = 59.3, P < 0.0001 Lat group X <sup>2</sup> = 268.1, P < 0.0001 Group x Total uses X <sup>2</sup> = 55.0, P < 0.0001	GLM X <sup>2</sup> = 292.7, P < 0.0001 Total uses X <sup>2</sup> = 50.4, P < 0.0001 Lat group X <sup>2</sup> = 237.6, P < 0.0001 Group x Total uses X <sup>2</sup> = 47.5, P < 0.0001	GLM X <sup>2</sup> = 152.8, P < 0.0001 Total uses X <sup>2</sup> = 18.7, P < 0.0001 Lat group X <sup>2</sup> = 127.3, P < 0.0001 Group x Total uses X <sup>2</sup> = 20.2, P < 0.0001
i) Relationship between strength of foot preference in <i>long</i> uses (absolute index) and total number of long uses. GLM Normal	GLM X <sup>2</sup> = 309.9, P < 0.0001 Total uses X <sup>2</sup> = 39.4, P < 0.0001 Lat group X <sup>2</sup> = 237.0, P < 0.0001 Group x Total uses X <sup>2</sup> = 29.9, P < 0.0001	GLM X <sup>2</sup> = 279.5, P < 0.0001 Total uses X <sup>2</sup> = 31.1, P < 0.0001 Lat group X <sup>2</sup> = 219.2, P < 0.0001 Group x Total uses X <sup>2</sup> = 24.0, P < 0.0001	GLM X <sup>2</sup> = 151.8, P < 0.0001 Total uses X <sup>2</sup> = 10.8, P = 0.001 Lat group X <sup>2</sup> = 134.1, P < 0.0001 Group x Total uses X <sup>2</sup> = 6.3, P = 0.04
j) Relationship between <i>transitory</i> and <i>long</i> use laterality indices Linear regression	R <sup>2</sup> = 0.02, N = 171 B = 0.01, P = 0.18	R <sup>2</sup> = 0.001, N = 186 B = 0.12, P = 0.11	R <sup>2</sup> = 0.05, N = 141 B = 0.22, P = 0.007

use observations per individual (Palmer, 2002). All figures were constructed in R 3.4 (Cran) using the “ggplot2”, and “funnelr” packages.

### 3. Results

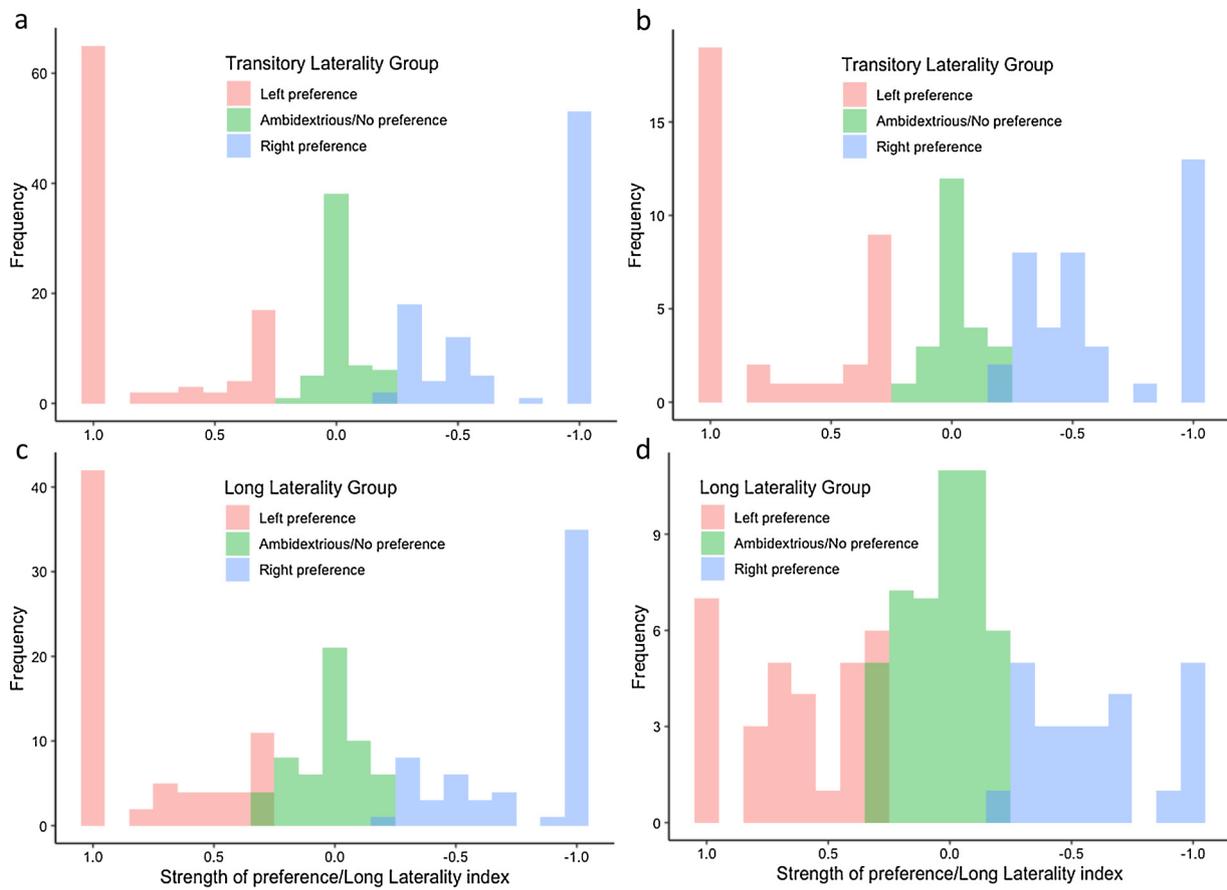
#### 3.1. Age differences in foot use and laterality

Individuals varied considerably in whether and how they used their feet during the observation time. Of the 359 individuals we observed, 309 used their foot at least once during the observations period (number of foot-uses: range, mean  $\pm$  SE; 0–37, 6.24  $\pm$  0.34 excluding chicks). Adults used their feet more frequently than juveniles when looking at the entire data set, but this difference was only marginal when restricting the data to individuals that used their feet at least five times (Five-use, Table 2a). Further, there were no age differences in transitory or long use laterality indices (Table 2b & c). These patterns were consistent when looking at all birds that used their feet (Full dataset) and Five-use birds.

#### 3.2. No side preference found at population level, limited evidence of individual level preference

Roughly similar proportions of the population were found in each preference group, both for transitory and long-use (Table 2d & e). There was no population level foot preference in either measure, though there were individuals with strong preferences producing a distribution with three peaks (Fig. 1a, c; Table 2c). Restricting the dataset to individuals that use their feet at least five times reduces the number of birds with an apparent side preference, producing a normal distribution of side preferences; but no overall population side preference was detected (Fig. 1b, d; Table 2d & e). This pattern held across the datasets. However, there was a trend for adults to slightly prefer left feet in long-use, but only when looking at the entire adult dataset, it was not observed in the five-use data set. Further, it was not observed when restricting transitory or long use to 10 or more uses (Long laterality score  $\pm$  SE, 0.04  $\pm$  0.07; *t*<sub>37</sub> = 0.5, P = 0.6; Transitory laterality score  $\pm$  SE, 0.05  $\pm$  0.1; *t*<sub>14</sub> = -0.5, P = 0.6).

Birds that used their feet more were more likely to be ambidextrous than have either left or right preferences in all of the datasets for transitory use, and for long use - in the full and adult datasets, but not five-use dataset (Fig. 2; Table 2f & g).

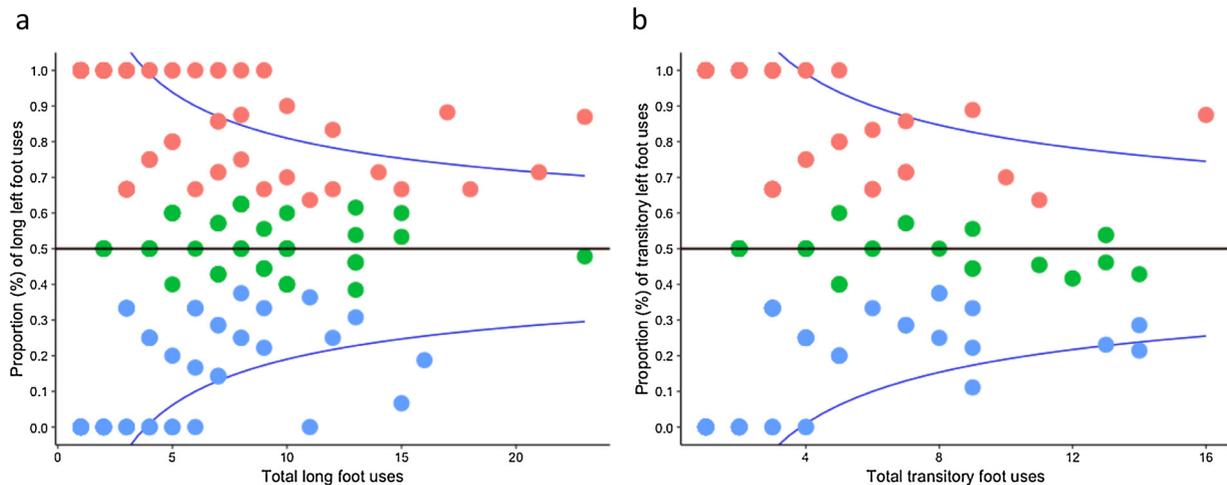


**Fig. 1.** Top row - histograms illustrating transitory laterality indices of individuals according to laterality group for all individuals (a) that used their feet, and individuals that use their feet at least 5 times during the observation period (b). Bottom row - histograms illustrating long-use laterality indices of individuals according to laterality group for all individuals that used their feet (c), and individuals that use their feet at least 5 times during the observation period (d). Note that the y-axis changes between the top and bottom rows.

**3.3. Negative relationship between frequency of foot-use and strength of side preference**

We found a negative relationship between the strength of foot absolute preference (absolute index) and the total number of foot-uses (Table 2h & i). In other words, individuals that used their feet less often

showed stronger side preferences than those who used their feet more often, but only in left and right groups; the overall effect was not present in the Ambidextrous group (Fig. 2; Table 2g). This pattern held for both transitory and long use behaviour.



**Fig. 2.** Funnel plots illustrating the relationship between strength of preference (% left uses) and total number of transitory uses (a) and long uses (b). Solid black line indicates the 50% foot usage, curved lines indicate 95% confidence limits. Points above or below the curved lines are individuals that were significantly biased for left or right foot use. Colours refer to index groups, red for left preference, green for ambidextrous, blue for right preference. Note that points are not jittered and often overlap.

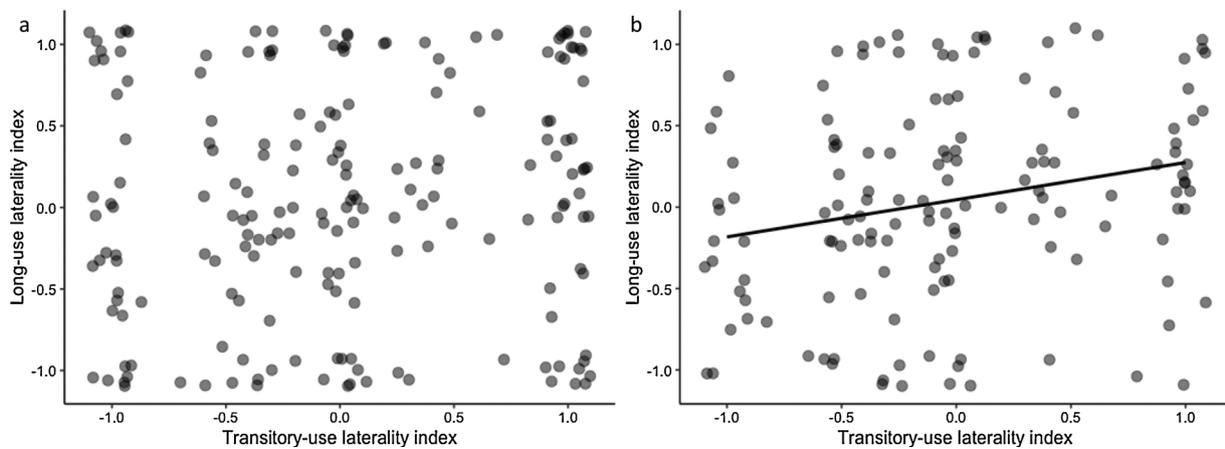


Fig. 3. Relationship between the strength of foot preference for transitory and long use. Panel a. includes all birds that have laterality scores for long and short uses, panel b. is the subset that use their feet at least five times during the observation period; the line indicates the linear regression line. Points are jittered slightly for visual clarity.

### 3.4. Correlation between transitory and long use laterality indexes

There was no relationship between transitory and long use laterality indexes in the Full or adult dataset. However, in the Five-use dataset, there was a weak ( $R^2 = 0.05$ ), but significant ( $P = 0.007$ ), relationship (Fig. 3, Table 2j).

## 4. Discussion

### 4.1. Population and individual level preference

Regardless of the type of foot action performed (transitory or long food-to-beak), and however we limited the dataset (at least 1 use, no juveniles, at least 5 uses, at least 10 uses), we found no significant population level foot preference in either direction (left or right). Although some birds showed an individual preference, there were similar amounts of left and right users overall, and an equal number using both feet in roughly equal amounts, i.e. ambidextrous. According to some definitions, only 51% of individuals in a population must be lateralised in the same direction for a population to be considered lateralised (Bisazza et al., 1998). Even by this low bar, pukeko do not appear to possess a population level side preference in foot-use, though other forms of behavioural lateralisation and side preferences may exist. This finding is in contrast to the most extensively researched birds for limb use preference, parrots, of which most species show strong side preference. Parrots and pukeko are distantly related and though both use their feet extensively to manipulate food items, there are large differences in ecology and behaviour.

Fewer studies have been done on limb preferences outside the parrots, but there is a large body of work examining side preferences in chickens, and other studies in pigeons, stilts, flamingos, crows, waders, and some songbird species (Table 1; Vince, 1964; Rogers and Workman, 1993; Tommasi, 1999; Franklin and Lima, 2001; Weir et al., 2004; Ventolini et al., 2005; Anderson et al., 2009). In each study, there is some evidence of side preference, indicating potential lateralisation, though these species rarely use limbs for manipulations, and these studies rely on other forms of preference (e.g. preferred eye etc.). Further, though studies generally report individual laterality, not all species show population level laterality (e.g. 15 of 23 species in Brown and Magat, 2011b; 11 of 16 species in Brown and Magat, 2011a). Limb preference have been less well-studied in taxa outside of birds and primates, but there is strong evidence for side preference and lateralisation, both at the population and individual levels, within some fish, mammals (placental and marsupial), reptiles, and invertebrate species (Table 1). The majority of these studies examine side preferences more

generally rather than limb-use and many find individual preferences without population level preference. For instance, horses and marmosets both show population level side preferences in the absence of population level limb preferences (Hook-Costigan and Rogers, 1998; Austin and Rogers, 2012). In contrast, research on rodents and bi-pedal marsupials that regularly use their front paws when feeding generally show both individual and population preferences, while quadrupedal marsupials, which do not use paws when feeding, show no such preferences (Betancur et al., 1991; Gilijov et al., 2015). It is important to consider here reasons for these patterns in the current research, and whether they are due to a publication bias or are actually reflective of the natural spread of lateralisation.

Because pukeko use their limbs extensively, particularly during manipulation of food items which requires strong foot-eye coordination, we predicted a population level side preference, but found no strong support for this possibility. However, we did find a weak trend for left foot preference when looking at only long-use preferences within adults (excluding juveniles and chicks), though not in the five-use dataset. Long-use behaviours may be a better measure of side preference as they are more reflective of extended manipulation and true skill, rather than an impulsive preference when quickly picking something up, for example. Although this preference was present, it was very weak when compared to other species. During tool use, where longer manipulation is required, New Caledonian crows (*Corvus moneduloides*) individuals show strong lateralisation, however the population could not be considered lateralised due to an even spread of limb preference between individuals (Weir et al., 2004). Additionally, handedness is believed to be linked to visualisation in many behaviours in animals. Brown and Magat (2011a) found strong correlation between foot and eye preferences in parrots during manipulative activities. These points suggest handedness may be most detectable, and most ecologically relevant, in the context of behaviours that require high levels of dexterity, and this should be considered in future studies.

Although we found no overall side preference in this pukeko population, roughly half of the population showed some individual preferences, but in equal number in either direction. A previous study by Magat and Brown (2009) showed that across multiple parrot species, within individuals, a stronger preference is related to a higher cognitive/problem solving ability, suggesting birds with stronger preferences may have improved cognitive ability. Similar results were also found in guppy species, where more lateralised individuals showed higher numerical skills (Dadda et al., 2015). It is possible that individual pukeko that show little or no preference have more limited cognitive abilities than birds with stronger preferences.

#### 4.2. Foot-use and strength of preference

We found a strong negative relationship between the frequency of foot-use and the strength of side preference. This suggests two possibilities. 1), that individuals using their feet less often have stronger side preferences than those using their feet more; or 2), birds appear to have stronger preferences when fewer observations are made as a by-product of limited sampling i.e. the apparent preference was a by-product of too few observations. We used a single focal observation period for each individual, and although we had a large sample size, the lack of repeat sampling of individuals means that we cannot determine how representative the single observation period was of that individual's overall behaviour. These results underscore the importance of repeated measures and multiple observation periods. For instance, [Brown and Magat \(2011a\)](#) tested 16 parrot species for foot and eye preference, including 10 replicate tests for each individual within every species. This is more challenging in free-living animals, but possible when individuals are uniquely tagged or banded.

#### 4.3. Lack of relationship between short and long hold laterality indexes

We found no clear relationship between the transitory and long use indices. In other words, a strong preference in one context was not predictive of preference in the other context. The lack of a strong relationship between transitory and long use indices suggests that either there are no overall limb preferences in pukeko, or that preference between different types of tasks are unrelated. [Tommasi \(1999\)](#) argued that in chicks, limb choice is based on maintaining postural and positional control by the grounded foot, rather than the behaviour being carried out by the lifted foot. Evidence from the [Tommasi \(1999\)](#) study indicates the brain hemisphere linked to the eye being used for visual identification of objects is activated for posture, and the other hemisphere takes control of manipulative action. However, if this were the case in pukeko, we would expect consistency among individuals, with the same foot to be used for either action (lifted or grounded), while instead we see marked variation. Importantly, this lack of relationship underscores the importance of examining foot use in a variety of behavioural contexts, as preference in one does not reflect preference in another.

#### 4.4. Varied use and age differences

In this pukeko population, we observed considerable variation in the frequency of foot-use. Most individuals used their feet for manipulative limb actions often, though a proportion did not use them at all. We also found differences in foot-use between age groups, with adults using their feet more often than juveniles. Age differences may indicate that pukeko develop the ability to use their feet for feeding, either as a learned or inherited/innate behaviour. There are mixed opinions on handedness or side preference being an inherited or learned trait, with evidence suggesting it is innate in some species, including humans, but learned in other species, such as primates ([Warren, 1980](#); [Forrester et al., 2013](#)). Heritability studies in lab populations suggests there is a strong genetic component to side preferences in some species (e.g. mice - [Betancur et al., 1991](#); teleost fish - [Bisazza et al., 2005](#)). Although the 'adult' birds in our study were of uncertain ages, if our observed pattern persists, the individuals that seem to rarely use their feet were the younger birds who may be still in the process of learning. Alternatively, adults and juveniles may have different diets or preferred food types. Chicks were rarely observed using their feet, likely due to development of diet with age, and were excluded from analyses, so no conclusions can be drawn on this possibility. Further studies including collection of detailed data across developmental stages would be required. Importantly, this study was conducted in a sanctuary free of mammalian predators (though avian predators are still present), which may affect the development and expression of some type of lateralised behaviours,

particularly processing the presence of a predator ([Rogers et al., 2004](#)). Some of the observed variation in foot use within adults may have been driven by individual differences in propensity to use feet while foraging or by different food or vegetation types requiring differing amounts of foot-usage. Different species of vegetation have different physical features, therefore require varying levels of manipulation for consumption. A future study including vegetative data is recommended, but was outside the scope of this study.

## 5. Conclusion

A broader understanding of the taxonomic diversity of limb side preference and cerebral lateralisation requires studies across taxa, however, few species use their limbs to manipulate items, making this breadth difficult to acquire. As indicated in [Table 1](#), side preference research is quite taxonomically biased, particularly in regards to limb preferences, and given the number of positive findings, may show stronger patterns due to publication bias. Pukeko provide an excellent model for future research, as they are phylogenetically distant from most other birds previously studied, yet show clear and well-developed limb use for manipulation of food items. Our results suggest that pukeko may also be an ideal model for investigating development of foot-use behaviours, the role of learning, and whether and to what extent side preference reflects broader cognitive ability. Further, they may represent a species that is somewhere along the continuum of lateralised versus non-lateralised, and thus a good model for understanding the evolution of lateralised limb preference or other behaviours.

## Ethical note

All data was obtained using only observational techniques. No direct handling or manipulation was involved in this research, thus it adheres to the ASAB/ABS Guidelines for the Use of Animals in Research.

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