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Brown, C., & Magat, M. (2011). The evolution of lateralized foot use in parrots: a phylogenetic approach. *Behavioral Ecology*, arr114.

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The Evolution of Lateralized Foot Use in Parrots: A Phylogenetic Approach

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KEYWORDS

behavior, ecology, foraging, laterality, lateralization, phylogeny

ABSTRACT

Cerebral lateralization refers to the division of cognitive function in either brain hemisphere and may be overtly expressed as behavioral asymmetries, such as handedness. The evolutionary history of laterality is of considerable interest due to its close link with the development of human language. Although considerable research effort has aimed at the proximate explanations of cerebral lateralization, considerably less attention has been paid to ultimate explanations. The extent to which laterality is constrained by phylogeny or shaped by ecological forces through natural selection has received little attention. Here, the foot preference of 23 species of Australian parrots was examined to investigate the link between laterality and body size. The raw data indicated that the strength of laterality was related to body size and an associated foraging mode. The results of the phylogenetic generalized least squares, however, indicated that both the pattern (left, right, or ambidextrous) and strength of laterality showed a high degree of phylogenetic inertia. Regressions based on independent contrasts revealed no relationship between laterality and body size. These results suggest that laterality in Australian parrots has been shaped by just a few events deep in their evolutionary history. We hypothesize that cerebral lateralization may provide a fitness benefit to larger bodied species that extract seeds from seedpods using coordinated foot-beak actions. The secondary loss of laterality in smaller body species may have been associated with a shift to grazing on small seeds and blossoms as Australia became increasingly arid.

INTRODUCTION

Cerebral lateralization (the division of cognitive processing between the 2 brain hemispheres) was considered a unique human trait for over a century because of its intimate relationship with the control of human speech and other “higher order” cognitive functions (Crow et al. 1998; Rogers 2000; Corballis 2002). Recent studies on lateralization of cognitive function have shown that it is in fact a ubiquitous vertebrate trait and may be common even among invertebrates (Vallortigara 2000; Byrne et al. 2002; Rogers and Vallortigara 2008). Cerebral lateralization is often expressed behaviorally and behavioral side biases that it produces are collectively referred to as laterality. Domestic chicks, for example, have a left-sided turning bias (Casey and Karpinski 1999), toads use the right paw to wipe objects from their head (Bisazza et al. 1996), and a number of parrot species favor the left or right foot to manipulate objects (Rogers 1980; Magat and Brown 2009). Cerebral lateralization, therefore, is most likely an ancient

evolutionary trait that has a substantial influence on behavioral expression in animals and provides a noninvasive insight into the workings of the animal mind.

Several lines of evidence suggest that laterality plays an important role in shaping the everyday behavior of animals and is subject to natural selection (Vallortigara and Rogers 2005). Firstly, there is ample evidence that laterality varies between individuals within populations. For example, individual chimps show different hand preferences while fishing for termites and strongly lateralized individuals are more efficient at extracting termites than ambidextrous individuals irrespective which hand they use (Marchant and McGrew 1996). Secondly, variation in laterality has fitness consequences; strongly lateralized parrots are better able to solve novel problems than nonlateralized parrots (Magat and Brown 2009). Similarly, schools comprised of strongly lateralized fish are more highly synchronized than schools of nonlateralized fish (Bisazza and Dadda 2005). Lastly, lines of strongly and left- and right-biased fish populations have been produced in the laboratory by artificial selection thus, in fish at least, laterality is partially heritable (Bisazza et al. 2000; Brown et al. 2007). Moreover, comparative data collected from fish populations that differ in their exposure to predation pressure reveal population level variation in laterality (Brown et al. 2004). Thus, there is also some evidence of evolution acting to shape lateralized characters in wild populations.

If laterality is favored by natural selection as illustrated above, it raises the intriguing question as to why we see so much variation at both the individual and species levels. Put simply, why are not all animals strongly lateralized? Some species of parrots contain left, right footed, and ambidextrous individuals approximating a normal distribution at the species level. In other species, however, the population distribution is strongly skewed with all individuals being strongly left footed, whereas in still other species, all individuals are strongly right footed (Brown and Magat 2011). This conundrum has received considerable attention in reviews addressing various factors that might contribute to population level biases in laterality (see e.g., Vallortigara and Rogers 2005; Corballis 2009; Ghirlanda et al. 2009). More generally, the lack of uniformity within species and across closely related species suggests that laterality must also incur costs that are likely to be context specific. Experimental work on fishes has shown that strongly lateralized individuals have a tendency to consistently turn in one direction, which reduces their ability to navigate efficiently within a maze (Brown and Braithwaite 2005). Similarly, strongly lateralized fish are more likely to make errors when attempting to choose between laterally positioned schools of varying sizes (Dadda et al. 2009). From a behavioral ecology perspective, we might expect the relative costs and benefits associated with laterality to vary depending on the physical and social environment in which animals live and the various selective forces that operate within that environment (e.g., predators, Brown et al. 2004).

One of the most obvious examples of laterality is right-hand preference to manipulate objects in humans. Lateralization of limb use at the population level akin to that observed in human handedness where approximately 90% of the population is right handed appears to be relatively uncommon in the animal world, although there have been multiple attempts to identify a nonhuman precursor particularly among primates. Pioneering work by Hopkins (reviewed by Corballis 2009) showed that captive chimps also display right-hand biases in a range of tasks, but the level of bias rarely exceeded 65%. Meta-analysis has revealed the species level laterality in primates is rare and almost entirely absent in wild populations (McGrew and Marchant 1997; Papademetriou et al. 2005). For example, studies examining termite fishing in wild chimpanzees have shown that limb biases can be found in individuals but no bias exists in the general population (Marchant and McGrew 1996). Recent evidence has suggested that captive chimpanzees prefer to use their right hand during communicative gesturing (Meguerditchian et al. 2010), but this is linked to language formation rather than object manipulation. Thus, there is to be continued debate regarding the evidence for hand biases while manipulating objects among primates (Hopkins and Cantalupo 2005). There is also some evidence of hand preferences in rats when reaching for food where

73% of the population showed a right paw preference (Guven et al. 2003). Walker (1980) has stated a general hypothesis that preferential use of a limb occurs only in those species that use their limbs for manipulative tasks. Rogers (2009) further suggests that the nature of the task is likely more important than the complexity of the task per second. Thus, the expression of limb preferences for manipulating objects may not show a consistent phylogenetic signal, and results could vary depending on the assay applied. Moreover, given that laterality varies between populations and may have varying costs and benefits depending on the context, it may be that ecological variables play a more important role in shaping the evolution of laterality than relatedness by descent (Brown et al. 2004).

Many species of parrots have strong preferences for using one foot for feeding (Harris 1989), and in contemporary debates about laterality in animals, the parrot is often cited as an exemplar of laterality in limb function at the population level comparable in kind and strength to handedness in humans (Friedmann and Davis 1938; Rogers 1980; Magat and Brown 2009). Brown and Magat 2011 analyzed the link between foot preferences and eye preferences in 16 species of parrots and found considerable variability between species. In all but one case, eye and foot preferences while viewing and manipulating potential food items were highly correlated suggesting the cerebral lateralization, eye and foot preferences are all functionally related. The comparative analysis revealed that some species are left handed at the population level, others are right handed, whereas others contain individuals spread across the spectrum. The reason for such variability and the evolutionary history of laterality in parrots in general has yet to be explored. Examination of the phylogenetic distribution of traits can provide information regarding their evolutionary history. When taken together with ecological data, one can elucidate the likely evolutionary forces that may have shaped the distribution of the trait over time.

Australian parrots occupy a wide range of habitats and feed on a variety of different food sources, some requiring manipulation with the foot (e.g., large banksia seedpods), whereas others do not (e.g., small grass seeds and nectar). Thus, we can use parrots as a model family to examine the link between foraging ecology and the evolution of lateralization. The preferential use of the left or right foot, however, may also be constrained by phylogeny whereby closely related species should show evidence of niche conservatism (i.e., identity by descent). In the latter case, we would expect to see consistent foot preferences within each of the major parrot clades, whereas in the former case, laterality ought to be correlated with ecological variables. Naturally, these are not mutually exclusive alternatives, thus the phylogenetic distribution of the trait may show evidence of both processes operating over various time scales. Moreover, our research examining the link between cognition and laterality in parrots revealed that there is no particular advantage to being left or right handed, so long as cognitive and/or motor function is lateralized the corresponding fitness advantage will be realized (Magat and Brown 2009). Thus, one might predict that the strength of laterality may be more strongly shaped by ecological variables than the direction of laterality.

Here, we examined laterality in 23 species of parrots encompassing most of the diversity across the Australian parrot phylogeny to investigate ecological and phylogenetic correlates of lateralization. There were 2 primary aims in this study: 1) to describe the pattern and strength of lateralized foot preferences in Australian parrots and 2) to establish to what extent laterality is constrained by phylogenetic relationships or varies according to important ecological variables, such as body size and foraging mode.

METHODS

This study examined the behavior of both captive and wild individuals. Captive parrots were observed at zoos (e.g., Taronga Park Zoo), animal parks (e.g., Featherdale Wildlife Park), pet stores (e.g., Crystal Pet and Wire Centre), and at the premises of parrot breeders. Wild parrots were observed on the Macquarie

University campus and surrounding areas. In all cases data for each species was obtained from multiple populations/sources.

To increase the power of the phylogenetic comparison, a wide range of parrot species representing the great variety of parrots in Australia were included in the study. In total, 23 native species of parrots and cockatoos were examined (Table 1). Adults were the primary focus of the study because laterality can vary with development (Hook and Rogers 2000). The aim was to observe 20 individuals per species in order to obtain a sensible approximation of the proportion of those that are left or right footed in any given species. For a few species, such as rare species in zoos, only a limited number of individuals were observed, thus some caution should be exercised when considering the results of those particular species. Specimens from each species were observed at multiple locations to attempt to capture some of the species diversity.

Determining foot preferences

Food items were placed on trays and introduced to the center of the enclosure. Only one animal was allowed access to the tray at a time. The foot used to grasp the food was recorded by an observer standing more than 2 m away. The test was repeated over several days, by substituting equivalent sized pieces of various fruit. Each bird was given 10 tests. Although other birds in the cage could observe the subject manipulating the food item, it is highly unlikely that they would imitate the hand used to grasp the food item as this is a very natural behavior for parrots and motor imitation in birds is exceptionally rare (Zentall 2004).

Nine species were examined in the wild as well as in captivity to determine if rearing environment influenced laterality. For wild birds in the field, food was provided on a platform a few meters from where a large flock was feeding on the ground. All observations were made through binoculars at least 20 m from the flock; a distance great enough to prevent the observers' presence interfering with their behavior. Only 2 individuals from each flock were observed at any one time. Two observers were needed to keep track of these individuals, and the test was repeated 10 times in 1 day using the same birds. The foot used to grasp the food item was tabulated.

The laterality score for each individual was calculated as the proportion of times the parrot used its left hand to grasp the food. The strength of laterality was also calculated for each individual as the deviation from ambidexterity (i.e., absolute value [% left foot score 250%]). For example, an individual parrot that used its left foot 10 times received a score of 50, similarly an individual who used the right foot 10 times scored 50 because both are equally strongly lateralized but in opposite directions. Thus, this score is a measure of the strength of lateralization independent of direction (L or R). Scores of 0 represent ambidextrous individuals, and scores of 50 represent completely lateralized individuals. From the individual data, we calculated the mean and standard error for each species.

Ecology

When one examines the body size of parrots across the phylogeny, it is apparent that a strong segregation by size between the major clades exists. Our previous observations suggested that large parrots tend to use their feet to manipulate large seedpods in order to extract the seeds, whereas the smaller body species primarily graze on grass seeds or extract pollen and nectar from flowers (Table 1). We hypothesized that those species that regularly use their feet to manipulate food items would be more strongly lateralized than those that do not (sensu Walker 1980). Firstly, a linear regression was used to determine if the level of foot lateralization (pattern and strength) was related to body size. Secondly, the species were split into 2 groups according to diet. The first group contained species that eat small seeds

and nectar, whereas the second group contained those that are reported to eat large seeds. We used an analysis of variance (ANOVA) to compare the strength and pattern of laterality of species in each group.

Table 1. Number of individuals observed, diet, body size, and foot laterality score for each species

Species	Common name	Number of individuals observed	Body size (cm)	Primary diet	Foot laterality score (%)
<i>Cacatua galerita</i>	Sulphur-crested Cockatoo	20	47.5	Large seeds, nuts, and bulbs	96
<i>Cac. sanguinea</i>	Little Corella	20	38.5	Large seeds, roots, and bulbs	90.5
<i>Cac. leadbeateri</i>	Major Mitchell's Cockatoo	15	36	Large seeds, roots, berries, and nuts	92
<i>Eolophus roseicapilla</i>	Galah	20	35	Small seeds of native or cultivated grasses	56.5
<i>Callocephalon fimbriatum</i>	Gang-gang Cockatoo	12	35	Large seeds of native trees	100
<i>Calyptorhynchus funereus</i>	Yellow-tailed Black Cockatoo	20	60	Large seeds and wood-boring larvae	96.5
<i>Cal. banksii</i>	Red-tailed Black Cockatoo	20	59	Large seeds of native trees	93
<i>Nymphicus hollandicus</i>	Cockatiel	20	32	Small seeds from native or cultivated plants	90
<i>Probosciger aterrimus</i>	Palm Cockatoo	5	60	Large seeds and fruits	80
<i>Eclectus roratus</i>	Eclectus Parrot	20	42	Large seeds, berries, fruits, nuts, and blossoms	26
<i>Alisterus scapularis</i>	Australian King Parrot	20	43	Large seeds, berries, fruits, and nuts	8.5
<i>Aprosmictus erythropterus</i>	Red-winged Parrot	10	32	Large seeds, fruits, buds, and blossoms	10
<i>Polytelis swainsonii</i>	Superb Parrot	20	40	Large seeds, eucalyptus blossoms, and fruits	27.5
<i>Neophema pulchella</i>	Turquoise Parrot	10	20	Small seeds of grasses and herbaceous plants	45
<i>Platycercus elegans</i>	Crimson Rosella	12	33.5	Large seeds and fruits	17.5
<i>Barnardius zonarius</i>	Australian Ringneck	5	35	Large seeds of native trees	20
<i>Purpureicephalus spurius</i>	Red-capped Parrot	5	36	Large seeds of the marri tree and other eucalyptus	72
<i>Psephotus haematonotus</i>	Red-rumped Parrot	20	28	Small seeds from grasses and cultivated crops	72
<i>Glossopsitta pusilla</i>	Little Lorikeet	15	15	Nectar, blossoms, and fruits	49.3
<i>Psitteuteles versicolor</i>	Varied Lorikeet	5	19	Nectar, blossoms, and fruits	48
<i>Trichoglossus haematodus</i>	Rainbow Lorikeet	20	30	Nectar, blossoms, and fruits	46
<i>Melopsittacus undulates</i>	Budgerigar	20	18	Small seeds of grass tussocks	52
<i>Neopsephotus bourkii</i>	Bourke's Parrot	20	20	Small seeds found on the ground	49.5

Diet and body size information were obtained from Lindsey 1998 and McNaughton 2002.

Phylogenetic analysis

The phylogeny of Australian parrots is still largely unresolved, with most species yet to be appropriately sampled and the position of various taxa is still disputed (Schweizer et al. 2010). We utilized a phylogeny recently published by Symonds and Tattersall (2010) which represents a composite tree. Our samples covered a broad selection of species within each of the major lineages of the Australian parrots. We reduced the tree to encompass only those species for which we had reasonable data. In order to investigate the distribution of the pattern and strength of laterality, we simply mapped the laterality traits onto the tree.

Phylogenetic comparisons were conducted using the phylogenetic generalized least squares (PGLS) approach (Martins and Hansen 1997) in the program COMPARE 4.6B (Martins 2004). Because of the lack of good phylogenetic data, all branch lengths were set to one. Similarly, where polytomy occurred, branch lengths were finely manipulated by arbitrarily assigning branch lengths of 0.001 to create bifurcating topologies that allow the program to resolve the tree. We used PGLS to examine the relationship between laterality (both strength and direction) and body size relative to phylogeny. Low values of λ are indicative of a strong phylogenetic signal, whereas high values suggest that the traits are distributed randomly across the phylogeny (Martins and Hansen 1997). Phylogenetic independent contrasts analysis was then performed. In essence, this analysis determines if the evolutionary divergences in one trait are significantly correlated with corresponding divergences in another trait. Standardized contrasts for each trait were extracted from the data set, and we then applied linear regression to determine the relationship between body size and laterality. Ancestral reconstruction of the traits was calculated by the generalized least squares (GLS) method of Martins and Hansen (1997). Briefly, the ancestral states are calculated based on the weighted averages of the other taxa in the phylogeny. The model assumes that evolution of traits occurs in a linear fashion (i.e., by Brownian motion), which is a common assumption of characters undergoing random drift or subject to directional selection. It should be noted, however, that the removal of taxa from the tree (i.e., incomplete data sets) can influence the weighted averages thus it is important to collect data on as many species as possible. This method allows us to identify the positions within the tree where significant evolutionary changes have occurred in each trait. Significant changes are identified by variations in trait values along the branches that exceeded 1.96 standard errors (a rough equivalent of 95% confident intervals; Rohlf 2001).

RESULTS

Foot preferences

A comparison of the wild versus captive reared parrots showed no significant differences in any of the 9 species tested in either the strength or direction of laterality ($P < 0.05$ in all cases). Thus, all individuals were included in the analysis irrespective of their rearing background.

The distribution of foot preferences across the phylogeny suggested that a significant divergence in laterality occurred very early on in the evolution of Australian parrots (Figure 1). Our results revealed that all of the large extant cockatoos were left footed with the exception of the Galah (*Cacatua roseicapillus*), which was nonlateralized at the species level and contained a mix of left, right, and ambidextrous individuals. The first tribe within the Psittacidae, the Psittaculini, was all right footed at the species level. The second tribe, the Platycercini, contains a mix of left, right and nonlateralized species. Lastly, the Loriinae were all nonlateralized at the species level.

Ecology—body size

The relationship between body size and foot lateralization revealed some interesting patterns (Figure 2). Small-bodied species tended to be nonlateralized, but species above 32 cm in length were either left or right footed. Only one species (the galah) broke the trend. Owing to the split between the left- and right-handed larger bodies species, the regression between percentage left-hand preference and body size was not significant ($F_{1,22} = 3.41$, $P = 0.079$, $R^2 = 0.10$). However, the relationship between body size and the strength of laterality was highly significant (linear regression: $F_{1,22} = 11.623$, $P = 0.002$, $R^2 = 0.36$) and clearly shows that larger parrots are generally more strongly lateralized than smaller parrots (Figure 3).

Ecology—diet

Examination of the food item preferences of each species suggests that those species that regularly use their feet to manipulate food items (e.g., large seeds) were strongly lateralized, whereas those that do not (e.g., they eat small seeds or blossom) were not lateralized (ANOVA: $F_{1,21} = 15.423$, $P < 0.001$; Figure 4). There was no significant difference in the pattern of laterality between small and large seed eaters (ANOVA: $F_{1,21} = 0.149$, $P = 0.703$).

Phylogenetic analysis

The results of the PGLS analysis found a very strong phylogenetic signal when examining the relationship between the pattern of laterality and body size ($\alpha = 2.07$); however, the signal was substantially reduced when examining the relationship between the strength of laterality and body size ($\alpha > 15.5$). Regression analysis of the standardized contrasts produced from the phylogenetic independent contrasts analysis for body size and laterality produced no relationship for both pattern and strength of laterality ($F_{1,21} < 0.185$, $P > 0.67$, $R^2 < 0.01$).

Lastly, ancestral reconstruction of the traits using the GLS method (Martins and Hansen 1997) identified a number of positions within the tree where significant evolutionary changes have occurred (Figure 1). Within the cockatoos, the galah (*Cac. roseicapilla*) has undergone a significant decrease in both the pattern and strength of laterality; however, this is not accompanied by a significant decrease in body size. Similarly the sulphur-crested cockatoo has shown a significant increase in the strength of laterality becoming extremely left biased. After the Psittacidae and Loriinae diverged from the cockatoos (Cacatuidae), a number of significant changes occurred. Firstly, there was a significant shift to right footedness in the ancestor of the Psittaculini, and this shift continued in *Alisterus scapularis* (Figure 1A). This shift was associated with various shifts in the strength of laterality within the clade. This shift in laterality, however, was not associated with a significant change in body size (Figure 1B), with the group as a whole retaining a fairly large body size typical of the ancestral state. When the Platycercini and Lorianae diverged, a significant decrease in body size occurred (Figure 1B), and this is associated with a general loss of laterality in this clade. The emergence of both left- and right-handed species within the Platycercini is particularly interesting, and it is likely the further sampling is needed to examine the evolutionary significance of these shifts. Only *Purpureicephalus spurius* showed a significant shift toward left handedness.

DISCUSSION

Adopting a comparative approach to examine behavioral traits across a broad range of species occupying a diverse array of environments offers powerful insights into the evolutionary history of the traits in question. The analysis of the foot preferences in Australian parrots revealed that direction and strength of laterality were both strongly associated with phylogeny, but the strength of laterality was clearly linked to ecological factors. Reconstruction of ancestral states revealed several significant shifts in trait values

during the course of evolution, but most importantly, the shift to nonlaterality from a putative lateralized ancestor was accompanied by a significant decrease in body size corresponding to a shift in diet from large seeds to small seeds and blossom. This strongly suggests that lateralization in Australian parrot foot preferences was driven by a shift in foraging mode with larger bodied strongly lateralized species eating large seeds extracted from seedpods requiring manipulation with a limb and small bodied nonlateralized species eating small seeds and blossom which need not be manipulated.

Examination of the distribution of the pattern of foot use and body size in the Australian parrots and reconstruction of the phylogenetic history revealed a number of interesting patterns. Firstly, the Cacatuidae retained the ancestral large body size and became strongly left handed. The only exception is the galah, *Cac. roseicapillus*, which contained a mix of left, right, and ambidextrous individuals and is one of the smaller cockatoo species that reportedly eat small seeds (Lindsey 1998; McNaughton 2002) but also spends considerable time extracting tubers from the ground. It appears likely that the loss of laterality in this species may be associated with a dietary shift. When the tribe Psittaculini (Psittacidae) diverged, members of the clade maintained a relatively large body size, but the common ancestor underwent significant shifts in the pattern of laterality resulting in a right-handed clade. The branch leading to the Platycercini and the Loriinae underwent a significant decrease in body size with a corresponding loss of laterality. Extant Platycercini contained a mix of left, right, and ambidextrous species. The 3 largest species in this tribe have reverted to the ancestral lateralized state, 1 becoming left handed, and 2 becoming right handed. Once again we find that this switch in laterality was associated with a shift in diet, in this instance eating seeds encased in large pods. All the small-bodied species in the Loriinae are nonlateralized and specialize on eating small seeds and blossom. The fact that these smaller bodied species lost their laterality suggest that maintenance of laterality may incur a cost of some sort, although it is difficult to determine what that might be. Alternatively laterality may be lost by random drift in the absence of selection.

The relationship between body size and the direction of laterality illustrates that parrots under a certain size are nonlateralized. With the exception of a single species (the galah), every species examined under 32 cm in length was nonlateralized (Figure 2). This relationship between laterality in foot preference is further confirmed by analysis of the strength of laterality where a highly significant linear relationship was revealed (Figure 3). Larger bodied parrots were significantly more strongly lateralized than their smaller bodied counterparts. This dichotomy into left- and right-handed species illustrates that natural selection is not directional when it comes to the pattern of laterality. That is, that the theorized fitness benefits associated with specializing in using one limb rather than being ambidextrous are realized irrespective of which hand is favored (Brown 2005; Magat and Brown 2009). This is further supported by the PGLS analysis found a very strong phylogenetic signal when examining the relationship between in the pattern of laterality and body size ($\alpha = 0.57$), but the signal was substantially reduced when examining the relationship between the strength of laterality and body size ($\alpha > 15.5$).

When comparing those species that specialize on large seeds with those that feed on small seeds and blossom, we found that the former are significantly more strongly lateralized than the latter (Figure 4). There is no doubt that large species tend to eat larger sized food particles, but what is significant here is not so much the size of the food item but the package it is delivered in and the mode of foraging. Grass seeds are simply too small to handle so these items are grazed on by the smaller bodied species rather than being manipulated by the foot in coordination with the beak. In this context, laterality of foot use would not provide any significant fitness advantage. At the other extreme, large-bodied cockatoos perch in a tree and extract seeds from seedpods by holding the pod in one hand and using a number of coordinated foot-beak actions (Homerger 2003). Because the eyes of parrots are laterally positioned, they often engage one eye to view the seedpod while they hold it in the corresponding foot and extract the seeds with their powerful beaks. It is likely, therefore, that footedness is a symptom of cerebral

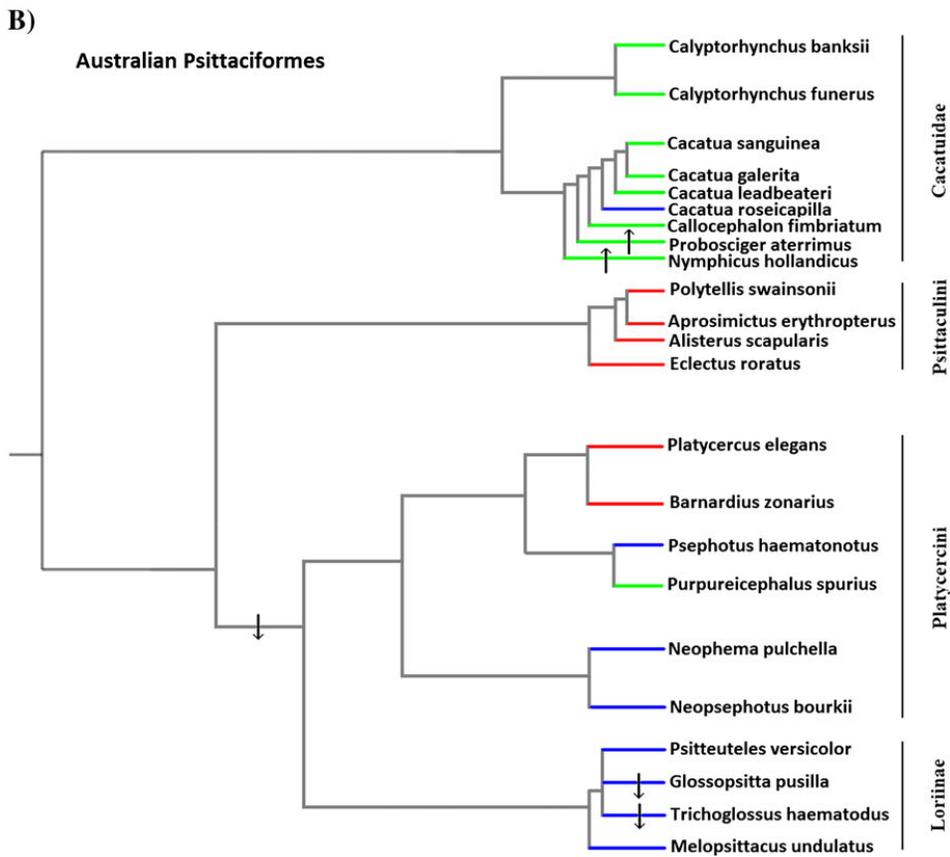
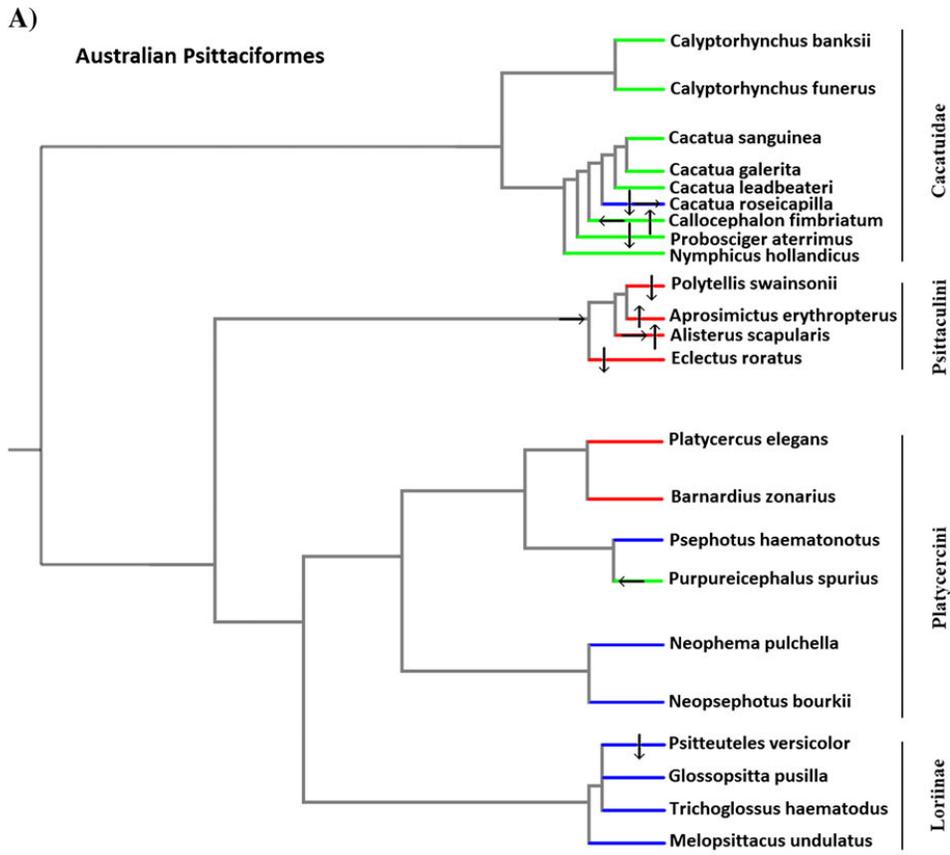


Figure 1. Phylogeny of the Australian Psittaciformes showing the distribution of hand preferences across the 23 species examined. Blue lines indicate nonlateralized species (30–70% left-hand preference), red lines indicate right-hand preferences (< 30% left-hand use) at the species level, and green lines are left footed (> 70% left hand use). A: shows significant shifts in both the strength (vertical arrows) and direction (horizontal arrows) of laterality; B: shows significant shifts in body size.

lateralization where the hemisphere responsible for analyzing information about food determines which eye is used to view potential food items, which in turn determines which foot is used for the task (Brown and Magat 2011). There is certainly evidence that laterality evolved long before the emergence of limbs (e.g., fish; see review by Bisazza and Brown 2011). Thus, foot preferences are probably a reflection of the associated specialization of the contralateral brain hemisphere used to differentiate potential food from nonfood items (Gunturkun et al. 2000; Rogers 2000). An alternative, but not mutually exclusive hypothesis relates to the fact that large-bodied cockatoos rarely feed on the ground and thus must perch on one foot in the trees while foraging (Joseph 1988). It is likely that the choice of perching foot is also a symptom of the hemisphere dominating food discrimination processing. It is interesting to note that there is some evidence in other species of birds that laterality of foot use is related to the control of posture (Tommasi and Vallortigara 1999).

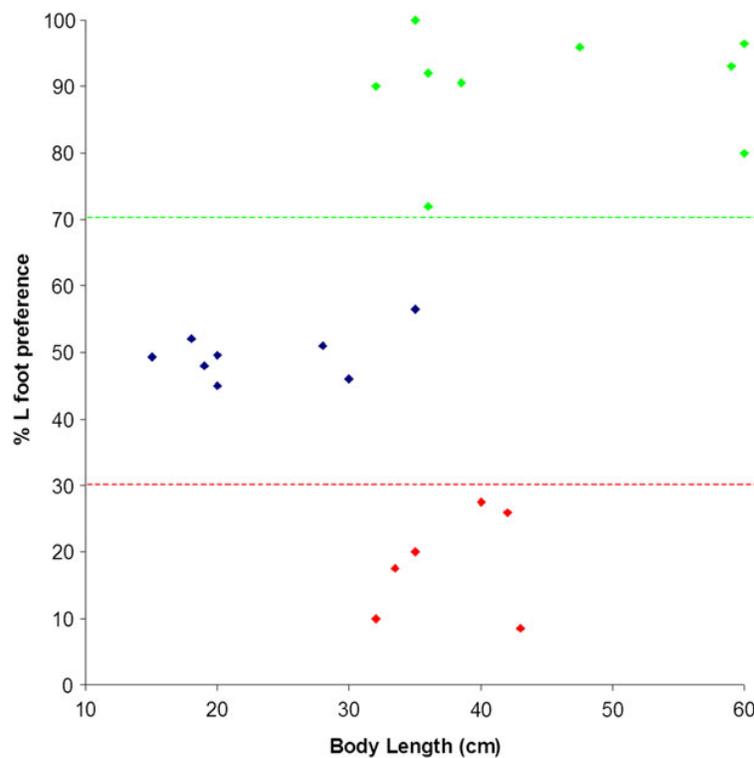


Figure 2. The relationship between body size and the foot preference. Green dots represent species that are left footed, blue dots represent nonlateralized species, and red dots represent right-footed species.

If one examines the distribution of body size within the various parrot clades, it is immediately apparent that body size increases as one moves from the little lorikeet (*Glossopsitta pusilla*, Loriinae) at just 15 cm in length, to the palm cockatoo (*Probosciger aterrimus*, Cacatuidae) reaching over 60 cm in length. Although our regression analyzing the relationship between the strength of laterality and the body size revealed a very significant association, the data this analysis is based on is not strictly independent from an evolutionary perspective because the various species are related to one another by descent to varying degrees. The results of phylogenetic independent contrasts analysis revealed no significant relationship between body size and either the strength or pattern of laterality. It may be that a small number of early evolutionary divergences deep within the phylogeny—where shifts in body size and laterality were correlated—underlies the strong correlation in these traits among present day species. One must bear in mind that the parrots date back to the early Tertiary (about 60 mya) and have shown continual adaptation

in response to large-scale environmental changes. In an Australian context, the primary environmental shift was increasing aridity and associated changes in food availability, as grasses and forbs became increasingly pervasive in the landscape (White 1994). We propose that the shift in food availability away from arboreal fruits in favor of grasses may explain the loss of laterality in the smaller bodied seed eating species that diverged later in the evolutionary history of the Psittaciformes.

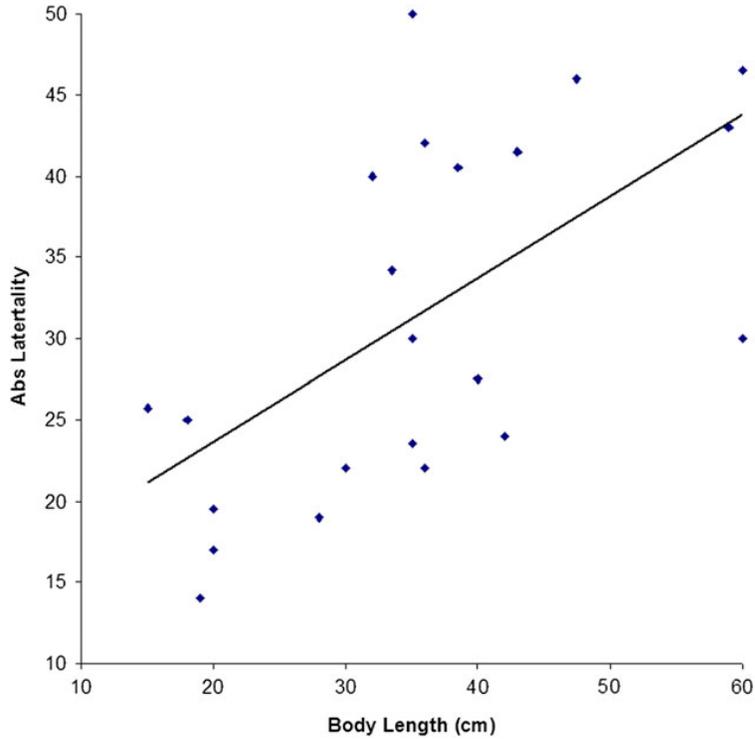


Figure 3. The relationship between body size (centimeter) and the strength of laterality (Abs Laterality) in Australian parrots (linear regression: $R^2 = 0.51$, $P = 0.002$). Values of 0 represent those species that are ambidextrous or contain a mix of left- and right-handed individuals. Values of 50 represent species where all individuals are completely left or right handed.



Figure 4. The mean strength of laterality (6 standard error) for parrot species that eat large seeds or small seeds and blossom.

To summarize, it is apparent that the foot preferences in the Australian parrots have a reasonably high degree of phylogenetic conservatism. The strength of laterality, however, is also intimately related to body size and the corresponding foraging mode. With the exception of the galah, the Cacatuidae are strongly left footed, large bodied, and use their beak and preferred foot in a coordinated fashion to extract seeds from large seedpods. A shift to right footedness has occurred in the Psittaculini, but this was not associated with a change in body size or diet. This provides rather nice evidence that the theorized cognitive and sensory-motor benefits of laterality are realized by both strongly left- and right-handed species in a foraging context. The loss of laterality, or more precisely the emergence of nonlateralized species, was tightly linked to a historical reduction in body size and a shift to a foraging mode that does not require foot-beak coordination. This single shift occurred just once deep in the evolutionary history of these taxa. This general shift is likely associated with the emergence of grass seeds as the predominant food source as Australia became increasingly arid. When taken together, our results suggest that the pattern and strength of laterality is inherited from a common ancestor and rarely shifts significantly over evolutionary time because it is unlikely to influence fitness. In addition, the strength of laterality may vary substantially within a clade, likely in response to ecological variables because it is closely linked to fitness traits (Magat and Brown 2009).

It is important to note that we have only investigated laterality in a single context, that of foraging behavior. Although we know that eye and foot preferences in this context are strongly correlated in most species of parrots (Brown and Magat 2011), there may be other contexts in which this is not the case. Future experiments should examine laterality in a broader range of contexts (e.g., predator and conspecific inspection). Such a course of action will provide further insight into how specific tasks are partitioned within the parrot brain and may yet illustrate further ecological or social factors that have shaped the evolution of cerebral lateralization in vertebrates.

FUNDING

This project was funded by Macquarie University and the Australian Research Council (DP0770396).

Thanks to the large number of parrot breeders and zoos that allowed us to work with their birds.

REFERENCES

- Bisazza A, Brown C. 2011. Lateralization of cognitive function in fish. In: Brown C, Laland KN, Krause J, editors. *Fish cognition and behavior*. 2nd ed. Cambridge: Wiley-Blackwell. p. 300–324.
- Bisazza A, Cantalupo C, Robins A, Rogers LJ, Vallortigara G. 1996. Right-pawedness in toads. *Nature*. 379:408.
- Bisazza A, Dadda M. 2005. Enhanced schooling performance in lateralized fishes. *Proc R Soc Lond Ser B Biol Sci*. 272:1677–1681.
- Bisazza A, Facchin L, Vallortigara G. 2000. Heritability of lateralization in fish: concordance of right-left asymmetry between parents and offspring. *Neuropsychologia*. 38:907–912.
- Brown C. 2005. Cerebral lateralisation, social constraints and coordinated anti-predator responses. *Behav Brain Sci*. 28:591–592.
- Brown C, Braithwaite VA. 2005. Effects of predation pressure on the cognitive ability of the poeciliid *Brachyraphis episcopi*. *Behav Ecol*. 16:482–497.

- Brown C, Gardner C, Braithwaite VA. 2004. Population variation in lateralised eye use in the poeciliid *Brachyraphis episcopi*. Proc R Soc Lond Ser B Biol Sci (Suppl). 271:S455–S457.
- Brown C, Magat D. 2011. Cerebral lateralisation determines hand preferences in Australian parrots. Biol Lett Online Early. doi:10.1098/rsbl.2010.1121.
- Brown C, Western J, Braithwaite VA. 2007. The influence of early experience on, and inheritance of, cerebral lateralization. Anim Behav. 74:231–238.
- Byrne RA, Kuba M, Griebel U. 2002. Lateral asymmetry of eye use in *Octopus vulgaris*. Anim Behav. 64:461–468.
- Casey MB, Karpinski S. 1999. The development of postnatal turning bias is influenced by prenatal visual experience in domestic chicks (*Gallus gallus*). Psychol Rec. 49:67–74.
- Corballis MC. 2002. From hand to mouth: the origins of language. Princeton (NJ): Princeton University Press.
- Corballis MC. 2009. The evolution and genetics of cerebral asymmetry. Philos Trans R Soc B Biol Sci. 364:867–879.
- Crow TJ, Crow LR, Done DJ, Leask S. 1998. Relative hand skill predicts academic ability: global deficits at the point of hemispheric indecision. Neuropsychologia. 36:1275–1282.
- Dadda M, Zandoni E, Agrillo C, Bisazza A. 2009. The costs of hemispheric specialization in a fish. Proc R Soc B Biol Sci. 276: 4399–4407.
- Friedmann H, Davis M. 1938. Left-footedness in parrots. Auk. 55: 478–480.
- Ghirlanda S, Frasnelli E, Vallortigara G. 2009. Intraspecific competition and coordination in the evolution of lateralization. Philos Trans R Soc B Biol Sci. 364:861–866.
- Gunturkun O, Diekamp B, Manns M, Nottelmann F, Prior H, Schwarz A, Skiba M. 2000. Asymmetry pays: visual lateralization improves discrimination success in pigeons. Curr Biol. 10:1079–1081.
- Güven M, Elalmış DD, Binokay S, Tan U. 2003. Population-level right-paw preference in rats assessed by a new computerized food-reaching test. Int J Neurosci. 113:1675–1689.
- Harris LJ. 1989. Footedness in parrots: three centuries of research, theory, and mere surmise. Can J Psychol. 43:369–396.
- Homberger DG. 2003. The comparative biomechanics of a prey-predator relationship: the adaptive morphologies of the feeding apparatus of Australian Black-Cockatoos and their foods as a basis for the reconstruction of the evolutionary history of the Psittaciformes. In: Bels VL, Gasc J-P, Casinos A, editors. Vertebrate biomechanics and evolution. Oxford: BIOS Scientific Publishers. p. 203–228.
- Hook MA, Rogers LJ. 2000. Development of hand preferences in marmosets (*Callithrix jacchus*) and effects of ageing. J Comp Psychol. 114:263–271.
- Hopkins WD, Cantalupo C. 2005. Individual and setting differences in the hand preferences of chimpanzees (*Pan troglodytes*): a critical analysis and some alternative explanations. Laterality. 10:65–80.
- Joseph L. 1988. Food holding behaviour in some Australian parrots. Corella. 13:143–144.
- Lindsey T. 1998. Parrots of Australia. Sydney (Australia): New Holland Publishers.
- Magat M, Brown C. 2009. Laterality enhances cognition in Australian parrots. Proc R Soc B Biol Sci. 276:4155–4162.
- Marchant LF, McGrew WC. 1996. Laterality of limb function in wild chimpanzees of Gombe National Park: comprehensive study of spontaneous activities. J Hum Evol. 30:427–443.
- Martins EP. 2004. COMPARE. Version 4.6b. Computer programs for the statistical analysis of comparative data. Bloomington (IN): Department of Biology, Indiana University; [cited 2010 September 20]. Available from: <http://compare.bio.indiana.edu/>.
- Martins EP, Hansen TF. 1997. Phylogenies and the comparative method: a general approach to incorporating phylogenetic information into the analysis of interspecific data. Am Nat. 149:646–667.

- McGrew WC, Marchant LF. 1997. On the other hand: current issues in and meta-analysis of the behavioral laterality of hand function in nonhuman primates. *Am J Phys Anthropol.* 104:201–232.
- McNaughton M. 2002. Australian parrots and finches. Seaford (Victoria): Bluestone Press.
- Meguerditchian A, Vauclair J, Hopkins WD. 2010. Captive chimpanzees use their right hand to communicate with each other: implications for the origin of the cerebral substrate for language. *Cortex.* 46:40–48.
- Papademetriou E, Sheu C-F, Michel GF. 2005. A meta-analysis of primate hand preferences, particularly for reaching. *J Comp Psychol.* 119:33–48.
- Rogers LJ. 1980. Lateralisation in the avian brain. *Bird Behav.* 2:1–12.
- Rogers LJ. 2000. Evolution of hemispheric specialization: advantages and disadvantages. *Brain Lang.* 73:236–253.
- Rogers LJ. 2009. Hand and paw preferences in relation to the lateralized brain. *Philos Trans R Soc B Biol Sci.* 364:943–954.
- Rogers LJ, Vallortigara G. 2008. From antenna to antenna: lateral shift of olfactory memory recall by honeybees. *PLoS One.* 3:e2340.
- Rohlf FJ. 2001. Comparative methods for the analysis of continuous variables: geometric interpretations. *Evolution.* 55:2143–2160.
- Schweizer M, Seehausen O, Güntert M, Hertwig ST. 2010. The evolutionary diversification of parrots supports a taxon pulse model with multiple trans-oceanic dispersal events and local radiations. *Mol Phylogenet Evol.* 54:984–994.
- Symonds MRE, Tattersall GJ. 2010. Geographical variation in bill size across bird species provides evidence for Allen's rule. *Am Nat.* 176:188–197.
- Tommasi L, Vallortigara G. 1999. Footedness in binocular and monocular chicks. *Laterality.* 4:89–95.
- Vallortigara G. 2000. Comparative neuropsychology of the dual brain: a stroll through animals' left and right perceptual worlds. *Brain Lang.* 73:189–219.
- Vallortigara G, Rogers LJ. 2005. Survival with an asymmetrical brain: advantages and disadvantages of cerebral lateralization. *Behav Brain Sci.* 28:575–633.
- Walker SF. 1980. Lateralization of functions in the vertebrate brain: a review. *Br J Psychol.* 71:329–367.
- White ME. 1994. After the greening-the browning of Australia. Kenthurst (Australia): Kangaroo Press. p. 288.
- Zentall TR. 2004. Action imitation in birds. *Learn Behav.* 32:15–23.