

Investigating laterality in the freely occurring behaviours of Budgerigars

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Abstract

Literature has long provided evidence that laterality (i.e. side preference in brain and behaviour) is demonstrated amongst populations in a variety of parrot species (Rogers 1980). Conversely, laterality in Budgerigars, Melopsittacus undulatus, an Australian parrot, appears to be limited to individual level preferences (Rogers and Workman 1993; Schiffner and Srinivasan 2013). However, laterality investigations in Budgerigars have mainly been confined to studies in which behavioural measurements are dependent upon the experimental task employed, and have not examined the freely occurring expression of lateral preferences outside of an experimental condition.

The present investigation yields conclusions from systematic behavioural observations on a colony of Budgerigars (N = 8) in which the occurrence of several different freely occurring behaviours are tracked. Significant individual level lateral preferences are obtained for several birds who evidenced left foot unipedal perching preferences and for one bird who evidenced a left foot scratching side preference. No significant individual level lateral preferences are obtained for preening side or stretching side, and no population level preferences are obtained for any of the observed behaviours. These results are consistent with previous conclusions suggesting the presence of individual level lateral preferences and the absence of population level lateral preferences in this species.

INTRODUCTION

Laterality refers to the consistent, asymmetric preference for either the left or right side in

performing a behaviour or mental process (MacNeilage, Studdertkennedy and Lindblom 1991). Although the term “laterality” commonly evokes anthropological concepts of right or left handedness, such tendencies amongst other species do exist and can dramatically impact fitness level and cognitive capabilities (Rogers 2000). These side preferences can be expressed both at the population level, where an entire population displays a specific behavioural preference, or at the individual level, where direction of lateralisation varies from one individual to the next (Schiffner and Srinivasan 2013). For instance, previous research suggests that many species of parrot readily demonstrate population level preferences, while some species demonstrate lateral tendencies only at the individual level (Brown and Magat 2011b). In one Australian parrot species, the Budgerigar, *Melopsittacus undulatus*, the existence of such preferences remains somewhat uncertain.

Laterality in a variety of avian species, particularly parrots, has been amply demonstrated. For example, observations of some Australian parrot species have revealed consistent population level preferences for using the left foot when manipulating food (Joseph 1989, 2003; Rogers 1980). Of the nine species investigated by Rogers (1980), only one species exhibited a preference for utilizing the right foot, and of the eight that exhibited significant preferences for the left, four species displayed strong preferences for left use.

Despite its prevalence, the ethological relevance of such laterality in parrots remains ambiguous.

The most prominent hypothesis predicts that laterality in parrots is dependent upon feeding type (Harris 1989). Thus, it has been suggested that if a species is predominantly an arboreal feeder, then its technique is considered prehensile, where large sized fruit require manipulation with one foot and unipedal perching with the other. Conversely, tether footed feeding behaviour occurs on the ground, where beak manipulation is overwhelmingly prevalent and lateral foot preferences are not reinforced. In support of this hypothesis, observations in Budgerigars (an Australian, tether footed parrot species) find no population level lateral preferences (Brown and Magat 2011a; Magat and Brown 2009; Rogers 1989). However, lateral behaviour in this species has typically been evaluated in a task-dependent manner where the behaviours were elicited in the specific experimental situation employed, as opposed to naturally / freely occurring observations (Bhagavatula *et al* 2014; Rogers 1989; Rogers and Workman 1993; Schiffner and Srinivasan 2013). Thus, further research on laterality in freely occurring Budgerigar behaviour appears warranted.

In the following procedures, laterality in freely occurring behaviours of Budgerigars was measured across two separate, week-long observational studies. In line with previous literature, researchers hypothesized no illustration of population level lateral preferences, and the expression of lateral preferences for specific behaviours within a small number of individuals.

METHOD

Subjects

The eight Budgerigars (four female and four male) utilized in this investigation were obtained from a pet store and were group-housed at Saint Joseph's University (SJU; Philadelphia, PA, USA) in line with an IUCAC approved protocol (PR 1403) for approximately six months prior to the start of the study; the subjects

were approximately twelve months old upon commencement of this study. Animals were identifiable via a coloured ID tag on one of their two feet, with the exception of one bird (Ariadne) who, given the bird's long history of removing the tag, remained tag-less.

Materials

Animals were group-housed in the SJU Aviary (room dimensions = 4.42 m x 2.59 m x 2.43 m) that contained multiple plants as well as several perches spaced throughout the room. Both Study 1 and Study 2 were conducted within the aviary room, which was lit on a 12L:12D light cycle (lights on 12:35 pm GMT/UTC, off 12:35 am GMT/UTC). Full-spectrum overhead lighting was utilized throughout daylight hours, and cages were cleaned every other week.

Light audio stimulation, (consisting of predominantly talk radio with intermittent classical music), was provided during the lighted portion of the day in the aviary via a radio tuned to an FM public radio station.

During standard housing, subjects were held in Prevue Pet Products Extra-Large Wrought Iron Flight Cages (cage dimensions = 1.52 m x 0.94 m x 0.58 m, with 1.27 cm bar spacing) with various forms of enrichment (i.e. toys, perches etc.), and *ad libitum* access to water and food (Zupreem FruitBlend Daily Bird Feed). In addition to their primary daily pellet diet, the birds in the colony were frequently provided with fresh foods (e.g. finely shredded baby carrots), and also had infrequent / occasional access to seed, which was employed sparingly when attempting to encourage out of cage foraging and socialization. Outside of the current study, cage doors were opened on most mornings so that subjects could engage in out-of-cage exercise for approximately six to eight hours; however, subjects were confined to standard housing throughout data collection and were not permitted out of cage exercise on observation days.

Procedure

Study 1

The first study served to gauge where lateral behaviours might be expressed and was conducted from October 5 to October 12, 2014. It took place over the course of eight consecutive days, during which three focal animal observation sessions (Altmann, 1974) were conducted each day (Morning [12:35 pm - 1:35 pm UTC/GMT], midday [4:35 pm - 5:35 pm UTC/GMT], and evening [11:35 pm - 12:35 am UTC/GMT] as defined by the light cycle of the colony room). Here, an investigator performed individual, five minute observations for each of the eight subjects (40 minutes total for each session).

The investigator recorded the frequency of four different behaviours: *unipedal foot support* (perching on only one foot), *scratching foot* (employing a foot to scratch the head, or sides of the crissum), *preening side* (nibbling of the feathers or pulling a feather through the bill, for cleaning purposes), and *stretching side* (extension of one wing together with the ipsilateral foot downwards and backwards from the body) (Brockway, 1964). In addition, the investigator recorded the side (*right vs left*) where each behaviour was expressed.

Each bout of a behaviour had to be separated by ~ten seconds of “calm” during which the behaviour did not occur in order to be counted as a separate bout. To avoid order effects, the order in which the birds were observed each session was randomized (via <http://stattrek.com/statistics/random-number-generator.aspx>). At the conclusion of the study all observed bouts of each behaviour were tallied.

Due to a power outage, subsequent lighting inconsistencies persisted throughout Day 1 of testing, with minor inconsistencies on Day 2. Therefore, instead of using the original eight consecutive days of observations, only the latter seven days were included in analyses.

Study 2

The second study served two purposes. As there was a 24 hour power outage at the University at the beginning of Study 1 that resulted in inconsistencies of the scheduled light cycle in the bird holding room, investigators firstly wanted to ensure conclusions regarding lateral preferences were unaffected by the inconsistent lighting. Additionally, investigators wanted to gather preliminary data on social behaviours, specifically pair bond strengths and social aggression, in order to potentially relate these measurements to any observed lateral preferences displayed (cf. Anderson, Williams and Bono 2010; Williams and Anderson 2012).

To confirm initial conclusions of individual preferences (Study 1), the systematic observation protocol employed in Study 1 was repeated for seven additional consecutive days, from November 3 to November 9, 2014. The procedures for Study 2 matched those described in Study 1 except that investigators only recorded the frequency of the two behaviours that had revealed significant individual lateral preferences, namely *unipedal foot support* and *scratching side*.

For partner preference information, a scan sample technique was employed (Altmann 1974), whereby an experimenter recorded which subjects were closest to one another at the beginning of each observation session. *Pair bond strength* was then quantified as a percentage of all observations in which the focal bird was seen next to its most preferred partner.

Data on social aggression was measured by recording bouts of *aggression received*, and *aggression displayed* (indicated by directed bill thrusts [striking another individual with the bill], bill gapes [bill open, head back, and oriented towards another individual] or squawk vocalizations [vocalization prior to an agonistic encounter that varies in pitch, frequency and duration]) (Brockway 1964). In addition, a measure of *total aggressive involvement* was

calculated by adding instances of aggression received and instances of aggression displayed.

Similar to Study 1, each bout of lateral behaviour had to be separated by ~ten seconds of “calm” during which the behaviour did not occur in order to be counted as a separate bout, while each bout of aggression had to be separated by ~thirty seconds of “calm”. All observed frequencies of each behaviour were tallied at the conclusion of the study. Due to an experimenter error, the number of observations used to calculate the *pair bond strength* of one subject (Helen) was reduced by one.

Statistical Analyses

Unless otherwise noted, all statistics were calculated using SPSS v22. For each bird on each behaviour, a lateral preference index was calculated ($[\# \text{ rights} - \# \text{ lefts}] / [\# \text{ rights} + \# \text{ lefts}]$). A score of -1 indicated an absolute preference for the left side, a score of + 1 indicated an absolute preference for the right, and a score of 0 corresponded to an absolute null preference for either side.

Population level lateral preferences for each behaviour were analyzed by means of one-sample *t*-test for each preference index compared to a test score of “0”. Individual level lateral preferences for each behaviour were calculated by hand by means of binomial analysis in the manner specified by Siegel (1956); specifically, $P = Q = \frac{1}{2}$ as subjects had an equal probability of either left ($P = 0.5$) or right ($P = 0.5$) preference for each behaviour.

For subjects with greater than 25 observations, a normal approximation to the binomial (with continuity correction) was employed.

For Study 2, a measure of pair bond strength was calculated for each subject (cf. Williams and Anderson 2012). Pair bond strength was calculated as a percentage: the number of observations with most frequent closest bird at start of observation sessions, divided by the total number of observation sessions, multiplied by 100. Bivariate correlations, both parametric (*Pearson’s r*) and non-parametric (*Spearman’s rho*), were conducted to determine the relationships between lateral preferences and social behaviours (within Study 2 observations), as well as between lateral preferences themselves (collapsed across all observations from both studies).

To confirm that there were not any differences in lateral preference indices from Study 1 to Study 2, paired-samples *t*-tests were conducted. To determine the influence of a subject’s ID tag location (right/left) on lateral tendencies, subjects with right leg tags and left leg tags were compared by means of independent samples *t*-tests on lateral preference indices (collapsed across all observations from both studies).

Similarly, to determine the influence of a subject’s sex, males and females were compared by means of independent samples *t*-tests on lateral preference indices (collapsed across all observations from both studies). For each given *t* statistic, an effect size (*Cohen’s d*) was calculated using Dr. L. A. Becker’s Effect Size Calculator (<http://www.uccs.edu/~lbecker/>).

Table 1. One sample t-tests examining population level lateral preferences from Study 1

	Unipedal foot support	Scratching side	Preening side	Stretching side
\bar{x}	-0.18	-0.02	-0.02	0.03
s.d.	0.41	0.39	0.19	0.27
<i>t</i>	-1.22	-0.13	-0.36	0.33
<i>p</i>	0.26	0.90	0.72	0.74
<i>d</i>	-0.63	-0.03	-0.15	0.16

RESULTS

Study 1

No population level lateral preferences were found when conducting two-tailed, one-sample *t*-tests comparing each lateral preference index to chance performance (a test score of "0") (Table 1). Binomial analysis (Siegel 1956) conducted for each bird on each behaviour revealed three significant individual level preferences: two birds (Echo and Narcissus) exhibited a left *unipedal foot support* preference (two-tailed, $p < 0.05$ and $p = 0.01$, respectively), and one (Ariadne) evidenced a left foot *scratching side* preference (one-tailed, $p = 0.04$).

Study 2

Again, no population level lateral preferences were found when conducting two-tailed, one-sample *t*-tests comparing each lateral preference index to chance performance (a test score of "0"): *unipedal foot support* ($\bar{x} = -0.05$, $s.d. = 0.39$, $t(7) = -0.37$, $p = 0.72$, $d = -0.18$) or *scratching side* ($\bar{x} = -0.16$, $s.d. = 0.38$, $t(7) = -1.23$, $p = 0.25$, $d = -0.59$). Binomial analysis (Siegel 1956) within each bird, on each behaviour revealed two individual-level preferences: Achilles exhibited

a left foot perching preference (one-tailed, $p = 0.04$) and Narcissus maintained his left foot perching preference (two-tailed, $p = 0.02$). *Ad hoc* evaluation of partner preferences suggested no strong pair bonds, with an average pair bond strength of 31.48% ($s.d. = 5.67\%$) and a maximum at 38.00% and a minimum at 24.00%. Correlations failed to demonstrate significant relationships between *unipedal foot support* and social behaviours as well as *scratching side* and social behaviors (Table 2).

Collapsed Data

Paired-samples *t*-tests revealed no significant differences in *unipedal foot support* lateral preference indices between Study 1 ($\bar{x} = -0.17$, $s.d. = 0.40$) and Study 2 ($\bar{x} = -0.05$, $s.d. = 0.39$), $t(7) = -0.74$, $p = 0.48$, $d = -0.30$. Similarly, paired-samples *t*-tests revealed no significant differences in *scratching side* lateral preference indices between Study 1 ($\bar{x} = -0.02$, $s.d. = 0.39$) and Study 2 ($\bar{x} = -0.16$, $s.d. = 0.38$), $t(7) = -1.09$, $p = 0.31$, $d = -0.39$. These results evidenced a general consistency between the two studies, and justified combining data from the two studies for those measures that were employed in both (i.e. *unipedal foot support* and *scratching side*).

Table 2. Correlations between lateral preference indices and social behaviours from Study 2

		Unipedal foot support	Scratching side
Unipedal foot support	<i>r</i> (<i>p</i>)	-	-0.15 (0.72)
	<i>rho</i> (<i>p</i>)	-	-0.32 (0.43)
Scratching side	<i>r</i> (<i>p</i>)	-0.15 (0.72)	-
	<i>rho</i> (<i>p</i>)	-0.32 (0.43)	-
Aggression received	<i>r</i> (<i>p</i>)	-0.36 (0.37)	-0.01 (0.98)
	<i>rho</i> (<i>p</i>)	-0.38 (0.34)	0.07 (0.86)
Aggression displayed	<i>r</i> (<i>p</i>)	0.23 (0.57)	0.10 (0.80)
	<i>rho</i> (<i>p</i>)	0.01 (0.97)	0.05 (0.91)
Total aggressive involvement	<i>r</i> (<i>p</i>)	-0.09 (0.84)	0.05 (0.91)
	<i>rho</i> (<i>p</i>)	-0.35 (0.39)	0.13 (0.76)
Pair bond strength	<i>r</i> (<i>p</i>)	-0.22 (0.58)	-0.45 (0.26)
	<i>rho</i> (<i>p</i>)	-0.34 (0.40)	-0.36 (0.37)

When all instances of foot support and scratching side from both Study 1 and Study 2 were combined, two-tailed, one-sample *t*-tests again failed to obtain population level preferences for either *unipedal foot support* ($\bar{x} = -0.12$, *s.d.* = 0.31) ($t(7) = -1.11$, $p = 0.30$, $d = -0.55$) or *scratching side* ($\bar{x} = -0.03$, *s.d.* = 0.29) ($t(7) = -0.25$, $p = 0.81$, $d = -0.09$). Binomial analysis (Siegel, 1956) conducted for each bird on each behaviour illustrated that Narcissus maintained a left foot preference for perching (two-tailed, $p < 0.05$) and Ariadne maintained a left foot scratching preference (one-tailed, $p = 0.03$). In addition, Achilles too exhibited a left foot perching preference (two-tailed, $p = 0.03$; Table 3). Non-parametric analysis revealed no significant correlation (ρ ($n = 8$) = -0.53, $p = 0.18$); however, parametric analysis revealed a significant negative correlation between *unipedal foot support* and *scratching side* ($r(7) = -0.82$, $p = 0.01$).

Independent samples *t*-tests examining tag location confirmed lateral preference indices for *unipedal foot support* were not significantly different ($t(5) = 0.23$, $p = 0.82$, $d = 0.16$) between

those with left leg tags ($\bar{x} = -0.12$, *s.d.* = 0.35) and right leg tags ($\bar{x} = -0.18$, *s.d.* = 0.39). In addition, lateral preference indices for *scratching side* were not significantly different ($t(5) = -0.67$, $p = 0.53$, $d = -0.55$) between those with left leg tags ($\bar{x} = -0.06$, *s.d.* = 0.36) and right leg tags ($\bar{x} = 0.10$, *s.d.* = 0.20).

Along with tag location, independent samples *t*-tests examining sex differences confirmed lateral preference indices for *unipedal foot support* were not significantly different ($t(6) = 1.48$, $p = 0.20$, $d = 1.05$) between males ($\bar{x} = -0.28$, *s.d.* = 0.37) and females ($\bar{x} = 0.03$, *s.d.* = 0.19). In addition, lateral preference indices for *scratching side* were not significantly different ($t(6) = -1.36$, $p = 0.25$, $d = 0.99$) between males ($\bar{x} = 0.11$, *s.d.* = 0.37) and females ($\bar{x} = -0.16$, *s.d.* = 0.10).

DISCUSSION

The purpose in conducting this research was to examine lateral preferences in freely occurring behaviours of Budgerigars, measured across two separate, week-long observational studies. On each of these seven consecutive days,

Table 3. Individual lateral preferences collapsing across Study 1 and Study 2

Individual	Sex	ID tag location	L.	R.	Preference	L.	R.	Preference
			<i>unipedal foot support</i>	<i>unipedal foot support</i>	<i>unipedal foot support</i>	<i>scratching side</i>	<i>scratching side</i>	<i>scratching side</i>
Echo	F	Left	22	15	-0.19	16	12	-0.14
Andromeda	F	Right	18	18	0.00	16	15	-0.03
Ariadne	F	N/A	15	16	0.03	**33	19	-0.27
Helen	F	Left	12	21	0.27	16	11	-0.19
Achilles	M	Left	*14	4	-0.56	4	11	0.47
Hector	M	Right	12	14	0.08	5	5	0.00
Narcissus	M	Right	*26	6	-0.63	7	14	0.33
Perseus	M	Left	17	17	0.00	11	5	-0.38
\bar{x}			13.88	17.00	-0.12	13.5	11.5	-0.02
<i>s.d.</i>			5.89	4.93	0.31	9.33	4.78	0.29

*Two tailed, significant at alpha 0.05, **One tailed, significant at alpha 0.05

experimenters recorded behaviours during three predetermined time intervals. Researchers hypothesized no illustration of population level lateral preferences, and the expression of lateral preferences for specific behaviours within some individual Budgerigars.

Consistent with the hypotheses and previous literature (Magat and Brown 2009; Rogers 1989), no population level lateral preferences were observed for any of the behaviours under investigation (unipedal foot support, scratching foot, preening side, or stretching side). The significant preferences that were demonstrated (two subjects displayed left foot *unipedal foot support* preferences, one subject displayed a left *side scratching* preference) existed only at the individual level, in a manner consistent with previous literature (Schiffner and Srinivasan 2013).

Similar to previous work in the Northern Bald Ibis (Anderson and Robinson 2012), we obtained evidence of a significant negative correlation between an animal's *unipedal foot support* preference and *scratching side* preference. This makes sense because if a subject is scratching itself with one foot, support must come from the opposite foot.

The absence of significant correlations between social aggression and lateral preferences is not surprising given the unlikelihood of an established hierarchy in the young colony. Similarly, the absence of significant correlations between pair bonds and lateral preferences is not surprising given the weak average pair bond strength for the birds in the flock (average = 31.48%).

Among the benefits of lab-based, randomized, systematic observational methods are a reduction in the potential influence of order effects and other unintended influences on observed behaviour; however, variables such as illumination are still sometimes unable to be appropriately controlled for, no matter what

procedural measures are employed or how well-intentioned the researchers are. As this was unfortunately the case with a power outage in Study 1, we saw fit to replicate procedures in Study 2 to confirm initial conclusions. Indeed, lighting inconsistencies did not impact lateral tendencies, due to the fact that both Study 1 and Study 2 yielded similar results. Ruling out an additional potential confound, the leg side of a subject's ID tag did not significantly influence lateral preferences.

While Budgerigars in the present study maintained individual level lateral preferences, there has been a long held disposition of population level lateral preferences within parrot species (Rogers 1980, 1989). Thus, previous researchers have proposed such a discrepancy might ultimately persist due to the differing foraging demands imposed on Budgerigars in comparison to most other parrot species (Harris 1989). Whereas the vast majority of parrot species feed primarily on fleshy fruits of relatively large size, Budgerigars inhabit an environment that provides only small seeds found on the ground, or small seeds that have been extracted from fruit. This differing diet is, in turn, accompanied by differing population level eating patterns. While most parrots exhibit a prehensile-footed feeding behaviour whereby foods of large size are manipulated with the assistance of the foot, Budgerigars employ tether-footed eating whereby food is small enough to be eaten off the ground, does not require foot manipulation, and thus does not reinforce the establishment of population level lateral preferences. Given this species' ethological predispositions, we can conclude that our results are in line with what is expected.

Current results evidence the existence of individual level lateral preferences in the freely occurring behaviour of Budgerigars, and are consistent with those previous studies that have failed to find evidence of population level lateral preferences in this species (Brown and Magat 2011a; Magat and Brown 2009; Rogers

1989); however, the evolutionary function of the observed individual level lateral preferences are in need of further study. It has been suggested by some authors that laterality in individual animals could serve to generally enhance mental processing ability through minimized redundancy and decreased interference in neurological systems (e.g. Rogers, Zucca and Vallortigara 2004; Rogers 2000; Magat and Brown 2009). For example, evidence has shown that cerebral lateralisation allows chicks (*Gallus gallus domesticus*) to simultaneously employ one eye to search for food, while using the other to monitor for predators (Rogers, Zucca and Vallortigara 2004). Whether the individual lateral preferences displayed in the present study serve similar functions is certainly worthy of future investigation.

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