

Article

Asymmetric Behavior in *Ptyodactylus guttatus*: Can a Digit Ratio Reflect Brain Laterality?

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Abstract: The digit ratio, an indicator of brain laterality, is the ratio of the second and fourth digits on the left (L24) or right foot (R24). Much of the research on the digit ratio and brain laterality focuses on primates, rather than other species such as reptiles. We tested whether the digit ratio in the gecko *Ptyodactylus guttatus* was associated with behaviors attributed to brain laterality. We examined risk-taking behavior (time spent under cover), foot preference (which foot was the first to start moving) and the side from which geckos bypassed an obstacle, in relation to the digit ratio. Geckos with longer fourth digits on their left hind foot (higher digit ratio) spent more time under cover. Geckos starting to move with their left leg were much more likely to bypass obstacles from the right side, and vice versa. This is the first evidence of laterality being associated with the digit ratio in reptiles. Comparisons among vertebrates are needed in order to decipher the evolutionary origin of the commonalities and peculiarities of brain asymmetry and disentangle the patterns and drivers of our evolutionary tree.

Keywords: brain laterality; digit ratio; foot preference; *Ptyodactylus guttatus*; risk behavior

1. Introduction

The focus of a majority of research by neurobiologists in brain asymmetries and brain laterality has mainly been with humans and other primates. This focus is somewhat surprising given that brain laterality was first described in fish, amphibians and reptiles [1]. Laterality studies of recent decades found consistent evidence amongst vertebrates of similar functionality of brain laterality [1–5]. In many vertebrates, left eye bias is more frequent in hostile gestures, e.g., lizards [6–8], but also other vertebrates [9–11], including humans [12–15], or domestic animals as dogs [16,17]. However, the eye bias is opposite in fish [18,19]. The more frequent use of the left eye in hostile gestures as mediated by the right brain hemisphere and subsequent hormone release is a well-studied mechanism in many vertebrates [1]. The left eye, which is controlled by the right hemisphere or diencephalic regions of the brain, is more specialized in vigilance towards predators. The right eye, controlled by the left side of the brain, is more specialized for searching for food [1,2,20]. Brain lateralization is sensitive to neonatal handling and prenatal maternal stress [19–23]. Prenatal maternal stress elevates corticoids and testosterone levels and is considered to be reflected in higher digit ratios when comparing the second to the fourth digit (i.e., 2/4 or longer fourth digit relative to the second digit) [24,25]. Brain laterality in lizards is reflected in asymmetrical eyes [6–8,26,27] and leg preference [28] as well as turning bias [29].

The preponderance of tail injuries in several species of lizards [30–33], tuatara [32,34] and snakes [35,36] is associated with left dominant asymmetry (of various morphological indices). In a similar fashion, eye and digit asymmetries are correlated with the risk-taking strategy in the gecko

Ptyodactylus guttatus [29]. A possible explanation is that morphological asymmetry is a proxy for brain laterality [29,37]. Thus, an association between eye or digit asymmetry and risk strategy (manifested in tail injury) may be derived from brain laterality. Another possible explanation is that brain asymmetry is derived from morphological asymmetry, especially of the eyes. These competing hypotheses need to be tested. Brain laterality and morphometry, such as hippocampus asymmetry [38,39], asymmetric distribution of receptors in the right vs. left hemisphere [38], risk perception [40], aggression [41] and spatial perception [42,43] are shaped by hormones during embryonic stages [44–47]. A byproduct of this phenomenon is the associated digit ratio [44–47]. The digit ratio and digit asymmetry are often correlated [29,37]. When the fourth digit is longer than the second digit, it has been shown to be a marker for higher testosterone levels in humans [44–47] and lizards [48]. Similarly, digit asymmetry is expected to be more left-biased as the fourth digit is longer on the left foot. Since eye and digit asymmetries correlate with hormones [29], it is possible that this is another facet of the same phenomena. Higher levels of testosterone may explain the correlation between digit asymmetry and tail injury [30], or tail injury and eye asymmetry in snakes [35] and lizards [28]. Elevated testosterone may result in a higher risk-taking strategy, and thus a higher rate of predation or tail injury. The exact mechanism is not entirely clear, although as the digit ratio and digit asymmetry are markers of testosterone level, then these same ratios and asymmetries can, therefore, indicate the level of risk strategy used in many vertebrates, such as humans [49] and lizards [50,51].

The morphometric ratio of the length of the second to fourth digits (D2/D4) on the manus (the distal portion of the forelimb, or hand) is an external marker of another process. The digit ratio (2D/4D) is considered to be a biomarker that reflects the balance between prenatal testosterone (pT) and estrogen (pE). Although the onset is only in a narrow window of early ontogeny, it is reflected in adult morphology [46,47]. There are some caveats [52] to this theory of prenatal androgen cerebral lateralization [53], especially as regards to speech laterality, where sexual dimorphism has not been observed. Even in studies of young children, who should have experienced fewer postnatal influences, the digit ratio as reflecting prenatal steroids was only found to be minimal [54]. Despite this, the second-to-fourth digit ratio is still considered as a proxy for prenatal testosterone [44–47]. Since pT levels also affect brain development and laterality [55–57], they have been found to be positively correlated with greater brain lateralization functions such as handedness, cognition and left hemisphere activity [57]. Higher levels of pT are related to increased left hemisphere dominance for language [57] and left-handedness [58]. It has been suggested that elevated levels of fetal testosterone are associated with adult levels of circulating testosterone [56,59], and these, in turn, are related to risk-related behavior in many vertebrates such as birds [60], humans [49], rats [61] and lizards [49,50]. In humans, a higher digit ratio (fourth digit longer than the second) reflects higher testosterone levels and has been linked to aggression [41,62] and with a tendency to take more financial risks [62,63]; therefore, we hypothesize that the digit ratio could be used to evaluate risk-taking strategies in other vertebrates. Using this hypothesis, the proportion of risk-taking individuals may be predicted from the degree of the digit ratio at the population level. Dizenzo and Stynoski [48] found that the digit ratio also reflects hormone levels (in frogs and lizards). The only behavioral experiments relating the digit ratio and hormone levels we are aware of was by Sion [29], which showed that in the gecko *P. guttatus*, corticosterone levels increased with lower digit ratios on the left hind foot. This suggests that the morphometric digit ratio is a marker for brain laterality in lizards in a similar way that it is a marker for laterality in humans.

When bird eggs of the collared flycatcher (*Ficedula albicollis*) were administered with testosterone, fledglings from eggs with elevated levels of yolk testosterone—regardless of sex—had longer second digits on their left feet than controls had; however, this was not the case for the right foot. This shows, experimentally, that early testosterone exposure can affect the second-to-fourth digit ratio in a wild population of vertebrates [64].

The right hand and leg are predominantly controlled by the left hemisphere and vice versa. Handedness can thus be a proxy for brain laterality [65]. Similarly to hand preference in primates,

we used foot preference in a lizard as a proxy for brain laterality. An association between a proxy for brain laterality and morphometric traits was never tested in reptiles, except in [29], when geckos with larger left eyes took more risks, and individuals with larger right eyes had a higher social status. Sion [28] found that lateral bite marks reflect asymmetric biting behavior and brain laterality via foot preference.

To examine the relationship between morphological and behavioral proxies of brain laterality, we studied the gecko *Ptyodactylus guttatus*. We aimed to examine whether risk taking, as reflected in the time spent under or away of cover, was associated with the digit ratio. We further tested whether the digit ratio was correlated with behavioral laterality as reflected in leg dominance during the first step and detour tests (on which side an animal chooses to pass an obstacle).

We hypothesized that the association of risk with brain laterality in vertebrates may tie both phenomena of the digit ratio and digit asymmetry towards one potential solution of being derived from brain laterality.

We predicted: (1) that the digit ratio (L24/R24) would correlate with behavioral laterality proxies associated with testosterone; (2) geckos with higher digit ratios on the left hind foot would tend to take higher risks; (3) left-footed individuals would tend to bypass obstacles from the right side; right-footed individuals will pass from the left side [66]; and (4) geckos turning right would tend to stay longer under cover, since detour direction is mediated via dopamine (higher dopamine levels equal higher probability of turning left [66] and lower risk-taking behavior [67]).

2. Materials and Methods

2.1. Subjects and Housing

The Sinai fan-fingered gecko *Ptyodactylus guttatus* Heyden, 1827 is a phyllodactylid species inhabiting the Sinai Peninsula of Egypt, NW Saudi Arabia, Palestine, Jordan and Israel. It is a rupicolous, scansorial lizard [28,29,68–74] that inhabits cliffs and masonry walls where it can be observed from a distance [28,37,68–74]. Though not usually a house gecko, it can nonetheless sometimes be found in human settlements [28,29,68,69,72,74]. It is active during both day and night and is very common in rocks throughout Israel. It is insectivorous and very much a “sit and wait” ambush predator [73,75].

We caught geckos twice: 22 during 2013 according to the Israeli law, under a permit from the Nature and Parks Authority (permit number: 2013/38003) and ethics (permit from the Hebrew University: OPRR-A01-5011) and 16 in 2017 (permit, 2017/41498), ethics from Tel-Aviv University (04-17-014). All geckos were captured on masonry walls in Jerusalem’s Yemin-Moshe neighborhood (Israel, lat. 31.77° N, long. 35.22° E, alt. 750 m a.s.l.)

The geckos were housed in standard plastic terraria (49 × 7.5 × 8 cm) at room temperature and fed with grasshoppers. Water was provided ad libitum. No food or water was provided during the experimental sessions, which took place in separate terraria (novel environment).

We removed one animal with an abnormal outlier measurement of the fourth digit on the left foot (L4). This animal was released back into the wild after experiments ended and we, therefore, could not measure its L4 again (the L4 abnormal outlier was consistent on two measurements). Therefore, tests involving L24 measurements were conducted on 37 animals and tests not involving L24 were run on the full dataset of 38 animals.

2.2. Sex and Age

The 2013 group comprised both adults and juveniles, whereas the 2017 group consisted of only juveniles. In 2013, we measured digit length and snout vent length (SVL), tested for foot preference and then the geckos were shortly released back to their place of capture, up to a week later. In 2017, the geckos were housed at Tel-Aviv University, and had the same morphometric measurements as the 2013 group, but additional behavioral tests (cover and detour tests) were conducted. Geckos in 2017

were measured on the same day they were tested. The geckos in 2017 were identified to sex once they attained a length of 50 mm. Male *P. guttatus*, which are longer than 50 mm SVL, display a paired bulge under the base of the tail housing the hemipenes [28,29,37,69,76]. Sex is known to affect testosterone levels, therefore, we accounted for sex in our analyses (see below), since sub-adults and juveniles <60 mm in SVL [28,29,37,69,76] are not territorial, have shorter hibernation and display riskier foraging strategies than adults [69,76]. We, therefore, controlled for sex using ANCOVA ($P > 0.4$ in all tests and thus we dropped it) and for body size in all our analyses (see below). Of the 16 geckos, we managed to sex 15 [77].

2.3. Measurements

All measurements were taken immediately prior to the behavioral observations, to avoid subconscious bias. Measurements were taken using digital calipers to 0.01 mm precision. We measured the 2nd and 4th digits on both hind feet (see Figure 1).



Figure 1. Measurement schematic for digit length in the gecko manus. The measurement is always from the inner side. The lines indicate measuring digits D2 and D4 on both sides of the third digit D3.

The digit ratio (2/4) was the length of the second digit divided by the fourth digit, for each hind pes (foot) separately: $R2/R4 = R24$; $L2/L4 = L24$ (except for the outlier described above, the 4th digit was always longer than the 2nd, and hence more complex ratios were unnecessary; [78]). The sample size for comparing the digit ratio with the detour test was $N = 37$, constituted from Tables 1 and 2 (gecko 7 from Table 2 was excluded), and the sample size for comparing the digit ratio with time under cover was $N = 15$ (Table 2).

Table 1. Comparing digit ratio with asymmetric behaviors.

Lizard	Sex	SVL	L24	R24	Foot-Preference
1	Female	68.3	0.598	0.972	0
2	Male	66.8	0.651	0.753	0.333
3	Female	66.5	0.657	0.783	−0.2
4	Female	64.4	0.672	0.62	0.5
5	Male	64.1	0.682	0.682	−1
6	Female	61.9	0.702	0.606	−0.6
7	Female	64.6	0.72	0.792	0.5
8	Female	65	0.731	0.8	0.143
9	Male	76.3	0.731	0.642	−0.5
10	Male	71.5	0.735	0.681	−1
11	Male	69	0.747	0.729	−0.2

Table 1. Cont.

Lizard	Sex	SVL	L24	R24	Foot-Preference
12	Female	66.8	0.747	0.762	−1
13	Female	65	0.753	0.829	0.6
14	Female	50	0.758	0.805	−0.667
15	Female	69.3	0.773	0.651	−1
16	Male	66.6	0.783	0.688	−0.333
17	Juvenile	45.6	0.796	0.964	0.5
18	Female	49.9	0.826	0.814	0.6
19	Female	61.7	0.847	0.667	−0.6
20	Female	67.2	0.854	0.738	0
21	Female	61.1	0.87	0.708	0.6
22	Female	68.8	0.872	0.812	0.2

Table 2. Comparing digit ratio with asymmetric behaviors.

Lizard	Sex	SVL	L24	R24	Foot-Preference	Detour-Test	Cover
1	Female	41.03	0.917	0.831	0	−0.333	0
2	Female	38.89	0.789	0.805	−0.333	0.333	0.667
3	Male	48.85	0.707	0.884	0	0.333	1
4	Male	36.35	0.879	0.72	0.333	−0.333	1
5	Female	37.09	0.97	0.959	0.333	−0.333	0
6	Female	43.44	0.85	0.721	0.333	−0.333	1
7 *	Female	47.17	1.306	0.824	0.667	−0.667	0
8	Female	48.46	0.735	0.805	0.667	−0.667	0.667
9	Female	48.38	0.915	0.973	0	−0.333	0
10	Female	34.06	0.741	0.779	−0.667	0.667	1
11	Male	51.07	0.839	0.711	0.333	−0.667	0
12	Female	38.79	0.736	0.785	−0.333	0	1
13	Juvenile	35.45	0.779	0.798	0.667	−0.667	0
14	Female	46.57	0.727	0.981	−0.667	1	1
15	Male	27.68	0.813	0.752	−0.333	0.333	0.667
16	Female	46.73	0.774	0.752	0	0	0.667

* Gecko No. 7. was excluded, since its left digit-ratio was an abnormal outlier. The results were significant with and without it.

2.4. Risk-Taking Strategy

To quantify the risk-taking strategy, we placed sixteen geckos, in turn, in a glass terrarium ($21 \times 61 \times 43$ cm) with a double-corrugated red plastic sheet (26×12 cm) as a cover. This enabled the gecko to hide, although the terrarium was transparent (see Figure 2).



Figure 2. When exposed to a novel environment, the geckos can choose either an exposed position or to hide under a double-corrugated red plastic sheet. The gecko on the left is exhibiting a risky strategy (exposed), while the gecko on the right is exhibiting the risk-averse strategy (under cover).

Risk-taking behavior was quantified by recording whether a gecko was observed under cover or out of cover during six observations (at 30-min intervals) during a 3-h trial. As *P. guttatus* is a classical “sit and wait” ambush predator [72,79], geckos were generally immobile when observed. It is unlikely that geckos moved much during the time they were not observed. Thus, we quantified risk taking as the proportions of observations in which the gecko remained under cover. Some of the geckos remained under the cover for the entire trial, while others chose to stay out during the whole experiment, and some changed their location between exposed and under cover. We calculated the proportion of geckos using a risky strategy during 180 min with 30-min intervals as 1/6 of the time up to 6/6 of the time with the same risk strategy, thus creating risk taking as a continuous variable. Although the animals were looked at during the whole three hours, we suggest from our experience that in such a “sit and wait” strategy [72,75], a half hour interval should suffice. We further defined animals as risk-averse if they spent 67% or more of the time under cover (4–6 of the observations).

2.5. Laboratory Conditions

The trials were performed during daylight, at a room temperature of 23 °C. Each gecko was tracked and its behavior was documented for three hours under constant lighting and temperature. All tests were conducted at the same hour of the day and during the same season.

2.6. Foot Preference

Foot preference was defined (following [28]) as the hindfoot the gecko uses when it starts walking in the experimental arena. The hindfoot was used because in all trials of all animals, the first leg to move was always a hind leg.

Individuals were placed alone in an open plastic box: 58 × 49 × 41 cm. Each gecko was tested six times and each trial (foot preference) was independent of the previous trial, since each lizard was individually hand-placed in the same initial location. All tests were performed after dark, (*P. guttatus* activity is mostly at dusk and the first few hours after dark) at room temperature (23 °C). Geckos were photographed using a Canon SX 60 HS video camera. Foot preference was documented using a camera and slow-motion analysis was used to determine which foot moved first. After each trial, the lizard was picked up and hand-placed in the same initial location within the arena. We used the Windows Media Player application to slow down the photographed movements. To calculate the degree of foot preference, we used six trials for each individual. The formula for calculating the asymmetric behavior was $(R-L)/(R+L)$, so it ranged between 1 and -1.

2.7. Detour Test

The detour test was conducted in the same box as the foot preference test. The side from which geckos bypassed an obstacle tested was not performed on the 22 geckos from 2013 (Table 1). It was tested only on the sixteen geckos from 2017 (Table 2). We rely on previous tests of detour tests (2015) that were not compared with the digit ratio but with eye asymmetry (2015). When compared with eye asymmetry, the detour test was conducted and compared on both day and night with the same results (significantly correlated and not significantly different). The detour test was conducted in an open space and a closed arena with the same results. The factor that the lizards were sensitive to was the environment. In a symmetric environment (open or closed), the results were consistent, but in a messy room with many places to find cover, it was not consistent, regardless of the time or temperature (2015).

2.8. Data Analysis

Kolmogorov–Smirnov analyses were performed using the software SPSS 15.0 for Windows™ (2006). All other tests were conducted in R (version 3.6.0, The R Foundation for Statistical Computing). The probability, set at $\alpha = 0.05$, was two-tailed. All data were tested for normality (Kolmogorov–Smirnov test). We initially conducted all tests while accounting for the effects of sex and SVL using an ANCOVA design. Sex was not significantly related to any of the response variables in any test ($-0.9 < t < 0.2$ and

$P > 0.40$ in all tests, detailed results not shown). We examined the effect of sex in our statistical models (see below, i.e., with 15 animals). Sex was not associated with any of our response variables (results not shown, all p values > 0.4), so we used the unsexed animal in subsequent tests. Hence, we repeated all the analyses as multiple regressions with SVL as a covariate and the data pooled for both sexes. In cases where SVL had no effect, we repeated the test as a single-predictor linear regression. We report results of the multiple regression when SVL was a significant predictor and of the single-predictor regression when it was not.

3. Results

3.1. Distributions of Variables

The distributions of all variables, digit ratios, time under cover, detour test and foot preference (Figures 3–7) did not significantly depart from a normal distribution according to a one sample Kolmogorov–Smirnov test:

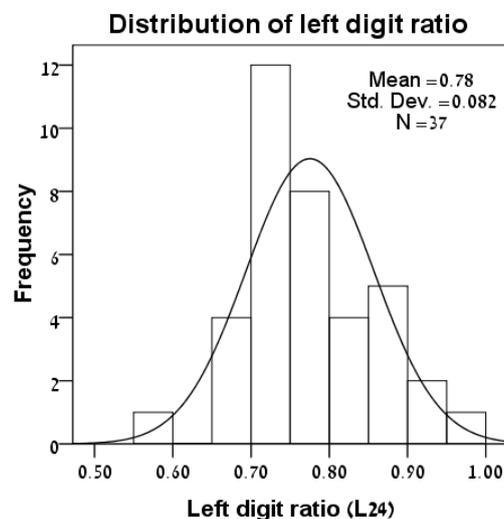


Figure 3. The distribution of the left digit ratio (L24). $N = 15$, $Mean = 0.8112 \pm SD = 0.081$, $Z = 0.548$, $P = 0.925$.

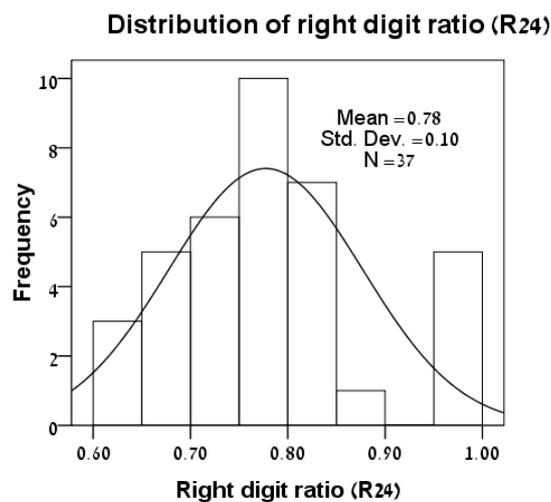


Figure 4. The distribution of the right digit ratio (R24). $N = 15$, $Mean = 0.817 \pm SD = 0.0916$, $Z = 0.854$, $P = 0.459$.

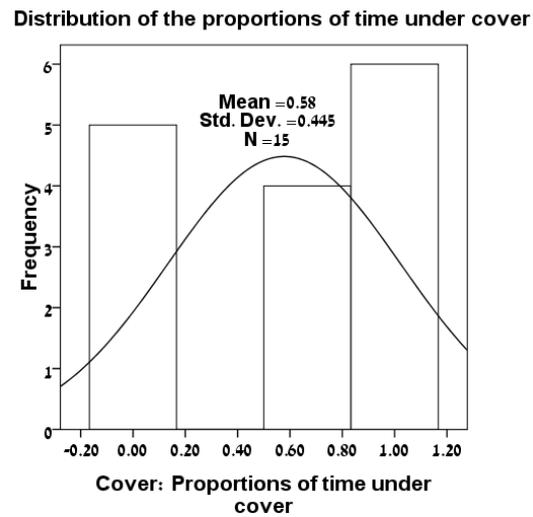


Figure 5. The distribution of the proportion of time under cover. $N = 15$, $Mean = 0.5778 \pm SD = 0.445$, $Z = 0.952$, $P = 0.325$.

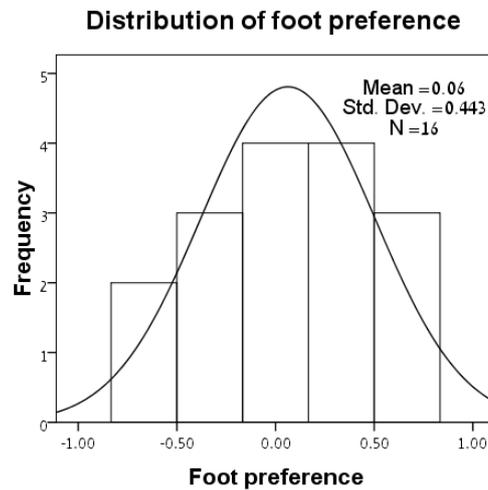


Figure 6. The distribution of foot preference. $N = 15$, $Mean = 0.022 \pm SD = 0.427$, $Z = 0.647$, $P = 0.797$.

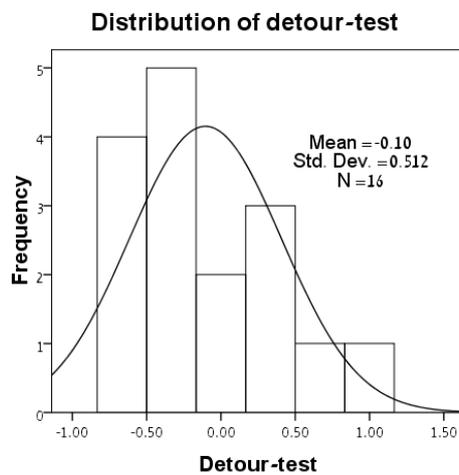


Figure 7. The distribution of the detour test. $N = 15$, $Mean = -0.067 \pm SD = 0.507$, $Z = 0.906$, $P = 0.385$.

3.2. Digit Ratio vs. Time under Cover

Higher ratios of the second to fourth digit on the left foot (L24) were associated (see Figure 8) with more time spent under cover (slope = 0.0159 ± 0.0070 , $t = 2.28$, $P = 0.0399$, $R^2 = 0.29$) but R24 was not (slope = 0.0049 ± 0.0090 , $t = 0.46$, $P = 0.65$; SVL was not significantly related to the digit ratio in either test).

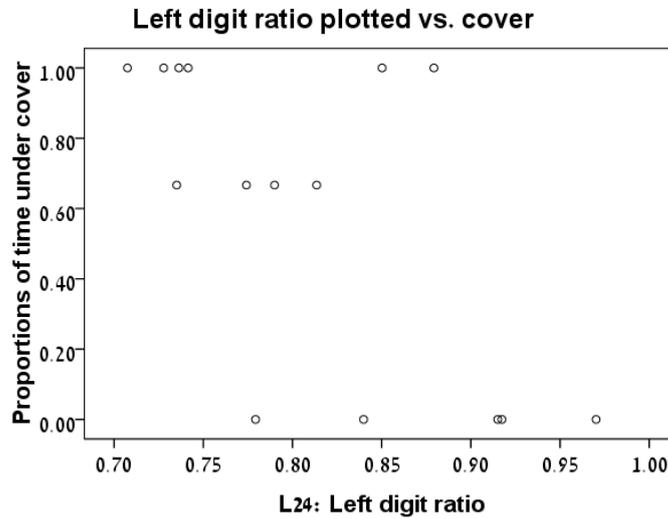


Figure 8. Left digit ratio vs. proportion of time under cover.

If we compare the digit ratio to a binary variable (in addition to the linear regression), in or out of cover, it is significant for the left digit ratio (L24). Exposed out of cover, we get a higher average of the digit ratio using a t-test:

Out of cover $N = 10$, $mean = 0.775 \pm 0.057$, under cover $N = 5$, $mean = 0.884 \pm 0.075$, $t_{13} = 3.152$, $P = 0.008$.

For the right digit ratio, the result is not significant using a t-test:

Out of cover $N = 10$, $mean = 0.799 \pm 0.080$, under cover $N = 5$, $mean = 0.855 \pm 0.111$, $t_{13} = 1.129$, $P = 0.279$.

3.3. Foot Preference vs. Detour Test

Geckos starting to move with the left foot were much more likely to bypass obstacles from the right side (see Figure 9), and vice versa (slope = -0.822 ± 0.099 , $t = 8.28$, $P < 0.0001$, $R^2 = 0.83$), as predicted.

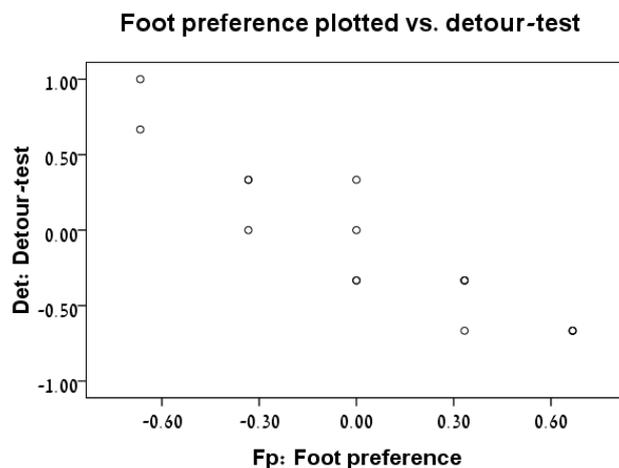


Figure 9. Foot preference plotted vs. detour test.

3.4. Detour Test vs. Time under Cover

There was no association between time spent under cover and the tendency to bypass an obstacle from the right or left (slope = 0.62 ± 0.49 , $t = 1.26$, $P = 0.23$).

All results are qualitatively the same with either 14 or 15 animals (i.e., removal of the single juvenile had no effect). However, when converting each variable to a binary unit, either below or above average, the correlation is significant (see Figure 10), using a non-parametric Spearman correlation: $N = 16$, $r_s = 0.683$, $P = 0.004$.

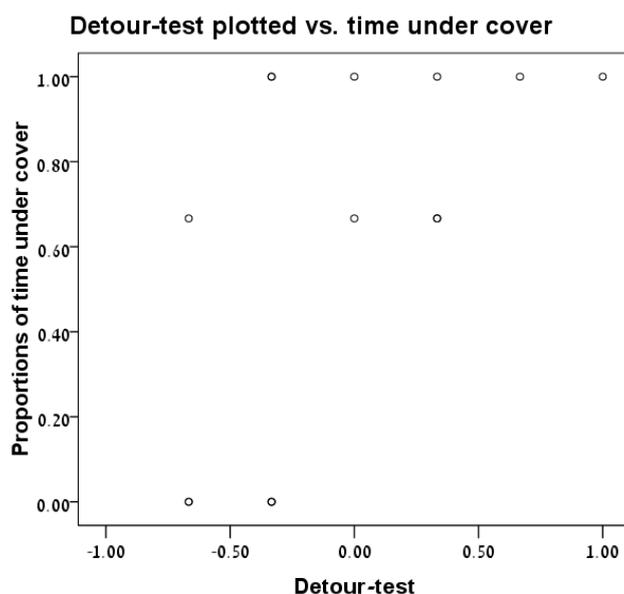


Figure 10. Detour test plotted vs. the proportion of time under cover.

4. Discussion

In this study, we showed a significant correlation between the digit ratio and risk strategy in lizards and between the digit ratio and foot preference. Moreover, similarly to humans, the longer the fourth digit was compared to the second, the higher the risk was [62,63]. It is a pilot study and, further, we strive to compare more behavioral patterns to the digit ratio in more reptiles and other vertebrates. Lizards show patterns of brain laterality, similar and consistent with what we know from other vertebrates, such as the left eye preference in aggression gestures [6–8,26]. In many vertebrates, including lizards (opposite in fish), the right eye preference and right eye lateralization (left brain hemisphere) are specialized for predatory responses to prey [80,81]. This is consistent with many other vertebrates [1,4]. The digit ratio, i.e., longer fourth digit as a biomarker for a higher level of testosterone for both prenatal stages and adults, was tested significantly for humans [44,45,47], for mice [46], rats [82], lizards and amphibia [48]. Some studies focus on pets or domesticated animals to study brain laterality [80], to neutralize the influence of the capturing procedure on the affective state of the tested animal and the consequent activation of the right hemisphere. We chose to address wild geckos and not pet geckos, since we chose to compare our results to those of other studies on *Ptyodactylus guttatus* from the wild that seem to manifest brain laterality as relating to foot preference [28], risk strategy [29] or digit ratio [29]. However, it should be pointed out and compared differentially and cautiously whether a wild animal was born in captivity or alternatively tested close to its capture as in this study, or months or even years later, since differences should be tested between wild animals that were born in captivity or habituated to their captivity and between wild animals shortly after capture.

The hypothesis that a morphometric trait, such as the digit ratio or digit asymmetry, reflects (or is affected by) brain laterality in lizards [29], or rats [82], as the digit ratio does in humans [44,63,83,84], should be tested in vertebrates other than primates. Only after mapping similarities and dissimilarities

would we be able to make a solid statement on the matter. However, this study case is the first step towards it. Higher left-side (but not right-side) digit ratio was correlated with risk-taking behavior (time under cover) but not with the preferred direction of bypassing an obstacle in a detour test. This pattern of a left morphometric-biased trait correlating with risk (indirectly via higher tail injury) is shown in lizards and *Sphenodon* digit asymmetry [30,32], and it is consistent with a left-biased digit ratio (longer fourth hind digit compared to the right one). Further, the detour test was highly significantly associated with foot preference—this association explaining over 80% of the variance. This further supports the efficacy of the detour test as an appropriate laterality index for lizards (as shown in other vertebrates) [37,82,85]. The digit ratio (2/4) reflects financial risk in humans [60,61] as longer fourth digits (relative to the second digit) reflect a tendency for higher risk taking. We obtained a similar result with the lizards, as staying under cover was associated with having much shorter fourth digits (relative to the relatively longer second digit: 0.775 vs. 0.91 on average).

We found that left-footed geckos did not differ in their risk-taking strategy from right-footed geckos. This is counter-intuitive since we would expect left-footed to be risk-averse, due to asset protection [86,87]. Left-footed gecko individuals usually have a higher social status [28], and therefore have more to lose. We thus expected them to take fewer risks. Interestingly, this is opposite to what we know of humans, as left-handed people are known to take higher risks [88,89]. The result of the digit ratio correlating with foot preference is interesting in two aspects: we did not expect it, since it is not described in the literature. Moreover, it strengthens the hypothesis that the digit ratio is derived from or associated with brain laterality. Our results support the hypothesis that digit ratios reflect brain laterality in vertebrates other than *Homo sapiens*. In birds, fledglings from eggs with elevated yolk testosterone, regardless of their sex, had higher ratios of the 2/4 digit ratio on their left but not on their right feet than controls [64]. This coincides with our results for lizards with a marker for testosterone (digit ratio) [48] and we think this is not coincidental. There is an advantage in elevating the testosterone level during continuous stress. Any elevation in testosterone level results in more developed muscle tissue, better running speed and stronger bite force [90]. Thus, in dire straits of continuous stress, better running speed is an advantage for either running away from predators or running after prey. However, the more risks they take, the more injuries we expect they will get.

A follow-up study with a testosterone measure and with more taxa is needed to determine if our results reflect a fundamental phenomenon in vertebrates or are due to mere chance. We think this is not a coincidence. The results we obtained in this controlled lab experiment are consistent with observations in the wild of risk-taking strategy and eye asymmetry of adult geckos [29]. We found that risk is correlated with the digit ratio in young (sub-adult) geckos in the lab. More importantly, the morphometric variable, the D2/D4 digit ratio, which is a known and accepted proxy of brain laterality in humans, is also a brain laterality proxy in the lizard *Ptyodactylus guttatus*. The implications of the digit ratio as a proxy for brain laterality in general and risk-taking strategy in particular may have practical value if proven in future studies.

We suggest testing more vertebrates, in particular reptiles, concerning possible correlations between the digit ratio and risk strategy, not only because of the accumulating evidence of tail injury (reflecting higher risk) and fourth digit asymmetry, but also since recent studies show the plasticity of the reptilian brain and the link between risk behavior and brain asymmetry in lizards [78,88,89]. If the result that the digit ratio and risk behavior are indeed correlated is consistent, we speculate it may be reflecting the levels of stress they deal with. Thus, longer fourth digits would be expected to predominate in stressful environments and shorter ones in stable environments. We suggest the notion that reptiles are an ideal model for brain research, since there is a growing literature on the flexibility of the reptilian brain [91,92] and there is a working theory supported by anecdotal reports of the supposition that the strength and direction of lateralization are dependent on experience [81].

Similarly to the cheap, simple tool of the detour test to measure brain laterality [68], if a morphometric trait such as the digit ratio, digit asymmetry or eye asymmetry can inform on the risk-taking strategy at the population level, it could be a cheap and useful ecological tool to assess

the stability of the environment or level of disturbance. This speculation can support the motivation to further study and test it. A simple demonstration of a correlation between brain laterality and a morphometric trait is not unprecedented [93]. The asymmetric distribution of scales (sub-lamellae scales) on the right vs. left hind foot may explain Figure 9 [93]. In an insular population of wild geckoes [93], the geckoes lift first from the substrate the hindlimb that has the lowest ability to stick to the substrate. We think it is important to study the differences and similarities of different taxa pertaining to brain asymmetries, particularly in non-humans, and especially on wild animals. It may enable us to decide if these similarities are imposed by brain architecture [28] or derived from a common evolutionary path [94,95].

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