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# Does a large brain equal higher intelligence?

A study of relative brain size and cognitive ability in the Guppy (*Poecilia reticulata*)

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## **Abstract**

The evolution of the vertebrate brain has fascinated and bewildered scientists for centuries. The brain is indeed a thrilling but also a very difficult organ to study with its extreme complexity, many functions and huge variation. One of the most studied features of the brain is the relative size, a highly variable trait where intelligence is thought to be the most important positive selective factor. However, all studies made within this field have been based on correlational analyses, a method which has met a lot of critique. With this study we wanted to investigate whether an enhanced brain size had a positive effect on cognitive ability, an important component of intelligence, using a different approach. The study was carried out by exposing guppies selected for small and large relative brain sizes to an associative learning experiment. We found that females with the larger brains seem to have a better cognitive ability as they did significantly more correct choices in our learning experiment compared to the down-selected females. These results indicate that cognitive ability is one of the positive selective factors causing the differences in relative brain size we see among vertebrates today.

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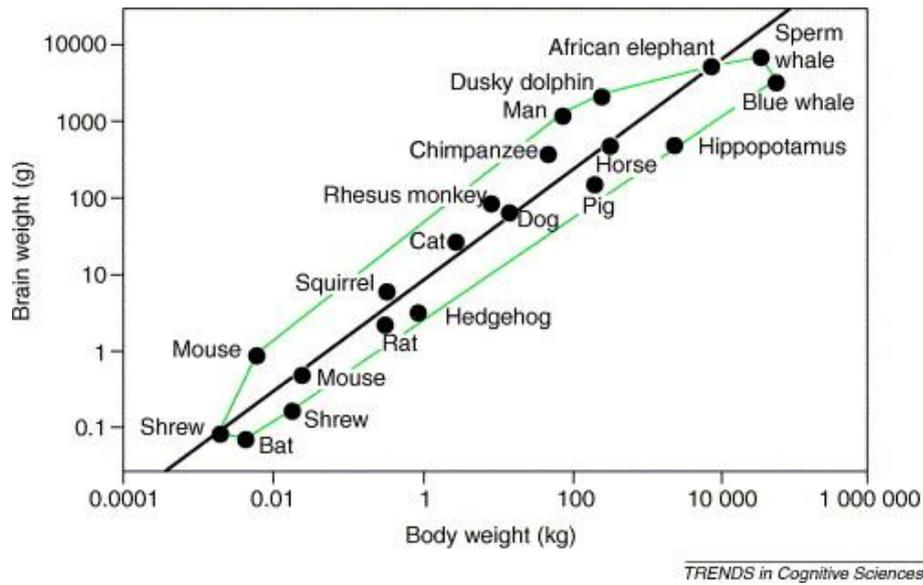
## Introduction

The vertebrate brain is a complex and intriguing organ that comes in many different shapes and sizes. It is involved in everything from basic body movements to intricate behavioral patterns (Ferrier, 1873; Striedter 2005) and is very likely to have a big impact on an individual's fitness. Many scientists, including Darwin himself (Darwin, 1871), have over the years tried to understand the evolutionary forces driving this divergence but because of the brain's complexity and its many functions this is a very difficult task.

Brain size (which is most often measured in weight) is one of the most variable features of the brain. It ranges from less than 0.1 gram, in for example shrews and bats, up to 8 kilogram in the sperm whale (Roth, 2005) (fig 1). We know that brain size positively covaries with body size where larger animals have larger brains (Roth, 2005; Striedter, 2005). This effect is often explained by the fact that larger bodies demand larger brains to control basic body functions (Northcutt, 2002). Apart from a variation in total brain size we also see variation in brain size among animals with a similar body size which indicates that there are differences existing independently of the size of the body (Jerison, 1973). The brain to body mass ratio, also known as relative brain size, is used to describe this variation in brain size that is left when corrected for body size (Striedter, 2005). Having a relatively large brain comes at a high cost as the brain is, together with skeletal muscles and the digestive tract, one of the most energy consuming organs in the body with a metabolic rate of around 11W/kg for a human brain (Aiello & Wheeler, 1995). A large brain will therefore demand a high energy intake and an effective nutrition uptake. Having a large brain will also make the distances between different brain structures longer resulting in less efficient information transportation between the brain structures (Watts & Strogartz, 1998). Furthermore, it causes problems when giving birth, takes a long time to develop which leads to prolonged nurturing times (Allman & Martin, 2000) and there is a link between low fertility rates and large brains (Kotrschal et al., Submitted). These are just a few examples implying that an increase in relative brain size should lower an individual's fitness. Regardless of the costs we know that for example humans, dolphins, chimpanzee and mice (fig. 1) all have large relative brain sizes (Roth, 2005), why is that?

To counterbalance all the negative effects of a large brain there must be one or several strong positive selection pressures. *Intelligence* has long been thought as an

important trait upon which the evolutionary forces are acting (Jerison, 1973). This is, however, a very difficult trait to study, partly so because there are yet no single definition which scientists agree upon. Today, most definitions of intelligence involves features like abstract thinking, understanding, self-awareness, communication, reasoning, learning, emotional knowledge, retaining, planning, and problem solving (Neisser et al. 1996). As it is such a broad concept most studies focus on one or a few behaviors linked to intelligence, for example behavioral repertoire sizes (Changizi, 2003), innovation propensity (Sol et al. 2005), tactical deception (Bryne & Corp, 2004), social intelligence (Scultz & Dunbar, 2006, Reader & Laland, 2002) and tool use (Lefevbre et al., 2002; Reader & Laland, 2002). Studies of intelligence and relative brain size have so far been based on comparative analysis of behaviors and brain sizes between related species. These are studies that also have met a lot of negative criticism from several researchers (Healy & Rowe, 2006; Chittika & Nieven, 2009). Most of the critique is focusing on the fact that almost all studies are correlational analyses and correlations cannot imply causation. Skeptics also point out that even closely related species may have behaviors with different selective advantages due to different ecologies. It is therefore difficult to compare intelligence between them as it is crucial to correlate behaviors of equal importance to both species. Comparing a behavior of greater value to one of the species will give a correlation between brain size and intelligence that in reality could be due to differences in life history and ecology traits (Shettleworth, 2003). Many independent studies have, however, succeeded in showing strong correlations between different highly evolved behaviors and relative brain size (Tebbish & Bshary 2004; Garamszegi & Eens, 2004; Iwaniuk & Arnold, 2004). Results which are, despite of the criticism, suggesting that further investigation is important within the field.



**Figure 1.** The correlation between brain size and body size among some vertebrates (Roth, 2005).

This is a study within a larger project of which the ambition is to address several important selective factors acting on the brain by using artificial selection. The artificial selection is made on a various number of aspects of brain morphology and functions. In this specific study we wanted to investigate whether an increased relative brain size would affect the cognitive ability, hence individuals selected for relatively small and large brain sizes were used. Cognitive ability, which is an essential trait when investigating intelligence, can be defined as “all mechanisms that invertebrates and vertebrates have for taking in information through senses, retaining it, and using it to adjust its behavior to local conditions” (Shettleworth, 2010). Cognition is an important trait for most organisms living in a changing environment as a good cognitive ability should improve an organism's capability to respond faster and more precise to the environmental variations. Individuals with an enhanced learning ability would therefore have a selective advantage (Shettleworth, 2010). This would be the first time it is possible to experimentally show positive effects of an increased relative brain size.

The experiments were made on the common vertebrate model species the Guppy (*Poecilia reticulata*), a small freshwater fish originating from Trinidad. By using artificially selected individuals within the same species we avoid the problems of comparative and correlational studies addressed above. The large- and small-brained fishes were exposed to an associative learning experiment which in this case meant that they had to learn to

associate a previously neutral stimulus (symbols) with a reward (food). To be able to learn where to find the food using symbols as guidelines the fish had to be able to memorize, associate, pay attention, perceive and act, all important processes of cognition (Shettleworth, 2010). By measuring learning speed we wanted to investigate whether the large brained fishes learned how to use the cues faster compared to the small brained individuals. This would suggest that a larger brain will increase your fitness due to a gain in cognitive ability.

## **Materials and methods**

### **Study species**

The Guppy (*Poecilia reticulata*), a common vertebrate model species, is convenient to work with since it's small, easy to keep in large populations and adapts quickly to new environments. It has been shown in several studies that guppies have a good learning ability as they are able to learn both mazes (Shohet & Watt, 2009), numbers (Piffer et al. 2011) and landmarks (Burns & Rodd, 2008). They possess a good eye-sight which can be compared to that of primates. They are, however, polymorphic in the long-wavelength sensitive cones with a  $\lambda_{\max}$  varying between 529-579nm (Archer, 1987) meaning that they perceive long-wave radiant colors differently. Hence only black and white symbols were used in this experiment. The individuals in this study were fed TetraMin® flake food both before and during the experiment. The light was artificial and was constantly held on a 12:12 l/d lighting schedule. The temperature in the room varied between 27°C and 28°C.

### **Selection**

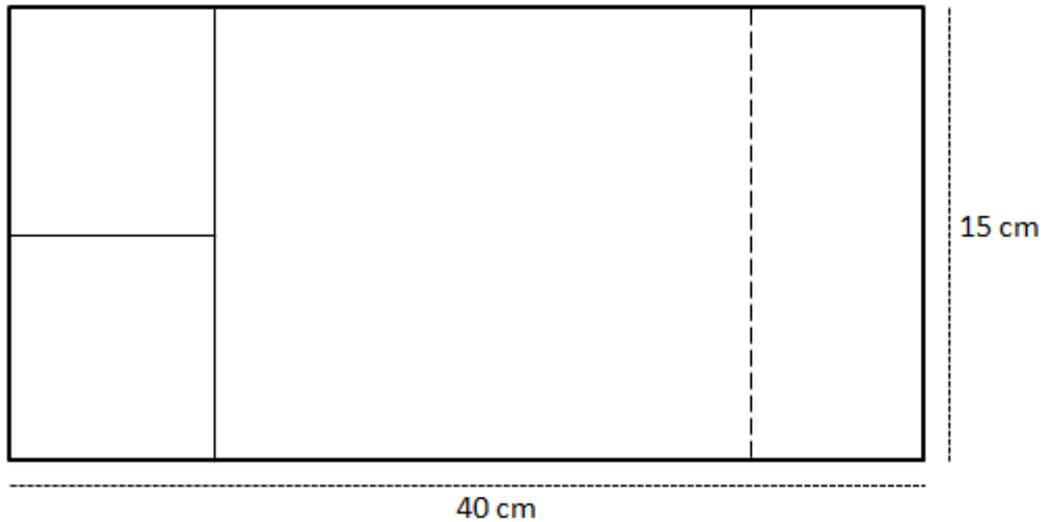
The selection experiment that was made to attain large- and small-brained guppies was conducted in the Kolm lab at EBC in Uppsala, Sweden. The fishes were originally caught in Trinidad and had been held in large (>500 individuals) populations since 1998, in which they were allowed to mate randomly. Four populations of 50 randomly selected individuals of each sex constituted the baseline populations for the selection experiment. Random mating was allowed within these four populations and the spawns were then transferred to smaller four liter tanks with three to five juveniles in each tank. The juveniles were separated as soon as they started to mature. At full maturity they were put in random pairs which now

represented the F0 generation. Three replicates were made for each generation. The pairs in the F0 generation were allowed to have two clutches before they were sacrificed using an overdose of benzocaine, after which they were measured and dissected. Body length and brain weight were used as measures of size and offspring from parents with a large relative brain size (top 25 % of the residuals of brain size on body size) and small relative brain size (bottom 25 % of the residuals of brain size on body size) were paired respectively to form the F1 generation pairs. Again the offspring from the F1 generation were put in small tanks with 5 juveniles in each which were separated at the first signs of maturity. Fully mature pairs were then again formed from the large respectively small brained F1 generation and full-sibling pairs were avoided. The difference in relative brain size in the F2 generation was on average 9% ( $p < 0.0001$ , Kotrschal et al. Submitted). Forty-eight randomly chosen adult individuals, 25 females and 23 males, from this generation were used in the cognitive experiment. The division was made so that we had equally many of the two selection lines. We also aimed to have equally many of each sex and replicate to the extent that it was possible (see enclosure on page 19 for the exact sectioning). Out of the 48 individuals three males died leaving 25 females and 19 males.

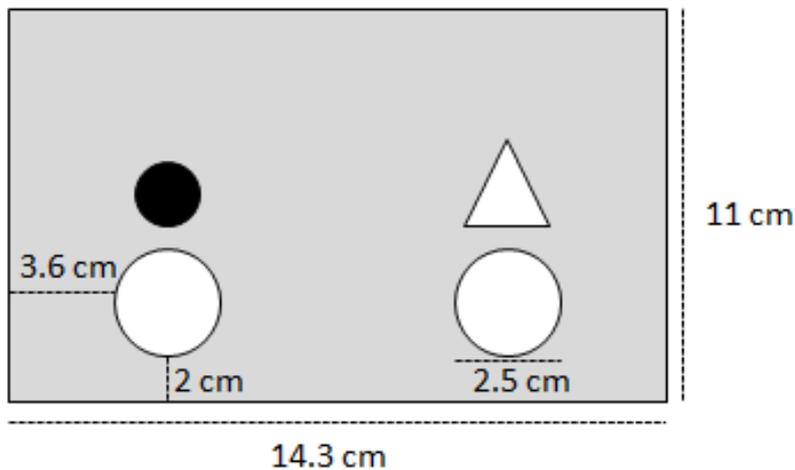
## **Setup**

Forty-eight plexiglas tanks with a size of 15x15x40 centimeters were used in this study (fig. 2). The selected individuals were held separately in the tanks during the whole experiment and were kept together with an unrelated juvenile fish to avoid the stress of being alone. The focal individuals were placed in the experimental tanks in a randomized order and they were prevented from visual contact with each other by card-board partitioning between the tanks. In the front of the tank were two compartments made out of PVC plates with a total area of  $115.2\text{cm}^2$ . These compartments had circular entrances, 2.5 cm in diameter, centered in the middle, 2cm from the bottom (fig. 3) which could be blocked when the fishes were not trained or tested. A sliding door was positioned eight centimeters from the rear of the tank door behind which the fish could be kept while preparing for the experiment. The separating wall was placed far in the back to avoid an effect of the fish swimming to the closest entrance. White triangles and black circles made out of PVC plates with an area  $3.75\text{cm}^2$  were used as cues for the association learning experiment. The white triangle was used as the rewarding stimulus and the black circle as the non rewarding

stimulus for all individuals throughout the experiment. As a reward they were given the same flake food as they had been fed before the experiment which they recognized and were used to.



**Figure 2.** The experimental tank seen from above with the compartments to the left and the separating wall to the right.



**Figure 3.** The wall to the compartments with entrances and symbols.

### Acclimatization

The focal individuals were allowed to acclimatize for eight days in order to avoid an effect of stress due to the new environment. During the acclimatization time individuals were allowed to swim freely in the whole tank, including the compartments, for three days. They were fed in both compartments all three days in order for them to know where the

food would be given. After three days the fishes were allowed to get used to the experimental procedure without symbols for one week. The fish was then put behind the separating wall whilst the entrances were opened up and the food was placed in one of the compartments. The fishes were kept behind the separating wall for at least two minutes. The wall was then opened and the individuals were allowed to swim freely to find the food for five hours. Afterwards the fish was gently removed from the compartment and the entrances closed. When all individuals were used to the set-up the learning trial started.

### **Experimental period**

During the experiment the fishes were trained for two days and tested on the third day. The experiment went on for 30 days meaning 20 days of training and 10 days of testing. During training, the individuals were exposed to a similar treatment as during the acclimatization time. The only difference being that symbols had been placed both above the entrances and in the compartments and food had been added to the compartment with the rewarding stimulus. The symbols were placed according to a random schedule made with the RANDBETWEEN function in Microsoft Excel 2007.

When the focal individual was tested there was no food added in the correct compartment until it made a choice, this to avoid the use of olfaction to solve the task. The time it took for the fish to make a choice, starting when the separating wall was lifted, was noted as well as if it made a correct choice or not. In addition, it was registered if the fish was scared, showed signs of panic (by swimming very fast or freezing for more than five minutes), did not care about the food or if it was unwilling to swim into the compartments. If it took the fish more than 15 minutes to make a choice the entrances were closed and the fish was re-tested at the end of the day. During both training and testing the fish were allowed to eat for one hour after which it was gently removed from the compartment. The entrances were then closed and the remaining food removed. In addition to time, it was also noted if the juvenile friend was the first or last to choose the same or the opposite compartment as the experimental fish.

### **Statistical analysis**

The main analysis, a binary probit generalized linear mixed model, was conducted in SPSS 19.0 where total amount of correct choices out of the ten testing days were used as an

indicator of learning ability. Sex, selection and replicate were used as fixed factors and individuals as a random factor. This model weights the data differently making it possible to exclude the trials where the focal individual was acting very scared and did not make a choice. After testing day two a large brained female (number 14) had jumped in to the tank of a small brained female (number 13). One of the females was then put back into tank 14 but it was not possible to tell them apart which make it necessary to do two complementary analyses. One additional analysis where individual 13 and 14 were interchanged after day two and another where they were excluded completely after day two.

To look at the temporal trends a binary logit generalized linear mixed model fit by Laplace approximation was conducted in R 2.12.1. Correct or wrong choice was used as the response variable, day, selection and sex as fixed factors and replicate and individuals as random factors. The intercept and slope that were attained for each individual were then analyzed with a Mann U Whitney-test comparing the differences between sexes and treatment. The intercept was measured between day 5 and 6 to get the mean value (i.e. the value of  $y$  when  $x=5.5$ ). Males and females were analyzed both separately and together.

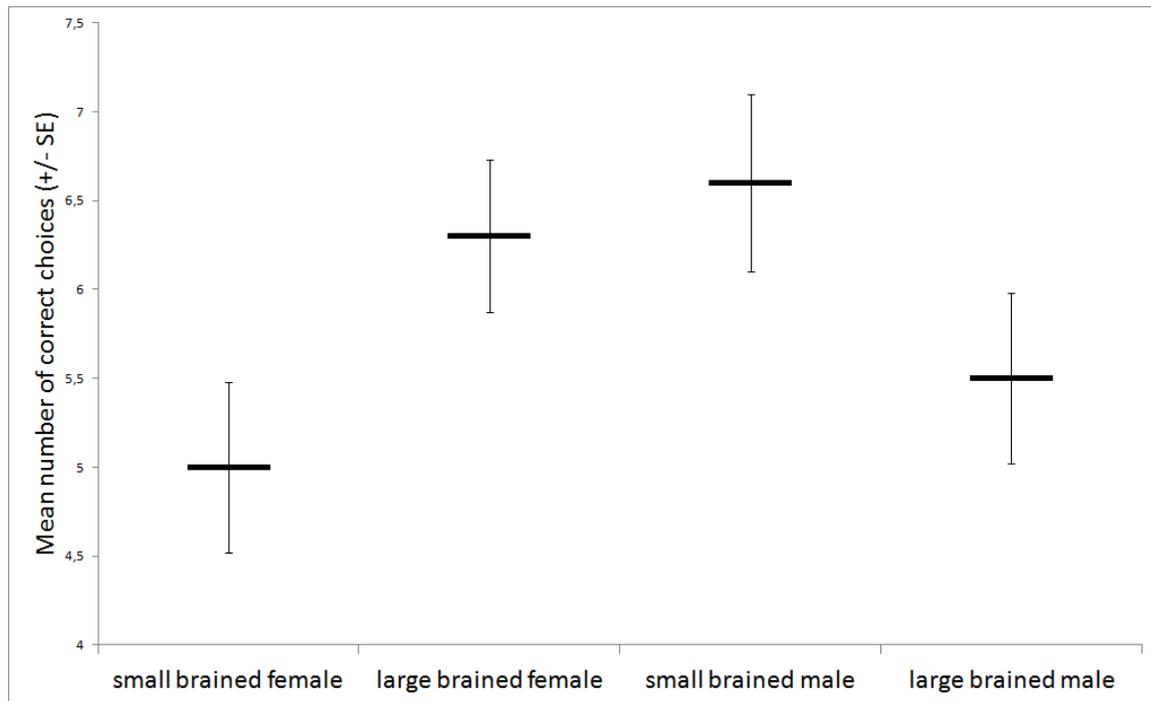
In addition, both the average number of times the individuals participated and the average number of times the focal individuals followed a friend were analyzed with a Mann-U Whitney test.

## **Results**

### **Number of correct choices**

The full model, including all individuals but excluding the times when the focal individuals were stressed, demonstrated no significant effect of replicate ( $p=0.249$ ), selection ( $p=0.781$ ) or sex ( $p=0.453$ ) on number of correct choices. A significant effect was found for the interaction between sex and selection ( $p=0.013$ ) on number of correct choices suggesting that a separate analysis was necessary for males and females. Importantly, when analyzing females separately a positive significant effect showed that large brained females had made significantly more correct choices compared to the small brained females ( $p=0.043$ , fig. 4). The analysis also showed that replicate did not seem to have any effect

( $p=0.323$ ). When analyzing males separately there were still no differences between the up and down selected lines ( $p=0.116$ , fig. 4) and neither between the replicates ( $p=0.144$ ).



**Figure 4.** Mean number of correct choices for small and large brained males and females (including 13 and 14) separately.

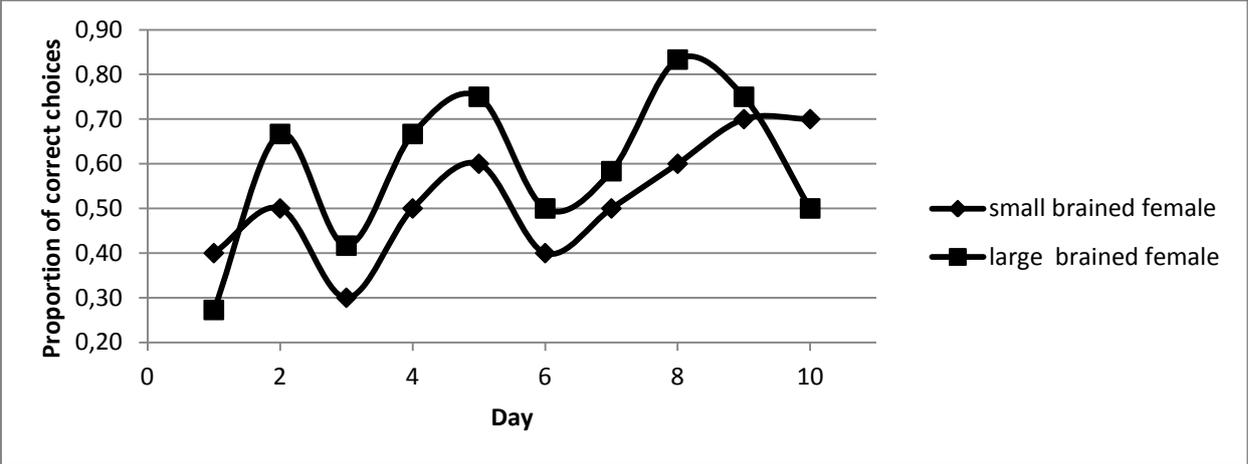
The results from the analysis when female 13 and 14 were interchanged after day 2 showed, like the previous analysis, a significant effect for the interaction of selection and sex on number of correct choices ( $p=0.034$ ) but no effect of replicate ( $p=0.391$ ), selection ( $p=0.931$ ) or sex ( $p=0.454$ ) alone. However, when looking at the females separately there were no significant effects of either selection ( $p=0.141$ ) or replicate ( $p=0.715$ ).

The results when female 13 and 14 were removed completely after day two were similar to the first analysis: even with this reduced sample, we found a trend suggesting a positive effect of selection on number of correct choices ( $p=0.063$ ).

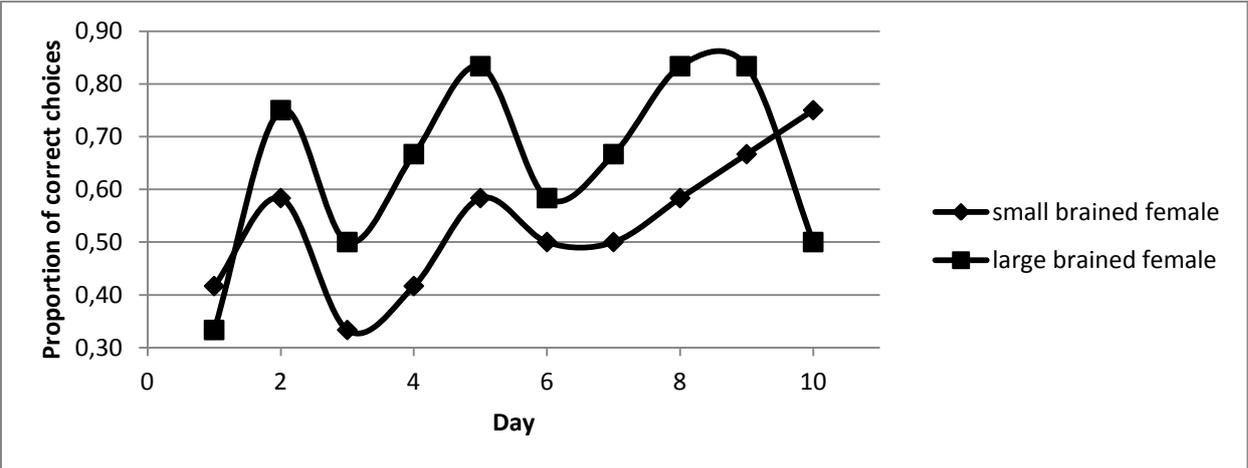
### Temporal trends

For females we found a trend suggesting that they were getting better and better over time ( $p=0.088$ ) but that there were no differences between the selected lines ( $p=0.121$ ). It seemed, however, that the large brained females almost always did better compared to the small brained females (fig. 5). We found no significant results for this effect

but a trend suggesting that there was a difference between the intercepts for the up and down selected females ( $p=0.113$ ). When the data was analyzed without number 13 and 14 the p-value increased from 0.113 to 0.193 and there was still no effect of the slope (fig. 6). No significant results were found when looking at the temporal trends analyzing either both sexes or males separately.



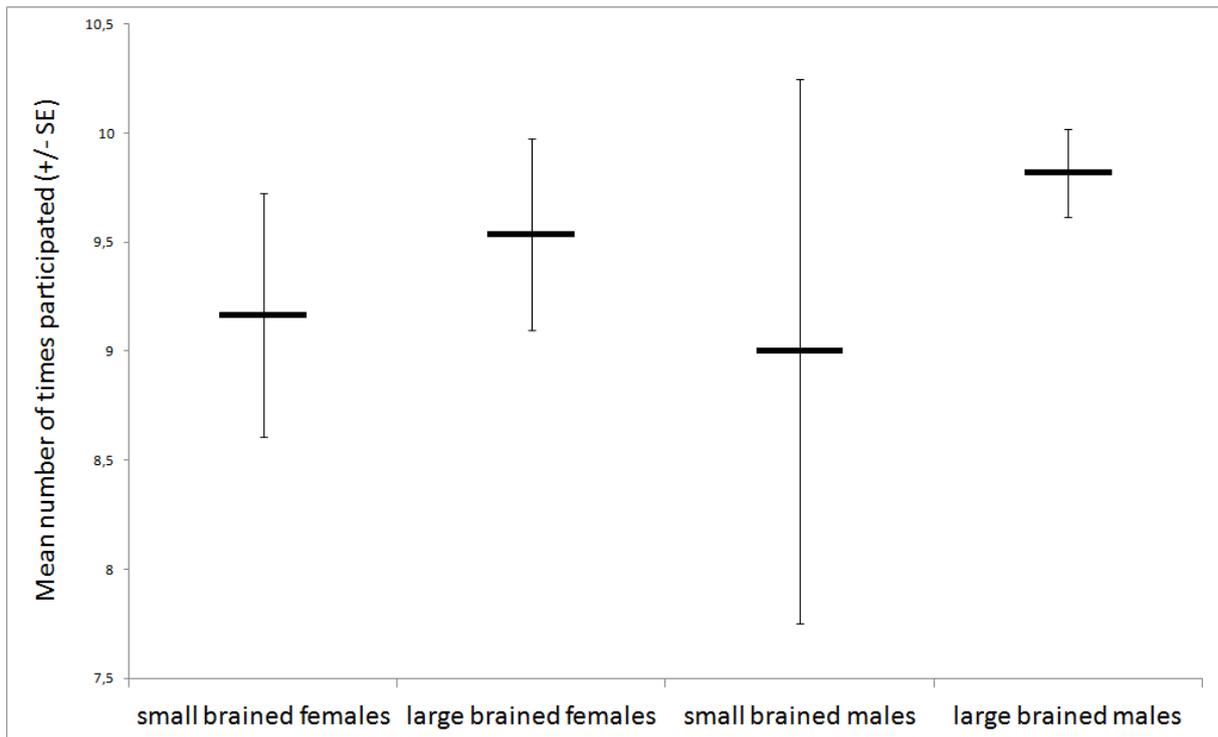
**Figure 5.** The proportional number of correct choices over the ten testing days for small and large brained females including female 13 and 14.



**Figure 6.** The proportional number of correct choices over the ten testing days for small and large brained females excluding female 13 and 14.

**Participation**

There was no difference between the up and down selected lines, neither for males nor for females ( $p>0.2$ ), in how many times the individuals participated in the tests (fig. 7).



**Figure 7.** Mean number of times that the individuals participated in the trials, separated by small and large brain size and males and females

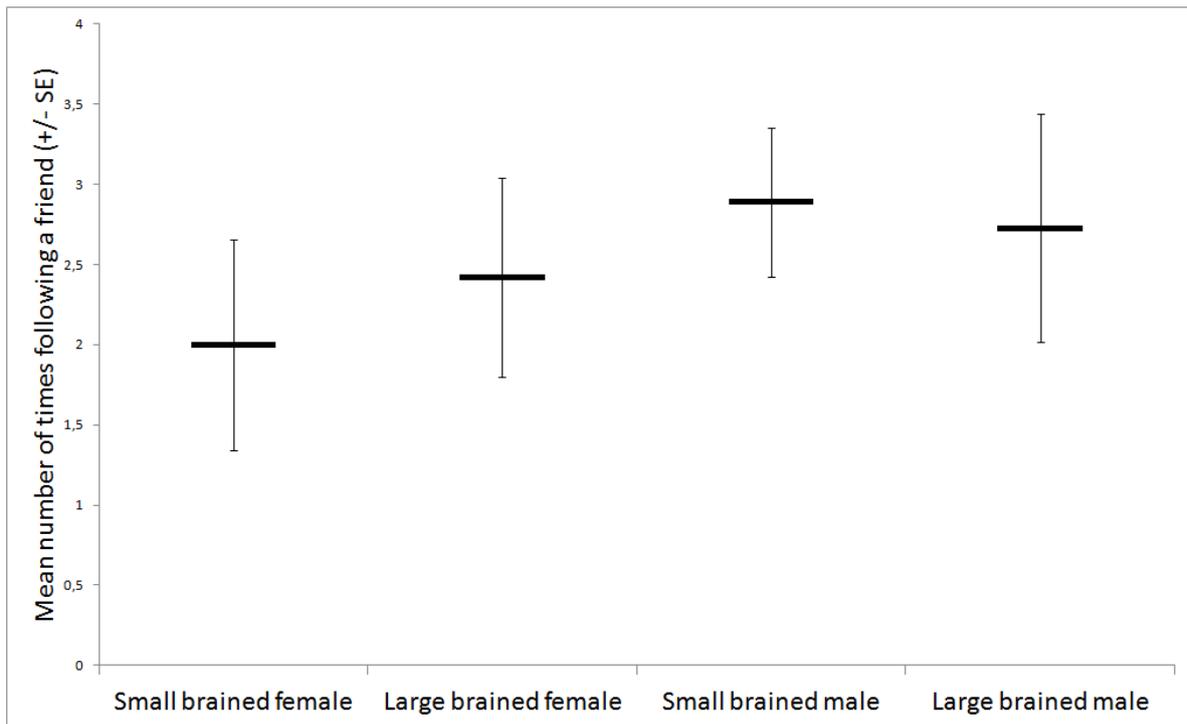
The coefficient of variation was calculated to look at the differences in standard deviation between the four groups (table 1) which show a greater variation in the small brained males compared to the three other groups.

**Table 1.** The coefficient of variation for participation of each sex and treatment.

Coefficient of variation	
small brained females	12,16%
large brained females	9,19%
small brained males	27,72%
large brained males	4,12%

### Friends

There was no significant difference between sexes or treatments (females;  $p=0.6289$  and males;  $p=0.6681$ ) in the number of times the focal individual followed a friend (fig. 8).



**Figure 8.** Mean number of times the individuals of the four groups, small and large brained males and females, choose to follow a friend.

## Discussion

The most striking outcome of this study is the significant difference in number of correct choices we found between the up and down selected females. A result which suggests that having a larger brain would be beneficial in terms of learning for females. This result supports the many comparative studies of brain size where the best predictive factor of a relatively larger brain can be linked to cognitive ability, for example studies of cognitive abilities in birds (Iwaniuk, 2006), flexibility in foraging behavior in ungulates (Schultz & Dunbar, 2006) and foraging ecology in bats (Hutcheon, 2002). Having a good cognitive ability should, as mentioned earlier, give an individual advantage in many important situations that arise in a variable environment. It is for example crucial in learning, remembering and localizing new foraging patches, in remembering and recognizing relatives and learning predator avoidance (Kieffer & Colgan, 1992). If, as this result implies, having a large brain results in a higher cognitive ability it is very likely that cognition is one of the traits upon which the selection for a relatively large brain is acting.

Unfortunately it is, as mentioned earlier in this text, problematic to use the whole dataset in the analysis since female 14 jumped into the tank of female number 13. The two complementary analyses that were made showed either a weak trend (when female 13 and 14 were removed) or no pattern at all (when female 13 and 14 were interchanged). The mix-up makes it difficult to, just with this study, tell whether a larger brain actually has an effect on cognitive ability or not. However, a similar experiment was conducted parallel to this one where effects of brain size on the ability to count were tested (Kotrschal et al., Submitted). That study shows, just as this one, no significant results for males but a significant positive effect among the females implying that large brained females were better at learning and discriminating between two and four symbols compared to the small brained individuals. These results indicate that we relocated the correct female back to tank 14 and that the large brained females actually were better at learning to use symbols as guideposts for where to find the food.

When looking at the temporal trend for the females we found no significant effect indicating any differences in learning speed. The graph (fig. 3) is nonetheless very interesting as it looks like both the up and down selected lines learn in a similar pattern but that the up selected individuals almost always do better. This effect is supported by the results of the main analysis where the up selected females did more correct choices and further a weak trend is suggesting that a difference in the mean value of the intercept might exist. Again results which are suggesting an enhanced cognitive ability for the large brained females.

One interesting aspect of this study, which is also shown in the parallel experiment, is that the only significant effects were found within females. An explanation to why we do not see any differences between the up and down selected males could be that we used food as a reward. Female guppies have been shown to be more food oriented compared to the males and the females could therefore have been searching for food more actively (Laland & Reader, 1999). Since they are more food oriented it might be easier for them to form associations between cues and food compared to male guppies. Moreover it is possible that the females spent more time eating in front of the rewarding symbol as they are larger (Magurran, 1995) and therefore have a greater need for energy compared to the males. A longer feeding time should make the association between the food and the symbol stronger (Gordon, 1981). As is demonstrated in figure 4 and table 1 we also see a large variation in participation within small brained males and as three out of the 12 down selected males

died the sample size for small brained males was very small. Even though the generalized linear model in SPSS weights the data differently the large variation and small sample size might affect the outcome as the effect size could be too small to show a possible difference.

If repeating this study I would suggest studying males and females separately as the sexes differ in level of food orientation and need for energy. For males it would be an idea to let them see a female as a reward instead, a method which has been used with good results in earlier studies (Burns & Rodd, 2008). It might also be a good idea to make it more costly to choose the wrong symbol, for example by making the distance between the rewarding and neutral stimuli longer. There is otherwise a risk that the focal individuals do not care about using the symbols as cues but instead just search for the food in both compartments. Replicate did not have an effect on the results and none of the up and down selected groups followed the juvenile friend in a higher grade than the other. This should make it safe to use individuals from different replicates and to add a companion in the upcoming experiments as well.

## **Conclusions**

The results of this study provide experimental evidence for the theory of cognitive ability as one of the traits upon which the selection or a relatively large brain size is acting. The next step towards fully understanding the causes of the variation we see in relative brain size today is to investigate the costs of evolving a larger brain as well.

## **Acknowledgement**

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**Enclosure.** Correct (1) and wrong (0) choice for each up- (1) and down-selected (0) individual each testing day where males are marked 1 and females 0. Individuals that died are marked with dark grey and no choice/scared with light grey.

ID	selection	replicate	sex	Day 1	Day 2	Day 3	Day 4	Day 5	Day 6	Day 7	Day 8	Day 9	Day 10
1	0	1	0	1	1	0	1	1	1	0	0	0	0
2	1	1	1	1	0	1	1	1	1	0	1	1	1
3	0	1	1	1	1	1	1	1	1	1	0	1	0
4	1	1	0	0	1	1	1	1	1	1	0	0	1
5	0	2	1	1	1	1	1	1	1	0	0	0	1
6	1	2	1	1	0	1	1	0	0	1	0	1	0
7	0	3	1	0	0	0	0	0	1	0	1	1	1
8	0	2	1	1	0								
9	0	1	0	1	0			1	0	0	1	0	1
10	0	3	0	0	1	0	1	1	0	0	0	1	0
11	1	1	0	1	0	1	1	1	1	1	0	1	0
12	1	3	1	1	1	0	0	1	0	0	0	0	0
13	1	1	0	1	1	1	0	1	1	1			
14	0	2	0	0	1	1	0	0	1	0			
15	0	3	1										
16	0	1	0	0	0		1	1	1	1		1	1
17	1	3	0	0	1	0	1	0	1	1	1	1	0
18	0	2	1		1	1	1	0	1	1	1	1	1
19	0	1	0	0	0	0	0	0	1	0	0	1	1
20	1	3	1	0	1	0	0	1	1	1	0	1	1
21	1	2	0	0	1	1	0	0	0	0	1	1	0
22	0	3	0	1	1	0	0	1	1	1		0	
23	1	3	0	0	1	1	1	1	0	1	1	1	1
24	1	1	1	1	0	0	0	1	0	0	0	1	1
25	1	2	0	0	0	0	1	1		0	1	1	1
26	0	1	1	1	1	1	1	1	1	1	1	0	0
27	1	3	1	0	1	1	1	1	0	0	1		1
28	0	2	0	0	1	1	1	0	0	1	1		1
29	0	1	1										
30	0	3	0	1	1	0	0	0	0	1	1	1	1
31	1	2	1	1	0	1	1	1	1	0	0	1	0
32	1	1	0		1	0	1	1	1	1	1	0	1
33	1	3	0	1	1	0	1	1	1	1	1	1	0
34	1	2	1	0	1	1	0	0	1	0	1	0	1
35	0	3	1	0	0	1	1	1	1	0	0		0
36	1	2	0	0	1	0	0	1	0	0	1	1	1
37	0	1	1	1	1	1	0	1	0	0	1	0	0
38	0	2	1	0	0	1	1	1	1	1	1	1	1
39	1	3	0	1	1	1	1	1	0	0	1	0	0
40	1	2	1		1	0	1	1	1	0	1	0	0
41	0	3	0	0	0	0	0	1	0	1	1	1	0
42	0	2	0	0	1	0	0	1	0	0	1	1	1
43	1	1	1	1	1	0	0	1	1	1	1	1	0
44	1	2	0	0	0	1	0	0	1	1	1	1	1
45	1	3	0	0		0	0	1	0	0	1	1	0
46	0	2	0	1	0	0	0	0	1	1	0	0	1
47	0	3	1	0	1	1	0	1	0	1	1	0	1
48	1	1	1	0	0	1	1	1	1	1	0	0	0