Head size and personality in great tits *Parus major*

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Abstract
Head size and personality in great tits Parus major*.* Behavior and decision–making depend on cognitive abilities and ultimately brain size and structure. I hypothesized that personality may be related to relative brain size adjusted for body size, and therefore, that selection acts against individuals that have small brains for their body size. I investigated standard personality scores in great tits *Parus major* from the field in relation to head volume, sex, age, capture date, and body size. Head volume and brain mass were strongly positively correlated, allowing for non–destructive estimation of brain size based on head volume. Personality score was positively correlated with head volume andwas higher in individuals captured later in the season. In an analysis of head volume in relation to sex, age, date of capture and body size, males had larger heads than females and older individuals had larger heads than yearlings. Head volume was larger in individuals captured later during the season. These findings are consistent with the prediction that personality is related to relative brain size and that selection acts on personality and relative head size as reflected by changes over time and between age classes.

Key words: Age effect, Brain size, Head size, Personality, Selection, Sex effect

Resumen
Tamaño cefálico y personalidad del carbonero común, Parus major. El comportamiento y la toma de decisiones dependen de las capacidades cognitivas y, en último término, del tamaño y la estructura del encéfalo. Nuestra hipótesis es que la personalidad puede estar relacionada con el tamaño relativo del encéfalo respecto del tamaño corporal y, por consiguiente, que la selección actúa en contra de los individuos que tienen encéfalos pequeños con respecto al tamaño del cuerpo. Analizamos las puntuaciones habituales de personalidad en individuos de carbonero común, *Parus major*, capturados en el campo, en relación con el volumen cefálico, el sexo, la edad, la fecha de captura y el tamaño corporal. Debido a la fuerte correlación positiva existente entre el volumen cefálico y la masa encefálica, se pudo emplear una técnica no destructiva para estimar el tamaño encefálico a partir del volumen cefálico. La puntuación de la personalidad estaba positivamente correlacionada con el volumen cefálico y fue superior en individuos que se capturaron más entrada la estación. En un análisis del volumen cefálico en relación con el sexo, la edad, la fecha de captura y el tamaño corporal, se observó que la cabeza era mayor en los machos y en los individuos de años anteriores que en las hembras y los jóvenes del año, respectivamente. El volumen cefálico era mayor en los individuos que se capturaron más entrada la estación. Estos resultados coinciden con la predicción de que la personalidad está relacionada con el tamaño encefálico relativo y que la selección actúa sobre la personalidad y el tamaño cefálico relativo, tal como reflejan los cambios producidos en el tiempo y entre clases de edad.

Palabras clave: Efecto de la edad, Tamaño encefálico, Tamaño cefálico, Personalidad, Selección, Efecto del sexo

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Introduction

While behavioural syndromes are generally defined as correlations between multiple behavioural traits, personality is defined as individual consistency within a single trait across time and contexts (Sih et al., 2004). Correlations between multiple behavioral traits show consistent variation over time and contexts (e. g. Drent et al., 2003; Bell et al., 2009; Dunn et al., 2011). Behavioral syndromes constitute the non–random association of different behaviors that are adaptations to specific environmental conditions or constitute links caused by pleiotropy (e.g. Sih et al., 2004; Réale et al., 2007; Møller and Garamszegi, 2012; Garamszegi et al., 2012). These aggregations of associated behavioral traits reflect differences in underlying personality (Gosling, 2001; Groothuis and Carere, 2005). Aspects of behavioural personality traits, such as the axis from shyness to boldness, may correlate with risk taking and be linked to exploration of habitats and hence to exploitation of natural resources (e.g. Sih et al., 2004; Garamszegi et al., 2012). Therefore, it is not surprising that the diversity of behavioural syndromes has implications for fitness components such as survival and mating (Klein, 2000; Smith and Blumstein, 2008; Biro, 2012; Wolf et al., 2007). Although many recent studies have described behavioral syndromes in a diverse array of species, there is limited information on how such syndromes and the underlying personalities relate to cognitive abilities and the associated neural substrate (Feldker et al., 2003; Carere and Locurto, 2011; Sih and Del Giudice, 2012). Such associations between behavior and the relative size of the brain would be expected (Jerison, 1973; Dukas, 2004).

Many studies have suggested that relative brain size after adjustment for the effects of body size and its component parts play an important role in mediating innovative behavior, risk of predation, foraging and hoarding, sexual selection, social behavior and even population trends of birds (e.g. DeVoogd et al., 1993; Dunbar, 1993; Madden, 2001; Garamszegi and Eens, 2016; Garamszegi et al., 2009; Nottebohm, 2005; Shultz et al., 2015; Sol et al., 2005; Gonda et al., 2012; Roth and Pravosudov, 2009). In contrast, very few intraspecific studies have attempted to link relative brain size to behavior or morphology of individuals (Riters et al., 2004; Møller, 2010; Møller et al., 2011). Gene expression studies in mice have shown that more than 80% of the genome is expressed in the brain (Lein et al., 2007; Sunkin and Hohmann, 2007). This makes it likely that many phenotypic characters will be linked to relative brain size.

It has been reported that head size is a non–destructive measure of brain size that allows investigation of the link between relative brain size and behavior (Møller, 2010; Møller et al., 2011). Because flying birds are strongly selected for aerodynamic properties and weight minimization, there is a tight correlation between external head volume and internal brain mass (Møller, 2010; this study). Head size can be measured non–destructively and hence provide a link between behavior and cognitive ability, as reflected by relative head size (Møller, 2010). For example, barn swallows *Hirundo rustica* with large heads are not simply larger individuals, and that they do not generally have larger wings, larger aspect ratios, or larger wing areas (Møller, 2010). Individuals with larger heads arrived earlier from the African winter quarters to their European breeding sites; furthermore, they were more difficult to catch and likely to be recaptured after having been caught previously than were individuals with smaller heads (Møller, 2010). Intensity of brood defense by females was stronger among individuals with larger heads (Møller, 2010). Barn swallows breeding in larger colonies had larger heads, suggesting that brain size and differential recruitment of large–headed individuals to large colonies play a role in social behavior (Møller, 2010). The same authors also found evidence of directional selection for larger head size because head size increased from yearlings to older individuals due to differential mortality of small–headed individuals (Møller, 2010). In a second study, Møller et al. (2011) showed that brain size was reduced by an average of 5 % in birds in radioactive areas at Chernobyl compared to nearby control areas with little or no contamination. This effect was hypothesized to arise from inferior environmental conditions for normal brain development, including severe depletion of antioxidant levels under radiation exposure. The same study revealed a significant increase in brain size when comparing head volume of yearlings and older individuals, suggesting differential mortality of small–headed individuals.

The objectives of the present study were to investigate the relationship between personality behavior and relative brain size in a model species commonly used for studies of personality and behavioral syndromes, the great tit *Parus major*. First, I tested whether personality score was related to head volume, while controlling for the potentially confounding effects of sex, age, body condition and body size. I used a standard procedure to quantify exploratory behavior using a novel environment and two novel object tests (Drent et al., 2003). Second, I tested whether head volume could be predicted by rearing environment, sex, age, date, body size, body mass and condition. Furthermore, I predicted that relatively large heads would be associated with specific personality behavior because a large head would allow for more diverse or more thorough processing of behaviour. Finally, I predicted that if there was selection against specific personality traits and head sizes, there should be an increase in standard personality score and head size over time and across age classes. This argument rests on the assumption that later captured individuals would be predicted to also have been present early during the season, and individuals over one–year of age would also have been present when yearlings. Again, previous studies in other species have shown that larger–headed individuals survive better as reflected by larger heads in older birds compared to yearlings (Møller, 2010; Møller et al., 2011).

Material and methods

Study area

The study was based on wild great tits caught at Orsay (48º 42' N, 2º 11' E), France, from January 23 to February 25, 2013. This study site is a mixture of urban habitats and a 300 ha chestnut *Castanea sativa* forest where great tits are one of the most common residents throughout the year.

Capture

Great tits were captured in mist nets in a suburb and an adjacent forest. They were then tested in exploratory and novel environment tests, after which they were immediately banded and released. I took care not to damage any of the individuals; none died, and all flew away on release.

Sexing and aging

I sexed great tits using the intensity of yellow breast coloration, the width of the breast band, and the presence of a large cloacal protuberance (males) or a brood patch (females) as criteria (Svensson, 2006). Birds were aged using molt of the wing coverts as a criterion (Svensson, 2006). These criteria are sufficient to reliably sex and age all adult great tits.

Head size, tarsus and beak length and body mass

I measured head length including beak length, head height and head width using a digital caliper to the nearest 0.01 mm, as described in detail by Møller (2010). I subsequently measured beak length to the skull (Møller, 2010). All characters were measured three times to allow estimation of repeatability. Head volume (cm^3) was then estimated as ((head length – beak length) x head width x head height x 1/6 x p), assuming that head volume can be approximated by an ellipsoid. Tarsus length was recorded with a digital caliper, while body mass was recorded with a Pesola spring balance.

J. Erritzøe kindly measured the three head dimensions described above while also recording brain mass for dead great tits that he received as a taxidermist. All specimens came from the same population around Christiansfeld, Denmark. Of 21 birds, 12 were males, 9 were females, 9 were adults and 12 were juveniles. There was a strong positive relationship between head volume and brain mass in all 21 great tits, implying that head volume is a reliable index of brain mass in these birds (fig. 1; F = 242.24, df = 1, 19, adjusted r^2 = 0.93, P < 0.0001, estimate (SE) = 0.289 (0.019)).

Personality score

I used a standard procedure to quantify exploratory behavior using a novel environment and two novel object tests (Drent et al., 2003). The novel environment test consisted of placing the birds individually in a test chamber (1 m x 1 m x 1 m) with five artificial trees. The size of this test chamber was smaller than that in previous studies of great tits (Drent et al., 2003), but this should not affect the relative ranking of individuals with respect to time required to perch on the individual trees. The birds were released from a holding bag. The behavioral score was the time it took for the bird to reach four of the five trees to convert this into a score ranging from 0 (slow) to fast (10) (Drent et al., 2003). Two novel object tests were conducted: these consisted of attaching an 8–cm bendable rubber toy (a Pink Panther) to the perch on one side of the cage in the first test, and a penlight battery in the second test. The behavioral score was recorded as the latency to approach the object and the closest distance to the object during the first 2 minutes. The results from these two tests were converted linearly to a scale from 0 (slow) to five (fast). I used a score that ranged from zero (the bird did not land on the perch), to one (it landed on the distant third of the perch during the two minutes), two (it landed on the distant third during the first minute), three (it landed on the central third of the perch), four (it landed on the third closest to the object), and five (the individual pecked at the novel object). Scores from the two novelty tests were analyzed separately for exploratory and novelty tests. Therefore, a higher score implies more exploratory or neophilic behavior, respectively. The use of two measurements allowed estimation of repeatability (Becker, 1984).

Ethical note

All birds were captured with permission from the local ringing center. All individuals were released at the site of capture and all flew away without difficulty when released.

Statistical analyses

I used generalized linear models to predict personality score. I started out with a full model that included sex (a categorical variable), age (a categorical variable), tarsus length, body mass, date, and time of day as predictors. The variables were subsequently eliminated with the least important predictor eliminated first until only predictor variables with an associated P < 0.10 remained. I made generalized linear models with head volume as the response variable and sex (a categorical variable), age (a categorical variable), tarsus length, body mass, date, and time of day as predictors. In a second model, I used personality score as a response variable. These models were subsequently reduced as described above. Repeatability (Becker, 1984) was above 0.95 for all three head dimensions , implying that measurement errors were small.

I evaluated the magnitude of associations between escape behavior and predictor variables based on effect sizes using Cohen's (1988) criteria for small (Pearson r = 0.10, explaining 1% of the variance), intermediate (Pearson r = 0.30, 9% of the variance) and large effects (Pearson r = 0.50, 25% of the variance). All analyses were made with JMP (SAS, 2012).

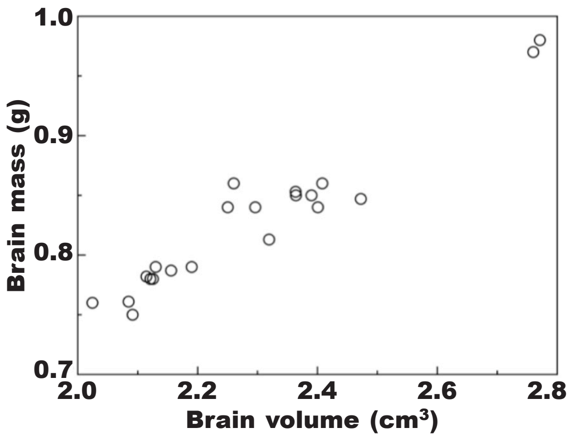

Fig. 1. Brain mass (g) in relation to head volume (cm^3) in 21 great tits.

Fig. 1. Masa encefálica (g) en relación con el volumen cefálico (cm^3) en 21 carboneros.

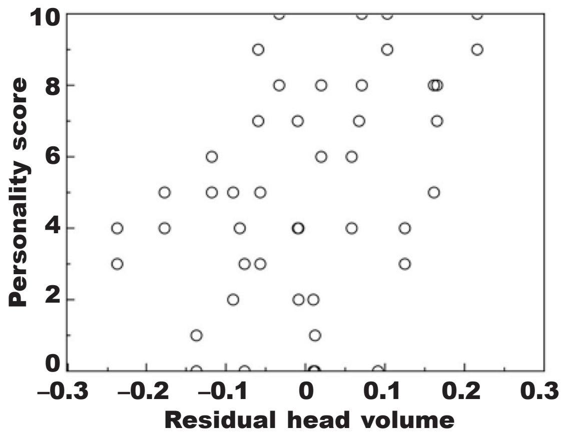

Fig. 2. Personality score in great tits in relation to residual head volume in 46 great tits (after adjustment for sex).

Fig. 2. Puntuación de la personalidad en relación con el volumen cefálico residual en 46 carboneros comunes (tras el ajuste por sexo).

Results

Personality score, head size and other predictors

The two novel object scores were significantly repeatable (F = 3.04, df = 44, 45, P = 0.0001, R = 0.51 (SE = 0.16)). The great tits showed significant correlations between exploratory behaviour and sex, date and head volume, respectively (fig. 2, table 1). Individuals with higher exploratory behaviour scores

Table 1. Generalized linear model of the relationship between exploratory and novelty components of behavior of great tits in relation to sex, date, time and head volume. The models had the statistics χ^2 = 19.66, df = 4, p = 0.0006 and χ^2 = 23.09, df = 4, p = 0.0001. Sample size was 46 individuals. Effect size is Pearson's product–moment correlation coefficient.

Tabla 1. Modelo lineal general de la relación entre el comportamiento de exploración y el comportamiento frente a la novedad del carbonero común en relación con el sexo, la fecha, el tiempo y el volumen cefálico. Los modelos dieron como resultados χ^2 = 19,66, gdl = 4, p *= 0,0006 y χ^2 = 23,09, gdl = 4,* p *= 0,0001. El tamaño de la muestra fue de 46 individuos. La magnitud del efecto es el coeficiente de correlación producto–momento de Pearson.*

Variable	χ^2	P	Estimate (SE)	95% CI	Effect size
Exploratory behaviour					
Sex	8.64	0.0033	0.841 (0.273)	0.295, 1.387	0.433
Date	3.89	0.049	0.054 (0.027)	0.000 (0.108)	0.291
Time	3.24	0.072	–0.669 (0.365)	–1.400, –0.061	0.265
Head volume	6.69	0.0097	8.328 (2.985)	1.283, 8.810	0.381
Novelty behaviour					
Sex	3.45	0.063	–0.413 (0.218)	0.024, 0.851	0.274
Date	6.02	0.014	0.054 (0.021)	0.011 (0.097)	0.362
Time	9.05	0.0026	–0.924 (0.292)	–1.509, –0.339	0.444
Head volume	4.62	0.032	3.320 (1.505)	0.307, 6.333	0.317

Table 2. Generalized linear model of the relationship between head volume of great tits in relation to sex, date, time, age and body mass. The model had the statistics χ^2 = 35.54, df = 4, p < 0.0001. Sample size was 46 individuals. Effect size is Pearson''s product–moment correlation coefficient

Tabla 2. Modelo lineal general de la relación entre el volumen cefálico del carbonero común en relación con el sexo, la fecha, el tiempo, la edad y la masa corporal. El modelo dio como resultado χ^2 = 35,54, gdl = 4, p *< 0,0001. El tamaño de la muestra fue de 46 individuos. La magnitud del efecto es el coeficiente de correlación producto–momento de Pearson.*

Variable	χ^2	p	Estimate (SE)	95% CI	Effect size
Sex	23.93	< 0.0001	–0.083 (0.015)	0.629, 2.066	0.721
Date	5.83	0.016	0.004 (0.002)	0.0009, 0.0081	0.356
Age	10.16	0.0014	0.050 (0.015)	0.020, 0.080	0.470
Body mass	3.57	0.059	0.004 (0.002)	–0.00015, 0.00768	0.279

had a larger head volume with an intermediate effect size (table 1). The interaction between sex and head size was not a significant predictor of exploratory behaviour (χ^2 = 1.04, df = 1, P = 0.31), implying that males and females did not show different patterns. Individuals with higher novelty score had larger head volume. In addition, novelty behaviour increased during spring (a large effect size), and individuals that were captured later during the day had higher personality scores (an intermediate effect size). The interaction between sex and head size was not a significant predictor of exploratory behaviour (χ^2 = 3.48, df = 1, P = 0.06), implying that males and females did not show different patterns.

Predictors of head volume

Head volume of 46 great tits showed a significant correlation with sex, with males having larger heads than females and with later captured birds having significantly larger heads than early captured individuals (table 2, fig. 3). The latter effect size was intermediate in magnitude. In addition, older individuals had larger heads than yearlings with a large effect size (table 2). Finally, there was a non–significant correlation for birds with a higher body mass having larger heads than birds with a lower mass (table 2). There were no significant correlations between head volume and tarsus length (χ^2 = 0.76, df = 1, P = 0.38) or time of day (χ^2 = 0.0004, df = 1, P = 0.98), and these relationships all had small effect sizes. Finally, the interaction between sex and date was not a significant predictor of head volume (χ^2 = 1.97, df = 1, P = 0.16), implying that males and females did not show different patterns of variation in head size.

Discussion

The main findings of this study were that the personality score in a model species for studying personality was related to head volume, which is an indirect measure of brain size, and head volume increased with date and age. The present study was based on correlative data from great tits captured in the field. However, data from captive reared great tits from the Netherlands showed similar relationships for personality score (K. van Oers and M. Naguib, pers. comm.). Furthermore, their great tits of lab origin had a smaller head size than field captured individuals, with consequences for personality score. This shows that the findings reported here go beyond the specific great tit population under study. I will briefly discuss these findings.

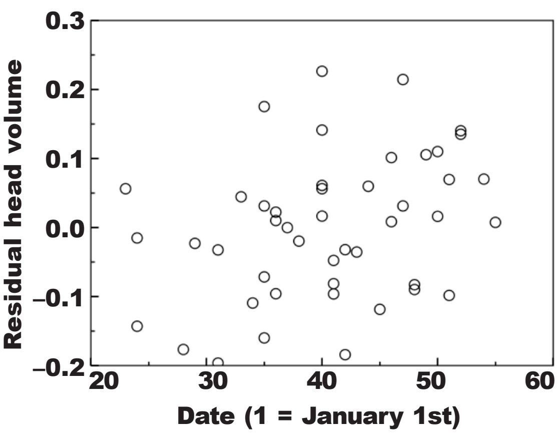

Fig. 3. Residual head volume (after adjusting for the effects of sex and age) in relation to capture date (1 = January 1) in 46 great tits (after adjustment for sex).

Fig. 3. Volumen cefálico residual (tras el ajuste por los efectos del sexo y la edad) en relación con la fecha de captura (1 = 1 de enero) en 46 carboneros comunes (tras el ajuste por sexo).

Head volume is a reliable index of brain mass in the great tit, as shown here for a sample of 21 individuals explaining more than 93% of variance. A similar tight relationship was previously reported for the barn swallow (Møller, 2010). Personality score was positively correlated with head size with an intermediate effect size. The significant relationships between personality score and head volume in the great tit may seem surprising, although there are no previous studies of great tits or other species linking personality behavior to morphological traits. This relationship between personality score and head volume was independent of the confounding effects of sex, age, capture date and time of day. Body size was not a confounding variable, as shown by the non–significant correlation between head size and tarsus length. This was also observed in the barn swallow where there were weak phenotypic correlations between head size and other morphological characters (Møller, 2010). Independently of head size, there was a sex difference in personality score. Personality is linked to sex in humans (e.g. reviews in Biglan et al., 1990; Sansone and Sansone, 2011) and animals (Duckworth, 2006; van Oers et al., 2008; While et al., 2009). Finally, individuals captured late during the season had higher personality scores than early captured individuals. The winter 2012–2013 was one of the coldest in France for many years, with snow falling in the Orsay study site intermittently between November 2012 and April 2013. In normal winters, snow is rare or non–existent in this area. I suggest that differential mortality during this very cold winter resulted in selective mortality among individuals with low personality scores. Such differential mortality among individuals with small brains has been reported previously (Møller, 2010; Møller et al., 2011). Here I hypothesize that the different results in mortality are linked to low personality scores. Alternatively, there may have been local movements of individuals with an influx of individuals with high personality scores late during the season. I consider this second possibility to be unlikely given that the main dispersal period is in autumn (Perrins, 1979). Furthermore, none of the 46 great tits were recaptured at one of the five study sites –separated by 5 km– other than that from which they were originally captured, suggesting that movement among sites was uncommon. I found a significantly weak correlation with time of day, suggesting that birds that were captured later in the day had lower personality scores, perhaps as mediated by diel rhythm in corticosterone that mediates activity (Carere et al., 2003).

Given that head volume was an important predictor of personality score, I investigated the determinants of head volume. There was a significant sex difference, and this was independent of structural body size as reflected by tarsus length. In a study of zebra finches *Taeniopygia guttata* reared on either a low or a high protein diet, reduced head size indirectly affected learning capacity (Bonaparte et al., 2011). In another study, Møller et al. (2011) reported a significantly reduced head size in birds at Chernobyl, linked to vitamin E, vitamin A and carotenoid deficiency during radiation exposure, extensive production of free radicals, and oxidative stress (Møller et al., 2005).

Natural selection may have acted on head size in great tits. Two pieces of evidence are consistent with this suggestion; correlations with date and age. Great tits captured later during winter 2012–2013 had larger heads than individuals captured earlier. Because 2012–2013 was a very cold winter with repeated snowfall, individual great tits captured later were also present at the start of the capture session due to their strictly resident status. It is unlikely that this difference is due to dispersal because I did not recapture any of the great tits at a site other than that at which they were initially captured. In contrast, I captured all of the individuals that were present at the end of the study multiple times, showing that they were indeed present in the neighborhood. The correlation between age and head volume of great tits showed that older individuals had larger heads than yearlings. Again, this finding is consistent with differential mortality of individuals with small heads. Such differential mortality of individuals with small heads has previously been reported for barn swallows (Møller, 2010) and birds in general including great tits in Chernobyl (Møller et al., 2011). We can exclude the possibility that this difference between age classes is due to growth among juveniles because juveniles are fully grown by the end of the summer, well before the capture of birds for this study.

The findings reported here open the possibility to study brain size in relation to personality behavior without sacrificing birds. Many different genes are expressed in the brain (Lein et al., 2017; Sunkin and Hohmann, 2007), and, therefore, it is likely that head volume as an index of brain size will be correlated with other behavioral traits. There is also evidence suggesting current selection for larger head volume, and that the quality of the rearing environment may constitute an important constraint on achieving optimal brain size.

In conclusion, personality as reflected by exploratory and novelty behavior is related to head size in a passerine bird, and head size in turn is associated with sex, age and date. These findings have important implications for our understanding of the link between personality behavior, cognition and relative brain size.

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