

# Egg Rejection and Brain Size among Potential Hosts of the Common Cuckoo

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## Abstract

Interspecific brood parasitism by the common cuckoo (*Cuculus canorus*) lowers host fitness, and has selected for discrimination and rejection of parasitic eggs in their commonly parasitized hosts. Cognitive demands needed to discriminate and reject cuckoo eggs may have led to augmentation of relative brain size among passerine hosts parasitized by cuckoos. This hypothesis predicts for across species positive relationships of brain size with rejection rate, host suitability and parasitism level. Here we test these predictions while controlling for phylogenetic, ecological and developmental factors known to affect brain size and egg rejection in a comparative study using the cuckoo and their hosts in Europe as a model system. Contrary to expected the rate of rejection of non-mimetic cuckoo eggs covaried negatively with relative brain size across bird species. Either suitability as cuckoo host, which reflects long-time duration of exposure to cuckoo parasitism, and level of parasitism, did not relate to brain size. Our results do not support the hypothesis that cuckoo parasitism was a main direct force affecting brain size variation across passerine hosts.

## Introduction

Many passerine species are parasitized by avian brood parasites. Parasites rely entirely on other host species that do all the work of nest building, incubation and chick rearing (Davies 2000). In Europe, interspecific brood parasitism by the European cuckoo (*Cuculus canorus*) (hereafter cuckoo) drastically lowers host fitness because of the eviction by the newly hatched cuckoo chick of the host eggs or chicks from their nests (Wyllie 1981). Discrimination and rejection of parasitic eggs is the most common and effective host behavioural trait evolved to counter cuckoo parasitism (Rothstein 1990). Experimentation has shown that many cuckoo hosts reject parasitic eggs from their nests, while species that

have not experienced cuckoo parasitism do not (e.g. Davies & Brooke 1989; Moksnes et al. 1991). Egg rejection protects host chicks from competition with the parasite chick or from being evicted, and it consequently has a high selective advantage. Also it is well known that species with a longer relation with the cuckoo have lower intraclutch variation in egg appearance, which is a trait enhancing cuckoo egg recognition (e.g. Øien et al. 1995; Soler & Møller 1996). Therefore, cuckoo parasitism is a major selective force shaping the evolution of both behavioural and morphological-based traits (Rothstein 1990).

Egg rejection, however, may be constrained by cognitive capacities. Rejection of parasite eggs requires of at least three cognitive tasks (Rothstein 1975; Lotem et al. 1995): (1) the capacity to recognize

a parasitic egg (i.e. egg discrimination), (2) a rejection ability (i.e. ejection or burial of the parasite egg and/or nest desertion) and (3) a linking motivational mechanism that triggers rejections once the parasite egg is recognized. Egg replacement experiments have shown that the time of exposure of a host to its own eggs affected rejection (Rothstein 1975; Lotem et al. 1995), suggesting that learning mechanisms (imprinting like processes) could be involved in egg discrimination. Also, egg discrimination appears to require long-term memory, as young great reed warblers (*Acrocephalus arundinaceus*) improve their rejection ability in their second nesting, after experiencing their own eggs during the first nesting (Lotem et al. 1995). Finally, it is plausible that host adaptation to egg rejection may require special visual and motor controls to discriminate the sometime perfectly mimicked cuckoo egg from the host own eggs, and, to reject it without causing damages to the host clutch. A further evidence that recognizing a cuckoo egg requires a certain level of cognitive specialization is provided by studies which have found an increased occurrence of recognition errors (i.e. misleading rejection of own eggs instead of the cuckoo egg) as cuckoo egg mimicry improved (reviewed in Davies 2000).

Much of cognitive ecology current effort is centred in the understanding of the link between brain space and cognitive function. Cognitive traits, like any other animal features, are determined by a mixture of genetic and environmental factors (reviewed in Dukas 2004). Therefore, those brain regions enabling particular cognitive tasks might occupy brain space that has been selected in a way proportional to the demand put upon them (Jerison 1973; Garamszegi & Eens 2004a; Healy et al. 2005). Indeed, several interspecific studies showed biological meaningful associations for overall brain size (Armstrong & Bergeron 1985; Bennett & Harvey 1985; Madden 2001; Garamszegi et al. 2002; Iwaniuk & Nelson 2003; Garamszegi & Eens 2004b; Lefebvre et al. 2004; Ricklefs 2004; Winkler et al. 2004).

Here, we explore the interspecific relationship between relative brain size of hosts and level of defences against brood parasites, as estimated by the rate of rejection of cuckoo eggs, using the cuckoo and their hosts across their breeding range in Europe as a model system. We specifically tested three predictions arisen from an evolutionary scenario in which increased cognitive demands to recognize and reject cuckoo eggs caused an increase in relative brain size among cuckoo hosts. This hypothesis relies on the assumption that discrimination and rejection

of cuckoo eggs implies significant cognitive demands for passerine hosts (see above). Accordingly, we predicted: (1) that total brain size may augment with the specialization of this behaviour because of the cognitive advantages that larger brains confer in terms of avoidance of cuckoo parasitism. Also, it is expected that (2) suitable cuckoo hosts (*sensu* Moksnes & Røskaft 1995) should have relative larger brains than unsuitable cuckoo hosts since they have been exposed for a longer time to cuckoo parasitism, which may have favoured defence mechanisms as a co-evolutionary response. Because of similar selection forces, we predict that (3) the level of parasitism is positively related to the relative brain size across species.

## Methods

### Data Set

We gathered information on brain size and cuckoo parasitism on 47 different European passerines (see Appendix). Discrimination abilities against cuckoo eggs based on host response against experimentally inserted parasitic eggs in its nests (e.g. Davies & Brooke 1989; Soler & Møller 1990; Lotem et al. 1995; Stokke et al. 2002). According to this methodology, individuals are classified as rejecters (nest deserters or egg ejectors) or acceptors of parasitic eggs. Based on published (Haartman 1981; Jarvinen 1984; Davies & Brooke 1989; Brown et al. 1990; Moksnes et al. 1991; Moksnes & Røskaft 1992; Moksnes et al. 1994; Lindholm 1999; Moskat & Fuisz 1999; Stokke et al. 1999; Grim & Honza 2001; Bartol et al. 2002; Rutila et al. 2002; Karcza et al. 2003), and unpublished sources (Martin-Vivaldi M. unpublished data; Avilés J. M. unpublished data), data on rejection rates (i.e. proportion of nests that rejected compared with the total number of nests tested) of experimentally added non-mimetic cuckoo eggs were retrieved for 47 species. In some species, rejection was tested in more than one population, which allowed calculating repeatability. Analyses of reliability revealed that rejection rate of non-mimetic eggs is highly repeatable among cuckoo hosts ( $r = 0.80$ ,  $F_{20,44} = 12.15$  and  $p < 0.00001$ ; see also Garamszegi & Avilés 2005). Consequently, if more than one estimate was available for a species, we used the average estimate from all studies. Because passerines possess advanced nervous systems, it could be argued that discriminating non-mimetic cuckoo eggs from own eggs is not a difficult task for cuckoo hosts. It is obvious that the hypothesis under evaluation

would have been more accurately examined whether rejection rates of highly mimetic egg instead of non-mimetic would have been used. Unfortunately, information on rejection of highly mimetic eggs is absent for most of the European cuckoo hosts. In our sampled species we could retrieve information from published (Davies & Brooke 1989) and unpublished sources (Martin-Vivaldi M. unpublished data) on rejection of mimetic eggs for 14 of 47 species with information on rejection of non-mimetic eggs. Interestingly, across specific variation in rejection of non-mimetic eggs was highly and positively correlated with across species variation in rejection of mimetic eggs in our sample ( $r = 0.81$ ,  $p < 0.0001$  and  $N = 14$  species), which supports the assumption that rejection of non-mimetic eggs is a reliable correlate of level of defences against cuckoos.

Level of parasitism was defined as the percentage of cuckoo parasitized nests of a given host species reported in the literature (Davies & Brooke 1989; Schulze-Hagen 1992; Soler 1999; Moskat & Honza 2002; Kleven et al. 2004; Lovaszi & Moskat 2004; Prochazka & Honza 2004). Unpublished data collected for woodchat shrike *Lanius senator*, grey shrike *Lanius excubitor*, corn bunting *Miliaria calandra* and European serin *Serinus serinus* by J. M. Avilés in Spain were also considered. Information on cuckoo parasitism for more than a single host population was only available for seven host species, which precluded a sound analysis of reliability. Nevertheless, repeatability analysis for these seven species revealed that parasitism was highly repeatable ( $r = 0.74$ ,  $F_{6,10} = 7.86$  and  $p = 0.0025$ ). Therefore, we used the mean estimate in the analyses when more than one estimate was available for a species.

Suitable hosts have more likely experienced a long-term relationship with the parasite, thus potentially providing more chance for selection toward host specific defences and/or brain characteristics. Thus, we divided host species into two groups regarding their suitability according to (Moksnes & Røskaft 1995). A species was classified as a suitable cuckoo host (scored as 1), if it provides their nestlings with insects, breeds in open or semi-open nests, and has eggs small enough for the cuckoo chick to evict (e.g. Davies & Brooke 1989; Moksnes et al. 1991; Moksnes & Røskaft 1995). The rest of species were considered as unsuitable cuckoo hosts (scored as 2). Reliability of this classification is inferred from the significant negative relationship between level of cuckoo parasitism and host suitability in our sample (i.e. unsuitable hosts are less parasitized) (analyses

based on raw data in Appendix:  $t = 3.83$ ,  $df = 46$  and  $p = 0.0003$ ).

Data for brain size (in grams) and the associated body mass were derived from three different sources (Mlíkovský 1990; Garamszegi et al. 2002; Iwaniuk & Nelson 2003). Iwaniuk & Nelson (2003) provide information on volumes, which can be converted to brain weights (Iwaniuk & Nelson 2002). In addition, highly significant repeatabilities between studies indicate that information on relative brain size can be combined across sources (Garamszegi & Eens 2004b; Garamszegi et al. 2005). We included information on body mass to control for allometric effects, but also to eliminate size-dependent effects on egg rejection, as the cost of this behaviour may be different between hosts that are small or big in relation to the cuckoo egg.

### Confounding Variables

A number of ecological and developmental factors may potentially affect the interspecific association under evaluation. For example, special capacity for the migration or food hoarding has been suggested to select for the enlargement of specific brain parts (e.g. Garamszegi & Eens 2004b; Winkler et al. 2004), thus potentially mediating the interspecific association between brain size and host defences against cuckoos, if these traits also relate to egg rejection. To control for this potential sources of biases, information on food hoarding and migration habits were simultaneously considered with the traits of interest in our comparative framework. Data on food hoarding behaviour was basically obtained from Garamszegi and Eens combined with the data from standard ornithological handbooks. We characterized the extent of food hoarding by using a two-point scale. Species with no evidence of food hoarding were considered as non-hoarders, whereas species that stored small amounts of food for short time intervals were categorized as hoarders. This two-point scale for food hoarding differs from the three grade scale used in Garamszegi and Eens because none of the considered species here can be classified as a specialized hoarder (i.e. species exhibiting typical caching behaviour by storing thousand of items in the autumn for later recovery). Migratory behaviour was scored on a three-point scale as 1 (resident), 2 (partial migrant) and 3 (migrant) according to the information in Cramp (1998).

Colonial species must be able to recognize other individuals and maintain social relationships with them. These demands, in turn, may favour the

evolution of brain structures that can process social information as compared with solitary breeders on one hand, but social leaning in colonial species may facilitate egg rejection on the other hand (Petrie & Møller 1991). Therefore we controlled for coloniality in our analyses. Information on coloniality, was retrieved from Cramp (1998) and species were classified on a three-point scale as 1 (nests aggregated in large groups), 2 (nest aggregated in small groups) and 3 (solitary, nests separated on large all-purpose territories).

Cuckoo hosts were also classified according to their diet, prey capture tactic and habitat type according to the information obtained from standard field guides (Cramp 1998; Glutz v. Blotzheim & Bauer 1985–1997) as these factors may potentially obscure the predicted associations between relative brain size and rejection rate, if they both associated with these factors. For diet, species were classified as mainly insect, seed or mixed (i.e. seed and insects) consumers. For prey capture technique, species feeding on plant material or being omnivorous or insectivorous while applying simple capturing techniques such as probing or gleaning from the vegetation were treated as having static preys; whereas birds hunting for actively moving prey in air or water were categorized as species with active prey. We recorded breeding habitats on a three-point scale from ground nesting species (1), via species nesting in bushes and shrubs (2) to species nesting in trees (3). These variables were treated as categorical variables in the analyses at the raw species data.

Comparative studies have revealed that developmental modes are related with relative brain size in birds (Iwaniuk & Nelson 2003). Developmental mode may also be related to rejection whether parasites would prefer host with a particular developmental mode in their hosts (see Soler et al. 1999), which should more likely evolve defensive behaviours against cuckoos. To control for this possible source of bias, we considered four variables likely to reflect differences in development mode among the considered host species in our comparative framework. From Cramp (1998) we retrieved information on the length in days of the incubation period, nestling period, post-fledgling period and total parental care (i.e. nestling period plus post-fledgling period).

Finally, the probability of finding egg rejection in different species may depend on the intensity of research on that species, as there may be more reports available for intensely studied species. We

estimated research effort by using the number of studies published since 1972 on each species as cited in the ISI Web of Science (<http://isiknowledge.com/>) and included this variable in our comparative framework to control for this possibility.

### Statistical and Comparative Analyses

Body size, brain size, incubation period, nestling period, post-fledgling period, total parental care and research effort were log-transformed before further analyses. Rejection rate was arcsine-square root transformed but still departed from normality. Hence, we sequentially ranked rejection rates which mean that species with zero rejection received random ranks from 0 to 10. Ranked rejection explained nearly whole variance in arcsine-square root transformed rejection ( $r = 0.98$ ,  $F_{1,45} = 2091.0$  and  $p < 0.00001$ ) and was normally distributed. Parasitism level was extremely left skewed and it did not fit a normal distribution after ranking. Therefore, we categorized each species in relation to parasitism level as no: for no parasitism, low: for parasitism between 0% and 5%, high: for parasitism >5%. We used a General Linear Model (GLM hereafter) on raw data, which allowed simultaneously assessing the effect of categorical and continuous normal distributed factors on brain size. Non-significant effects were excluded from the model following a stepwise deletion procedure in which the threshold p-value was set at 0.05. We removed non-significant effects, starting with the least significant term.

Taxonomic groups such as species cannot be considered statistically independent observations, and a phylogenetic control is required to eliminate the confounding effects of common ancestry (Felsenstein 1985). We applied the general method of comparative analysis for correlated evolution of traits based on Generalized Least Squares (GLS) Models implemented in software *Continuous* (Pagel 1997, 1999). Before modelling the correlated evolution of traits of interest, we assessed the contribution of different branch lengths and the importance of phylogenetic relationships. These assessments were achieved by estimating the maximum likelihood values of the branch length scaling parameter  $\kappa$  and the phylogeny scaling factor  $\lambda$ . If a significant effect was found ( $p < 0.05$ ), the estimated values were used in the final model; otherwise default (=1) settings were used. Secondly, using the appropriate scaling parameters, the correlation between the pairs of traits was tested by log-likelihood ratio statistics. These statistics are used to compare model  $H_0$ , fitting the data

while forcing the correlation to be zero, with the alternative  $H_1$  model, and permitting correlated evolution of the two characters. Thirdly, using the model best fitting the data, we estimated the phylogenetic correlation between traits. The appropriate scaling parameters and the log-likelihood ratio statistics testing for correlated trait evolution are presented. Brain mass is strongly dependent on body mass. To control for this allometric effect, we calculated the phylogenetically corrected regression of brain size on body size, using *Continuous*. Based on this phylogenetic equation, residuals were obtained for the raw species (see also Purvis & Rambaut 1995). We considered several potentially confounding variables (see above). However, to control for many discrete and continuous variables at the same time is difficult under our evolutionary modelling based on GLS approach. Therefore, we only took variables into account in the phylogenetic context that had had significant effects in the models based on the raw species data (Table 1). The other variables that are not in the model in Table 1, may have confound the phylogenetic results only if they become significant when the phylogenetic angle is

**Table 1:** Determinants of brain size as revealed by general linear mixed models with stepwise backward model selection, and involving body size, rejection rate, host suitability, and level of parasitism together with confounding ecological and developmental variables likely to affect brain size. Analysis based on raw species data. The effect of each non-significant term was obtained from the final model to which the given effect was added

Dependent variable, brain size	Slope ( $\pm$ SE)	Statistic
Overall, final model, $R^2 = 0.92$		$F_{4,42} = 122.7, p < 0.0001$
Intercept	$-0.858 (\pm 0.054)$	$t_{42} = -15.77, p < 0.0001$
Independent variables		
Body size	$0.628 (\pm 0.030)$	$F_{1,42} = 441.1, p < 0.0001$
Food hoarding	$0.148 (\pm 0.035)$	$F_{1,42} = 17.58, p = 0.0001$
Coloniality	Not in the model <sup>a</sup>	$F_{2,40} = 0.057, p = 0.945$
Prey capture	$0.075 (\pm 0.027)$	$F_{1,42} = 7.740, p = 0.008$
Rejection rate	$-0.002 (\pm 0.001)$	$F_{1,42} = 6.908, p = 0.012$
Food type	Not in the model <sup>a</sup>	$F_{2,40} = 0.326, p = 0.724$
Cuckoo parasitism	Not in the model <sup>a</sup>	$F_{2,40} = 0.380, p = 0.686$
Habitat type	Not in the model <sup>a</sup>	$F_{2,40} = 2.055, p = 0.141$
Migration	Not in the model <sup>a</sup>	$F_{2,40} = 1.048, p = 0.360$
Host suitability	Not in the model <sup>a</sup>	$F_{1,41} = 0.940, p = 0.338$
Research effort	Not in the model <sup>a</sup>	$F_{1,41} = 1.759, p = 0.192$
Incubation period	Not in the model <sup>a</sup>	$F_{1,40} = 0.078, p = 0.782$
Nestling period	Not in the model <sup>a</sup>	$F_{1,40} = 2.864, p = 0.098$
Post-fledging period	Not in the model <sup>a</sup>	$F_{1,31} = 0.671, p = 0.419$
Total parental care	Not in the model <sup>a</sup>	$F_{1,31} = 2.820, p = 0.103$

<sup>a</sup>Not selected by the stepwise procedure.

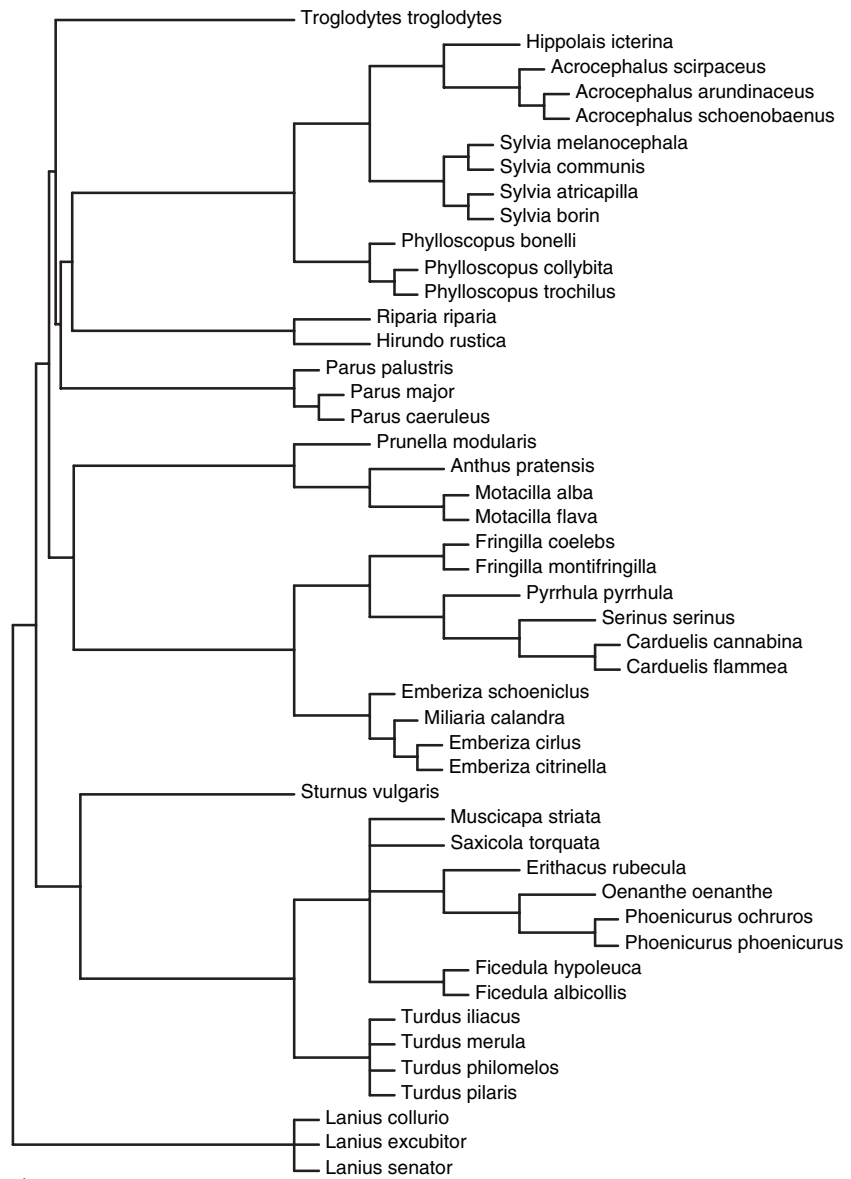
added. However, this is unlikely, because typically when one simulates data phylogenetically the critical values for the 'F' distribution are larger than what you get from a standard table.

The general topology of the phylogenetic tree (Fig. 1) for our comparative analyses was derived from a number of sources using molecular techniques. We constructed a composite phylogenetic hypothesis at the family level mainly based on the information in Sibley & Ahlquist (1990) obtained from extensive studies of DNA-DNA hybridization. This phylogeny was supplemented at the subfamily level with information from Arnaiz-Villena et al. (1998) and Blondel et al. (1996). Although Sibley & Ahlquist's (1990) phylogeny has been criticized, (Barker et al. 2002; Gill & Sheldon 1991; Lanyon 1992; Sheldon & Gill 1996), other analyses have emphasized its robustness to sophisticated phylogenetic analyses (Harshman 1994; Mooers & Coghlan 1999). We applied branch lengths from the tapestry tree of Sibley and Ahlquist (Harshman 1994) for higher taxonomic levels. Within families the distance between different genera was set to  $3.4\Delta T_{50H}$  units, and between species within genera to  $1.1\Delta T_{50H}$  units (Bennett & Owens 2002; Sibley & Ahlquist 1990).

## Results

A GLM approach using the raw species data revealed that the brain size of the European passerines was dependent on the rejection rate of cuckoo eggs, while body size, food hoarding also explained a significant amount of variance on brain size (Table 1). More specifically, species with relative larger brains are less prone to reject cuckoo eggs (Fig. 2). Neither host suitability nor level of parasitism was significantly related to brain size (Table 1).

When we estimated the effects of potentially confounding factors at the species level while using categories for the coded traits in a linear model for which statistical assumptions were not violated, we found significant effects for food hoarding and prey capture. Hence, eliminating the confounding effects of hoarding and prey capture, we can test for the phylogenetic relationship between egg rejection and relative brain size. Accordingly, we removed hoarding species and those that hunt for actively moving preys, and used the remaining species ( $N = 39$ ) to assess the effect of common ancestry. Using Pagel's continuous methods, we found a significant and negative relationship between relative brain size and egg rejection rate ( $\kappa = 0, \lambda = 0.592$ , Likelihood



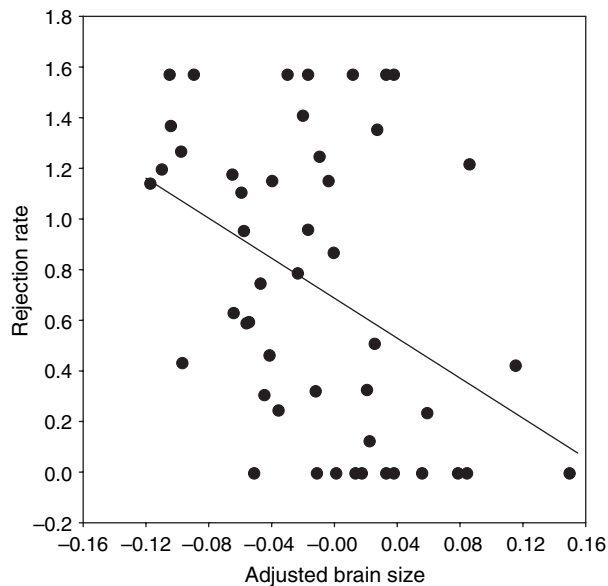
**Fig. 1:** Phylogenetic relationships among passerine cuckoo-host species included in the analyses

Ratio Test (LN) ratio = 3.535, df = 1, p = 0.008, r = -0.407 and p = 0.031).

**Discussion**

Comparative studies have previously shown that spatial abilities required for locating host nests may have induced sexual and/or species-specific changes in the volume of specific brain regions among obligate avian brood parasites (Reboreda et al. 1996; Clayton et al. 1997; Astie et al. 1998). The main finding of this comparative study is that the relative mass of the brain covaried negatively with the most important component of defences against cuckoo

parasitism. More specifically, we showed that species that reject cuckoo eggs at higher rates have a smaller relative brain size than non-rejecter species (Fig. 2). This pattern was consistent when analyses were based on raw species data or when considering the phylogenetic relationships among the cuckoo hosts. In addition, this association appeared to be independent of confounding ecological and developmental factors known to affect brain size and/or level of defences against cuckoo parasitism and of research effort. We found no evidence of significant covariation between the mass of the brain and host suitability, which is a variable likely reflecting duration of exposure to cuckoo parasitism by a particular host.



**Fig. 2:** Relationship between the rejection rate of artificial non-mimetic cuckoo eggs and adjusted brain volume (residuals of the regression of brain volume on body size, food hoarding and prey capture) among passerine hosts of the common cuckoo. Raw species data are shown

Similarly, brain size did not significantly relate to the level of parasitism suffered by hosts.

Considering the co-evolutionary relationship between hosts and avian brood parasites, we have hypothesized a causal mechanism linking relative brain size and the level of defences against cuckoo parasitism among passerines. The scenario proposes that, such as other tasks (e.g. food hoarding: Garamszegi & Eens (2004b); nest location: Reboreda et al. (1996); migration: Winkler et al. (2004) discriminating and rejecting cuckoo eggs may need particular cognitive demands leading to the augmentation of brain size among cuckoo hosts. This hypothesis relies on the assumption that discrimination and rejection of parasite eggs imply significant cognitive demands for passerine hosts, and thus predicts a positive association between egg rejection rate and relative brain size across species. Contrary to expectation from the hypothesis, we found that brain size was negatively associated with the rejection rate when allometric effects were controlled. Furthermore, we failed to find any significant association between brain size and variables likely to reflect exposure to cuckoo parasitism (i.e. parasitism and suitability as cuckoo host).

The negative relationship between brain size and the rate of rejection of cuckoo eggs across species is puzzling. It could be argued that hosts with relat-

ively larger brains may escape from cuckoos because they display more flexible behaviour and thus these species will need lower rejection rate than hosts with smaller brains. Indeed, species with relatively larger brains better respond to new environmental challenges, if they have improved behavioural flexibility (e.g. Sol et al. 2005). Also, plastic rejection of cuckoo eggs by host may reduce the peril of incurring in rejection costs when the risk of cuckoo parasitism is low (Brooke et al. 1998). According to this post hoc hypothesis, hosts with relatively larger brains may escape from cuckoos because they have higher plasticity for an unknown behavioural trait that is responsible for cuckoo avoidance. This scenario would also predict that big-brained species would suffer less parasitism than small-brained species. We do not found, however, signs of covariation between brain size and current level of cuckoo parasitism among hosts once possible confound were considered into account (Table 1).

In conclusion, relying on a wide range of passerine cuckoo hosts, we found consistent evidence that rejection rate of cuckoo eggs was negatively associated with volumetric augmentation of the brain. This finding does not support the expectation from our a priori hypothesis that cognitive demands to recognize and reject cuckoo eggs caused an increase in relative brain size among cuckoo hosts. Furthermore, it seems unlikely that the evolution of complex behaviour to escape from cuckoo parasitism was the mechanism behind the found pattern, because although rejection rate related to brain size, neither host suitability nor parasitism level, which are variables likely to express long- and short-term degree of constrains by cuckoo parasitism, related to brain size.

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### Literature Cited

- Armstrong, E. & Bergeron, R. 1985: Relative brain size and metabolism in birds. *Brain, Behav. Evol.* **26**, 141–153.

- Arnaiz-Villena, A., Álvarez-Tejado, M., Ruíz del Valle, V., García de la Torre, C., Varela, P., Recio, M. J., Ferre, S. & Martínez-Laso, J. 1998: Phylogeny and rapid Northern and Southern Hemisphere speciation of goldfinches during the Miocene and Pliocene Epochs. *Cell. Mol. Life Sci.* **54**, 1031—1041.
- Astie, A. A., Kacelnik, A. & Reboreda, J. C. 1998: Sexual differences in memory in shiny cowbirds. *Anim. Cogn.* **1**, 77—82.
- Barker, F. K., Barrowclough, G. F. & Groth, J. G. 2002: A phylogenetic hypothesis for passerine birds: taxonomic and biogeographic implications of an analysis of nuclear DNA sequence data. *Proc. R. Soc. Lond. B* **269**, 295—308.
- Bartol, I., Karcza, Z., Moskat, C., Røskaft, E. & Kisbenedek, T. 2002: Responses of great reed warblers *Acrocephalus arundinaceus* to experimental brood parasitism: the effects of a cuckoo *Cuculus canorus* dummy and egg mimicry. *J. Avian Biol.* **33**, 420—425.
- Bennett, P. M. & Harvey, P. H. 1985: Relative brain size and ecology in birds. *J. Zool.* **207**, 151—169.
- Bennett, P. M. & Owens, I. P. F. 2002: *Evolutionary Ecology of Birds*. Oxford Univ. Press, Oxford.
- Blondel, J., Catzeflis, F. & Perret, P. 1996: Molecular phylogeny and the historical biogeography of the warblers of the genus *Sylvia* (Aves). *J. Evol. Biol.* **9**, 871—891.
- Brooke, M. de L., Davies, N. B. & Noble, D. G. 1998: Rapid decline of host defences in response to reduced cuckoo parasitism: behavioural flexibility of reed warblers in a changing world. *Proc. R. Soc. Lond. B* **265**, 1277—1282.
- Brown, R. J., Brown, M. N., Brooke, M. de L. & Davies, N. B. 1990: Reactions of parasitized and unparasitized populations of *Acrocephalus* warblers to model cuckoo eggs. *Ibis* **132**, 109—111.
- Clayton, N. S., Reboreda, J. C. & Kacelnik, A. 1997: Seasonal changes of hippocampus volume in parasitic cowbirds. *Behav. Process* **41**, 237—243.
- Cramp, S. 1998: *Cramp's the Complete Birds of the Western Palaearctic*. Optimedia, Oxford Univ. Press, Oxford.
- Davies, N. B. 2000: *Cuckoos Cowbirds, and Others Cheats*. T & A D Poyser, London.
- Davies, N. B. & Brooke, M. de L. 1989: An experimental study of co-evolution between the cuckoo, *Cuculus canorus*, and its hosts. 1. Host egg discrimination. *J. Anim. Ecol.* **58**, 207—224.
- Dukas, R. 2004: Evolutionary biology of animal cognition. *Annu. Rev. Ecol. Evol. Syst.* **35**, 347—374.
- Felsenstein, J. 1985: Phylogenies and the comparative method. *Am. Nat.* **125**, 1—15.
- Garamszegi, L. Z. & Avilés, J. M. 2005: Brood parasitism by brown-headed cowbirds and the expression of sexual characters in their hosts. *Oecologia* **143**, 167—177.
- Garamszegi, L. Z. & Eens, M. 2004a: Brain space for a learned task: strong intraspecific evidence for neural correlates of singing behavior in songbirds. *Brain Res. Rev.* **44**, 187—193.
- Garamszegi, L. Z. & Eens, M. 2004b: The evolution of hippocampus volume and brain size in relation to food hoarding in birds. *Ecol. Lett.* **7**, 1216—1224.
- Garamszegi, L. Z., Møller, A. P. & Erritzoe, J. 2002: Coevolving avian eye size and brain size in relation to prey capture and nocturnality. *Proc. R. Soc. Lond. B* **269**, 961—967.
- Garamszegi, L. Z., Eens, M., Erritzoe, J. & Møller, A. P. 2005: Sexually size dimorphic brains and song complexity in passerine birds. *Behav. Ecol.* **16**, 335—345.
- Gill, F. B. & Sheldon, F. H. 1991: The birds reclassified. *Science* **252**, 1003—1005.
- Glutz, v., Blotzheim, U. N. & Bauer, K. M. 1985—1977: *Handbuch der Vögel Mitteleuropas Band 10–15: Passiformes*. Aula-Verlag, Wiesbaden.
- Grim, T. & Honza, M. 2001: Differences in behaviour of closely related thrushes (*Turdus philomelos* and *T. merula*) to experimental parasitism by the common cuckoo *Cuculus canorus*. *Biologia* **56**, 549—556.
- Haartman, L. V. 1981: Co-evolution of the cuckoo *Cuculus canorus* and a regular cuckoo host. *Ornis Fenn.* **58**, 1—10.
- Harshman, J. 1994: Reweaving the tapestry: what can we learn from Sibley and Ahlquist (1990)? *Auk* **111**, 377—388.
- Healy, S. D., de Kort, S. R. & Clayton, N. S. 2005: The hippocampus, spatial memory and food hoarding: a puzzle revisited. *Trends Ecol. Evol.* **20**, 17—22.
- Iwaniuk, A. N. & Nelson, J. E. 2002: Can endocranial volume be used as an estimate of brain size in birds? *Can. J. Zool.* **80**, 16—23.
- Iwaniuk, A. N. & Nelson, J. E. 2003: Developmental differences are correlated with relative brain size in birds: a comparative analysis. *Can. J. Zool.* **81**, 1913—1928.
- Jarvinen, A. 1984: Relationship between the common cuckoo *Cuculus canorus* and its host the redstart *Phoenicurus phoenicurus*. *Ornis Fen.* **61**, 84—88.
- Jerison, H. J. 1973: *Evolution of the Brain and Intelligence*. Academia Press, New York.
- Karcza, Z., Moskat, C., Cherry, M. I. & Kisbenedek, T. 2003: Experimental manipulation of intraclutch variation in the great reed warbler shows no effect on rejection of parasitic eggs. *Ethology* **109**, 15—22.
- Kleven, O., Moksnes, A., Røskaft, E., Rudolfson, G., Stokke, B. G. & Honza, M. 2004: Breeding success of common cuckoos *Cuculus canorus* parasitising four sympatric species of *Acrocephalus* warblers. *J. Avian Biol.* **35**, 394—398.



- Lanyon, S. M. 1992: Phylogeny and classification of birds: a study in molecular evolution, by C. G. Sibley and J. E. Ahlquist. *Condor* **94**, 304—310.
- Lefebvre, L., Reader, S. M. & Sol, D. 2004: Brains, innovations and evolution in birds and primates. *Brain. Behav. Evol.* **63**, 233—246.
- Lindholm, A. K. 1999: Brood parasitism by the cuckoo on patchy reed warbler populations in Britain. *J. Anim. Ecol.* **68**, 293—309.
- Lotem, A., Nakamura, H. & Zahavi, A. 1995: Constraints on egg discrimination and cuckoo host coevolution. *Anim. Behav.* **49**, 1185—1209.
- Lovasz, P. & Moskat, C. 2004: Break-down of arms race between the red-backed shrike (*Lanius collurio*) and common cuckoo (*Cuculus canorus*). *Behaviour* **141**, 245—262.
- Madden, J. 2001: Sex, bowers and brains. *Proc. R. Soc. Lond. B* **268**, 833—838.
- Mlíkovský, J. 1990: Brain size in birds: 4. Passeriformes. *Acta Soc. Zool. Bohem.* **54**, 27—37.
- Moksnes, A. & Røskaft, E. 1992: Responses of some rare cuckoo hosts to mimetic model cuckoo eggs and to foreign conspecific eggs. *Ornis Scand.* **23**, 17—23.
- Moksnes, A. & Røskaft, E. 1995: Egg-morphs and host preferences in the common cuckoo (*Cuculus canorus*): an analysis of cuckoo and host eggs from European museum collections. *J. Zool.* **236**, 625—648.
- Moksnes, A., Røskaft, E., Braa, A. T., Korsnes, L., Lampe, H. M. & Pedersen, H. C. 1991: Behavioral-responses of potential hosts towards artificial cuckoo eggs and dummies. *Behaviour* **116**, 64—89.
- Moksnes, A., Røskaft, E. & Solli, M. M. 1994: Documenting puncture ejection of parasitic eggs by chaffinches *Fringilla coelebs* and blackcaps *Sylvia atricapilla*. *Fauna Norveg. C Cinclus* **17**, 115—118.
- Mooers, A. O. & Cotgreave, P. 1999: Sibley and Ahlquist's tapestry dusted off. *Trends Ecol. Evol.* **9**, 458—459.
- Moskat, C. & Fuisz, T. I. 1999: Reactions of red-backed shrikes *Lanius collurio* to artificial cuckoo *Cuculus canorus* eggs. *J. Avian Biol.* **30**, 175—181.
- Moskat, C. & Honza, M. 2002: European cuckoo *Cuculus canorus* parasitism and host's rejection behaviour in a heavily parasitized great reed warbler *Acrocephalus arundinaceus* population. *Ibis* **144**, 614—622.
- Øien, I. J., Moksnes, A. & Røskaft, E. 1995: Evolution of variation in egg color and marking pattern in European passerines: adaptations in a coevolutionary arms race with the cuckoo, *Cuculus canorus*. *Behav. Ecol.* **6**, 166—171.
- Pagel, M. 1997: Inferring evolutionary processes from phylogenies. *Zool. Scr.* **26**, 331—348.
- Pagel, M. 1999: Inferring the historical patterns of biological evolution. *Nature*. **401**, 877—884.
- Petrie, M. & Møller, A. P. 1991: Laying eggs in others' nests: intraspecific brood parasitism in birds. *Trends Ecol. Evol.* **6**, 315—320.
- Prochazka, P. & Honza, M. 2004: Egg discrimination in the Yellowhammer. *Condor* **106**, 405—410.
- Purvis, A. & Rambaut, A. 1995: Comparative analysis by independent contrasts (CAIC): an Apple Macintosh application for analysing comparative data. *Computer Appl. Biosci.* **11**, 247—251.
- Reboreda, J. C., Clayton, N. S. & Kacelnik, A. 1996: Species and sex-differences in hippocampus size in parasitic and nonparasitic cowbirds. *Neuroreport* **7**, 505—508.
- Ricklefs, R. E. 2004: The cognitive face of avian life histories – the 2003 Margaret Morse Nice Lecture. *Wilson Bull.* **116**, 119—196.
- Rothstein, S. I. 1975: Mechanisms of avian egg-recognition: do birds know their own eggs. *Anim. Behav.* **23**, 268—278.
- Rothstein, S. I. 1990: A model system for coevolution: avian brood parasitism. *Annu. Rev. Ecol. Evol. Syst.* **21**, 481—508.
- Rutila, J., Latja, R. & Koskela, K. 2002: The common cuckoo *Cuculus canorus* and its cavity nesting host, the redstart *Phoenicurus phoenicurus*: a peculiar cuckoo-host system? *J. Avian Biol.* **33**, 414—419.
- Schulze, K. 1992: Parasitism and egg losses due to the cuckoo (*Cuculus canorus*) in reed and marsh warblers (*Acrocephalus scirpaceus*, *A. palustris*) in central and western-Europe. *J. Ornithol.* **133**, 237—249.
- Sheldon, F. H. & Gill, F. B. 1996: A reconsideration of songbird phylogeny, with emphasis on the evolution of titmice and their sylvioid relatives. *Syst. Biol.* **45**, 473—495.
- Sibley, C. G. & Ahlquist, J. E. 1990: *Phylogeny and Classification of Birds: a Study in Molecular Evolution*. Yale Univ. Press, New Haven, CT.
- Sol, D., Duncan, R. P., Blackburn, T. M., Cassey, P. & Lefebvre, L. 2005: Big brains, enhanced cognition, and response of birds to novel environments. *Proc. Natl. Acad. Sci. U.S.A.* **81**, 6232—6234.
- Soler, J. J. 1999: Do life-history variables of European cuckoo hosts explain their egg-rejection behavior? *Behav. Ecol.* **10**, 1—6.
- Soler, M. & Møller, A. P. 1990: Duration of sympatry and coevolution between the great spotted cuckoo and its magpie host. *Nature* **343**, 748—750.
- Soler, J. J. & Møller, A. P. 1996: A comparative analysis of the evolution of variation in appearance of eggs of European passerines in relation to brood parasitism. *Behav. Ecol.* **7**, 89—94.
- Soler, J. J., Møller, A. P. & Soler, M. 1999: A comparative study of host selection in the European cuckoo *Cuculus canorus*. *Oecologia* **118**, 265—276.

Stokke, B. G., Moksnes, A., Røskaft, E., Rudolfson, G. & Honza, M. 1999: Rejection of artificial cuckoo (*Cuculus canorus*) eggs in relation to variation in egg appearance among reed warblers (*Acrocephalus scirpaceus*). Proc. R. Soc. Lond. B **266**, 1483–1488.

Stokke, B. G., Moksnes, A. & Røskaft, E. 2002: Obligate brood parasites as selective agents for evolution of

egg appearance in passerine birds. Evolution **56**, 199–205.

Winkler, H., Leisler, B. & Bernroider, G. 2004: Ecological constraints on the evolution of avian brains.

J. Ornithol. **145**, 238–244.

Wyllie, I. 1981: The Cuckoo. B.T.Batsford Ltd., London.

## Appendix

Species brain mass (BRAIN, in grams), species body mass (BODY, in grams), habitat type (HAB), coloniality (COL), food hoarding (HOAR), prey capture (PC), migration (MIGR), food type (FOOD), suitability for cuckoo parasitism (SUIT), brood parasitism by cuckoos (PAR, frequency of nests parasitized, in percentage), rejection rate (REJECT, frequency of rejected cuckoo eggs, in percentage), research effort (RES, number of papers), incubation period (INC, in days), nestling period (NP, in days), post-fledging period (PFP, in days) and total parental care (TPC, in days) in passerine birds of Europe. See main text for sources of data

Species	BRAIN	BODY	HAB	COL	HOAR	PC	MIGR	FOOD	SUIT	PAR	REJECT	RES	IP	NP	PFP	TPC
<i>Acrocephalus arundinaceus</i>	0.94	21.90	1	3	1	1	3	1	1	48.9	88.2	134	14	13	13	26
<i>Acrocephalus schoenobaenus</i>	0.45	11.40	1	3	1	1	3	1	1	13.42	20	50	14	13.5		
<i>Acrocephalus scirpaceus</i>	0.48	13.00	1	3	1	1	3	1	1	8.48	31.28	100	10.6	10.9	12	22.9
<i>Anthus pratensis</i>	0.53	17.50	1	3	1	1	2	1	1	2.66	17.58	43	13	12.5	13	25.5
<i>Carduelis cannabina</i>	0.69	17.53	2	2	1	1	2	2	2	0.11	0	23	12	13.5	14	27.5
<i>Carduelis flammea</i>	0.62	12.94	2	3	1	1	2	3	2		0	32	11	11	15	26
<i>Carduelis chloris</i>	0.90	25.75	3	3	1	1	2	2	2	0.025	10.29	88	12.9	14.4	14	28.4
<i>Emberiza cirulus</i>	0.79	25.00	2	3	1	1	1	2	1	0	100	30	12.5	12.5	12	24.5
<i>Emberiza citronella</i>	0.72	27.93	2	3	1	1	2	2	1	0.01	96	87	13	12	11	23
<i>Emberiza schoeniclus</i>	0.69	19.79	1	3	1	1	2	2	1	0.15	97.5	45	13	11	20	31
<i>Erithacus rubecula</i>	0.66	17.99	3	3	1	1	2	1	1	0.29	10	192	13.7	13.4	20	33.4
<i>Ficedula albicollis</i>	0.47	10.30	3	3	1	2	3	1	2	0	0	169	12.8	15.9	8	23.9
<i>Ficedula hypoleuca</i>	0.45	12.76	3	3	1	2	3	1	2	0	0	715	14	15.5		
<i>Fringilla coelebs</i>	0.77	22.07	3	3	1	1	2	2	1	0.01	83.35	177	12.6	13.3	21	34.3
<i>Fringilla montifringilla</i>	0.82	24.47	3	2	1	1	3	1	1	0.04	90	35	11.8	13.5		
<i>Hippolais icterina</i>	0.51	13.67	3	3	1	1	3	1	1		83.5	12	13.7	14.5	11.3	25.8
<i>Hirundo rustica</i>	0.63	18.78	1	1	1	2	3	1	2	0.01	0	562	14	20.3	7	27.3
<i>Lanius collurio</i>	1.02	29.02	2	3	2	2	3	1	1	1.75	100	67	14	14.5		
<i>Lanius excubitor</i>	1.48	59.63	2	3	2	2	2	1	2	0	85.42	35	16	16.5		
<i>Lanius senator</i>	1.11	27.80	2	3	2	2	3	1	1	0	100	11	15.3	17.7	24.5	42.2
<i>Miliaria calandra</i>	1.20	50.00	1	2	1	1	2	3	1	0.01	0	58	13	10.5	8.5	19
<i>Motacilla alba</i>	0.62	21.84	1	3	1	1	2	1	1	0.42	91.06	42	12.5	13.5	16	29.5
<i>Motacilla flava</i>	0.55	15.95	1	3	1	1	3	1	1	0.13	80	28	12.4	12	14	26
<i>Muscicapa striata</i>	0.49	14.70	3	3	1	2	3	1	1	0.12	58.11	14	13.2	13	22	35
<i>Oenanthe oenanthe</i>	0.76	24.30	1	3	1	1	3	1	2	0	5.9	75	13.2	15.5	12.5	28
<i>Parus caeruleus</i>	0.66	10.40	3	3	1	1	2	1	2	0	0	325	14.2	19		
<i>Parus major</i>	0.86	17.24	3	3	1	1	2	1	2	0	16.7	1195	13.9	18.9	7	25.9
<i>Parus palustris</i>	0.68	12.00	3	3	2	1	1	1	2	0	0	90	14	18.5	11	29.5
<i>Phoenicurus ochrurus</i>	0.70	27.00	1	3	1	1	2	1	2	0	100	24	15	15.5	11	26.5
<i>Phoenicurus phoenicurus</i>	0.51	14.29	3	3	1	1	3	1	1	0.03	30.98	36	12.9	14.5	17.5	32
<i>Phylloscopus bonelli</i>	0.35	7.40	3	3	1	1	3	1	1		50	4	12.5	12		
<i>Phylloscopus collybita</i>	0.31	7.64	3	3	1	1	2	1	1	0	100	57	14	15	14.5	29.5
<i>Phylloscopus trochilus</i>	0.34	9.24	3	3	1	1	3	1	1	0.06	86.67	128	13	13	14	27
<i>Prunella modularis</i>	0.75	19.37	3	3	1	1	2	1	1	1.93	1.56	169	12.5	11.5	15.5	27
<i>Pyrrhula pyrrhula</i>	0.97	23.00	3	2	1	1	1	2	2	0.04	0	30				
<i>Riparia riparia</i>	0.43	13.80	1	1	1	2	3	1	2	0	46	91	14.5	20.1	4.7	24.8
<i>Saxicola torquata</i>	0.63	15.30	1	3	1	1	2	1	1	0.12	0	57	13.5	13.5	12	25.5
<i>Serinus serinus</i>	0.48	9.50	3	3	1	1	2	2	2	0	0	32	12.6	15.2	9	24.2
<i>Sturnus vulgaris</i>	1.99	81.51	3	1	1	1	2	1	2	0	23.8	1196	12.1	21	11	32
<i>Sylvia atricapilla</i>	0.71	17.59	3	3	1	1	2	1	1	0.17	95.38	179	11.6	11.5		
<i>Sylvia borin</i>	0.62	19.21	3	3	1	1	3	1	1	0.32	66.67	157	11.9	10.6	12	22.6

**Appendix** Continued

Species	BRAIN	BODY	HAB	COL	HOAR	PC	MIGR	FOOD	SUIT	PAR	REJECT	RES	IP	NP	PFP	TPC
<i>Sylvia communis</i>	0.58	13.55	2	3	1	1	3	1	1	0.07	100	44	11.5	11	17.5	28.5
<i>Sylvia melanocephala</i>	0.53	10.98	2	3	1	1	1	1	1		100	9	13	12.5	17.5	30
<i>Troglodytes troglodytes</i>	0.50	9.42	3	3	1	1	2	1	1	0.04	5.56	128	16	17.3	13.5	30.8
<i>Turdus iliacus</i>	1.53	75.00	3	2	1	1	2	1	2	0	34.88	21	12.7	10	14	24
<i>Turdus merula</i>	1.63	98.79	3	3	1	1	2	1	2	0.01	82.64	272	13	13.5	6.6	20.1
<i>Turdus philomelos</i>	1.59	67.48	3	3	1	1	2	1	2	0.01	67.03	61	13.4	13.2		
<i>Turdus pilaris</i>	1.93	98.60	3	1	1	1	2	1	2	0	9.09	51	12	12.9	30	42.9

Habitat: 1, ground; 2, shrub; 3, tree. Coloniality: 1, colonial; 2 small groups; 3, solitary. Food hoarding: 1, non-hoarder; 2 hoarder. Prey capture: 1, static prey; 2, active prey. Migration: 1, resident; 2, partial migrant; 3, migrant. Food: 1, insects; 2, mixed; 3, seeds. Suitability: 1, suitable; 2, unsuitable.