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The Social Brain Hypothesis: A Survey Of Evidence

Hypotéza sociálního mozku: přehled dostupné evidence

Bakalářská práce

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Poděkování

Na tomto místě bych chtěla poděkovat svému školiteli, Pavlu Němcovi, za jeho podporu a za cenné připomínky. Dík patří také všem mým blízkým za trpělivost, se kterou snášeli mou fyzickou i duševní nepřítomnost a monotematické rozhovory po dobu sepisování práce.

Prohlášení

Prohlašuji, že jsem závěrečnou práci zpracovala samostatně a že jsem uvedla všechny použité informační zdroje a literaturu. Tato práce ani její podstatná část nebyla předložena k získání jiného nebo stejného akademického titulu.

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Podpis

Abstract

The social brain hypothesis was first proposed to explain the remarkable cognitive abilities of primates and has since been extended to other taxa. Generally, it posits that sociality is a major selection pressure driving the evolution of large brains and intelligence. However, there is no single version of the hypothesis and different underlying mechanisms have been proposed. Tests of the hypothesis rely on appropriate indices of social complexity and brain size, as a proxy for cognitive abilities, and difficulties are associated with choosing both these variables and obtaining precise data. Situation is further complicated by that fact that a multitude of factors potentially contributing to or constraining encephalization is highly intercorrelated. This bachelor's thesis reviews approaches to research in this field and presents a survey of relevant evidence accumulated so far. The social brain hypothesis has been tested in various ways in primates, carnivores, ungulates, cetaceans, insectivores, bats, birds, fish (cichlids), and insects. The jury is still out, since contrasting results exist for most of these groups, warranting more research to help elucidate the influence of sociality on brain evolution.

Key words: relative brain size, sociality, encephalization, pairbondedness, mating system, comparative analysis

Abstrakt

Hypotéza sociálního mozku byla původně navržena jako vysvětlení mimořádných kognitivních schopností primátů, byla však postupem času rozšířena i na další taxony. Obecně tato hypotéza tvrdí, že socialita je jedním ze zásadních selekčních tlaků vedoucích v evoluci ke zvětšování mozku a inteligence. Neexistuje však v jednotné podobě a bylo navrženo několik různých mechanismů, kterými by socialita mohla takto působit. K testování hypotézy je zapotřebí použít vhodné vyjádření sociální komplexity a velikosti mozku, jakožto zástupné veličiny pro kognitivní schopnosti, přičemž volba a co nejpřesnější zjištění obou těchto údajů se pojí s jistými úskalími. Situaci dále komplikuje skutečnost, že celá řada faktorů, jež by se mohly na encefalizaci potenciálně podílet, nebo ji naopak omezovat, spolu vzájemně vysoce koreluje. Tato bakalářská práce shrnuje přístupy ke zkoumání dané problematiky a podává přehled dosud získaných poznatků, které jsou pro tuto hypotézu relevantní. Hypotéza sociálního mozku byla různými způsoby zkoumána u primátů, šelem, kopytníků, kytovců, hmyzožravců, letounů, ptáků, ryb (cichlid) a hmyzu. U většiny těchto skupin se objevují výsledky, které si navzájem odporují, proto rozhodně nelze prohlásit tuto otázku za uzavřenou a je na místě další výzkum, který by vliv sociality na evoluci mozku lépe objasnil.

Klíčová slova: relativní velikost mozku, socialita, encefalizace, párovací systémy, srovnávací analýza

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1 Introduction

People have long been intrigued by the variation in cognitive abilities and brain sizes across the animal kingdom, this curiosity perhaps fuelled by the self-centred interest in what makes our “oversized” brains so special. Consequently, a wealth of explanations has been generated, stressing all the different components acting on brain size evolution. While most variability in brain size can be explained by body size alone (Jerison, 1973) and while the link between brain size and intelligence is more tacitly assumed than settled (Roth & Dicke, 2005), flexible behaviour does confer its benefits (Sol & Lefebvre, 2000) and can thus be the subject of natural selection. However, no single factor works in isolation, the resultant effect is due to an intrinsically interwoven net of selection pressures and constraints. Attempts to disentangle such net prove tricky, but we can ask about the relative contributions of particular elements.

The various effects proposed to explain brain size variation beyond that due to body size are reviewed elsewhere (e.g. Healy & Rowe, 2007; Isler & van Schaik, 2009a; Isler & van Schaik, 2014; van Schaik et al., 2012; Swanson et al., 2012; Willemet, 2013) and can be broadly categorized as either life history (longevity, age at first reproduction, maternal investment), developmental (size at birth, developmental mode, gestation length, lactation length), ecological (diet, extractive foraging, tool use, habitat complexity, arboreality/terrestriality, activity pattern, home range, day journey length), social (mating system, care for young, cooperative breeding, group size, social learning), or energetic (trade-offs between expensive tissues, basal metabolic rate, body temperature). And this list is certainly not exhaustive, which attests to the appealing nature of the problem.

Our perception of what constitutes intelligent behaviour is inevitably influenced by our own experience. Humans are extremely social, and we tend to see cleverness in other animals that behave “like us”, although we know very little about the cognitive mechanisms that underpin this behaviour. If asked to come up with examples of “clever” animals, hardly anyone would think of solitary ones first. Not surprisingly then, the social explanations, dubbed the social brain hypothesis, have been generally well received and gained much traction. It seems like the social brain meme is on the rise.

Despite a multitude of studies exploring this hypothesis in recent years, no specific review of evidence has been published since the work of Dunbar and Shultz (2007a), although some studies were included in the more general reviews. The aim of this bachelor's thesis is to present such review of the existing body of literature, especially covering comparative studies of brain size in non-human animals, to see just how strong and general the support is, and perhaps identify possible areas of future study.

2 Evolution of the social brain hypothesis

What is the social brain hypothesis (SBH)? Although often referred to in literature, it is somewhat loosely defined, and in fact, there seems to be no generally accepted definition. Rather, the SBH, also referred to as the social intelligence, Machiavellian intelligence, or social challenge hypothesis, encompasses a related set of ideas, all centred around the evolutionary relationship between social complexity and cognitive abilities. Various researchers formulated their own versions, based on different assumptions as to the directionality, underlying mechanisms, and generality of such a relationship. For this reason, I will describe the origins and genesis of this “social brain” concept, with some subtle and not so subtle shifts of focus along the way, and present a working definition for the purposes of this thesis.

Traditionally, the evolution of intelligence was believed to be driven by selection pressures exerted by the environment (e.g. Eisenberg & Wilson, 1978; Harvey et al., 1980; Jerison, 1973). Although insightful observations about the possible link between the intense social lives of primates and their apparent intelligence had been published before (Chance & Mead 1953; Jolly, 1966), the general interest of the scientific community got sparked by Nicholas Humphrey's seminal paper *The social function of the intellect* (Humphrey, 1976).

Humphrey argued that primates have essentially no need to employ higher intelligence in solving the ecological tasks they encounter on a daily basis. Therefore, he suggested that their remarkable reasoning faculties must have evolved for a different reason, and proposed that their essential function is to cope with the demands of sociality. Social living brings advantages, but also presents challenges, such as increased competition for food or mates. An individual would thus gain in terms of fitness by outsmarting other members of the group. This intragroup competition can set into motion a runaway process of ever-increasing intelligence. Another factor adding to the selection pressure would then be the need to make up for the time “lost” in such social strategizing, by putting this primarily social intelligence to more general use, such as more efficient foraging. And society further facilitates this by providing the young with ample opportunities for imitation and social learning.

Humphrey thus mentions cooperation, competition and social learning as factors contributing to the emergence of higher cognition in primates and suggests that this primarily social intelligence needs not be limited to the social domain, but can be co-opted for dealing with environmental problems as well. If this holds true, it follows that there should be a positive correlation between a species' social complexity and level of intelligence. In his paper, Humphrey notes that there is no agreed definition or standard measure of either of these parameters, which is remarkably still true today, nearly 40 years later.

Perhaps for the lack of such measures, there were not many attempts at directly testing the assumptions of the hypothesis in the decade or so following the publication of Humphrey's paper. Nevertheless, a number of theoretical and empirical works exploring the “social intelligence” in primates appeared, resulting in the book *Machiavellian Intelligence*, edited by Byrne and Whiten (1989).

It comprises several papers providing evidence for sophisticated social behaviours in primates, generally arguing that this is what sets them apart from other taxonomic groups and what translates to their apparent general-purpose intelligence. Most of these proclaimed primate-specific social skills pertain to the ability to maintain alliances, keep track of third-party relationships, understand others' intentions, deceive, and manipulate, therefore warranting the name Machiavellian intelligence. Social learning, though still mentioned, was rather downplayed in importance. This body of work provided compelling evidence for the exceptional social cognition in primates and even uncovered some patterns within the order. Yet, there was no explicitly stated, falsifiable hypothesis.

After the publication of the above mentioned volume, a surge of studies followed, with the aim of rigorously testing the association of social complexity and intellectual capacity. This time not just contrasting primates with other mammals, but trying to find specific evidence stemming from interspecies differences. The hypothesis now claimed that there should be a correlation between group size, as an index of social complexity, and brain size, as an index of cognitive power (Dunbar, 1992; Sawaguchi & Kudo, 1990). These indices will be discussed at more length in the following chapters.

Robin Dunbar became a prominent proponent of the hypothesis and introduced a new distinction: ultimately, social living had driven the evolution of larger brains in primates, but proximately, current brain size imposes a constraint on group size (Dunbar, 1992). This further led him to postulate that it should be possible to predict the group size based on neocortex size alone (Dunbar, 1995).

As a leading figure, Dunbar popularized the actual name "social brain hypothesis" (Barton & Dunbar, 1997; Dunbar, 1998), although it was originally coined by Brothers (1990) in a different meaning, referring to the neural system for social cognition.

So far, the focus had been solely on primates (and especially humans) and explaining their uniqueness among animals. In the second collection of papers devoted to Machiavellian intelligence, Byrne and Whiten (1997) suggested that the hypothesis should apply to any long-lived species found in large groups. The year 1998 marked the first full-blown attempt to generalize the hypothesis to other mammalian groups (Dunbar & Bever, 1998), and others soon followed. The SBH has since been extended to not just mammals, but as diverse taxa as birds (e.g. Beauchamp & Fernández-Juricic, 2004), fish (e.g. Shumway, 2010) and insects (e.g. Lihoreau et al., 2012). While this allows to draw interesting parallels in search for the universal principles shaping brain evolution, it inevitably forces different approaches and reformulations for each group, since it would be hard pressed to assume the same underlying proximate mechanisms across all these taxa.

Lindenfors (2005) started another trend – noting that males and females of the same species sometimes display different social behaviours and turning the attention of some researchers to sexual differences in sociality and brain size.

More recently, there has been an important change of perspective, claiming that while group size is a good correlate of brain size in primates, in other vertebrates, dyadic social bonds characteristic of monogamous pairs are a more important predictor (Dunbar & Shultz, 2007b, 2010; Shultz & Dunbar, 2007).

In contrast with the Machiavellian version, more emphasis is put on the affiliative, cooperative aspect of social interaction, although not exclusively so. This new spin on the hypothesis introduces a lot of incongruity with previous results showing a relationship between group size and brain size in non-primates (Dunbar & Bever, 1998; Tschudin, 1997). Are they in support of the SBH, or not? The presumed mechanism has also changed: Dunbar and Shultz (2007b) explicitly claim that the SBH differs from the ecological hypotheses only in the assumption that “one or more ecological problems (survival, foraging, rearing offspring) are more effectively solved socially than by an individual’s unaided efforts”. This leads them to postulate that in social species there should be a tendency to solve novel tasks by social, rather than individual learning.

One particular aspect of the hypothesis that struck a cord with a more general audience is the infamous Dunbar's number (Dunbar, 1993) – a putative limit on the number of social relationships people can handle. The rise of internet social networks sparked a debate about whether such new media can help us break through this ceiling (Dunbar, 2012).

While the SBH, especially as it pertains to primates, has been generally well accepted, a new wave of criticism is appearing (e.g. Charvet & Finlay, 2012; van Schaik et al., 2012). The latter gave rise to another related concept: the cultural intelligence, stressing the importance of the propensity to innovate and skills acquired through social transmission in the juvenile period.

Throughout this thesis, I will use the SBH as an umbrella term for all the specific hypotheses dealing with the causal link between some measure of social complexity and brain size in animals. In the end, I hope to be able to show which of its variants have the soundest empirical support.

3 Approaches to testing the hypothesis

What are the assumptions of the SBH, and how to test them?

The basic premise of the SBH is that species with greater social complexity should be more intelligent than solitary ones. Leaving social complexity aside for now, the task of comparing intelligence across (or even within) species is far from simple. A test that would be fair to all species would have to take into account their perceptual and motor abilities, motivation, and ecological relevance of the task at hand. Even the interpretation of the subject's performance is not immune to bias. The case of a fish outperforming great apes illustrates both points (Salwiczek et al., 2012).

A slight modification is determining if social species are better equipped for dealing with socio-cognitive tasks. Again, the decision as to what should be regarded as specifically social cognition is largely arbitrary. As a case in point, inhibitory control has been treated in different studies as both social (Amici et al., 2008) and non-social (Maclean et al., 2013). Social learning has been implicated as an important mechanism in the SBH (Dunbar & Shultz, 2007b), propensity for learning from conspecifics is thus another factor that can be tested (e.g. Briefer et al., 2014; Greco et al., 2013).

Even if the perfect experimental set-up was available, it is seldom practical to test a representative sample for each species. Another approach avoids the need to present the animals with a devised task. Instead, observations from field studies are compared and evaluated for signs of cognitive complexity (e.g. Byrne & Corp, 2004; Reader & Laland, 2002). This, in turn, presents a problem with unequal research effort devoted to different species. Rare or hard to observe behaviours are more likely to be reported in well-studied species. And drawing conclusions requires caution, since animals engaging in seemingly complex behaviours might be following simple rules of thumb (Stevens & King, 2012). For instance, while the well-known fungus-growing ants strike us as a remarkable curiosity, if such a behaviour was observed in apes, with little doubt it would be interpreted as the pinnacle of intelligence.

The majority of researchers therefore opt for using brain size as a proxy for intelligence. While the exact relationship between these variables is far from simple, and will be dealt with in more detail in the following chapter, hardly anyone would dispute that brains do form the neural substrate for cognition (for recent experimental evidence see Kotrschal et al., 2013).

Whatever the chosen proxy, all these approaches produce correlational evidence, but do not prove a causal link. Since many potentially relevant variables can be highly intercorrelated, any comparative studies should strive to avoid such confounding effects as much as possible. In practice, that might be accomplished by comparing species that differ with respect to the studied parameter, while being similar in other related parameters, or by properly partialling out any possible confounders in statistical analyses. There are statistical models that allow to look for a correlated evolutionary change in two traits (Pagel, 1997), and evidence of tight coevolution is more convincing than simple correlation, but this approach is contingent on reliable phylogenetic information and, ideally, a good fossil record. However, even the concerted change of social living and brain size does not necessarily mean causation. It is not inconceivable that the same pressure selecting for larger group size, such as predation, might act on brain size at the same time, be it directly, or indirectly through favouring larger bodies.

Studies are further hampered by the limited number of species where both data for brain size (let alone tests of cognitive ability) and social complexity are available. In turn, both the selection of species to be included in the analysis and the quality of data are impacted by relative research effort. Finally, comparative studies need to address the issue of phylogenetic inertia, i.e. the fact that related species might share some characteristics due to their common descent. Treating species as independent data points is thus not justified, as it inflates the degrees of freedom (Felsenstein, 1985). Several approaches to deal with this have been proposed, the most commonly used being independent contrasts (Garland et al., 1992), and phylogenetic generalized least squares – PGLS (Pagel, 1994). However, using these methods comes at a cost of decreasing the sample size and carries the risk of introducing noise, when the phylogeny is not well resolved (Symonds, 2002).

Since a direct manipulation of either brain size or group size in relation to each other seems impractical at best, correlational studies remain the standard. Such experiments are not entirely

inconceivable, though. In fact, some recent explorations have been headed in that direction (Ott & Rogers, 2010; Sallet et al., 2011).

With the advent of modern IT, modelling using computer simulations becomes an increasingly more accessible option for testing evolutionary hypotheses. Interestingly, two such recent studies highlight both cooperation (McNally et al., 2012) and competition (Arbilly et al., 2014) as the driving force of cognitive evolution.

3.1 Measures of brain size

Although, as mentioned above, any measure of “brain size” as a proxy for “brain complexity” and, in turn, “intelligence” is bound to be an oversimplification, some approaches might be more appropriate than others. While a comprehensive coverage is beyond the scope of this thesis, I will briefly summarize the different options used in the studies discussed below, and point out some associated caveats. The main questions are whether to use the whole brain or specific parts, whether to consider the absolute or relative size, and whether to measure by mass, volume or other property.

3.1.1 Measures of the whole brain

Perhaps the most straightforward approach is to use absolute brain size. Endocranial volumes (ECV) can be estimated from skulls, which is advantageous in that it allows to make use of large museum collections and to include fossil species. ECVs can be obtained by different methods: filling the skull with some small-grained material, such as lead shots, glass beads or similar (Iwaniuk & Nelson, 2002), using external skull measurements (Finarelli, 2006), using X-ray (Madden, 2001), or using CT to create a virtual endocast (Sakai et al., 2011). All these might give different results, which could be a problem when using multiple data sources. Even when measuring actual brains, there is the issue of seasonal changes and different treatments leading to different levels of dehydration, and the mass and volume might not be equivalent across species, due to different proportions of grey and white matter and different sizes of ventricles (Stephan, 1981, as cited in Deacon, 1990). All of this can lead to distortion of data, especially when combining different data sources.

Somehow, it does not seem intuitive that larger animals with absolutely larger brains should be automatically smarter than smaller ones. Apart from the elephant in the room, other examples come to mind, such as a shepherd dog herding sheep with brains twice its size (Haug, 1987). There surely is more to cognitive power than just sheer brain size. Accordingly, several ways to arrive at a more appropriate relative measure of brain size have been put forward. The most common one is to use brain mass relative to body mass. Although it is easily objected that body weight can be subject to sexual dimorphism, can differ between individuals and even fluctuate in the same individual, it is the most readily available and widely applied way to correct for body size. Overall brain size in vertebrates scales with a negative allometry with respect to body size, so using a simple ratio of brain to body size is not appropriate (Jerison, 1973). Instead,

it is possible to derive equations for the expected brain size at a given body size and compare that to the actual brain size. The relative merits of using expected and observed exponents in these equations are discussed by Harvey and Krebs (1990). More recently, it has been pointed out that when correcting for body size, phylogeny should be taken into account (Revell, 2009).

Measures of relative whole brain size used in the studies discussed below include:

Encephalization quotient (EQ) (Jerison, 1973): the ratio of actual brain size to the expected brain size, where the expected brain size is derived using the equation (1).

$$\log(\text{brain mass}) = \log(0.12) + 0.67 \times \log(\text{body mass}) \quad (1)$$

Comparative brain size (CBS) (Clutton-Brock & Harvey, 1980): residuals (the difference between actual and expected brain size) from regression of $\log(\text{brain mass})$ on $\log(\text{body mass})$ for congeneric groups, where the regression line slope is derived for the family.

Relative brain size (RBS) will refer to the generalized version of CBS, that is the use of residuals from regression of $\log(\text{brain mass})$ on $\log(\text{body mass})$, where the residuals are used for species and the slope can be derived for any taxonomic level. Although this is not, strictly speaking, a single measure, since there are different ways to derive it, the specifics can always be found in the referenced paper.

3.1.2 Measures of brain parts

Since body size alone accounts for the overwhelming majority of brain size variation (Jerison, 1973), it might be advantageous to adopt a finer-grained approach and look at specific brain regions that would be most likely involved in processing social information. According to the principle of proper mass, “the mass of neural tissue controlling a particular function is appropriate to the amount of information processing involved in performing the function” (Jerison, 1973, p. 8), so it might be worth investigating if these regions are particularly enlarged. Although note that this principle has been questioned (Iwaniuk et al., 1999).

Social information processing might include perception (after all, the individual has to be able to accurately identify and monitor its conspecifics), memory, and some kind of cognitive reasoning (even just following simple heuristics). In any case, these are all functions mostly associated with the telencephalon at the crudest level, so not surprisingly, telencephalon as a whole, or some of its components are most often used. As is the case with the whole brain, brain part measures are also usually relativized. In mammals, the region of interest has been mostly the neocortex. Neocortex is not an independent unit in itself. Just like every other brain part, it is interconnected both developmentally and functionally with the rest of the brain. Vertebrate brains generally follow a conserved allometric scaling pattern and the neocortex becomes disproportionately larger with increasing absolute brain size (Finlay & Darlington, 1995). Therefore large-brained mammals tend to have the highest neocortex proportion. However, deviations from the expected

value for a given taxonomic group might reflect selection for cortical enlargement/reduction. Evidence for specific cases of such mosaic evolution has been collected (e.g. Barton & Harvey, 2000; Iwaniuk et al., 2004; Smaers & Soligo, 2013). Brain enlargement may in fact be mediated by two different mechanisms: passive, due to body size increases, accounting for concerted evolution, and active, due to selection on processing capacity in specific brain regions, resulting in mosaic evolution (Aboitiz, 1996).

Measures of relative brain region size used in the studies discussed below include:

Telencephalic volume fraction (TF) (Burish et al., 2004): telencephalon volume/whole brain volume.

Relative size of neocortex (RSN) (Sawaguchi & Kudo, 1990): residuals from regression of $\log(\text{neocortex mass})$ on $\log(\text{whole brain mass})$.

Neocortex/rest-of-brain residuals (Barton, 1996): residuals from regression of $\log(\text{neocortex volume})$ on $\log(\text{rest of the brain volume})$.

Neocortex ratio (C_R) (Dunbar, 1992): neocortex volume/rest of the brain volume.

Estimated neocortex ratio (EC_R) : neocortex ratio calculated with estimated, rather than actual neocortex volume.

Due to poor data availability, some authors (e.g. Dunbar, 1995) resorted to calculating the neocortical volume from the whole brain volume using an allometric relationship. However, this is questionable, since it essentially obscures any potential variation in actual neocortex volumes. What it reflects is just a transformed absolute brain size, and while that might be a legitimate measure in its own right, it would be preferable to use the actual whole brain mass or volume. This whole approach defeats the asserted purpose of focusing on the neocortex as a target of selection for cognitive abilities.

Relative neocortex ratio (Schillaci, 2008): residuals from regression of $\log(\text{neocortex ratio})$ on $\log(\text{male body mass})$.

Executive brain residuals (Keverne et al., 1996): residuals from regression of $\log(\text{neocortex} + \text{striatum volume})$ on $\log(\text{brainstem volume})$.

Executive brain ratio (Reader & Laland, 2002): $(\text{neocortex} + \text{striatum volume}) / \text{brainstem volume}$.

3.1.3 Choosing the appropriate measure

Which of these measures are then most appropriate? This is no trivial matter and is clearly worth considering, as Deaner et al. (2000) highlight that depending on the choice of the scaling method when using relative brain region size, opposing conclusions can be reached with the same data.

Since the brain size index is supposed to reflect cognitive power, it would be best to choose one that has strong empirical evidence for being associated with some measure of cognitive abilities. Such evidence for relative brain size is scarce (e.g. Ratcliffe, et al., 2006), and most recent studies do not support it (Deaner et al., 2007; MacLean et al., 2014; Stevens, 2014; Willemet, 2013). Byrne and Corp (2004) show that the frequency of tactical deception in primates, corrected for research effort, correlates with C_R , however, McNally and Jackson (2013) did not confirm this. In field studies not involving any human intervention, a significant correlation was found between reported frequency of innovation, tool use, and social learning with both executive brain volume and executive brain ratio in primates, after controlling for phylogenetic relatedness (Reader & Laland, 2002). Similar conclusions were reached by Deaner et al. (2007), who show that the variability in observed cognitive ability explained by absolute brain size and absolute neocortex size is about the same, and non-neocortical size is even a slightly better predictor. This growing case for absolute brain size being a good correlate of “intelligence” was recently extended to a wider selection of taxa (MacLean et al., 2014).

How is that in line with the paradox previously hinted at? The key lies in comparing brains across lower taxonomic groups. Since brain evolution took different paths in different phylogenetic lineages, brains of distantly related animals can vary substantially in the number of neurons, even if they are about the same size (Herculano-Houzel, 2011). Of course, brain complexity and “effectiveness” does not lie just in the number of neurons, but other factors come into play, such as neuronal interconnections (DeFelipe et al., 2002), or myelin sheath thickness, which translates to conduction velocity (Hartline & Colman, 2007). Even though the number of neurons is by no means the best imaginable predictor of cognitive capacity, at present it seems to be the best feasible one.

3.2 Measures of social complexity

Social complexity in itself is a vague concept and can be interpreted in many different ways. Not surprisingly then, proxies for social complexity take various forms. The most readily available seems to be group size. Dunbar (1992) defines the group size as the “number of individuals that an individual animal knows and interacts regularly with”. Such definition sounds sensible and simple enough, but trying to employ it raises a plethora of questions. How do you tell which individuals the animal knows and which it does *not* know? What does regularly mean? What kind of interaction is sufficient – physical contact, proximity, vocalisation, visual signals? What about territorial interactions? Is this number the same for males and females? Is it the

same across different populations? Estimating this number gets even more problematic, when we consider cases like physically mostly solitary animals that still remain in close touch with conspecifics, such as orang-utans (Spillmann et al. 2010), or fission-fusion societies, displaying varying degrees of cohesion, and stability of group composition and size in time (Aureli et al., 2008). Dunbar (1995) tried to identify the appropriate group level in Cercopithecinae living in fission-fusion societies based on the relationship he derived between neocortex ratio and group size. There is a glaring drawback to this approach, in the form of a circular argument: this is the group size consistent with our predictions, therefore it is the appropriate measure to test our hypothesis.

Although average group size might not be so informative when it comes to the assumption that cognitive abilities place an upper limit on group size, trying to identify maximum group sizes seems futile (Dunbar, 1992).

In any case, accurate capture of data on social complexity can be a tricky task: results depend quite obviously on the amount of invested time, but also on the method of data collection (Gibson & Mann, 2009). As a result, the dependability of data is sometimes questionable. In fact, as Patterson et al. (2014) poignantly show, different estimates of group size in the same species can be so discordant as not to correlate at all, or correlate very poorly. This is a critical issue, especially when using the group size as a quantitative variable.

While social group size is the most frequently used index of social complexity, over time, it became overwhelmingly clear that there is much more nuance to social relationships (e.g. Byrne & Bates, 2007). Alternative measures have thus been proposed, such as grooming clique size, that is tight groups with intense relationships within a larger group (Kudo & Dunbar, 2001), other more sophisticated network parameters (Lehmann & Dunbar 2009), or the proportion of time-budget spent on social activities (Shultz & Dunbar, 2007). Tactical deception and coalition forming are good examples of complex social lives in primates, however using them for the purposes of testing the SBH (as did Dunbar & Shultz, 2007a, 2007b) is problematic, because it leads to correlating two measures of cognitive power, instead of actually testing the hypothesis.

Mating system, not social group size *per se*, might hold the key to social complexity. Although it remains unclear what exactly is the source of higher cognitive demands: multi-male/multi-female groups in primates have been traditionally treated as more complex, because they require tracking of multiple dominance hierarchies (Cheney & Seyfarth, 1985), but in non-primates, monogamous pair-bonded system is considered to be the most cognitively taxing, due to the need of coordinating behaviour and taking the partner's needs into account (Shultz & Dunbar, 2007). Another related factor to consider seems to be cooperative breeding (e.g. Burkart & van Schaik, 2010; Iwaniuk & Arnold, 2004; Lukas & Clutton-Brock, 2012).

4 Review of evidence

In this part, I shall present an overview of representative studies for each taxonomic group, where some form of the SBH has been put to test. Due to restricted space, the presented evidence is focused on studies that use brain size as a proxy for cognitive abilities.

4.1 Evidence in primates

The SBH was originally posited to explain the unusually large brains and remarkable behaviour of primates and the evolution of distinctly human intellect. Not surprisingly then, the bulk of studies testing this proposition has been focused on primates. A lot of studies were done at the level of the order Primates (e.g. Dunbar, 1992; Dunbar, 1995; Keverne et al., 1996), which may be too wide, since the two suborders are estimated to have diverged at around 74 to 64 mya (Pozzi et al., 2014; Chatterjee et al., 2009, respectively). There has long been an assumption that strepsirhines¹ would be somehow qualitatively different from haplorhines in their sociality (Byrne & Whiten, 1989). Jolly (1966) argued that sociality in primates preceded and facilitated the rise of complex cognition, on the basis that lemurs, some of which lead rather complicated social lives, do not fare as well as monkeys and apes on cognitive tasks. In context of the SBH, this leads to the question what (if anything) is so different about haplorhine societies, if it is not sheer size – the range of troop sizes is overlapping (e.g. Dunbar, 1995). Actually, there is recent evidence hinting that there might not be such a sharp cognitive divide between the primate lineages in the social domain (Sandel et al., 2011). Perhaps in strepsirhines social cognition does not readily transfer to other areas, for some reason. Since the question whether the SBH applies to both haplorhines and strepsirhines in the same way is one of the more debatable points, I will first present studies across primates, and then separately studies that either included only one of the suborders or reported distinct results for the two groups.

4.1.1 Primates in general

A multivariate study across primates (Dunbar, 1992) aimed to identify the brain measure that would best predict group size, and to test the SBH against various ecological variables. Generic groups were used in the analysis to control for phylogeny. The best predictor of group size turned out to be C_R , as compared to absolute neocortex volume, RSN, neocortex residuals/rest-of-brain, and neocortex ratio to hindbrain, but all of these were significantly correlated with group size. This was interpreted as reflecting the actual number of neocortical neurons acting as the constraint on group size. Rather perplexingly, however, use of absolute neocortex size was not encouraged. Instead, C_R was established as the gold standard in similar studies. The uncovered relationship between C_R and group size is not linear, implying that the sheer number of group

¹ I will use the division of primates to suborders Strepsirrhini and Haplorhini, although some studies used Prosimii and Anthropoidea, since these groups are largely overlapping, with the exception of Tarsiiformes, which are very rarely included in the studies.

members might not be the critical factor. The ecological variables (extractive foraging, day journey length, and home range) were tested only with C_R and no link was revealed.

When trying to repeat the study with a larger sample, Dunbar (1995) in a series of equations converted brain mass calculated from cranial capacity back to ECV and then estimated C_R using this parameter, inevitably increasing error in each step. This EC_R shows a relationship with group size for the larger sample, albeit weaker than the one mentioned above.

Kudo and Dunbar (2001) proposed that coalitions are the glue that holds larger primate groups together and that the number of allies an individual can maintain is dependent on its cognitive abilities, indexed by C_R and EC_R . Coalitions, or “social cliques”, were defined as the number of dyads that exceed the mean frequency of grooming between dyads (i.e. if an individual engages in allogrooming with three members of the group more often than average, this implies a clique size of four). Calling these groups coalitions thus seems a little misleading. In both strepsirhines and haplorhines, clique size was shown to grow with C_R . However, strepsirhines were found to have larger cliques for a given C_R than haplorhines, and within haplorhines, hominoids had smaller clique sizes for a given C_R . According to the authors, that implies progressively more cognitively taxing relationships. (But no data were given on the overall time spent on grooming and no other possible mechanisms for group cohesion besides grooming were discussed). This raises the question why would haplorhines need to keep their groups more bonded, if strepsirhines can reap the same benefits of group living without this apparent cohesion. Interestingly, a closer look at the data shows that the mean clique size is often (in over a half of strepsirhines and over a third of haplorhines, excluding humans) under 2, implying a conspicuous *lack* of stable grooming relationships.

Schillaci (2008) points out that body size explains 89% of variation in C_R and shows that after partialling out the effect of body size, group size alone is not a significant predictor of C_R in the primate data set used by Kudo and Dunbar (2001). Schillaci (2008) further found that relative neocortex ratio was not related to either group size or clique size in primates. A significant relationship emerged for mating system, with monogamous primates having larger relative neocortex ratio than those in either single-male or multi-male polygamous groups, but significance was not reached after excluding humans from the analysis.

According to Keverne et al. (1996), across primates, group size correlates positively with executive brain residuals when the effect of phylogeny is controlled for. Moreover, primates with mating restricted to oestrus were reported to have smaller executive brains than primates who mate throughout the female cycle, perhaps reflecting a greater social complexity in species where mating is not strictly related to reproduction and might be another social interaction to keep track of.

Shultz and Dunbar (2007) investigated the link of RBS controlled for phylogeny with several ecological and social variables in primates, artiodactyls and carnivores, with the aim of verifying if the previously reported relationship between brain size and group size holds across distantly related taxa (however, choosing a different index of brain size this time). All the variables were both examined separately and used in constructing statistical models. The included species were categorized with respect to their mating system as solitary, monogamous (pair-bonded), harem, or multi-male group. Pair-bonded species

showed consistently higher RBS, with the exception of primates, where RBS gets progressively larger from solitary to multi-male groups, and correlates thus with group size. In contrast, no relationship between average group size and RBS emerged in artiodactyls or carnivores, whereas in primates these two variables are positively correlated. This is interpreted as a consequence of primate social lives being qualitatively different from the other groups. The authors further suggest that the social bonds present in monogamous non-primate mammals are generalized in primates to give rise to cohesive groups. They also proposed new indices of social complexity – stable bonds between female group members, and time devoted to social activity (all affiliative and agonistic interactions) – and demonstrated that species with various mating systems differed with respect to these indices, but did not attempt to separately correlate the indices with brain size.

Coevolution of RBS and sociality in the same three groups of mammals (and perissodactyls) was the subject of another study conducted at around the same time (Pérez-Barbería et al., 2007). The results support coevolution of sociality and brain size in all of these taxa, with primates exhibiting the tightest relationship. Although, due to the chosen statistical method, encephalization and sociality had to be treated as categorical variables, so the quantitative relationship could not be confirmed.

Generally, there seems to be a relationship between neocortex size and group size across primates, the link to mating system is not clear. Interestingly, though, the size of foraging groups and population groups did not correlate with a composite score of performance on different cognitive tasks in primates (MacLean et al., 2014). More useful information can be perhaps obtained at the level of suborders.

4.1.2 Strepsirhines

Sawaguchi and Kudo (1990) identified a significant positive relationship between RSN and troop size in strepsirhines. In contrast, Barton (1996) did not report any association between neocortex/rest-of-brain residuals and group size. In addition to using a slightly different measure of brain size and controlling for phylogeny using independent contrasts, Barton included more species and used different sources, which resulted in discordant group sizes for the same species. For example, Sawaguchi and Kudo classify the dwarf lemur *Cheirogaleus medius* as solitary, whereas Barton reports a group size of 5.5. Shultz and Dunbar (2007) note that bonded relationships are significantly less common in strepsirhines compared with haplorhines, but are not clear about whether the rest of the conclusions apply to primates in general, or just haplorhines. Another more recent study (MacLean et al., 2009) examined the link between RBS (with brain mass calculated from ECV) and several ecological and social factors in lemurs and found no significant correlation between RBS and group size or pairbondedness, although a negative trend for group size was present. In fact, negative correlation of relative brain size with group size in lemurs has been shown before by Hemmer (1979, as cited in Hemmer, 1981). Clutton-Brock and Harvey (1980) found that polygynous Lemuridae had significantly higher CBS than monogamous ones, but the sample was far from sufficient for reaching any conclusions, since only one species was classified as monogamous.

This suggests that the relationship previously reported by Sawaguchi and Kudo (1990) might be largely due to the unequal distribution of group sizes in the sample, where the genus *Lemur*, having a large neocortex and big troops, contrasted with the other strepsirhines, most of which were treated as solitary. Determining what is the “right” group size is tricky, given how difficult to observe a lot of these species are. Thus, for now, there seems to be little consensus for the relationship between brain size and sociality in strepsirhine primates.

4.1.3 Haplorhines

After partialling out the effect of diet, Sawaguchi (1990) showed an association between RBS and mating system, with polygynous haplorhines having larger RBS than monogamous ones, which is in line with later findings of Shultz and Dunbar (2007). The same relationship was shown for RSN as well, which additionally positively correlated with group size (Sawaguchi, 1992). Independent contrasts in neocortex/rest-of-brain residuals were positively linked with group size in diurnal haplorhines, even after controlling for body size (Barton, 1996).

Lehmann and Dunbar (2009) focused on different aspects of primate social complexity and their associations with different measures of brain size. In Cercopithecidae, female group size correlates better with C_R (and EC_R), than with ECV. When controlled for group size, species with larger neocortices had less dense and less connected networks, composed of smaller subgroups. Additionally, the authors concluded that female social networks are more resistant to disruption in species with higher C_R , although they are less interconnected in the first place. This finding is explained by the fact that monkeys with larger neocortices are better at maintaining group cohesion, and can do so by exploiting the weak links joining the relatively separate subgroups. That might offer additional support and explanation for the findings of Kudo and Dunbar (2001).

Pawłowski et al. (1998) examined EC_R and social complexity as indexed by the correlation between male rank and mating success (access to females) in polygamous primates. There is a negative relationship, i.e. in species with higher EC_R , dominant males failed in monopolizing access to females more often, which is interpreted as evidence for superior strategizing abilities of the lower ranking males. The effect of group size was controlled for, but the relationship holds only for groups over 4 males. This might implicate that, perhaps, Machiavellian intelligence can only manifest in sufficiently large groups, regardless of whether the underlying cognitive ability is present.

An interesting implication of this relationship between C_R and group size in haplorhines was proposed by Dunbar (1993), extending its applicability to modern humans. He extrapolated the mean group size for humans from C_R using the previously derived equation (Dunbar, 1992) to be 148.9, a figure that would later become to be known as the Dunbar's number in a rounded form. Dunbar (1993) argues that this predicted group size crops up frequently in natural human groupings, and that language evolved to facilitate the social cohesion necessary to support groups of this size, since the amount of time that would have to be devoted to

grooming would be impractical. Aiello and Dunbar (1993) build on this, and using EC_R for fossil hominids, show that grooming as the means of ensuring group cohesion started getting unfeasible with the emergence of the genus *Homo*, requiring some sort of vocal supplement.

A more impetuous interpretation of the Dunbar's number is that it limits the amount of “friends” people can have, although it was originally supposed to be the average, not maximum. This has been tested in various ways, including monitoring of Christmas card sending (Hill & Dunbar, 2003), and, more recently, using internet social networks, such as Twitter (Gonçalves et al., 2011) and Facebook (Dunbar, 2012; Kanai et al., 2011). Due to Dunbar's popular lectures and articles on the topic, this number now seems to live a life of its own, in a quite distorted form, finding its way into such practical considerations as designing office floors (Oseland, 2009).

When studying the SBH in non-human haplorhines, a new approach was adopted by Lindenfors (2005), who noted that male and female primates often differ in their social behaviours and experience distinct social challenges, and that the sex composition of social groups is not uniform. From that he hypothesised that different selection pressures are acting on females, who can benefit more from social interactions, and males, who rely on aggressive behaviour in order to secure access to females. Although separate data about female and male brains were not available for analysis, the effect on brain size, if any, should still be observable at the species level. Lindenfors showed that in haplorhines, neocortex volume, independently of whole brain volume, correlates with female group size, but not with male group size, which even shows a negative trend. This could perhaps reflect differences in mating system, and imply that relatively larger neocortices are present in harem species. However, a test for body-size dimorphism did not reveal any relationship to relative neocortex size. Similar findings were confirmed later, with more detailed parcelling of brain regions (Lindenfors et al., 2007). The two studies conclude that social strategizing is limited to females, who have more to gain, and that intrasexual competition in males relies more on brawn than brain. That is somewhat going against the previously mentioned conclusions of Pawłowski et al. (1998).

Joffe and Dunbar (1997) attempted a finer-grained search for the actual neural substrate for social cognition in haplorhine primates. To differentiate between visual input processing and social information processing, neocortex was separated into primary visual cortex and the remaining parts, referred to as the non-visual cortex (NVC). In addition, the volumes of lateral geniculate nucleus, to represent a noncortical visual circuit, and amygdala, to assess the influence of emotional response, were examined. For all these brain regions, linear regression residuals on the rest of the brain were calculated. The analysis revealed NVC to be the best predictor of group size, whereas primary visual cortex on its own and amygdala did not correlate with group size. Although NVC is not just the seat of “higher cognition” and contains other sensory processing and motor areas, a case is being made for the assumption that social information manipulation is the critical factor influencing brain size.

To complement the comparative data, Sallet et al. (2011) undertook an experimental study: housing young adult rhesus macaques *Macaca mulatta* in groups of different sizes for over a year and then conducting a series of MRI scans to assess their grey matter density. The larger the group the macaques had

been housed in, the more grey matter they had in areas of the temporal lobe and prefrontal cortex. Similarly, within groups, social rank was positively correlated with grey matter in the rostral prefrontal cortex. However, other parts of the “social brain” were unrelated to either of these parameters. This is a clear demonstration of the intuitive assumption that larger groups are more challenging and illustrates that social stimuli can have a quantifiable effect on neural matter through phenotypic plasticity. The second finding implies a possible genetic component and thus a variation selection might act on, but it is not inconceivable that this effect might be due to plasticity as well.

Thus, there seems to be strong support for the relationship between (female) group size and neocortical enlargement in haplorhines, while relative brain size seems to be more connected to mating system.

4.2 Evidence in carnivores

Carnivores are a mammalian group with a broad range of social systems, reasonably well resolved phylogenetic relationships and enough of brain or skull specimens available for study. As such, they have been used to test the SBH numerous times, as is presented below. All studies are limited to terrestrial carnivores, although some pinnipeds have the largest brains among carnivores, and even rank among the largest in mammals (Manger et al., 2013).

Sociality was first included as a factor in a multivariate study of encephalization in 7 carnivore families, conducted by Gittleman (1986). No relationship between CBS and group size (defined as the number of individuals that regularly aggregate and share the same home-range) was discovered, nor were any differences between species with monogamous/polygamous mating systems and different parental care systems. However, there was an observable effect of breeding group type, with multi-male species having larger CBS than single-male species. The most significant differences, though, were found among families, with the solitary Ursidae in the lead.

Comparing brain sizes across the whole order might thus be too crude and perhaps more meaningful information could be obtained from studies focusing on a single family, whose members employ diverse social systems.

A recent study (Sakai et al., 2011) examined the SBH in the family Hyaenidae. Hyaenids seem amenable to this kind of study thanks to their spectrum of social systems. The complex social life of the spotted hyaena *Crocuta crocuta* is of particular interest for testing the predictions of the SBH, because of its striking similarity to that of some primate species (Holekamp et al., 2007). On the other hand, there are only four extant hyaenid species, which rather limits the statistical power, and moreover, these species differ substantially in their feeding ecology, which may confound the results.

Sakai et al. estimated ECV from skull specimens using computed tomography and found that mean social group size correlates positively both with ECV relative to the basal skull length, and with anterior cerebrum volume (roughly corresponding to frontal neocortex) relative to the overall ECV. The authors

further suggest that the relatively large frontal neocortex of the spotted hyaena *Crocuta crocuta* might be explained by its superior inhibitory control associated with living in a fission-fusion society (previously experimentally shown in primates by Amici et al. [2008]). Nevertheless, this can just as well be simply due to allometric scaling, since the spotted hyaena has by far the largest absolute ECV of the four species. Alternatively, the differences could reflect different foraging strategies, ranging from the termite-eating *Proteles cristata* to cooperatively hunting *Crocuta crocuta*.

The same methodology was adopted by Arsznov and Sakai (2013) for comparison of three procyonid species. Whereas no significant differences in total ECV related to sociality could be detected, relative anterior cerebrum volume was found to be largest in the social coati *Nasua nasua* and smallest in the mostly solitary racoon *Procyon lotor*. Since the overall ECVs of these two species are on par, the finding is probably not attributable to allometry. Additionally, male and female relative regional ECVs were tested for sexual differences. While no such differences were revealed in either racoons or kinkajous *Potos flavus*, female coatis, which lead more socially intense lives compared with males, had larger relative ECVs and anterior cerebrum volumes than males did.

Similar findings were reported by the same authors for African lions, where females spend their lives in the natal group, whereas males experience periods of solitary existence (As a side note: male lions are among the few non-primate mammals known to form alliances [Bygott et al., 1979]. Are the females' social interactions really more complex?). They report that females have a larger relative frontal cortex (anterior cerebrum surface) than males, in the absence of overall ECV differences. In the predominantly solitary cougar *Puma concolor* no sexual differences in overall or regional brain size were observed (Arsznov & Sakai, 2012).

An earlier study (Gittleman, 1994) uncovered sex-specific interspecies differences in carnivores with respect to parental care. According to this study, females have relatively larger brains in species where females exclusively care for the young, compared with females of species with biparental or communal care. No relation between parental care system and brain size was found in males. It is of note, that although not specifically claimed by the author, this might go against the SBH, since communal care occurs in highly social species, whereas "single mothers" among carnivores often imply solitary, unbonded species.

Such sexual differences in brain size raise a potential caveat: disregarding sexual dimorphism and using brain size data pooled from both sexes may mask such effects. Until fairly recently, information about the sex of the animals used was rarely available in comparative studies.

And sexual differences are not the only source of intraspecies variation in brain size. A study of encephalization within the genus *Panthera* (Yamaguchi et al., 2009), based on large sample sizes of skull specimens, revealed no significant differences between the sexes of any of the four extant species. Nevertheless, such differences were found among subspecies and wild and captive individuals. Interestingly, tigers seem to have the largest ECV relative to skull length, compared with lions, jaguars and leopards, among which no significant differences were uncovered. Since lions are the only social big cats, this provides some evidence against sociality being associated with larger relative brain size.

A more complex study (Swanson et al., 2012), encompassing seven carnivoran families, considered several life-history, ecological and social factors at once. ECVs estimated by computed tomography and corrected for body mass/skull size were used as a measure of encephalization. Moreover, relative regional brain volumes were examined. Rather than simply using group size, social complexity was expressed as a composite score derived from social group size, feeding/hunting group size and the degree of social cohesion. No relationship was identified between social complexity and overall encephalization, however, a positive correlation was found with relative cerebral volume and a negative correlation with combined brainstem and cerebellum volume, suggesting a possible constraint on absolute brain size. The relationship between anterior cerebrum and sociality reported by Sakai et al. (2011) in hyaenids was not confirmed.

A previously mentioned study (Pérez-Barbería et al., 2007) attempted to elucidate the coevolutionary history of encephalization and sociality, the conclusion being that there is an evolutionary coupling of larger RBS and sociality in carnivores, albeit not as tight as in primates. Further analysis identified transitional states, indicating that large brains are not a necessary condition for developing sociality, and sociality on its own does not necessarily lead to encephalization. However, these were interpreted as exceptions to the general pattern of coevolution.

An attempt to tackle brain-size evolution in carnivores from a different angle (Finarelli & Flynn, 2009) included 164 extant and 125 fossil species across the order. Using ECVs (and estimates thereof) corrected for actual or estimated body weights, the authors discovered two grade shifts in encephalization allometry relative to the plesiomorphic carnivoran condition: in Canidae and Ursidae. Since canids have various social systems and ursids are solitary, this does not lend much support to the SBH. The results are thus in disagreement with the findings of Pérez-Barbería et al. (2007). Finarelli and Flynn point out that canids are mostly responsible for the observed coevolution of these two traits in carnivores and that after excluding them from the analysis, the effect disappears. In fact, one of the authors reported a possible evolutionary relationship between the emergence of sociality (cooperative hunting) and encephalization in canids in an earlier study (Finarelli, 2008). Shultz and Dunbar (2010a) criticize Finarelli and Flynn (2009) for comparing allometric relationships to show evolutionary change, and advocate their approach of tracking changes in brain size in different lineages over time. They show an encephalization trend in carnivores, perissodactyls, cetaceans and primates, but not in artiodactyls and insectivores, and argue that encephalization in mammals is related to sociality, as indexed by the percentage of extant species living in groups (giving up on their earlier use of the bondedness criterion).

Furthermore, in a comparison of the degree of encephalization in social and non-social species across Hyaenidae and Herpestidae, Finarelli and Flynn (2009) found that sociality is not significantly associated with higher than expected brain volumes, in contrast with the observations of Sakai et al. (2011).

Such opposing conclusions of two similar studies deserve further commentary. Although the same relationship in the same four hyaenid species was examined, the methodologies differed in several aspects. The earlier study used estimates of ECV based on filling the skull with glass beads, whereas Sakai et al. estimated ECV using computed tomography. The latter approach resulted in about 10 % higher volumes

overall, and the contrasts among species differed as well. To calculate relative brain size, Sakai et al. used basal skull length as a proxy for body size, and to indicate social complexity, they employed mean group size. Finarelli and Flynn used body mass and described sociality simply as a social/non-social dichotomy. Furthermore, Sakai et al. treated individuals as data points, while Finarelli and Flynn used species averages in their analysis.

A recent analysis of evolutionary rates of brain and body size suggests that in carnivores as a whole, changes in encephalization are largely due to selection for body size (Smaers et al., 2012). Consequently, encephalization as such might not be very informative as to the adaptive response of brain size to the challenges of social life.

Dunbar and Bever (1998) set to find out if the previously reported positive correlation between C_R and group size in primates holds for other mammals as well. However, data on neocortex volumes were available only for a limited subset of carnivore species with known ECVs. When using independent contrasts to control for phylogeny, no significant relationship between the tested variables was demonstrated. In an attempt to broaden the sample, the authors then derived EC_R . A subsequent independent contrasts analysis uncovered a significant, but rather weak, positive correlation of EC_R with group size.

In the previously mentioned study comparing several larger taxa (Shultz & Dunbar, 2007), carnivores do not show any significant relationship between RBS and group size. In contrast, species with monogamous mating systems had consistently larger RBS than harem and multi-male groups and solitary species.

Thus, there is mixed evidence for and against the SBH in carnivores, the main sources of discrepancy being data sources and choice of appropriate measures, as illustrated by the two contradictory conclusions about hyaenids. It seems that the association of sociality with relatively larger neocortex is better supported than that with overall relative brain size, particularly at intraspecies level between the sexes, although it should be noted that most research showing this originated from one team. The conclusions about mating system are based on just one study. Among carnivores, the relatively large-brained non-social Ursidae and Mustelidae are an obvious example of encephalization not predicted by the SBH.

In the future, it would be interesting to see a study focused on Pinnipedia, which exhibit generally larger brains, marked sexual dimorphism and varying degrees of sociality, or Hesperstidae, where sociality is not coupled with larger bodies (Veron et al., 2004) as is the case e.g. in Hyaenidae.

4.3 Evidence in cetaceans

Cetacea are nested within Artiodactyla (Montgelard et al., 1997), but have been treated separately for good reasons – their ecology and societies bear almost no resemblance. Cetaceans possess famously large brains. They can even exceed humans both in absolute brain mass and in neocortex surface area (Haug, 1987) and this has attracted much attention. Humphrey (1976) noted that toothed whales present something of a mystery, since at open sea, there is little to be gained from complex societies and thus there should be little pressure to increase intelligence. Yet, tool use and traditions have been well documented in cetaceans, as

well as complex social behaviour and impressive cognitive faculties (reviewed e.g. in Marino, 2002; Marino et al., 2007; but cf. Manger, 2013). Cetaceans seem to be an excellent group for comparative studies, since species with very similar body sizes can differ widely in brain sizes (Marino, 1998). Perhaps due to the difficulties associated with detailed long-term field studies at open sea and scarcity of brain specimens, however, there has been more theoretical debate than actual hypotheses testing (e.g. Connor & Mann, 2006). Within cetaceans, odontocetes are more encephalized than mysticetes (Montgomery et al., 2013) and have received more attention. Odontocetes studied so far engage in intricate social interactions convergent with that of elephants or chimpanzees (e.g. Connor et al., 1998), but it has proven difficult to determine the appropriate group size, since they have fluid societies and range over huge areas (e.g. Connor et al., 2000). Several levels of grouping have been suggested, in the order of increasing tightness: schools, groups, and pods (Connor et al., 1998).

Marino (1995, as cited in Marino, 1996) uncovered a significant positive correlation between EQ and pod size in odontocetes, hinting at a relationship similar to primates. However, Manger (2006) argues that this relationship is just a weak trend and does not reach significance. For cetaceans, specifically, encephalization might not be an appropriate measure due to relaxed constraints on body size in an aquatic environment and the large proportion of body mass accounted for by blubber, as admitted by Marino (1998).

An attempt at a comprehensive study of different correlates of cetacean brains (Tschudin, 1997) included 19 species of toothed whales. Actual total brain volumes and neocortex volumes of six dolphin species were measured using magnetic resonance imaging in specimens by-caught in nets. C_R was then calculated for these species, and estimated for other odontocetes from ECVs, to increase the sample size. Correlational analysis did not yield any significant results, but linear regression (weighted by the number of individuals from each species) revealed a significant relationship of C_R with mean group size and maximum aggregation size in dolphins, whereas no such relationship was reported for the species where EC_R was used. Possibly, the nature of this association differs in the six dolphin species and the other odontocetes (other Delphinidae, Phocaenidae, Kogiidae, and Ziphiidae), or C_R and EC_R are not equivalent measures. It should also be noted that phylogeny was not taken into account in these analyses and that reliability of data on group sizes likely varies for different species.

A study limited to just delphinids could be more informative, since the behaviour of specific dolphin populations has been studied in detail (e.g. Stanton & Mann, 2014). There might not be enough data across all cetaceans or even odontocetes to allow for a meaningful comparison.

4.4 Evidence in ungulates

Variation in feeding ecology in ungulates² is rather subtle, compared to variation in social systems (Geist, 1974), and hence they present good opportunities for studying the SBH without major confounders in the form of foraging and diet differences.

The first such study investigating several correlates of brain size in ungulates encompassed the orders Perissodactyla, Artiodactyla and, surprisingly, Proboscidea (Pérez-Barbería & Gordon, 2005). Most of these ungulates do not exhibit bonds as tight as primates or carnivores (with the notable exception of elephants), hence the measure of social complexity was represented by a simple dichotomy of gregarious (stable social groups over 6 members) and non-gregarious. Using statistical modelling, the authors found that besides phylogeny, gregariousness and gestation length explained most of the variability in brain mass (and ECV converted to brain mass) adjusted for body mass. This was presented as evidence in favour of the SBH, although the study did not look for a quantitative relationship as had been done in other taxa.

Shultz and Dunbar (2006) looked for such quantitative relationship in ungulates, but failed to identify a link between mean social group size and either RBS or C_R and neocortex/body mass residuals. Instead, all of these indices were significantly higher in social (generally observed in pairs or groups) vs. solitary species. RBS and neocortex/body mass residuals were additionally associated with mating system, with monogamous and harem groups having larger residuals than solitary and large mixed groups. Habitat complexity, as a potential confounder, was not related to any measure of brain size. At face value, this seems consistent with the results of the above mentioned study (Pérez-Barbería & Gordon, 2005). However, due to different categorization criteria, large mixed groups would fall into the gregarious, and monogamous into the non-gregarious category in the previous study. This highlights how the non-existence of consistent criteria hinders comparability between different studies.

Two other previously mentioned studies presented evidence for the coevolution of RBS and sociality (as opposed to solitary living) (Pérez-Barbería et al., 2007) and for the association of monogamous mating systems with larger RBS controlled for phylogeny (Shultz & Dunbar, 2007). Both were restricted to artiodactyls.

In a recent study (Briefer et al., 2014), goats demonstrated a high capacity for individual learning and long-term memory in a non-trivial food extraction task, but also a lack of social learning, despite the fact that they maintain complex societies (Stanley & Dunbar, 2013).

Overall, there appears to be some support for the link between sociality and relative brain size in ungulates, but it is not straightforward and seems to be dependent on the mating system.

² The term ungulates is used here as a descriptive name for hoofed mammals and does not represent a taxonomic unit.

4.5 Evidence in other mammalian groups

4.5.1 Proboscids

Elephants, with their absolutely large brains, and striking social complexity and cognition (reviewed by Byrne et al., 2009), are of great interest for the SBH, but not very suitable for comparative studies of brain size. Still, they can be used to test some of the more refined predictions, such as the one that highly social species should favour social over individual learning, as has been done by Greco et al. (2013). African elephants were presented with various puzzles they had to solve in order to get to a food reward. Those that first watched a conspecific demonstrator succeeding in getting the reward failed to solve the task more quickly and did not copy the actions of the demonstrator. The only observable effect was at the level of stimulus enhancement. From this result, along with that in goats (Briefer et al., 2014), it would seem that social learning does not play a crucial role in these animal societies, however, it is quite possible that such foraging tasks are simply not the subject of social learning in these grazers/browsers.

4.5.2 Bats

Two unrelated bat species forming stable groups (*Desmodus rotundus* and *Phyllostomus discolor*) were found to have greater neocortex/rest-of-brain residuals than nine other species living in unstable groups (Barton & Dunbar, 1997). However, no indication of group stability criteria or associated mating systems was given. Another study focused on bats (Pitnick et al., 2006) considered both the complexity of group composition (in order of increasing complexity: single-male/single-female, single-male/multiple-female, multiple-male/multiple-female) and the mating system (monogamous, polygynous or polygynandrous). No significant relationship between RBS or neocortex/body mass residuals and group composition was uncovered, although there was a trend towards diminishing brain size with growing group complexity. Conversely, monogamous species and species without female promiscuity had relatively larger brains. That might be opposite to the expectations of the SBH in the original form, but supporting of the pair-bonded version. An alternative explanation proposed by the authors is a possible trade-off between two expensive tissues: brain and testes, substantiated by the finding of a negative correlation between the sizes of these two organs.

Bats, being such a species-rich and diverse group, are clearly understudied with respect to the SBH, even more so in light of the recent finding that some bats are able to maintain stable social ties in fission-fusion groups (Kerth et al., 2011). From the available evidence, no firm conclusions can be drawn.

4.5.3 Insectivores

In addition to carnivores, the study of Dunbar and Bever (1998) included 25 genera of the order Insectivores, which has since been split into Eulipotyphla and Afrosoricida. They were further divided into “basal” and “advanced”, based on cerebral morphology criteria established by Stephan (1972), but these categories do not reflect any actual phylogenetic relationships. The study found that the link between C_R and group size holds only for the “advanced” insectivores. That is hardly surprising, given that within the “basal” group, there was virtually no variation in reported group size (all but one had group size of 1). An improved fit was obtained with absolute neocortical volume instead of C_R , but the relationship was not very convincing. Given the poorly known phylogenetic relationships and mostly secretive nocturnal lifestyles with very little reliable information on their social lives, insectivores might not be well-suited to test the hypothesis in the first place.

4.6 Evidence in birds

Among birds, corvids are considered unusually smart, warranting even comparisons to apes (Emery & Clayton, 2004; Seed et al., 2009), together with parrots and hornbills. Incidentally, all of these groups display a high level of sociality. On the other hand, other such “smart” birds, like woodpeckers and owls, are territorial or solitary, and some social birds, such as pigeons and fowl, do not enjoy such a good cognitive reputation (as reviewed by Emery, 2006). Is there a pattern?

A large-scale study examined 155 bird species across multiple orders (Burish et al., 2004). Telencephalic volume fraction (TF) was compared in birds assigned to four categories based on social group size, defined as the number of birds typically found together, excluding migration flocks and birds on breeding grounds, (“solitary”, “covey”, “colonial”), and on presence of transactional social interactions (“transactional”). This categorization is somewhat puzzling, as it mixes quantitative and qualitative criteria – birds included in the transactional category must simultaneously belong to one of the other three. Significant differences in TF between most groups were detected, where increasing TF was associated with increasing level of sociality, and especially between transactional vs. non-transactional birds. Owls were excluded from the analysis, since they did not conform to the pattern, and there is no mention of whether including them would lead to different results. Additionally, the authors examined the relationship between social complexity and residuals from regressing telencephalic volume on body mass, and arrived at mixed results, depending on the grouping used to calculate the residuals. At a finer taxonomic level, the differences between transactional and non-transactional species largely disappeared.

These conclusions are in stark contrast to the results of another study examining the same relationship between telencephalon size and group size and using partially the same data set (Beauchamp & Fernández-Juricic, 2004). This study found no association between sociality and telencephalon size in any of the three investigated data sets. While using the same residuals from regressing telencephalon volume on body mass and additionally using TF, the authors employed different measures of sociality, namely mean and maximum

group size in non-breeding season (mixed-species flocks were included as well), and “flocking propensity”, dividing species into solitary and gregarious. Their criteria were thus purely quantitative, without taking actual interactions into account. Since the most robust associations uncovered by the previous study involved the transactional/non-transactional dichotomy, it is possible that mere flock size does not appropriately reflect social complexity. That said, the transactional category was fairly arbitrarily defined, based on a number of widely different behaviours, and of course does not rule out complex social interactions in species, where it has not been reported.

Emery et al. (2007) investigated the link between RBS and sociality, as classified by group size in 7 categories, from solitary to very gregarious. No linear relationship emerged, instead, small groups (5-30 individuals) had significantly larger RBS than all the other groups. The authors offer an explanation that avian brain size is constrained by the demands of flight and would not be able to “store” much more relationship information. That seems rather improbable, given the impressive memory abilities of even such ordinary birds as pigeons (Fagot and Cook, 2006). Maybe these groups are more complex and differ from loose large flocks, where it would be unlikely to maintain close relationships with all the individuals. Another factor considered was the mating system – promiscuity, polygyny, polyandry, serial (one year) monogamy, monogamy for more than one year, long-term monogamy (which serves as a substitution for the term “life-long”, as that is technically hard to prove), and cooperative breeding. Birds with cooperative breeding and long-term monogamy had relatively largest brains. Pondering the differences between distant groups of long-term monogamous birds, the authors speculate that it is the need to cooperate closely in care for altricial offspring that is cognitively taxing and leads to brain enlargement. However, the same reasoning would apply to all altricial birds (which has in fact been shown by Iwaniuk and Nelson [2003]). Cooperative breeding thus might be associated with larger brains, because it allows for a prolonged developmental period that helps to overcome a constraint on brain size (Isler & Van Schaik, 2009b). Emery et al. (2007) further contrast the social behaviour of the smaller brained grey-lag geese *Anser anser* with that of rooks *Corvus frugilegus* and jackdaws *Corvus monedula*, and highlight the need to coordinate and to read and anticipate the behaviour of the partner. Such “relationship intelligence” might be important in favouring brain enlargement.

This is in agreement with Dunbar's argumentation (2009), but elicited criticism from Scheiber et al. (2008), based on the grounds of underestimating the complexity of social behaviour in greylag geese, examples of large-brained non-social birds (Strigidae, Podargidae), and long-term bonds in non-brainy species. Scheiber et al. (2008) thus conclude that cognitive skills are not a prerequisite for long-term pair bonding, but do not offer much systematic data to back up the claim.

Shultz & Dunbar (2010b) report migratory status, pair-bond duration, developmental mode, foraging group size, and mating system as correlates of RBS controlled for phylogeny. Interestingly, absolute brain size and TF correlated significantly only with migratory status and pair-bond duration. Additionally, based on modelling of evolutionary pathways, Shultz and Dunbar argue that pairbondedness and biparental care are prerequisites for altricial development, which they claim is not related to encephalization directly.

Garamszegi et al. (2005) offer some insight into the alternative mechanisms for the proposed link between monogamy and larger brain size: the effect might be due to the need to cooperate and synchronize behaviour (Dunbar, 2009), or due to the “cheating game” (trying to secure extra pair copulations or prevent the partner from doing so). The study revealed no link between extra pair paternity (EPP) and RBS across species. However, within species with high levels of EPP, females had larger brains than males, and vice versa, implying an evolutionary “arms race” between the sexes. West (2014) shows that up to a point, levels of EPP correlate positively with RBS, but after reaching a certain threshold, brains start to get smaller, probably because such high levels of EPP favour transition to polygamy and the selection pressure relaxes.

Unlike all the above mentioned studies, Iwaniuk and Arnold (2004) focused on a lower taxonomic group: the parvorder Corvida *sensu* Sibley & Ahlquist (1990), whose monophyly has since been contested (e.g. Barker et al., 2004), but whose members nevertheless share the same developmental mode and are distinguished by a high frequency of cooperative breeding. Brain masses and ECVs were measured in specimens from museum collections and other sources and these two measures were combined by converting brain mass to ECV. Analysis of both raw data and independent contrasts did not find any relationship between the presence of cooperative breeding and ECV corrected for body mass, or between RBS and cooperative breeding group size (number of birds participating in raising the young). The only significant result emerged within Meliphagidae, where cooperative breeders had relatively larger brains.

Recent findings about the cellular scaling rules for bird brains (Olkowicz et al., unpublished data) raise serious doubts as to whether comparing brains across Aves is substantiated. That gets further complicated by the issue that high-level bird phylogeny is still up for debate. If there is any consensus from these studies, it would be the support for monogamy as a driving force for absolute and relative brain enlargement. The evidence implying intrasex competition as the mechanism responsible for this trend is intriguing. However, monogamy correlates tightly with other important factors, such as altriciality and cooperative breeding, and the effect might thus be mediated by removing energetic constraints.

4.7 Evidence in fish

Fish constitute an interesting, albeit seldom used, group to test the SBH. Although long regarded mostly as mindless automata, fish do display a range of higher cognitive abilities and social behaviours, including individual recognition, cooperation, cheating and reconciliation, as well as social learning and traditions (reviewed e.g. in Brown, 2014; Bshary et al., 2002). Coral reef fishes living in mixed-species communities and especially cleaner fish maintaining complex relationships with their clients (Salwiczek et al., 2012) lend themselves to studying the effects of interspecific social interactions. However, cichlids remain to be the only studied group.

Some cartilaginous fishes possess levels of encephalization comparable to those of mammals and birds (Northcutt, 1978). While the SBH has not been explicitly tested in cartilaginous fishes and the availability of

data on brain sizes leaves much to be desired (Yopak, 2012), there are observable trends towards larger brains in more social, gregarious, and school-forming species (e.g. Yopak et al., 2007) and in species engaging in complex mating behaviour (e.g. Chapman et al., 2003; Yano et al., 1999).

Pollen et al. (2007) examined brain size, and social and habitat complexity in the cichlids from the Lake Tanganyika. Relative telencephalon volume correlated positively with social system, with monogamous species having larger volumes than polygamous ones, and with the total number of fish living in their habitat. Conversely, hypothalamus was relatively smaller in monogamous species. Whole brain volume was associated with species richness in the habitat, while interestingly no measure of brain size was related to the number of conspecifics. This is in agreement with the previous observation of Bauchot et al. (1988) that, in general, fishes living in a complex community comprising a high number of species, such as a coral reef, have higher EQs.

Monogamy can also be related to biparental care. Gonzalez-Voyer et al. (2009) showed that in African cichlids, species where only females care for the young have larger brains, when the effects of phylogeny are partialled out. Sex-specific analyses revealed that female brain mass correlates significantly with parental care type, while male brains are unaffected. This is an interesting parallel to the findings of Gittleman (1994) in carnivores.

Shumway (2010) shows that although telencephalon is enlarged in monogamous species of cichlids (Pollen et al., 2007), polygamous (lekking) species display significantly greater visual acuity, possibly advantageous in quickly recognizing and appropriately reacting to different conspecifics.

In contrast to primates (Joffe & Dunbar, 1997), group size/mating system seems to affect visual acuity in fish and may also be linked to the amygdalar homologue, represented by the dorso-medial area of the telencephalon (Shumway, 2010). And the claim for monogamy as a driving factor in brain evolution (Dunbar & Shultz, 2007b) gets some support in fish as well. Additionally, though, fish attest to the fact that heterospecifics can provide a complex social environment as well. This might be a more universal phenomenon worth exploring.

4.8 Evidence in insects

Insects illustrate the possibility of evolving what we see as complex behaviours with brains that are miniscule in absolute terms (reviewed by Chittka & Niven, 2009). Lately, there has been some investigation into the link of brain size and sociality in insects, to see if comparatively more neural matter is needed to manage its demands, or if it can be circumvented by different mechanisms.

Many social hymenopterans have conspicuously enlarged, complex mushroom bodies (Farris & Schulmeister, 2011) that are considered the insect equivalent of vertebrate higher brain centres (Farris, 2008). While this might be interpreted in favour of the SBH, it has been shown that these evolved before the rise of sociality, possibly as an adaptation to parasitoid lifestyle, ensuring more effective host location (Farris & Schulmeister, 2011). The existing neural structures might have been later exapted for social functions,

such as individual recognition. Although, when Gronenberg et al. (2007) compared species of paper wasps within the genus *Polistes* that recognize individuals by their facial patterns with that which do not exhibit such recognition, they could not find any difference in the size of optical lobes. Instead, the face recognizing species had relatively smaller antennal lobes, indicating they may rely less on olfactory cues.

As evidenced by many eusocial insects, colony coordination and communication may require some sophisticated behaviours, on the other hand, in cast-based societies, cognitive demands might be relieved by specialization in a single task. A recent study by Riveros et al. (2012) lends some support to this reasoning. After examining brain masses across 18 species of fungus-growing ants (Attini), they found a quadratic relationship with colony size, suggesting there is a point where the relationship gets reversed. In addition to group size, the authors performed a scale analysis, an originally anthropological method based on a matrix of present and absent social traits (Carneiro, 1962), and showed a negative correlation of the number of traits with relative brain size. However, most results were dependent on the treatment of outliers and effects of controlling for phylogeny, and further complicated by the fact that the full observed range of brain size variation was displayed *within* some species.

Interesting patterns might thus be uncovered at the intraspecific level. It has been shown that the gregarious, migratory phase of the desert locust *Schistocerca gregaria* has a significantly larger brain compared to the solitary phase (Ott & Rogers, 2010). Moreover, this effect was most prominent in the mushroom bodies. Although the two forms differ in other aspects of their biology in the wild, in the experiment, they were kept under identical conditions. The results of Smith et al. (2010) in the sweat bee *Megalopta genalis* support this finding. In these facultatively social bees, social reproductives (even those living in very small groups) had larger mushroom bodies than either social non-reproductives or non-social reproductives, which was interpreted as a possible response to the need of asserting dominance.

Other similar studies have been conducted, and in their review, Lihoreau et al. (2012) conclude that most failed to show a link between sociality and brain size in insects. They argue that brains get more specialized, rather than simply bigger, and that research in all taxonomic groups should refocus on the specific neural circuits underpinning social tasks. While the relevance of studying insect brains for drawing conclusions about vertebrate brain evolution is limited, insects nevertheless present unique opportunities for detailed studies that should be made use of.

5 Critique of the social brain hypothesis

While the SBH is generally well received, some criticism has been voiced. Holekamp (2007) draws attention to the fact that despite living in societies of comparable complexity, primates and canids differ in terms of general cognition, with primates displaying more behavioural flexibility, as do the solitary bears. She criticises the SBH on being too vague, emphasizes the need to consider the interplay of social and environmental factors, and calls for more intense uniting of behavioural and neuroanatomical approaches.

Byrne and Bates (2010) point out that while the SBH may apply in the case of quantitative cognitive differences between species, based mostly on memory capacity, it does not have a good explanation for the qualitative differences between great apes and monkeys, since apes do not experience any more complex social environments. They argue that the abilities associated with a degree of theory-of-mind are due to having to deal with environmental challenges and competition, because they emerged independently in different phylogenetic lineages (some birds, elephants, and great apes). In this context, it is worth mentioning that tactical deception of some kind can be employed even in cephalopods (Brown et al., 2012), which are famously “smart”, but also do not qualify for most of the criteria employed by the SBH.

Barrett et al. (2007) dispute the assumption that grooming in primates leads to coalition forming, increasing in turn the social environment complexity and creating the necessity to track third party relationships, and cite evidence that coalitions are rarely observed in the wild. They do not agree that navigating the social environment requires abstract reasoning. Instead, they propose that social skills rely on pattern recognition, thus arguing that primates cultivate the art of observation, not necessarily that of deduction. Similarly, Henzi et al. (2009) call into question one of the central premises of the SBH, as it applies to primates. According to their study, female baboons do not display long-term relationships, and their groups become loose in times of food abundance, with no consequences for group stability. This is clearly contrary to the claim that close relationships are necessary to maintain group cohesion (Kudo and Dunbar, 2001).

In their general critique of theories about brain evolution, Charvet and Finlay (2012) mention that the amount of brain size variability explicable by the SBH is extremely small. While the relationship between social complexity and some proxy of brain size is apparent in primates, they question the conclusion that neocortex places a quantifiable limit on group size. Moreover, they suggest that changes in developmental schedules might lead to changes in social behaviour, which is just reflected in neocortex size, without any causal relationship between the two.

Van Schaik et al. (2012) define several conditions that have to be met in order for an organism to be able to reap the cognitive benefits of a large brain, explaining why the demands of social living might not lead to encephalization in some taxa. They further posit that specific socio-cognitive skills can evolve even in small-brained species, while general behavioural flexibility requires larger brains and leads to innovation, which is then perpetuated by social transmission. This diverges from the SBH in that the mechanism does not have to involve social interaction in adults, as long as there is a sufficient period when the young can learn from conspecifics.

While most of the criticism focused on the SBH in primates, Barret and Würsig (2014) denounce the generalization of the hypothesis to fit a broad range of diverse taxa, based on the heavily anthropocentric premises and flawed assumptions that sociality would be expressed in the same way in very different animals.

6 Conclusions

Over the last 20 years or so, there have been numerous studies trying to shed some light on the relationship between sociality and brain enlargement. Primates have been the focus of most of them, but virtually all other suitable mammalian groups received some attention, with the notable exception of rodents. Birds have been the subject of many studies, and some considered fish and insects. Other groups were left out, because they do not display much variation in social behaviour, although that might not be the case for reptiles (Doody et al., 2013).

The problem with the SBH is that due to the vague definition, results can be flexibly interpreted as evidence for or against it, depending on what version is invoked. Perhaps the search for an all-encompassing explanation is just not fruitful and efforts should shift to testing more specific claims that can be formulated at a finer taxonomic level, where it makes sense, rather than trying to fit the results with an explanation *post hoc*. If there is a general pattern, it could emerge on its own.

From the evidence presented in preceding chapters, it is clear that on many topics consensus is far from being reached. A more detailed break-down might be helpful in uncovering what has been established so far.

As for the relationship between group size and some measure of brain size, relative brain size does not seem to be supported, with the exception of one study in odontocetes, which has been contested, while neocortex ratio (which is more indicative of absolute brain size) is related to group size in haplorhine primates, carnivores, to a lesser degree, and perhaps odontocetes, where the evidence is mixed.

The very strong claim that “the only reason primates live in larger groups than carnivores is that they have larger neocortices” (Dunbar & Bever, 1998) seems preposterous and does not take into account that different taxa have quite different reasons for group living. The assertion that neocortex places an upper limit on group size in primates does not appear to be justified either. Even one example from Dunbar's own data (1992), where he explains the exclusion of synanthropic populations of *Miopithecus* on the basis that they tend to be larger, documents that group size gets limited by other factors long before the theoretical constraint posed by neocortex size would come into effect. The same reasoning can be applied to the Dunbar's number. In my opinion, maintaining much over 150 relationships would be unfeasible in terms of invested time, rather than cognitively impossible. Besides, the question remains why intense social relationships would exist at all, if loose aggregations can still provide the benefits of group living without these relationships.

As for the relationship between monogamous pair-bonded relationships and RBS, this seems to hold well for birds. There is an intriguing suggestion that a battle between the sexes over extra-pair copulations might be partly responsible, but it is also inextricably related to having altricial young and does not explain variability at lower taxonomic levels. In the case of carnivores, where it might hold as well, monogamous species are oftentimes cooperative breeders (Kleiman, 1977) and cooperative breeding has been implicated in removing the constraints on brain enlargement due to diluting the investment in raising young over more

individuals (Burkart et al., 2009; Burkart & van Schaik, 2010). This brings up the question of possible mechanisms behind these empirical findings.

The need for cooperation is definitely common to monogamy, group living and cooperative breeding, so it seems as a good candidate for mediating the effect on cognitive abilities. But as mentioned above, social insects show the ultimate cooperation without any linear effect on their brain size. Yet, cooperation and competition might be just two sides of the same coin. Where there is cooperation, the opportunity for cheating lurks around the corner. McNally and Jackson (2013) have shown this in primates: the degree of cooperativeness correlates with frequency of tactical deception, even when controlled for confounders. Thus, the initial Machiavellian intelligence comes into play again. One of the distinguishing claims of the first version of the SBH is that the environment does not strike back and can be dealt with by innate strategies, whereas conspecifics can engage in “battle of the minds”. It might be worth considering that this is not limited to conspecifics, but there are other such flexibly responding partners, so this pressure may be faced by not-so-social species as well. This applies to predators and prey (as evidenced by the case of the shrinking brain in *Myotragus* [Köhler & Moyà-Solà, 2004]), cleaner fish and their clients (Tebbich et al., 2002), or the drongo tricking other animals by false alarm calls and stealing their food (Flower, 2011).

Finally, social learning features as an important component in some versions of the SBH, but it is not unique to social species (Wilkinson et al., 2010), social animals do not seem to favour it over individual learning Greco et al. (2013), nor does it correlate with group size in primates (Reader & Lefebvre, 2001).

Notwithstanding, there is one paradox concerning any purported selection factor acting on improved cognition. Many species in captivity seem to have a cognitive potential above that which they display in the wild and that only manifests once they are put to tests by scientists (e.g. Benson-Amram et al. 2013; Bird & Emery, 2009; Haslam, 2013). That does not apply to any other characteristic, animals cannot run faster or hear better in experiments than they do in their natural environment. Perhaps our own cognitive abilities are the best example. Clearly, anything akin to the ability to solve differential equations was not selected for in our ancestors, yet our brains (at least some of them) are capable of doing so. If the cognitive demands of challenges animals face are not pushing the limits, how can they be the driving force behind brain evolution? Maybe we are just underestimating the complexity of problems animals solve in the wild, or maybe this only becomes an issue when times get hard. Or is it possible that this spare cognitive capacity is an epiphenomenon of having brains that evolved to manage other functions?

The support for any variant of the SBH is by no means overwhelming. Clearly, we are left with more question than answers. To provide some, more detailed and reliable data on both animal behaviour in the wild and the morphology and development of their brains need to be collected. After all, any analysis can be only as good as the information input. I believe that future studies on the SBH should be performed at a finer taxonomic level, to avoid comparing apes and oranges. Last but not least, the use of relative brain size as a proxy for “intelligence” seems not justified in light of the accumulated evidence for absolute brain size being a much better correlate. While probably not providing the definitive answer, future studies that address these issues might bring us one step closer.

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