FROM BRAINS TO BEARS. UNDERSTANDING BRAIN SIZE EVOLUTION: CAUSES, COSTS AND BENEFITS

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Dedication

This thesis is dedicated to Riku, Kai, Amu and Hanako.

Credit. By Yorkshire Wildlife Park, 2018.

Declaration

The research titled '*Why big brains? A comparison of models for both primate and carnivore brain size evolution*', that is presented and discussed in chapters 2 to 5, has been published as a research article in PLoS One. This involved collaboration with Dr Sandra Heldstab from the University of Zurich, in terms of assistance regarding statistical analyses and methodologies, as well as reviewing and editing of the manuscript. However, I was the principal researcher in this study and the lead author of the paper (see Chambers et al. (2021)).

Glossary

Glossary Term	Glossary Definition
Behavioural flexibility	"*The ability to alter behavior following environmental feedback and to inhibit previously successful behaviors*" (Harrison et al., 2021).
Body size correction factor	The techniques used to account for body size when calculating relative brain size[1].
Cognition	"*Information processing in the broadest sense, from gathering information through the senses to making decisions and performing functionally appropriate actions, regardless of the complexity of any internal representational processes that behavior might imply*" (Shettleworth, 1998, 2000).
Cognition (broad)	"*The mechanisms by which animals acquire, process, store, and act on information from the environment*" (Shettleworth, 1998).
Cognitive buffer hypothesis (CBH)	A hypothesis proposed by Sol (Sol, 2009a, 2009b) which posits that big brains facilitate the production of behavioural responses that serve as a '*buffer*' in light of socioecological challenges.
Concerted evolution[2]	"*Individual components (brain and body size, or individual brain components) tend to evolve together because natural selection operates on relatively simple developmental mechanisms that affect the growth of all parts in a concerted manner*" (Finlay & Darlington, 1995; Finlay et al., 2001; Montgomery et al., 2016).
Domain-general abilities	"*An overarching ability, not tied to any domain in particular (i.e., content-neutral), to respond flexibly to new or complex situations, to learn and to innovate*" (van Schaik et al., 2012).

Domain-specific abilities	Adaptive specialisations, often defined as modules, which have evolved to solve a *specific* adaptive problem (Duchaine et al., 2001). Such modules are thought to "*exclusively process information from a specific domain and to produce a correspondingly specific output in the form of representations and/or a behavioral response*" (Burkart et al., 2017). For example, a species may have particularly strong spatial memory to retrieve stored food, without possessing more powerful cognitive capacities in other contexts (Sherry, 2006).
Encephalisation	When brain size is larger than expected for relative body size (Jerison, 1985).
Encephalisation quotient (EQ)	A measure of relative brain size. Calculated as the ratio of *observed* brain size to *expected* brain size (for body size).
Endocranial volume (ECV)	A measure of brain size. The standard technique for estimating ECV involves filling the cranium with beads (or similar) and measuring using a graduated cylinder or by weighing the beads and converting the weight to volume (Isler et al., 2008).
General intelligence (*G*)	"*The suite of cognitive mechanisms that appear to enhance an animal's ability to engage in flexible, innovative behaviours when confronted with a problem*" (Farris, 2015; Holekamp & Benson-Amram, 2017).
Innovation	An individual's ability to utilise previous knowledge to solve a new problem or apply new techniques to solve an existing problem (Kummer et al., 1985; Reader & Laland, 2003).
Intelligence	"*An individual's ability to acquire new knowledge from interactions with the physical or social environment, use this knowledge to organize effective behavior in both familiar and novel contexts, and engage with and solve novel*

	problems" (Burkart et al., 2017; Byrne, 1994; Rumbaugh & Washburn, 2003; Yoerg, 2001).
Mosaic evolution	Contrasts with concerted evolution[2], in that each *distributed functional system* (connecting different *sub-components*) is under *different* selection pressures, which results in different brain structures evolving *independently* of each other (Barton, 2001; Montgomery et al., 2016).
Problem-solving ability	"*Cognitive processing directed at achieving a goal when the problem solver does not initially know a solution method*" (Mayer, 2013).
Relative brain size[1] (RBS)	Brain size after accounting for body size e.g., residuals from a regression line.
Social brain hypothesis (SBH)	A hypothesis proposed by Dunbar (1998) which implicated sociality as the major driving force behind the evolution of increased brain size.
Technical intelligence hypothesis Also known as the **Extractive Foraging** or **Ecological Intelligence** hypothesis	A hypothesis proposed by Byrne (1997) which stated that *material* and *object*-orientated behavioural skills (such as caching food, extracting embedded food and using tools) to be a major driving force behind the evolution of increased brain size.

Abstract

Developmental and energetic costs result in brains being expensive organs to grow and maintain, yet large brains have evolved in many mammalian species. The adaptive value of increased brain size has come under scrutiny over the past few decades and despite considerable research effort, much uncertainty remains regarding: (i) the selective pressures responsible and (ii) the potential benefits that big brains provide. Here, both topics are investigated.

Firstly, the influence of social, ecological and life-history traits were assessed on whole and regional brain size in two well-studied orders: Primates and Carnivora. In primates, consistent associations are found between brain size and dietary factors, such as dietary breadth; however, evidence is also found indicating sociality as a selection pressure driving brain size. In carnivores, evidence suggests ecological variables, most notably home range size, is influencing brain size, whereas no support is found for the social brain hypothesis. Life-history associations reveal complex selection mechanisms counterbalance the costs associated with expensive brain tissue through extended developmental periods, reduced fertility and extended maximum lifespan.

Secondly, to better understand the proposed benefits afforded by encephalisation, the cognitive abilities of 17 captive European brown bears (*Ursus arctos arctos*) were tested via two behavioural problem-solving trials. Results revealed evidence of trial-and-error learning; however, two juveniles appeared to acquire an association between the latch and access to the box, suggesting some individuals have potential to adopt successful strategies and draw perceptive associations. Individual variation in motivation levels

appears to be an important factor influencing cognitive performance. The bears failed to spontaneously use a tool but still managed to retrieve the food reward, instead using alternative techniques. Analyses revealed both age and sex (using female as the reference category) to be negatively associated with time-to-solve in our sample, indicating that younger male bears solved the task more quickly. Results suggest social dynamics of group-living bears to be influencing cognitive performance, as the collective nature of testing resulted in increased competition over a high-value reward. European brown bears are confirmed to be an excellent model species for testing the benefits of increased brain size, as well as theories of cognitive evolution.

The findings of the first study, together with other recent re-examinations of brain size evolution, are shifting long-standing viewpoints on the variables responsible for encephalisation. Meanwhile the second study is one of the first to explore the cognitive abilities of captive European brown bears; this approach is at the forefront of cognitive evolution research, since it seeks to test the benefits afforded by encephalisation.

1. Introduction

1.1. Background

Brain size increases with increasing body size. Despite this common allometric scaling principle, ratios of brain size to body size differ considerably between taxonomic groups (Jerison, 1973). For example, there are taxonomic differences, often considered ‘*grade shifts*’ between primates and insectivores, and within the primates, between the strepsirrhines and haplorrhines (Barton & Harvey, 2000). There are also structural differences, with apes possessing larger cerebellums than monkeys, proving that not all primate brains are organised similarly (Rilling & Insel, 1998). The presence of such variation in brain size has interested researchers for decades.

Encephalisation, when brain size is found to be bigger than expected for relative body size (Jerison, 1985), occurs despite the fact that brain tissue is expensive (Aiello & Wheeler, 1995) and incurs substantial developmental costs through extended growth and maturation periods (Barton & Capellini, 2011; Chambers et al., 2021; Weisbecker & Goswami, 2010). This raises questions regarding which selective pressures have overcome such costs (Potts, 2011; Seyfarth & Cheney, 2002) and has resulted in the diverse array of specialised brains and behavioural competencies seen today (DeFelipe, 2011).

Much research effort has gone into confirming the potential evolutionary pressures resulting in enlarged brains. Particular focus has been devoted to investigating the social lives of species since Brothers (1990b) first coined the term the “*social brain*” and researchers became interested in the evolution of this “*social brain*” (Barton & Dunbar, 1997). Dunbar (1998) summarised these early proposals when he suggested the "*social brain*" hypothesis (hereafter SBH), which brought awareness to the importance of social interactions between individuals. This hypothesis has received substantial support from data related primates (Dunbar, 1992), as well as other taxa including carnivores (Dunbar & Bever, 1998; Holekamp et al., 2015; Sakai et al., 2011) and birds (Emery et al., 2007; Scheiber et al., 2008; Shultz & Dunbar, 2010b). Despite this, more recent work contests the SBH, finding no support for the role of sociality in brain evolution (DeCasien et al., 2017; MacLean et al., 2014; Powell et al., 2017; Swanson et al., 2012).

Other factors, such as those related to the physical environment, are also thought to explain variation in brain size. Ecological hypotheses mainly involve investigating the role of diet (DeCasien et al., 2017; MacLean et al., 2009; Swanson et al., 2012; van Woerden et al., 2010; Walker et al., 2006), home range (Parker, 2015; Powell et al., 2017), and foraging techniques (Gibson, 1986; Plante et al., 2014; Reader et al., 2011) in overall encephalisation. This work stems from the idea that certain diets are thought to be more cognitively demanding; for example, frugivorous species are believed to require greater spatial memory and food processing competencies, potentially leading to increased brain size (Barton, 2000; Milton, 1981; Parker & Gibson, 1977). The importance of these ecological factors have only recently returned to the fore, as when Dunbar (1998) suggested the SBH, he discredited the role of ecology in encephalisation and shifted the focus towards the importance of sociality.

In contrast to hypotheses like the SBH or those related to ecological variables, which aim to confirm the presence of domain-specific abilities (evolved to solve a *specific* adaptive problem), there is now considerable research investigating the presence of domain-general (not fixed to any domain in particular) cognitive abilities. One such hypothesis is the "*cognitive buffer*" hypothesis (hereafter CBH), which posits that big brains facilitate the production of behavioural responses that serve as a '*buffer*' in light of socioecological challenges (Sol, 2009a, 2009b). Support has started to surface for this hypothesis, primarily coming from data related to birds (Fristoe et al., 2017; Minias & Podlaszczuk, 2017; Sayol, Maspons, et al., 2016; Sol et al., 2007), but also mammals (González-Lagos et al., 2010; Sol et al., 2008) including some primate species (van Woerden et al., 2010; van Woerden et al., 2012). It also improves on other theories by not being restricted to one factor or variable, integrating previous hypotheses and acknowledging that the brain carries out multiple functions (González-Lagos et al., 2010).

In addition to external factors influencing brain size, life-history variables are thought to exert considerable influence on cognitive evolution, especially in terms of acting as a '*filter*' in the production and growth of large brains (Deaner et al., 2003; Isler & van Schaik, 2014). This is because they are crucial in determining the potential adaptive pathways available to a species (Dunbar & Shultz, 2007b). For example, extended gestation length is thought to bypass the constraints of precociality (being mature-born) on brain development in mammals and facilitate brain growth (Weisbecker & Goswami, 2010). Ultimately, encephalisation has been found to correlate with the expansion of most developmental stages, including an extended reproductive lifespan (Barrickman et al., 2008).

Furthermore, many researchers who study the presence of big brains, also question what function big brains serve and what potential benefits they can provide. One long-held assumption is that the production of large brains facilitates the production of superior cognitive abilities (Boddy et al., 2012; Weisbecker et al., 2015). Comparative studies lending support to the assumption have started to arise, using indicators of superior abilities such as behavioural flexibility (Amici et al., 2018), innovation (Benson-Amram et al., 2016), learning (Kotrschal et al., 2013b), invasion success (Amiel et al., 2011; Sol et al., 2005), predator evasion (Kotrschal et al., 2015) and self-control (MacLean et al., 2014). Thus, it is now thought that larger brains facilitate the production of more, and potentially more specialised, *modules* that can ultimately be used for novel cognitive functions (Chittka & Niven, 2009). These *modules*, or adaptive specialisations, evolve to solve a specific cognitive challenge (Duchaine et al., 2001), and therefore, the production of more of these *modules* should result in increased cognitive ability. However, despite decades of research, this idea remains highly controversial, with much scepticism surrounding the advantages of increased brain size (Deaner et al., 2007; Deaner et al., 2000; Smaers et al., 2012; van Valen, 1974; Willerman et al., 1991).

One area of research which investigates the potential benefits of enlarged brains, which has become prominent in the field of animal cognition, involves studying one’s ability to innovate and solve unique socioecological problems (Bandini & Harrison, 2020). Such innovative behaviours have become of specific interest to behavioural researchers (Arbilly & Laland, 2017), with innovation rate now commonly used as a tool to quantify differences in cognitive ability and test brain evolution hypotheses (Lefebvre et al., 2004). Commonly, it is thought that innovation is a direct product of cognition and a direct target of selection, however innovativeness is perhaps best considered just one component of a larger array of abilities, evolved to cope with environmental variation (Griffin, 2016). A substantial number of studies now concern the evolution of problem-solving abilities and species abilities to be innovative under pressure e.g., (Benson-Amram et al., 2016; Benson-Amram & Holekamp, 2012; Benson-Amram et al., 2013; Borrego & Gaines, 2016; Drea & Carter, 2009; von Bayern et al., 2009; Wat et al., 2020).

Whilst the field of brain evolution is progressing, there is considerable confusion and uncertainty in the current literature, in terms of the specific selective pressures driving the evolution of big brains, and whether species appear to possess domain-general cognitive abilities as suggested by the CBH (Sol, 2009a, 2009b) or whether skillsets are more domain-specific as suggested by the SBH (Dunbar, 1998) or ecological hypotheses (for example (Parker & Gibson, 1977)). The prominent SBH (Dunbar, 1998), whilst once considered the most highly supported theory of brain evolution, has recently come under considerable scrutiny and now the statistical link between brain size and measures of sociality appears uncertain and no longer holds strong after updated phylogenetic statistical analyses e.g., (DeCasien et al., 2017; MacLean et al., 2014; Powell et al., 2017; Swanson et al., 2012). Thus, greater clarity is needed within the field to understand both the drivers and constraints on brain size evolution.

One tool that is imperative to furthering the field of brain evolution is the use of comparative analyses. When used appropriately, comparative analyses allow us to address evolutionary questions which would otherwise be impossible to investigate using alternative methods (Healy & Rowe, 2007). Such comparative methods make it possible to incorporate the influence of phylogeny into analyses and model phenotypic evolution in ways which uncover patterns which may have remained hidden without such methods (Miller et al., 2019). Thus, by drawing on more recently published datasets, applying more robust statistical analyses, and including multiple variables to address several hypotheses simultaneously (Dechmann & Safi, 2009; Dunbar & Shultz, 2007b; Swanson et al., 2012), greater clarity can be achieved regarding the proposed correlates of brain size. Primates have been the focus of many brain size evolution studies (e.g., (DeCasien & Higham, 2019; Isler & van Schaik, 2012)), most likely due to the availability of primate data, as well as interest surrounding human evolution. Similarly, carnivorans are becoming more prevalent in studies (e.g., (Heldstab & Isler, 2019; Sakai et al., 2016)) since they vary greatly in brain and body sizes, whilst occupying differing social and physical environments. Therefore, drawing greater clarity within these two groups may move the field forward.

Another way to clarify some of the uncertainty within the field is to address any shortfalls of already proposed hypotheses. One major grey area of the SBH is highlighted by the presence of taxa who possess large brains, but are not considered social, whose mere presence suggest factors other than sociality are influencing brain size (Holekamp, 2007; Swanson et al., 2012; van Schaik et al., 2012). Bears are one striking example of this, as they have unusually large relative brain sizes, even when compared to their close relatives, despite living minimally social lives (Gittleman, 1999). Thus, by investigating the presence of big brains and the proposed subsequent cognitive abilities in solitary species, greater clarity can be gained on how encephalisation leads to superior cognitive abilities and more understanding can be achieved in terms of the variables influencing cognitive performance. For example, motivational differences were found to better explain cognitive performance (at the behavioural level), rather than complex cognitive processes (van Horik & Madden, 2016). In addition, play behaviour was found to influence bear cub survival (Fagen & Fagen, 2004, 2009), with this highly investigatory nature of young bears (see (Bacon, 1980)), perhaps suggesting age may impact cognitive ability in bears.

1.2. Aims and objectives

Aim 1: What are the selection pressures influencing the evolution of big brains in primates and carnivores?

Objectives:

- Gather data on whole and regional brain volumes for primate and carnivore species, as well as data related to social, ecological and life-history variables,
- Create different models using the collected data, with each model using whole or regional brain volume as the dependent variable,
- Use statistical analyses to uncover the potential correlates with brain size.

Aim 2: Do European brown bears possess problem-solving abilities? Do European brown bears possess object-manipulation abilities? Which variables predict success in cognitive trials?

Objectives:

- Test both problem-solving and object-manipulation abilities of captive European brown bears (N = 17),
- Extract data on performance measures from video recordings of trials,
- Use statistical analyses to determine which variable e.g., age or motivation, if any, predicts cognitive performance.

1.3. Overview of thesis

This thesis is organised into 10 chapters. Chapter 1 outlines the background to the research and briefly states the research aims. A literature review relevant to Aim 1 is presented in chapter 2, after which chapter 3 describes the research methodology used. Results are summarised in chapter 4 and discussed and concluded upon in chapter 5. Chapter 6 presents a literature review relevant to Aim 2, with the corresponding research methodology mentioned in chapter 7. Results of the study are displayed in chapter 8, which are examined and summarised in chapter 9. Lastly, chapter 10 provides a synthesis of the overall conclusions of the research.

‘Why big brains? A comparison of models for both primate and carnivore brain size evolution’

2. ‘Why big brains?’ Literature review

Brain size varies considerably amongst mammals. This is principally thought to be the result of variation in body size, and only secondarily accounted for by variation in encephalisation (Jerison, 1973). Consequently, body size is considered perhaps the most important statistical predictor of brain size, due to the common allometric scaling principle; however, substantial variation still remains after accounting for the influence of body size (Isler et al., 2008; Jerison, 1973). Substantial variation is seen amongst primates, for example, where brain size varies almost a thousand-fold across the order (Barton, 2012), with mouse lemurs having an endocranial volume of 1.63 mL (Isler et al., 2008), whereas humans average 1478 mL (Robson & Wood, 2008). Thus, primates are often considered the best example of brain size variation, as brain expansion began early in primate evolution, and increases have occurred in all major clades (Montgomery et al., 2010). The adaptive value of such variation has come under scrutiny over the past few decades and yet despite considerable research effort, much uncertainty remains regarding the selection pressures responsible.

2.1. The “social brain” hypothesis (SBH)

Perhaps one of, if not, *the* most widely known and commonly accepted hypothesis is the SBH, which implicates sociality as the major driving force behind the evolution of big brains. First suggested by Chance and Mead (1953), (later Jolly (1966), Humphrey (1976), Brothers (1990b), Barton and Dunbar (1997), Whiten & Byrne (1988) and Moll & Tomasello (2007)), the SBH highlighted the importance of one’s ability to track, maintain and repair social relationships, in groups of increasing size and suggested this domain-specific ability spurred increased neocortex size (Dunbar, 1998). This theory became influential in the field of cognitive evolution and the value placed on social interactions in socially complex species.

The SBH received substantial empirical support, especially from tests using primate data, showing neocortex relative to brain size to correlate with many social proxies, such as social group size (Dunbar, 1992), tactical deception (Byrne & Corp, 2004), grooming clique size (Kudo & Dunbar, 2001), male mating strategies (Pawlowski et al., 1998), innovation rate (Reader & Laland, 2002) and number of females within the group (Lindenfors, 2005). Work conducted on spotted hyaenas (*Crocuta crocuta*), whose social complexity shows parallels with that of cercopithecine primates (Drea & Frank, 2003; Holekamp, 2007), most notably the presence of complex societies and certain life-history traits (Holekamp et al., 2015), also supported the SBH. In fact, data from Hyaenidae are consistent with the proposition that social complexity has driven the expansion of the frontal cortex (Sakai et al., 2011). More general support for the hypothesis comes from data related to mammals (Shultz & Dunbar, 2010a), other carnivores (Dunbar & Bever, 1998; Pérez-Barbería et al., 2007; Shultz & Dunbar, 2007), ungulates (Perez-Barberia & Gordon, 2005; Pérez-Barbería et al., 2007; Shultz & Dunbar, 2006), birds (Beauchamp & Fernández-Juricic, 2004; Dunbar & Shultz, 2017; Emery et al., 2007; Scheiber et al., 2008; Shultz & Dunbar, 2010b; West, 2014) and some fish species (Bshary, 2011; Gonzalez-Voyer et al., 2009; Triki et al., 2019). Mammalian orders have become the focus of much of this research, as sociality and relative brain size were found to be closely correlated over evolutionary time in these orders (Dunbar & Shultz, 2007a; Pérez-Barbería et al., 2007).

The focal point of much of the early research was social group size, based on the simple principle that as group size increases the demand on information-processing should also increase (Dunbar, 1992, 1998). Yet, whilst the relationship between group size and neocortex ratio appears robust for primates (Dunbar & Shultz, 2007a; Sandel et al., 2016), the use of this proxy is often considered crude, weak, and not always relevant; group size holding little significance in certain species (Byrne & Bates, 2007). In addition, intraspecific variation in group size is thought to influence support for the SBH since overlooking within-species variation can lead to spurious results and biases in comparative analyses (Sandel et al., 2016). Instead, the focus shifted to the consequences of varying levels of relationship complexity (Bergman & Beehner, 2015) and toward investigating the influence of pair-bondedness (Dunbar, 2009; MacLean et al., 2009; Schillaci, 2006, 2008). This developed from the findings that primates appear to have extended the bonds usually reserved for monogamous pairings to include other members of their social group (Dunbar & Shultz, 2007a; Shultz & Dunbar, 2007). Primate societies are characterised by these bonded social relationships, leading to multi-level social systems (Chapais, 2014; Dunbar, 2012; Grueter et al., 2012), which, ultimately, puts greater emphasis on the *value* of relationships since relationship quality appears to connote complexity (Bergman & Beehner, 2015; Silk, 2012). For example, much emphasis has been placed on the influence of cooperative breeding (Burkart et al., 2009; Burkart & van Schaik, 2010, 2016).

Despite its wide acceptance, there are grey areas that do not fit the SBH, such as non-social large-brained taxa, suggesting factors other than sociality are influencing brain size (Holekamp, 2007; Swanson et al., 2012; van Schaik et al., 2012). Bears are one striking example of this. They have unusually large relative brain sizes, even when compared to their closest relatives, despite living minimally social lives (Gittleman, 1999). Thus, if sociality is to be accepted as the main causal agent for increased brain size in mammals, sociality should be wide-spread across bears and musteloids, which show similar increases to Canidae (Finarelli & Flynn, 2009). This raises questions as to what selective pressures beyond sociality play a role in driving increases in brain size and influence subsequent cognitive abilities (Waroff et al., 2017). Furthermore, this raises questions regarding the comparability of social behaviours, whether sociality uniformly impacts brain evolution across disparate groups and how this complicates comparative studies of the SBH.

Moreover, recent research has revealed further limitations to the SBH, failing to find a link between brain size and sociality e.g., (Beauchamp & Fernández-Juricic, 2004; De Meester et al., 2019; DeCasien et al., 2017; Fedorova et al., 2017; Kverková et al., 2018; Lihoreau et al., 2012; MacLean et al., 2014; Powell et al., 2017; Swanson et al., 2012; van Schaik et al., 2016). Cooperative breeding, a breeding system thought to impose a cognitive challenge, is found to be not related to increased encephalisation in cichlid fishes (Reddon et al., 2016). Additionally, predation is thought to cause spurious correlations between sociality and brain size (van der Bijl & Kolm, 2016). Concerns have also been raised regarding the quality of data used in analyses of the SBH; for example, Smith and Jungers (1997) found problems with the primate body mass data used commonly in comparative analyses, whilst Sandel et al. (2016) highlighted how uncertainties in group size data may influence statistical inferences. Powell et al. (2017) suggested error variances in behavioural predictors likely substantially influences results of regression analyses and thus, make much of the current research unreliable. Moreover, Acedo-Carmona & Gomila (2016) argue the SBH no longer remains ‘robustly established’; for example, ‘Dunbar’s number’ no longer holds reliable after more robust statistical analyses are applied (Lindenfors et al., 2021), with the choice of variables used in statistical models essentially influencing the results produced and conclusions drawn (Wartel et al., 2019). Thus, many still scrutinise the role sociality has in brain evolution and, the evidence to support an increase in brain size for the *isolated* ability of managing social relationships remains weak (Charvet & Finlay, 2012).

2.2. Ecological hypotheses

Early ecological hypotheses, investigating the role of ecology in encephalisation, developed from work comparing the diets of howler and spider monkeys, leading to the proposal that large brains are the evolutionary product of the extensive spatiotemporal requirements faced by frugivorous species (Milton, 1981). Reinforced by findings showing diurnal frugivorous species have brain increases primarily found in the visual system, nocturnal frugivores instead show increases in the olfactory structure, indicating that the brain has directly responded to the demands of foraging (Barton et al., 1995). Substantial neurocircuitry is required to memorise and integrate information related to the location in space and time of patchy and ephemeral food sources such as fruit (Barton, 2000). Developing from this early work, further research has emerged that is particularly interested in foraging (Barton et al., 1995; Hutcheon et al., 2002; Mace et al., 1981; Milton, 1981; Parker & Gibson, 1977; Winkler et al., 2004) and features of the diet (DeCasien et al., 2017; Ratcliffe, 2009; Swanson et al., 2012; van Woerden et al., 2010; Walker et al., 2006), including the complex spatiotemporal distribution of foods (Barton, 2000; Bernard & Nurton, 1993; Clutton-Brock & Harvey, 1980; Harvey et al., 1980; Heldstab et al., 2016), home range size (Clutton-Brock & Harvey, 1980; Milton & May, 1976; Parker, 2015; Powell et al., 2017), use of extractive foraging techniques (Gibson, 1986; Heldstab et al., 2016; Parker & Gibson, 1977; Plante et al., 2014; Reader et al., 2011) and responses in a fluctuating environment (Sol et al., 2005).

Extractive foraging techniques became of particular interest, following the work of Gibson (1986), Parker and Gibson (1977) and Wynn (1988), who highlighted the importance of object-manipulation abilities. This lead to the proposal of the "technical intelligence" hypothesis (Byrne, 1997), one of the first ecological hypotheses for large brains. This was initially suggested in an effort to explain the grade-shift in intelligence present between monkeys and apes, specifically in terms of technical and mechanical pressures. More broadly, this refers to how increased brain size allows individuals to use innovation to modify their technical skills (Navarrete et al., 2016). In fact, such extractive foraging was found to be central to primate cognition and brain evolution (Reader et al., 2011). The evolution of such technical intelligence and 'smart' foraging techniques are thought to counteract the energetic, physiological and time budget demands of producing big brains (Dunbar & Shultz, 2017).

Until recently, there were few studies investigating the relationship between ecology and brain size evolution. Dunbar (1998) found a lack of support for any of his ecological proxies when he first suggested the SBH, consequently the importance of ecological factors became largely discredited. This caused much focus to shift to the influence of social measures on brain size, and many researchers concluded that primate intelligence arose as social rather than ecological adaptations (Parker, 2015). However, recent research has once again accentuated the importance of ecological variation (Rosati, 2017) and significant ecological associations are found across multiple datasets (Powell et al., 2017). Diet, specifically frugivory, better explains brain size than multiple measures of sociality (DeCasien et al., 2017). Thus, there is now comparative data reinforcing the suggestion that diet better predicts brain size in both primates and carnivores (DeCasien et al., 2017; Holekamp & Benson-Amram, 2017; Powell et al., 2017). This more recent work reconfirms the patterns already highlighted by the likes of Parker & Gibson (1977), Milton & May (1976) and Clutton-Brock & Harvey (1980).

Where sociality once held precedence in the variables suggested to explain brain evolution, ecology is again suggested to be one of the main drivers (Heldstab & Isler, 2019), with diet quality predicting relative neocortex size “at least as well as, if not better than, social complexity” (DeCasien & Higham, 2019, p. 1489). Indeed, ecological factors appear to exert greatest influence on brain size, especially in mammalian lineages. Behavioural flexibility involving skills to exploit food resources, including spatial memory, decision-making, extractive foraging and inhibitory control (Rosati, 2017) and the potential to find and exploit varied and novel resources (Wright et al., 2010) suggests a clear selective advantage.

2.3. Life-history influence

Brain size and life-history variables appear to have direct evolutionary links, showing signs of correlated evolution (Deaner et al., 2003). This relationship has been explained in terms of both developmental costs, as larger brains take longer to grow, and cognitive benefits, as larger brains enhance survival and increase lifespan (Barton & Capellini, 2011). Evidence is consistent with both explanations, suggesting that brain size is positively associated with longevity (González-Lagos et al., 2010; Minias & Podlaszczuk, 2017; Sol, 2009b), as well as with the length of gestation, lactation and juvenile periods (Isler & Schaik, 2009; Isler & van Schaik, 2009; Jones & MacLarnon, 2004; Weisbecker & Goswami, 2010). Simple models neglecting these factors can risk generating spurious results. The robust correlation of relative brain size has influential consequences, with larger-brained mammals and birds possessing slower life-histories and living longer than smaller-brained species (Powell et al., 2019). Additionally, slower life-histories have been found to accompany increased cortical neurons in warm-blooded species (Herculano-Houzel, 2019). Ultimately, encephalisation is shown to correlate with elongations of most developmental stages and is significantly correlated with an extended reproductive lifespan (Barrickman et al., 2008). Thus, mammals are understood to counterbalance the cost of producing a large brain with a longer reproductive lifespan (González-Lagos et al., 2010). As such, slow life-histories in large-brained species are thought to be a direct consequence of developmental costs (Barton & Capellini, 2011), although this trend possibly does not extend to fish species (see Sowersby et al. (2021)).

In the specific case of primates, there are distinct life-history adaptations present within primate lineages, with potentially important consequences for primate cognition (Leigh, 2004) and considerable variation in life-history traits, including litter size, gestation period and maximum longevity (Harvey & Clutton-Brock, 1985). Variation imposes constraints on developmental processes and is central to understanding the potential adaptive pathways available to a species (Dunbar & Shultz, 2007b). One example of this is how placentals focus on gestation length to counteract the costs of increased brain size, whereas marsupials focus on lactation to do so (Weisbecker & Goswami, 2010). In addition, developmental costs are thought to influence correlations between specific primate brain structures and life-history variables, with the neocortex most strongly correlated with gestation length, and the cerebellum with juvenile period length, suggesting these brain regions exhibit distinct life-history correlations which concur with their unique development trajectories (Powell et al., 2019). Despite the obvious variation between species, results suggest there is a general pattern which remains consistent across vertebrate clades between brain evolution and life-history traits (Yu et al., 2018).

2.4. Whole or relative brain size

A further problem to have dogged comparative analyses of brain evolution is deciding on the correct brain measure. Whilst most studies tend to focus on whole brain size, even this can become an arduous task since there is little clarity in the literature regarding the most appropriate way to account for the influence of body size (Font et al., 2019), making decisions on the correct method of choice challenging. It is well understood that body size explains the majority of variation found in brain size amongst mammals (Changizi, 2009; Jerison, 1973; Jerison, 1985) and brain and body size are tightly coupled allometrically across vertebrates (Shultz & Dunbar, 2010a). Therefore, accounting for this allometric relationship is of great importance, especially in comparative analyses (Pérez-Barbería et al., 2007; Shultz & Dunbar, 2010a).

When it is necessary to calculate relative brain size, there is great uncertainty regarding the most appropriate body size correction factor; there is no single standard approach and opinions about the different methods have changed over time. Relative brain size has previously been estimated either by taking residuals from a regression curve or calculating encephalisation quotients (EQ) (Deaner et al., 2007; Jerison, 1973; van Schaik et al., 2012). In order to calculate residuals, certain studies have regressed brain size on body mass, whereas others have regressed brain size on another brain structure or are taken from ratios (Deaner et al., 2000). These statistically controlled techniques were formerly preferred as absolute brain size was found to be ‘invariably strongly correlated with body size’ in most taxa (Pérez-Barbería et al., 2007). Moreover, relative brain size has been found to be associated with problem-solving abilities in carnivores (Benson-Amram et al., 2016), and guppies (Kotrschal et al., 2013b) as well as occurrences of innovations in birds (Lefebvre et al., 1997) and primates (Reader et al., 2011). Thus, many still consider statistically calculated measures of relative brain size to be a robust proxy of cognition (Burkart et al., 2017; Fristoe et al., 2017; Iwaniuk, 2017; Pollen et al., 2007) as long as the differences between taxa are accounted for, in terms of selection pressures influencing body size and design (Font et al., 2019).

Despite this, the use of relative brain size and EQs are now often criticised (Deaner et al., 2007). Brain size is thought to lag behind rapid evolutionary changes in body size resulting in inaccurate brain calculations from EQs (Barton, 2000). This was proven to be the case in carnivores; Swanson et al. (2012) finding carnivoran brain size to lag behind body size over evolutionary time. However, no evidence for a lag is found for primates (Deaner & Nunn, 1999), suggesting a taxonomic difference for this group. Still, the use of EQs has been discouraged as EQ scores repeatedly fail to accurately predict cognitive ability (van Schaik et al., 2021). Alongside this, the use of relative brain size as a proxy for intelligence may possibly obscure other evolutionary pathways underlying adaptations in body mass (Smaers et al., 2012). For example, Smaers et al. (2021) found the brain-to-body relationship to uncover more than just selection on brain size, suggesting relative brain size measures may not accurately capture brain size variation. Additionally, variables in ecological datasets often covary, producing possibly biased parameter estimates when calculating residuals (Freckleton, 2002, 2009; Garcia-Berthou, 2001).

Thus, absolute brain size measures are now commonly preferred as they have been shown to be the best predictor of primate cognitive abilities over statistically controlled methods i.e., residuals (Deaner et al., 2007). Moreover, absolute brain size has been found to be associated with many proxies, including executive function in dogs (Horschler et al., 2019), sociality in ground squirrels (Matějů et al., 2016), environmental variation in birds (Sayol, Maspons, et al., 2016) and self-control in 36 species (MacLean et al., 2014). When using absolute brain size measures, the method of incorporating body mass as a covariate in statistical models is now commonly preferred and considered the statistically correct approach (see Cowl and Shultz (2017); Fitzpatrick et al. (2012); Heldstab et al. (2018); Powell et al. (2017)). By addressing the problem of inaccurate body correction methods, researchers can produce more reliable and replicable results, thereby strengthening the field of cognitive evolution (Chambers et al., 2021).

2.5. Regional brain components

Brain components are thought to either evolve in a coordinated manner (Finlay & Darlington, 1995) or show ‘divergent evolutionary trajectories’ as suggested by a mosaic pattern of variation (Gómez-Robles et al., 2014). Mosaic evolution suggests that different functional *systems*, connecting different *sub-components*, evolve independently of each other with natural selection acting *independently* of evolutionary change in other systems (Barton, 2001; Montgomery et al., 2016). Understanding this pattern of evolution is important in understanding how mosaic change is linked to brain structure evolution

(Barton & Harvey, 2000). There is support for the role of mosaic evolution (Powell et al., 2019; Smaers & Soligo, 2013; Whiting & Barton, 2003), specifically at the level of functional systems (Montgomery et al., 2016), all of which is highlighted by the fact that different species show wide variability in terms of components volumes, proportional sizes of different subdivisions and neural systems (D'Aniello et al., 2019). This indicates that brain size does not reflect just one neural adaptation but multiple adaptations which differ across taxonomic groups and ecological niches, rather than strict changes in overall brain size (Smaers & Soligo, 2013). This is further discussed by Logan et al. (2018) who highlight how variation in behaviours found to be correlated with whole brain size may in fact emerge from localised changes in brain development that do not affect total size. Moreover, studies that focus on specific brain regions are thought to be advantageous since they are focus on areas of the brain likely to be specifically involved in the production of a particular behaviour (Healy & Rowe, 2007). One such example is research into the hippocampus, which has been found to be important for both spatial and recognition memory (Broadbent et al., 2004).

2.5.1. Neocortex significance

The neocortex attracted research interest as a potential focus of mammalian brain evolution (Barton, 1996) and is a characteristic unique to mammals (Aboitiz et al., 2003). This structure is thought to handle the more demanding cognitive and social skills associated with intelligent and flexible behaviour (Barton & Harvey, 2000; Innocenti & Kaas, 1995; Kaas, 1995) and is considered crucial for complex thought and cognition (Franco & Müller, 2013).

Large-brained mammals possess a disproportionately expanded neocortex when compared to other structures (Finlay & Darlington, 1995) and taxonomic differences often underlie grade-shifts in neocortex size and corresponding cognitive ability; for example, between primates and insectivores and, within primates, between strepsirrhines and haplorrhine sub-orders (Barton & Harvey, 2000). This is illustrated in Fig. 1, taken from Barton and Harvey (2000). A similarly significant grade-shift is proposed to have occurred within mammalian evolution, specifically in terms of cognitive abilities and required neocortex-based processing power (Dunbar & Bever, 1998) and that the large brain seen in primates and most mammals, is primarily the result of neocortical enlargement (Cantania, 2004). Therefore, the neocortex became the structure to focus on, particularly when wanting to investigate the evolution of higher cognitive functions (Lindenfors, 2005).

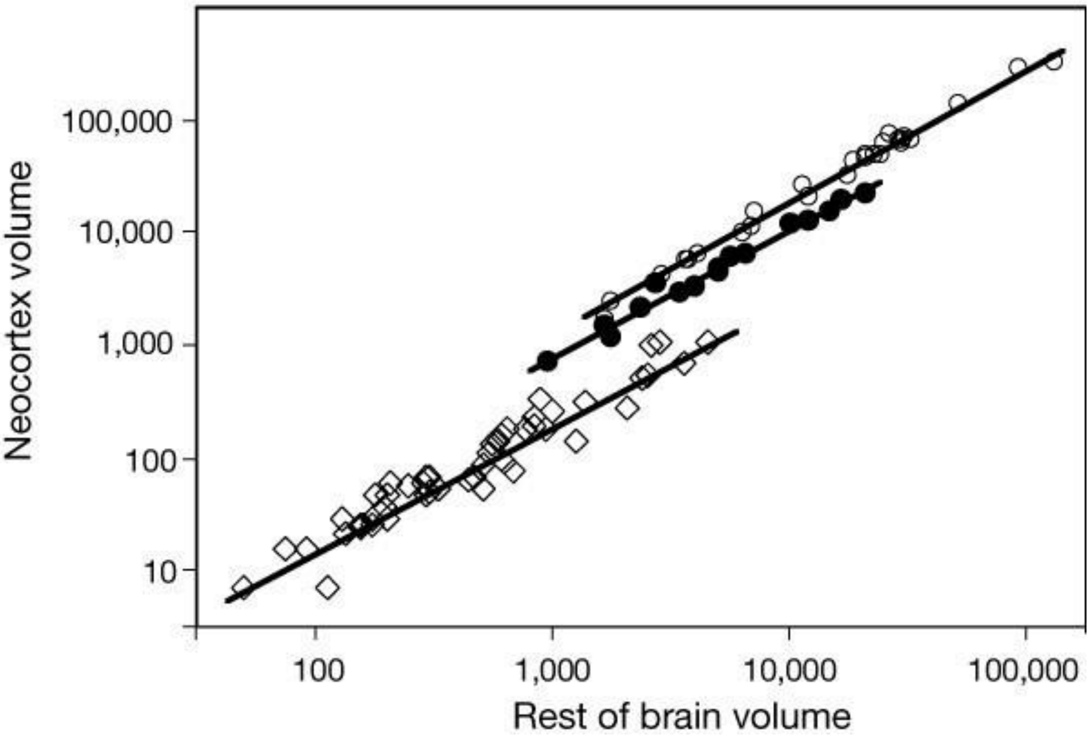

Figure 1. Taxonomic differences in relative neocortex size among primates (strepsirrhines and haplorrhines) and insectivores. Brain part volumes are in cubic millimetres. Open circles, haplorrhine primates; closed circles, strepsirrhine primates; diamonds, insectivores.

Credit. From “Mosaic evolution of brain structure in mammals” by R. A. Barton & P. H. Harvey. 2000. *Nature 405*, p. 1055 (https://doi.org/10.1038/35016580). Copyright 2000 by R. A. Barton & P. H. Harvey.

Neocortical enlargement in primates is thought to be partly due to selection on visual mechanisms (Barton, 1998) which is important for frugivorous species, for example when needing to distinguish between fruits of different colours (Jacobs, 1993; Jacobs, 1994; Jacobs, 1996) or when manipulating small fruit and seeds that require fine motor coordination (Sussman, 1991). Alternatively, these visual mechanisms are thought to be important for processing complex and rapid social interactions, including understanding facial expressions, gaze direction and posture (Brothers, 1990a), suggesting that neocortical modifications associated with complex social life primarily involve areas specialised for visual processing of social information (Barton, 1996). In primates, the neocortex constitutes a substantial portion of the brain (Finlay & Darlington, 1995; Finlay et al., 2001) and a large proportion of the neocortex is comprised of visual information processing areas (Barton, 1998, 2004, 2006), which is thought to explain links found between frugivory and brain size (see DeCasien et al. (2017)) as well as social group size and neocortex volume (see Barton (1998, 2012)).

An area in the brain thought to be equivalent to the neocortex in birds is the associative pallium. This area has been found to be associated with innovation rate in birds, supporting the suggestion that the mammalian neocortex and associative pallium in birds share similar roles (Lefebvre et al., 2004; Timmermans et al., 2000). Additionally, the pallium represents a large proportion of whole brain size and is highly correlated with changes in relative brain size (Sayol, Lefebvre, et al., 2016). This is illustrated in Fig. 2, taken from Sayol, Lefebvre, et al. (2016). When compared, neuronal densities in the avian pallium are found to exceed those in the primate pallium, suggesting that avian brains have higher pallial neuron packing densities (Olkowicz et al., 2016), with more neurons in the pallium suggested to indicate greater cognitive capacity (Němec & Osten, 2020). Therefore, when investigating the neural circuits and cognitive capacity of birds, the associative pallium appears to be of importance.

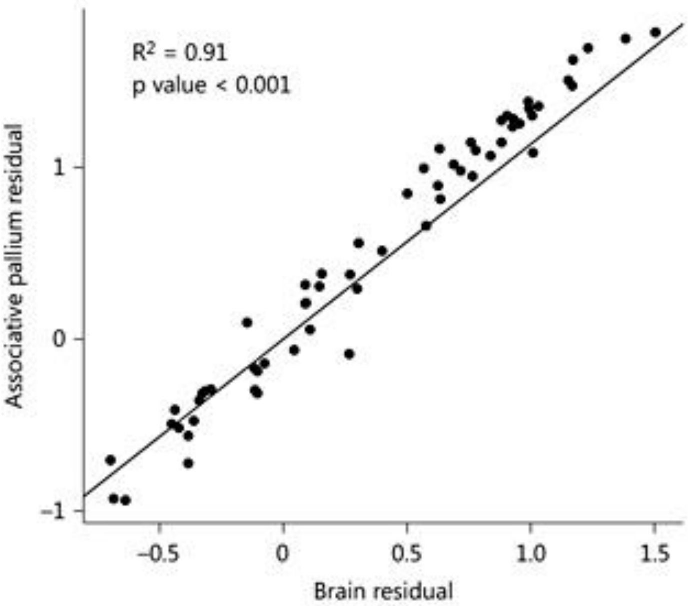

Figure 2. Residual of whole-brain size against body size plotted against residual of associative pallium size against brainstem size. The data points represent actual species, while the line represents the PGLS model. The slightly lower slope of the regression with respect to the cloud of data points is due to the phylogenetic corrections.

Credit. From “Relative brain size and its relation with the associative pallium in birds” By F. Sayol, L. Lefebvre & D. Sol. 2016. *Brain, Behavior and Evolution, 87*(2), p. 74 (https://doi.org/10.1159/000444670). Copyright 2016 by F. Sayol, L. Lefebvre & D. Sol.

2.5.2. Cerebellum significance

More recently, the cerebellum has gained interest as a result of the findings that it tends to evolve together with the neocortex (Barton & Harvey, 2000) and the two brain regions are correlated (Barton, 2002). This is illustrated in Fig. 3, taken from Barton (2012). In fact, natural selection acting on the neural systems which connect the neocortex and the cerebellum has resulted in them exhibiting correlated evolution (Whiting & Barton, 2003). Furthermore, evidence now suggests the human neocortex is not as exceptionally large relative to other brain structures as previously thought. Instead, it appears there was an increase in relative neocortex volume in haplorrhines and an increase in relative cerebellar volume in apes (Barton & Venditti, 2014; Miller et al., 2019). Simply, apes are found to have larger cerebella than monkeys, implying specific selection for an increase in cerebellar volume at one or more points in primate evolution (Rilling & Insel, 1998). In addition, it is thought that commonly used measures such as neocortex ratio, overestimate the significance of the neocortex and underestimate the significance of the cerebellum, which does not correspond with the relative number of neurons, as the cerebellum contains about four times more neurons than the neocortex (Barton, 2012).

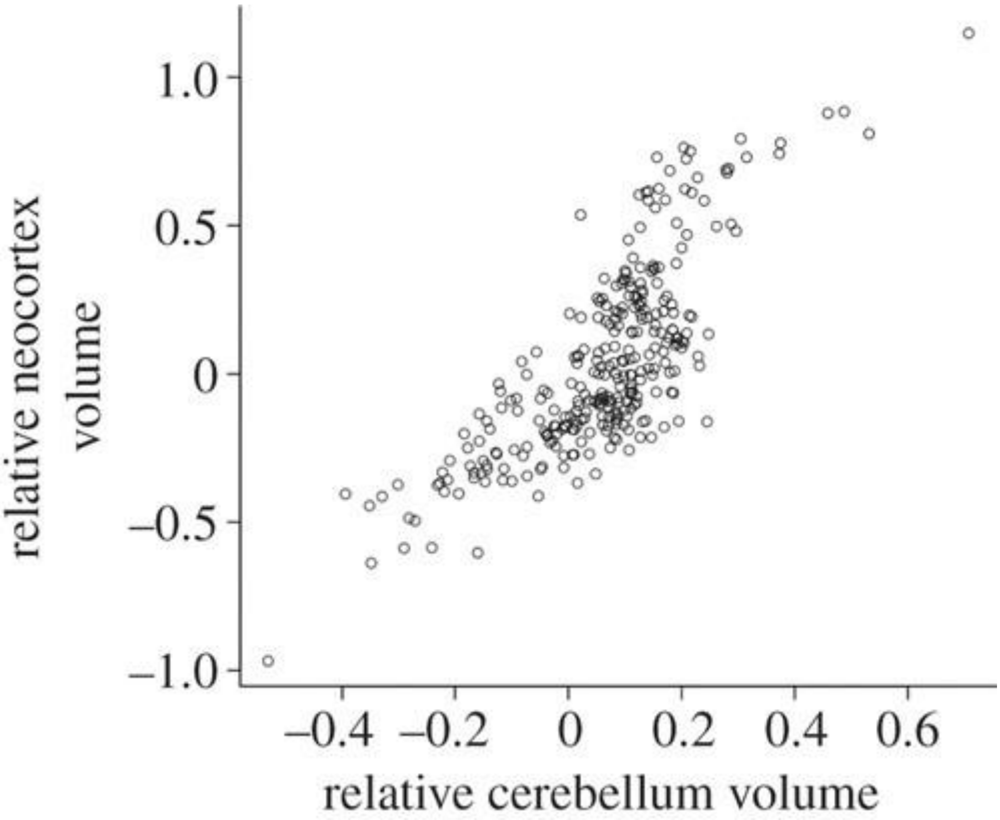

Figure 3. Correlated evolution of neocortex and cerebellum size in mammals. Neocortex size and cerebellum size are positively correlated after controlling for phylogenetic effects and volume of other brain regions.

Credit. From "Embodied cognitive evolution and the cerebellum" by R. A. Barton. 2012. *Philos. Trans. R. Soc. B, 367*(1599), p. 2100 (https://doi.org/10.1098/rstb.2012.0112). Copyright 2012 by R. A. Barton.

The cerebellum is known to be involved in a number of different tasks, including optimising motor movements (Bloedel et al., 1997; Thach, 1998), aiding control of motor-coordination and balance (Houk et al., 1996; Kandel et al., 1995; Smith, 1996), tracking the motor patterns of other individuals and objects (Paulin, 1993), as well as enabling conscious and unconscious action, thus facilitating sequential movement (Cotterill, 2001; Nixon & Passingham, 2001). Hence, increased cerebellar volume is suggested to allow increased processing capacity, in terms of enhanced motor abilities and manipulative abilities (Butler & Hodos, 2005; Iwaniuk et al., 2009). For example, positive correlations are found between cerebellum volume and extractive foraging techniques in primates (Barton, 2012), as well as the presence of neural activation in the cerebellum during tool use in monkeys (Obayashi et al., 2001). This highlights the influential role played by the cerebellum in technical intelligence (Barton & Venditti, 2014). Alongside this, the cerebellum is thought to be important in social intelligence (Barton, 2012), particularly in terms of the links between sensory-motor control and social interactions and understanding (Oztop et al., 2005; Wolpert et al., 2003).

Indeed, it is now thought the expansion of the cortico-cerebellar system is the primary driver of brain expansion in anthropoid primates (Barton, 2012; Smaers & Vanier, 2019; Whiting & Barton, 2003), with the increased behavioural complexity seen in mammals partly explained by selection on the cerebellum (Smaers et al., 2018). So much so, that Fernandes et al. (2020) found residual cerebellar size to be the most appropriate proxy when compared to a measure of general intelligence. While primates have been the main focal group of this research, comparative evidence is now available from cetaceans who have similarly dramatically enlarged cerebellums, indicating a pattern of brain evolution which is convergent with primates, suggesting the trend may be widespread across taxa (Muller & Montgomery, 2019). For example, mormyrid fishes have evolved extremely large relative brain sizes, rivalling even that of humans (Nilsson, 1996), with this encephalisation found to be mainly achieved through enlargement of the cerebellum (Sukhum et al., 2018). Thus, the assumption that the neocortex is the sole “intelligent” part of the brain is too simplistic (Barton, 2012) and studying the cerebellum now appears fundamental to understanding the evolution of complex cognitive functions.

2.6. Where are we now?

Since the initial insights of Chance & Mead (1953), who first hinted at the presence of social intelligence from observations of male baboons, considerable research effort has been invested. The SBH (Dunbar, 1998, 2009) promoted much research activity focused on this domain-specific mechanism (e.g., Dunbar and Shultz (2007a); Kudo and Dunbar (2001)) but more recently studies have failed to find support for the SBH, instead pointing to ecological (DeCasien et al., 2017; MacLean et al., 2014; Powell et al., 2017; Swanson et al., 2012) and life-history influences (Deaner et al., 2003; Powell et al., 2019). The literature now consists of contrasting results (DeCasien et al., 2017; Heldstab et al., 2016; Sakai et al., 2011). For example, in primates both social (e.g., Meguerditchian et al. (2021)) and ecological (e.g., Louail et al. (2019)) skills have been proven to explain brain size, which could indicate that their skills are not limited to just one domain. Perhaps, it suggests increased encephalisation gives rise to brain flexibility, resulting in general intelligence (e.g., Burkart et al. (2017)) as suggested by the CBH (Sol, 2009a, 2009b). Nevertheless, it is increasingly obvious that much clarity is needed regarding the selective pressures responsible for increased brain size in order to move the field forward.

3. 'Why big brains?' Methods

To address the current disparity within the field, data aggregated from the literature is used to assess the relative importance of social, ecological and life-history traits on both overall encephalisation and specific brain regions different models of brain size evolution are tested. Considerable attention has been paid to primate brain evolution (e.g., DeCasien and Higham (2019); DeCasien et al. (2017); Isler and van Schaik (2012); Powell et al. (2017)), which could be the result of anthropocentricism. Consequently, there are substantial data available on this taxonomic group making comparative tests easy to implement. Likewise, carnivorans are also now receiving attention (e.g., Heldstab and Isler (2019); Sakai et al. (2016); Smaers et al. (2018); Swanson et al. (2012)) since variation in their brain and body size, and ranging social and physical environments, makes them excellent models for these tests too. Indeed, most of the literature surrounding brain size hypotheses is based on analyses of these two groups. Therefore, the aim here is to provide greater clarity within these two groups.

Integrating predictors into a framework which allow the assessment of multiple hypotheses simultaneously has become increasingly important for tests of brain evolution (Dunbar & Shultz, 2007b, 2017). Therefore, phylogenetically corrected generalised least squares (PGLS) models were used to account for shared evolutionary history, whilst assessing the potential variables influencing encephalisation. A recently updated phylogenetic tree was used to ensure contemporary phylogenetic relationships. Further, the inclusion of multiple variables allowed the comparison of multiple hypotheses, as well as models of varying complexity. While brain data are available for more taxa than were included in this dataset, some limitations were found on the completeness of the necessary covariate data. Therefore, presented here are the analyses of two orders where complete datasets with all covariates were available for all species, ensuring the most robust model comparisons.

3.1. Data collection

3.1.1. Brain data

Endocranial volume (ECV) (mL) and body mass (g) data for primates (n = 83) and carnivores (n = 85) were compiled from multiple sources (see Chambers et al. (2021) for sources). Volumes were matched for species composition and predictor variables and whilst this resulted in smaller sample sizes when compared to available brain data, in doing so it provided a complete dataset with all covariates available for all species, which better enabled robust analyses. ECV data were preferred over brain mass data since it is thought ECV provides a more reliable estimate of brain size, due to the influence of preservation techniques on brain mass (Isler et al., 2008). The standard technique for estimation of ECV is through filling the cranium with beads (or similar), which is then measured using a graduated cylinder or by weighing the beads and converting the weight to volume (Isler et al., 2008). Neocortex and cerebellum volumes (mm^3) were also collated, where available, for both primates (Neo = 52, Cere = 49) and carnivores (Neo = 44, Cere = 38). These two brain regions were selected for use in the analyses since both have received much attention from researchers in recent years (e.g., Barton (2012); Dunbar (2009)). Regional brain volumes are commonly measured using one of two different techniques: virtual endocasts (e.g., Swanson et al. (2012)) or physical sectioning of the individual brain volumes using paraffin and staining substances (e.g., Stephan et al. (1981)). While on the one hand conducting large-scale comparative studies can enable powerful tests of evolutionary hypotheses, on the other hand a limitation is that data sources used are presumed comparable, when they may not be so. To mitigate against this, when sourcing whole and regional brain volumes these measurement methods were considered to best ensure the data were comparable; for example, all ECV data sources used common measurement techniques (as described above) making the whole brain data comparable across multiple studies.

Further taxonomic groups would have been included in the analyses, such as birds and ungulates, as these groups have received considerable attention in the literature (e.g., Emery et al. (2007); Grisham et al. (2020); Perez-Barberia and Gordon (2005); Sayol, Maspons, et al. (2016); Scheiber et al. (2008); Shultz and Dunbar (2006)). However, substantial gaps were present in available datasets (highlighted by Burger et al. (2019)), particularly in terms of the predictor variables, which resulted in these groups being excluded for further analyses.

3.1.2. Social data

Both social group size and social cohesion data were collected for primates and carnivores. Group size – based on the simple principle that as group size increases the information-processing demands (Dunbar, 1998) and corresponding internal structures (Powell et al., 2012; Sallet et al., 2011) should also increase – became perhaps the most commonly used proxy for social complexity. Despite this, the use of this proxy has been criticised as it is often considered crude, weak and not always relevant (Byrne & Bates, 2007). Greater attention is now paid to differing levels of relationship complexity (Bergman & Beehner, 2015) often indicated through the presence of pair-bonds (Dunbar, 2009; Dunbar & Shultz, 2007a; Shultz & Dunbar, 2007). Therefore, to ensure the influence of sociality was fully captured, alongside group size, a social cohesion proxy was used: a categorisation system ranging from 1) being primarily solitary living aside from breeding seasons, 2) pair-living, 3) fission-fusion societies, to 4) being obligatorily social (e.g., DeCasien and Higham (2019); Stankowich et al. (2014)). This index aims to better encapsulate sociality, rather than relying solely on group size numbers.

3.1.3. Ecological data

Four ecological variables were chosen for analysis: dietary categories, dietary breadth, habitat variability and home range size. Dietary categories were assigned following previous designations in the published literature (see Chambers et al. (2021) for sources) and included six different categories: carnivorous, herbivorous, piscivorous, folivorous, frugivorous and omnivorous. Alongside this traditional classification system, dietary breadth was also used, estimated using the total number of food sources used by a species, with data taken from (Wilman et al., 2014). This included a total of 10 different food types: invertebrates, mammals and birds, reptiles, fish, unknown vertebrates, scavenge, fruit, nectar, seed or other plant material, marked either as absent (0) or present (1). For this dataset, this resulted in a dietary breadth scale of one to six. This proxy was implemented to investigate whether the number of food sources used by a species has implications for brain size. Habitat variability, another ecological measure, was formed using data from the IUCN Red List (2021), based on the total number of habitat-types used by a species, following the same habitat classification system used in the IUCN Red List. This resulted in a habitat variability scale of one to nine. Additionally, home range size (HA) data were collected. By including variables related both to diet and habitat (i.e., imposing both temporal and spatial cognitive demands), it allowed greater incorporation of possible variables within the physical environment affecting brain size. It is important to note, however, such proxies measure ecological variability in the broadest sense, often producing large margins of error. Notwithstanding, these measures are widely used due to data availability and since data consistency across groups can be achieved.

3.1.4. Life-history data

Five life-history variables were chosen for analysis: gestation length (days), maximum longevity (years), fertility (offspring per year), age at first reproduction (years) and weaning age (days). Gestation length was chosen as it has received considerable attention and is thought to be of great importance in bypassing the constraints of precociality on brain development in mammals and facilitating brain growth (Weisbecker & Goswami, 2010). Maximum longevity was included as there is substantial support that encephalisation is correlated with extended longevity (Deaner et al., 2003), especially in primates (DeCasien et al., 2018; Street et al., 2017). The relationship found between brain size and longevity is thought to be driven primarily by maternal investment, with subsequent correlations found between specific brain regions and developmental periods, reflecting this brain size-longevity association (see Barton and Capellini (2011); Powell et al. (2019)). Ultimately encephalisation has been found to correlated with the expansion of most developmental life-history stages, including an extended reproductive lifespan (Barrickman et al., 2008). Therefore, data on age at first reproduction, weaning age and fertility were also included in the dataset (see Chambers et al. (2021) for sources). This allowed the study of both the developmental costs and cognitive benefits explanations proposed to explain the relationship between brain size and life-history variables.

3.2. Statistical analyses

3.2.1. Brain transformations

Whole brain volumes were incorporated in analyses by simple incorporation of log ECV volume with log body mass included as a covariate. This method is often preferred over the use of statistically produced methods as ecological variables often covary, producing possibly biased parameter estimates when calculating residuals (Freckleton, 2002, 2009), and EQs are thought to represent inaccurate brain calculations due to the proposed evolutionary lag between brain size and body size (Barton, 2000). Including body mass as a covariate in the model avoids these problems, controls for its effect on brain volume, as well as potentially controlling for any effects body mass may have on other variables included. Regional brain volumes were incorporated in analyses by simple incorporation of log ROB (rest of brain) volume. To calculate ROB volume for both the neocortex and cerebellum, a calculation was performed: whole brain volume minus the region volume of interest. This method has been previously implemented and proved useful in measuring relative regional brain volume (e.g., DeCasien and Higham (2019)).

3.2.2. PGLS analyses

All statistical analyses were performed using *R* 4.0.1 (R Core Team, 2020), using the 'caper' (Orme et al., 2018), 'ape' (Paradis et al., 2004) and 'geiger'(Pennell et al., 2014) packages. Phylogenetic generalised least-squares (PGLS) regression analysis was used to identify those variables influencing whole and regional brain evolution, whilst avoiding the problem of phylogenetic non-independence. This technique differs from standard generalised least-squares analysis, as it uses knowledge of phylogenetic relationships or relatedness to produce estimates of the expected covariance across species (Garamszegi, 2014; Symonds & Blomberg, 2014). This technique is now commonly preferred; in fact, it is probably the most frequently used phylogenetic comparative method (Wartel et al., 2019). Pagel's λ was estimated by maximum likelihood (see Molina-Venegas and Rodríguez (2017); Pagel (1999)). When Pagel's λ is close to one this is indicative of a Brownian motion model of trait evolution; whereas, when λ equal to zero, this implies the data have no phylogenetic structure (Barton & Venditti, 2014). The tree used for all phylogenetic analyses was that of Upham et al. (2019). All continuous variables, brain volumes and body mass were log transformed prior to analysis to satisfy the assumption of normality. Variance Inflation Factors (VIF) are used to detect for the presence of collinearity or correlations among predictors in regression models (Salmerón et al., 2018). VIFs were checked and almost all scores were found to be <5, and no scores >7. There were no scores of concern, and thus, all socioecological and life-history variables were retained for analyses (see Chambers et al. (2021) for scores).

3.2.3. Model comparisons

A series of PGLS models were implemented which varied in complexity, including 1) social, 2) ecological, 3) social and ecological, 4) life-history and 5) variables of interest. Models included all possible combinations of the selected variables; for example, the social models included i) group size, ii) social cohesion, iii) group size and social cohesion. BIC (Bayesian Information Criterion) values of each model were then compared (Schwarz, 1978). BIC values were preferred over Akaike Information Criterion (AIC) values because BIC resolves the problem of overfitting, by using a more conservative penalty for additional variables (Jones, 2011). Model number five was constructed using all variables previously highlighted of interest within the social, ecological, and life-history models. As well as separating out proximate and ultimate causes of brain size evolution, this allowed the comparison of social versus ecological models, constructing models that included those variables best explaining the data. Once computed, model five was compared alongside the previous models, and those found to have the lowest BIC value were then considered the '*best fit*' models, which in some cases represents a subset of models (simply, any model within dBIC<2 of the lowest model). This is because BIC values with a difference between 2 and 6 indicate moderate evidence that the model with the lower BIC provides a relatively better model fit, whilst greater than 6 indicates strong evidence for improved fit.

Concerns have been raised regarding the influence of variable inclusion on results produced in brain size analyses (see Hooper et al. (2021); Wartel et al. (2019)), therefore this model comparison system was used to ensure the results produced best represent the data present and thus, any conclusions drawn are of greater reliability.

4. ‘Why big brains?’ Results

4.1. Summary of results

The results from PGLS analyses on the primate and carnivore data are summarized below (Table 1).

Table 1. Summary of results from PGLS analyses on primate and carnivore data.

Primate Results	Significant Associations	Carnivores Results	Significant Associations
ECV	GS, SC, DB, GL, ML, WA	**ECV**	F
ROBN	D, HR, ML, WA	**ROBN**	FR
ROBC	D, HR, ML, WA,	**ROBC**	HR, GL, ML, FR

Note. *GS = Group size, SC = Social cohesion, D = Diet, DB = Dietary breadth, HV = Habitat variability, HR = Home range, GL = Gestation length, ML = Maximum longevity, F = Fertility, FR = Age at first reproduction, WA = Weaning age.

4.2. Primates

The results from PGLS analysis on the primate data show that almost all models were highly significant (Table 2). For most models, Pagel’s lambda λ was close to one, however, certain neocortex models stand in contrast to this, with λ equal to zero. The overall model section represents the different categories of PGLS models i.e., social, ecological. The preferred model section presents the model with the lowest BIC score within that respective category. For example, when investigating endocranial volume (with body mass), in the social category, the model with social cohesion produced the lowest score, whereas in the ecological category, the model with dietary breadth produced the lowest score. When comparing BIC scores across all the models, combined models were preferred when investigating both whole and regional brain volumes (highlighted in bold), with significantly improved (equal or greater than two BIC units lower than another) BIC scores when combining variables indicated to be of importance in previous model iterations. When comparing the influence of ecology versus sociality, ecological models were found to be preferable to social models, evidenced by the presence of significantly improved BIC scores.

Table 2. Phylogenetic generalised least-squares (PGLS) regression analyses examining the effects of social, ecological and life-history variables* on primate whole and regional brain volumes. Preferred models represent the '*best fit*' model (with the lowest BIC score) of the overall model category (i.e., social or ecological). The combined models represent the '*best fit*' model after running all combinations of the previous '*best fit*' models (models one to four). Boldness indicates the model(s) with the lowest BIC score across all models (dBIC<2).

Brain input	Overall model	Preferred model	BIC score	*P*-value	λ	Adj. r^2	Sample size (n)
Endocranial volume (ECV)	Social	ECV ~ Mass + SC	-184.199	<0.001	1	0.8774	83
	Ecological	ECV ~ Mass + DB	-190.8458	<0.001	1	0.8868	83
	Social & Ecological	ECV ~ Mass + SC + DB	-192.0528	<0.001	1	0.8929	83
	Life History	ECV ~ Mass + GL + ML + WA	-201.2257	<0.001	1	0.9079	83
	Combined	**ECV ~ Mass + GS + DB + GL + ML + WA**	**-208.5244**	**<0.001**	**1**	**0.9222**	**83**
	All	ECV ~ Mass + GS + SC + D + DB + HV + HR + GL + ML + F + FR + WA	-183.9911	<0.001	1	0.9207	83
Rest of brain neocortex volume (ROBN)	Social	Neo ~ SC	36.43372	<0.05	0.991	0.08278	52
	Ecological	Neo ~ D + HR	20.04	<0.001	0.843	0.481	52
	Social & Ecological	Neo ~ SC + D + HR	23.04369	<0.001	0.866	0.4672	52
	Life History	Neo ~ ML + WA	-9.507772	<0.001	0	0.8602	52
	Combined	**Neo ~ D + HR + ML + WA**	**-17.54041**	**<0.001**	**0**	**0.8984**	**52**
	All	Neo ~ GS + SC + D + DB + HV + HR + GL + ML + F + FR + WA	9.397628	<0.001	0	0.8818	52
Rest of brain cerebellum	Social	Cere ~ SC	26.55957	<0.05	1	0.08632	49
	Ecological	Cere ~ D + HR	0.2775847	<0.001	1	0.5238	49
	Social & Ecological	Cere ~ SC + D + HR	3.144599	<0.001	1	0.5231	49

volume (ROBC)	Life History	Cere ~ ML + WA	-17.40863	<0.001	1	0.6485	49
	Combined	**Cere ~ D + HR + ML + WA**	**-25.9437**	**<0.001**	**0.986**	**0.7631**	**49**
	All	Cere ~ GS + SC + D + DB + HV + HR + GL + ML + F + FR + WA	-10.45452	<0.001	0.996	0.7699	49

Note. *GS = Group size, SC = Social cohesion, D = Diet, DB = Dietary breadth, HV = Habitat variability, HR = Home range, GL = Gestation length, ML = Maximum longevity, F = Fertility, FR = Age at first reproduction, WA = Weaning age.

4.2.1. Overall encephalisation

The results of PGLS analysis on endocranial volume data are presented in Table 2, with the ‘*best fit*’ models presented in Table 3. The variables which were indicated to be of importance and included in the ‘*best fit*’ endocranial volume models were: group size, dietary breadth, gestation length, maximum longevity and weaning age. Also present in the subset of ‘best fit’ models were: social cohesion and home range. After accounting for phylogeny, both group size and social cohesion were found to be positively associated with ECV ($\lambda = 1$, $r^2 = 0.9222$, $P < 0.05$) ($\lambda = 1$, $r^2 = 0.922$, $P < 0.05$). Although, social cohesion failed to reach significance in certain model iterations ($\lambda = 1$, $r^2 = 0.9236$, $P = 0.06$). In terms of the ecological variables, dietary breadth was consistently associated with ECV ($\lambda = 1$, $r^2 = 0.922$, $P < 0.001$); however, home range size failed to reach significance ($\lambda = 1$, $r^2 = 0.9209$, $P = 0.08$). Three of the life-history variables were significantly associated with ECV: gestation length, maximum longevity and weaning age ($\lambda = 1$, $r^2 = 0.9222$, $P < 0.01$).

Table 3. Phylogenetic generalised least-squares (PGLS) regression analyses examining the effects of social, ecological and life-history variables* on primate whole and regional brain volumes. Preferred models represent all the ‘*best fit*’ models for each brain input, which in most cases represents a subset of models (any model within dBIC<2 of the lowest model). This can include any category of model (i.e., social or combined), and is dependent on the BIC score produced. Boldness indicates <0.05.

Brain input	**Preferred models**	**BIC score**	**Predictor**	**Estimate**	***t*-value**	***P*-value**
Endocranial volume (ECV)	ECV ~ Mass + GS + DB + GL + ML + WA	-208.5244	Intercept	-1.8599	-6.6214	**<0.001**
			LogMass	0.5479	18.9909	**<0.001**
			LogGS	0.0432	2.1248	**<0.05**
			DB	0.0213	3.2392	**<0.01**
			LogGL	0.4021	2.8949	**<0.01**
			LogML	0.1488	3.0356	**<0.01**
			LogWA	0.1294	3.3570	**<0.01**
	ECV ~ Mass + SC + DB + GL + ML + WA	<2	Intercept	-1.8367	-6.5280	**<0.001**
			LogMass	0.5463	18.8287	**<0.001**
			SC	0.0212	2.0765	**<0.05**
			DB	0.0233	3.5498	**<0.001**
			LogGL	0.3950	2.8406	**<0.01**
			LogML	0.1374	2.7985	**<0.01**
			LogWA	0.1257	3.2441	**<0.01**
	ECV ~ Mass + DB + GL + ML + WA	<2	Intercept	0.2872	-6.4578	**<0.001**
			LogMass	0.0293	18.9869	**<0.001**
			DB	0.0067	3.3586	**<0.01**
			LogGL	0.1420	2.7831	**<0.01**
			LogML	0.0501	2.8653	**<0.01**
			LogWA	0.0393	3.4476	**<0.001**
	ECV ~ Mass + DB + HR + GL + ML + WA	<2	Intercept	-1.8559	-6.5533	**<0.001**
			LogMass	0.5387	17.7337	**<0.001**
			DB	0.0230	3.4826	**<0.001**
			LogHR	0.0178	1.7881	0.08
			LogGL	0.4195	2.9817	**<0.01**
			LogML	0.1383	2.7961	**<0.01**
			LogWA	0.1271	3.2575	**<0.01**
	Mass + SC + DB +	<2	Intercept	-1.8391	-6.6062	**<0.001**
			LogMass	0.5318	17.6895	**<0.001**
			SC	0.0196	1.9298	0.06

	HR + GL + ML + WA		DB	0.0237	3.6480	**<0.001**
			LogHR	0.0159	1.6222	0.11
			LogGL	0.4167	3.0146	**<0.01**
			LogML	0.1333	2.7384	**<0.01**
			LogWA	0.1190	3.0851	**<0.01**
Rest of brain neocortex volume (ROBN)	Neo ~ D + HR + ML + WA	-17.54041	Intercept	1.5482	6.0124	**<0.001**
			DFrug	-0.1570	-2.1200	**<0.05**
			DOmni	-0.3093	-3.9187	**<0.001**
			LogHR	0.1139	3.2303	**<0.01**
			LogML	0.6851	4.4548	**<0.001**
			LogWA	0.6482	6.4547	**<0.001**
Rest of brain cerebellum volume (ROBC)	Cere ~ D + HR + ML + WA	-25.9437	Intercept	2.3101	7.4158	**<0.001**
			DFrug	-0.1131	-1.5536	0.13
			DOmni	-0.2645	-3.0869	**<0.01**
			LogHR	0.1480	4.2338	**<0.001**
			LogML	0.4402	3.0810	**<0.01**
			LogWA	0.5789	5.8047	**<0.001**
	Cere ~ D + HR + GL + ML + WA	<2	Intercept	0.9767	1.2227	0.23
			DFrug	-0.0762	-1.0319	0.31
			DOmni	-0.2336	-2.7180	**<0.01**
			LogHR	0.1529	4.4768	**<0.001**
			LogGL	0.7857	1.8597	0.07
			LogML	0.3589	2.4562	**<0.05**
			LogWA	0.4390	3.6953	**<0.001**

Note. *GS = Group size, SC = Social cohesion, D = Diet, DB = Dietary breadth, HV = Habitat variability, HR = Home range, GL = Gestation length, ML = Maximum longevity, F = Fertility, FR = Age at first reproduction, WA = Weaning age.

4.2.2. Regional brain volumes

The results of PGLS analysis on the neocortex and cerebellum data are presented in Table 2, with the '*best fit*' models presented in Table 3. The variables which were indicated to be of importance and included within the '*best fit*' 'rest of brain' neocortex volume model were: diet, home range size, maximum longevity and weaning age. After accounting for phylogeny, diet (specifically frugivory and omnivory) was found to be negatively associated with neocortex volume ($\lambda = 0$, $r^2 = 0.8984$, $P < 0.05$, $P < 0.001$). This is the result produced when a folivorous diet is used as the baseline category, therefore the dietary category results produced here only demonstrates differences between these dietary groups (frugivory and omnivory) and folivory. Alongside these associations, home range size was positively correlated with neocortex volume ($\lambda = 0$, $r^2 = 0.8984$, $P < 0.01$). Similar to whole brain models, both maximum longevity and weaning age were significantly associated with neocortex volume ($\lambda = 0$, $r^2 = 0.8984$, $P < 0.001$).

The variables which were indicated to be of importance and included in the '*best fit*' 'rest of brain' cerebellum volume models were: diet, home range size, maximum longevity and weaning age. Also present within the subset of '*best fit*' models was: gestation length. After accounting for phylogeny, diet, specifically omnivory was found to be negatively associated with cerebellum volume ($\lambda = 0.986$, $r^2 = 0.7631$, $P < 0.01$). Frugivory failed to be significant ($\lambda = 0.986$, $r^2 = 0.7631$, $P = 0.13$). As above, this results when folivorous diet is used as the baseline category. Home range size was positively associated with cerebellum volume ($\lambda = 0.986$, $r^2 = 0.7631$, $P < 0.001$). Similar to previous life-history results, maximum longevity and weaning age were significantly associated with cerebellum volume ($\lambda = 0.986$, $r^2 = 0.7631$, $P < 0.01$, $P < 0.001$). Gestation length failed to be significant ($\lambda = 1$, $r^2 = 0.7643$, $P = 0.07$).

4.3. Carnivores

The results of PGLS analysis on the carnivore data are presented in Table 4. Almost all models were highly significant. Lambda was not consistent between the models, ranging from one to zero across the dataset. The overall model section represents the different categories of PGLS models i.e., social, ecological. The preferred models section presents the model with the lowest BIC score within that respective category. In terms of the '*best fit*' models, those producing the lowest BIC score (or any score within dBIC<2 of the lowest model), there was no significant difference between life history and combined models (highlighted in bold) and thus the results of all these models are discussed below. When comparing the influence of ecology versus sociality, ecological models were found to be preferable to social models when investigating regional brain volumes, evidenced by the presence of significantly improved BIC scores. However, this was not the case in whole brain models, where there was no significant difference between the preferred social and ecological models.

Table 4. Phylogenetic generalised least-squares (PGLS) regression analyses examining the effects of social, ecological and life-history variables* on carnivoran whole and regional brain volumes. Preferred models represent the '*best fit*' model (with the lowest BIC score) of the overall model category (i.e., social or ecological). The combined models represent the '*best fit*' model after running all combinations of the previous '*best fit*' models (models one to four). Boldness indicates the model(s) with the lowest BIC score across all models (dBIC<2).

Brain input	**Overall model**	**Preferred model**	**BIC score**	***P*-value**	**λ**	**Adj. r^2**	**Sample size (n)**
Endocranial volume (ECV)	Social	ECV ~ Mass + GS	-137.3671	<0.001	0.784	0.911	85
	Ecological	ECV ~ Mass + HV	-138.8228	<0.001	0.810	0.9102	85
	Social & Ecological	ECV ~ Mass + GS + HV	-135.0748	<0.001	0.814	0.9095	85
	Life History	**ECV ~ Mass + F**	**-140.9778**	**<0.001**	**0.762**	**0.9166**	**85**
	Combined	**ECV ~ Mass + DB + F**	**-140.4778**	**<0.001**	**0.753**	**0.9201**	**85**
	All	ECV ~ Mass + GS + SC + D + DB + HV + HR + GL + ML + F + FR + WA	-106.9128	<0.001	0.724	0.9221	85
Rest of brain neocortex volume (ROBN)	Social	Neo ~ GS	71.58854	0.06425	0.954	0.05726	44
	Ecological	Neo ~ HR	68.10774	<0.01	0.334	0.196	44
	Social & Ecological	Neo ~ GS + HR	70.20444	<0.01	0.400	0.1938	44
	Life History	**Neo ~ FR**	**58.64386**	**<0.001**	**0.097**	**0.414**	**44**
	Combined	**Neo ~ HR + FR**	**59.78632**	**<0.001**	**0**	**0.48**	**44**
	All	Neo ~ GS + SC + D + DB + HV + HR + GL + ML + F + FR + WA	87.42208	<0.001	0	0.4546	44
Rest of brain cerebellum	Social	Cere ~ GS	35.60386	0.07056	1	0.06265	38
	Ecological	Cere ~ HR	20.3267	<0.001	1	0.3729	38
	Social & Ecological	Cere ~ GS + HR	22.22221	<0.001	1	0.3839	38

volume (ROBC)	**Life History**	**Cere ~ GL + ML + FR**	**4.668459**	**<0.001**	**1**	**0.6369**	**38**
	Combined	**Cere ~ HR + GL + ML + FR**	**3.803654**	**<0.001**	**1**	**0.6677**	**38**
	All	Cere ~ GS + SC + D + DB + HV + HR + GL + ML + F + FR + WA	28.10051	<0.001	1	0.6135	38

Note. *GS = Group size, SC = Social cohesion, D = Diet, DB = Dietary breadth, HV = Habitat variability, HR = Home range, GL = Gestation length, ML = Maximum longevity, F = Fertility, FR = Age at first reproduction, WA = Weaning age.

4.3.1. Overall encephalisation

The results of PGLS analysis on endocranial volume data are presented in Table 4, with the '*best fit*' models shown in Table 5. The variables which were indicated to be of importance and included within the '*best fit*' endocranial volume models were: fertility, dietary breadth, maximum longevity and age at first reproduction. After accounting for phylogeny, fertility was found to be negatively associated with ECV ($\lambda = 0.762$, $r^2 = 0.9166$, $P < 0.05$), with this being the only variable significantly associated with endocranial volume. For example, dietary breadth fell short of significance ($\lambda = 0.753$, $r^2 = 0.9201$, $P = 0.05$). In addition, both maximum longevity and age at first reproduction, failed to reach significance ($\lambda = 0.742$, $r^2 = 0.9171$, $P = 0.08$) ($\lambda = 0.785$, $r^2 = 0.9131$, $P = 0.10$).

Table 5. Phylogenetic generalised least-squares (PGLS) regression analyses examining the effects of social, ecological and life-history variables* on carnivoran whole and regional brain volumes. Preferred models represent all the '*best fit*' models for each brain input, which in most cases represents a subset of models (any model within dBIC<2 of the lowest model). This can include any category of model (i.e., social or combined), and is dependent on the BIC score produced. Boldness indicates <0.05.

Brain input	**Preferred models**	**BIC score**	**Predictor**	**Estimate**	***t*-value**	***P*-value**
Endocranial volume (ECV)	ECV ~ Mass + F	-140.9778	Intercept	-0.6057	-5.3678	**<0.001**
			LogMass	0.5870	25.7757	**<0.001**
			LogF	-0.1113	-2.0993	**<0.05**
	ECV ~ Mass + DB + F	<2	Intercept	-0.5245	-4.4263	**<0.001**
			LogMass	0.5810	25.6777	**<0.001**
			DB	-0.0154	-1.9622	0.05
			LogF	-0.1318	-2.4784	**<0.05**
	ECV ~ Mass + ML	<2	Intercept	-0.9083	-7.0336	**<0.001**
			LogMass	0.5867	24.0699	**<0.001**
			LogML	0.1906	1.7925	0.08
	ECV ~ Mass + FR	<2	Intercept	-0.6513	-6.0877	**<0.001**
			LogMass	0.5783	21.5774	**<0.001**
			LogFR	0.1145	1.6682	0.1
Rest of brain neocortex volume (ROBN)	Neo ~ FR	58.64386	Intercept	4.0097	35.4993	**<0.001**
			LogFR	1.4150	5.6022	**<0.001**
	Neo ~ ML + FR	<2	Intercept	2.8747	3.3575	**<0.01**
			LogML	0.9151	1.3334	0.19
			LogFR	1.0190	2.6229	**<0.05**
	Neo ~ HR + FR	<2	Intercept	3.6343	17.222	**<0.01**
			LogHR	0.1437	1.856	0.07
			LogFR	1.0956	3.786	**<0.001**
Rest of brain cerebellum volume (ROBC)	Cere ~ HR + GL + ML + FR	3.803654	Intercept	1.5075	1.8971	0.07
			LogHR	0.0753	2.0374	**<0.05**
			LogGL	0.8236	2.0974	**<0.05**
			LogML	0.9084	2.7665	**<0.01**
			LogFR	0.4524	2.1567	**<0.05**
		<2	Intercept	1.7089	2.0734	**<0.05**

	Cere ~ GL + ML + FR		LogGL	0.7669	1.8730	0.07
			LogML	0.9706	2.8402	**<0.01**
			LogFR	0.6920	3.8113	**<0.001**
	Cere ~ ML + FR	<2	Intercept	2.9664	5.9931	**<0.001**
			LogML	1.0852	3.1178	**<0.01**
			LogFR	0.8402	4.9662	**<0.001**
	Cere ~ HR + ML + FR	<2	Intercept	2.8682	5.9347	**<0.001**
			LogHR	0.0702	1.8137	0.08
			LogML	1.0316	3.0414	**<0.01**
			LogFR	0.6336	3.1242	**<0.01**
	Cere ~ ML + FR + WA	<2	Intercept	2.5812	4.7991	**<0.001**
			LogML	0.9485	2.7130	**<0.05**
			LogFR	0.7819	4.4666	**<0.001**
			LogWA	0.2815	1.6954	0.1

Note. *GS = Group size, SC = Social cohesion, D = Diet, DB = Dietary breadth, HV = Habitat variability, HR = Home range, GL = Gestation length, ML = Maximum longevity, F = Fertility, FR = Age at first reproduction, WA = Weaning age.

4.3.2. Regional brain volumes

The results of PGLS analysis on the neocortex and cerebellum data are presented in Table 4, with the '*best fit*' models shown in Table 5. The variables which were indicated to be of importance and included in the '*best fit*' 'rest of brain' neocortex volume models were: age at first reproduction, maximum longevity and home range size. After accounting for phylogeny, age at first reproduction was found to be positively associated with neocortex ($\lambda = 0.097$, $r^2 = 0.414$, $P < 0.001$), with this being the only variable significantly associated with neocortex volume. For example, home range size fell short of significance ($\lambda = 0$, $r^2 = 0.48$, $P = 0.07$). In addition, maximum longevity failed to reach significance ($\lambda = 0.079$, $r^2 = 0.4315$, $P = 0.19$).

The variables which were indicated to be of importance and included within the '*best fit*' 'rest of brain' cerebellum volume models were: home range size, gestation length, maximum longevity and age at first reproduction. Also present within the subset of '*best fit*' models were: different iterations of the previously mentioned variables and weaning age. After accounting for phylogeny, home range size was found to be significantly associated with cerebellum volume ($\lambda = 1$, $r^2 = 0.6677$, $P < 0.05$). Three of the life-history variables were significantly associated with cerebellum volume: gestation length, maximum longevity and age at first reproduction ($\lambda = 1$, $r^2 = 0.6677$, $P < 0.05$) ($\lambda = 1$, $r^2 = 0.6677$, $P < 0.01$) ($\lambda = 0.990$, $r^2 = 0.6338$, $P < 0.001$). Although, home range size and gestation length failed to reach significance in certain model iterations ($\lambda = 0.997$, $r^2 = 0.6358$, $P = 0.08$) ($\lambda = 1$, $r^2 = 0.6369$, $P = 0.07$). Weaning age also failed to reach significance ($\lambda = 0.990$, $r^2 = 0.6338$, $P = 0.10$).

5. ‘Why big brains?’ Discussion

The aim of the research presented here was to investigate the selective pressures influencing brain size evolution in primates and carnivores, whilst testing the reliability of different body size correction methods. Applying robust statistical analyses, a recently updated phylogenetic tree, a comprehensive dataset and models of varying complexity, the correlates of brain size in primates and carnivores were reconsidered. Consistent associations were found between brain size and ecological variables in primates, thus highlighting the influence of ecology on encephalisation. However, support was also found for the prominent SBH, specifically revealing evidence for a link between whole brain volumes and two measures of sociality. In carnivores, data suggest ecological variables shape brain size, suggesting alternative evolutionary patterns influencing carnivoran encephalisation. In both groups, life-history variables appear crucial in counterbalancing the costs of producing and maintaining increased brain size, through extended developmental periods, reduced fertility and increased maximum lifespan.

It is worth noting, however, the potential sources of instability within the study. Powell et al. (2017) highlight how error variance in predictor datasets has an impact on the results produced during regression analyses, which could be influencing the results found here. This is especially a problem for behavioural measures which are collected during field studies (Powell et al., 2017). In addition, Wartel et al. (2019) emphasise how the choice of variables included within models influences the results found and subsequent conclusions made, with model comparison methods perhaps not resolving the issue of instability of results. These issues undermine confidence in comparative studies of brain size evolution, and more work is needed to ensure robust results can be obtained using various predictor datasets and varying models.

5.1. Primates

Here, consistent with current literature, robust correlations were found between brain size and ecological variables. The most prominent of these were diet-related, with dietary categories or dietary breadth appearing in all '*best fit*' models, for both whole brain and regional brain data. These findings are similar to those of DeCasien et al. (2017) and Powell et al. (2017), who found stronger and more consistent associations with ecological variables than those related to the social environment. Akin to the result of DeCasien et al. (2017), support was found for omnivory, as well as frugivory, as correlates of brain size. However, in contrast to the literature, here the correlations between regional brain volumes and dietary categories, were negatively correlated. This perhaps reflects both the need to sustain the energetic cost of brain tissue (highlighted by Aiello and Wheeler (1995); Fish and Lockwood (2003)), as well as meeting the cognitive foraging challenges imposed by omnivorous and frugivorous diets (Barton, 2000; Milton, 1981; Parker & Gibson, 1977). In addition to the dietary categories, dietary breadth was significantly (positively) correlated with whole brain volumes, further reinforcing the proposition that diet influences brain size, whilst highlighting how useful this proxy can be in understanding how availability and variety of food source can be important in setting the cognitive challenge. For example, MacLean et al. (2014) also suggested dietary breadth to be an important ecological correlate, with greater cognitive flexibility allowing individuals to explore and exploit new food sources, as well as deploy extractive foraging techniques. Evidence for associations between regional brain volumes and home range size were also found, supporting the view of Powell et al. (2017) in that certain dietary categories, such as frugivory, may covary with home range. Similar results were also found by Graber et al. (2017).

In the past, considerable support indicated that sociality was the major driver of encephalisation in primates. However, more recent works contest this long-held viewpoint by failing to find support for a link between brain size and sociality measures (DeCasien et al., 2017; MacLean et al., 2014; Powell et al., 2017; Swanson et al., 2012; van Schaik et al., 2016). This study, however, confirms support for the SBH. Here, the models revealed evidence of a link between brain size and sociality in primates, potentially as a result of the model selection techniques used here which allowed the inclusion of multiple variables and because aspects of the social and ecological hypotheses are likely to covary. This highlights how an ‘embodied’ approach is needed, which accounts for both social and physical forms of sensorimotor coordination, acknowledging the role physical action has in brain evolution (Barrett & Henzi, 2005; Barrett et al., 2007; Barrett et al., 2022). This association was present only in the whole brain ‘*best fit*’ models, with both variables reaching significance, indicating both increasing social group size and varying levels of social cohesion are influencing brain size in primates. Interestingly, the use of the social cohesion proxy was often preferred when comparing models, thereby suggesting the use of this proxy is superior when testing multiple ecological and social variables simultaneously. The inference too is that there may be greater importance in relationship quality, over quantity, as suggested by past research into primate sociality and pair-bonds (Bergman & Beehner, 2015; Dunbar & Shultz, 2017; Layton & O'Hara, 2010; Shultz & Dunbar, 2007; Silk, 2012). It is important to note, however, that whilst there was support for this hypothesis, ecological models were preferrable over social ones and ecological variables appear to be more robust correlates of brain size when compared to measures of sociality (see Graber (2017)). Similarly, Mitchell (2018) found support for a significant association between group size and cognition, and yet, model comparisons found ecological models provided a similar fit to the data as social ones.

Consistent with the literature support was found for correlations between life-history variables and brain size. As suggested within the developmental cost (Barton & Capellini, 2011) and maternal energy hypotheses (Martin, 1996), relationships found possibly reflect the developmental costs associated with growing large brains, which appear to be bypassed through extended developmental periods and increased maternal investment (Heldstab et al., 2019; Isler & van Schaik, 2009). Similarly, Powell et al. (2019) found correlations between neocortex volume and gestation length, as well as cerebellum volume and juvenile period. The associations found here differ in terms of the specific regions involved, with methodological differences likely to underscore those differences in results. Powell et al. (2019) for example, used body mass to control for allometric scaling of regional brain volumes whereas here the rest of brain technique was used, with this method also producing different results when investigating regional brain volumes and the influence of diet (see **5.4**). Thus, the associations found here are representative of the specific regions after controlling for the rest of the brain volume, suggestive that the life-history variables are specifically influencing the brain region of interest, rather than the brain as a whole. Despite these disparities, these results still support the theory as to why relatively large-brained mammals often exhibit slow maturation times and reduced fertility; thus, by increasing developmental periods and maternal investment, primates possess these slow life-histories which ultimately facilitates the production of big brains. This therefore makes the 'extended parenting' association critical to the evolution of cognition (Heldstab et al., 2019; Heldstab et al., 2020; Isler & van Schaik, 2012; Uomini et al., 2020). One thing that remains unclear is the reasoning behind the association found here between brain size and maximum longevity. One proposition is that selection mechanisms work towards counterbalancing the costs of large brains in mammals with a longer reproductive lifespan (González-Lagos et al., 2010) and thus, by extending the reproductive lifespan of a species, it counteracts the time and effort spent producing and maintaining large brains and aims to maximise the time species can spend producing young, which in turn have large brains. Whereas others propose the correlation is indirect and that a longer reproductive lifespan is a by-product of shifting developmental and maturation periods (Powell et al., 2019).

5.2. Carnivores

Akin to the primate results, the results presented for carnivores provides support by identifying a link between regional brain volumes and home range size. This relationship was significant in the cerebellum models, concurring with research suggesting this region is important for spatial memory processing (Barton, 2012; Leggio et al., 2011; Rochefort et al., 2011). Simply, larger home range sizes are thought to require the use of complex information about food location and distribution (Clutton-Brock & Harvey, 1980), which for example in carnivores, may represent the challenges of locating travelling herds of herbivores. Alongside this association, which indicates that spatial demands influence brain size in carnivores, dietary breadth was another ecological variable included in the '*best fit*' endocranial volume models. However, in contrast to the results of MacLean et al. (2014) and Swanson et al. (2012), the relationship between dietary breadth and brain size is negatively directed, suggesting greater dietary breadth is actually associated with smaller brain size in carnivores. This result could perhaps be a consequence of those species who are classified as obligate meat-eaters, whose dietary breath is limited to one or two categories, thereby producing this negative correlation. Despite this, obligate meat-eating carnivores consume the highest caloric diet, which is thought to provide greater energy for producing large brains. This highlights how carnivores cannot simply be compared and likened to other mammalian orders, such as Primates, and suggests different evolutionary mechanisms at work in carnivoran lineages. However, it is important to note that this association was not significant (P = 0.05), suggesting this relationship is not a significantly strong influence on brain size in carnivores.

Whilst previous work has suggested sociality plays a role in the evolution of brain size in carnivoran lineages (Dunbar & Bever, 1998; Holekamp et al., 2015; Pérez-Barbería et al., 2007; Shultz & Dunbar, 2007), here, no support is found for a link between measures of sociality and brain size in carnivores. Similarly, MacLean et al. (2014), Benson-Amram et al. (2016) and Swanson et al. (2012) found no support for the SBH in mammals. The contrasting results present in the literature could be due to the fact that sociality appears to be limited to a select few carnivore taxa, specifically social species from the families Hyaenidae, Procyonidae and Felidae (Sakai & Arsznov, 2020). This is suggested in the findings of Finarelli & Flynn (2009), who identified that support for the SBH in Carnivora was dependent on data from Canidae, without which, no association is found. Thus, whilst sociality evidently plays an important role in primates, leading to complex, multifaceted societies, this is less common in carnivore species, and therefore does not hold the same importance.

Consistent with the previously discussed primate results, associations were found between life-history variables and brain size in carnivores. Age at first reproduction, gestation length and maximum lifespan were all found to positively correlate with regional brain volumes, suggesting both an increase in developmental periods as well as an extension in reproductive lifespans. Additionally, findings are consistent with the expensive brain hypothesis (Isler & van Schaik, 2009), which proposes either an increase in energy turnover or a reduction in energy allocation is needed in order to meet the costs of increased brain size. This is seen here with a negative correlation between fertility and endocranial volume, suggesting a reduction in reproductive output. This, when paired with an increase in maternal investment and developmental periods, as suggested by the aforementioned results, bypasses the developmental constraints of producing a large brain through reduced fertility and slow maturation times.

5.3. Whole versus regional brain volumes

This study highlights the benefit of investigating both whole brain and regional brain volumes. Whole brain volumes are often more readily available for species and thus by choosing to use this brain measure it increases sample sizes and commensurate statistical power. In addition, it has been argued the neocortex comprises a large proportion of whole brain volume, making the two brain volumes closely related (Dunbar & Shultz, 2017; Shultz & Dunbar, 2007). However, it is possible the inclusion of specific brain regions may uncover further associations that were not significant or present before. This was the case here, where for primates, the home range association only became significant in the neocortex and cerebellum models, having not reached significance in endocranial volume models. Additionally, in carnivores, many of the life-history associations, for example age at first reproduction, only reached significance in the regional brain volume models. Therefore, without investigating specific brain regions, the influence of these associations would have been missed. In addition to this, the use of whole brain size does not necessarily allow the study of the ways in which different selective pressures act on different neural systems, as proposed by theories of mosaic evolution (Barton & Harvey, 2000; Barton et al., 1995). This often makes it difficult to relate whole brain size to individual selection pressures (Healy & Rowe, 2007). By investigating specific brain regions, where brain data and the corresponding covariates are available, it allows the further analysis of how multiple functional systems can evolve in a mosaic fashion in response to different selection pressures.

5.4. Conclusion

To conclude, the evidence presented here supports the proposition that ecological variables hold greater influence, when compared to social variables, in determining brain size in primate lineages. However, critical support is also found for the SBH in primates, confirming sociality does hold significance in encephalisation. Ecological variables, most notably home range size, appear to shape carnivoran brain size. However, no support is found there for measures of sociality, indicating that sociality may not hold the same importance within that order. Life-history traits reveal evidence for the transition to slow life histories, which work toward facilitating the production of big brains and bypassing the cost of expensive brain tissue. Future studies should strive to integrate multiple variables, fully encompassing all the potential variables influencing brain size. In addition, where possible, researchers should investigate both whole brain and specific brain regions, as the inclusion of such may reveal further associations, capturing how different brain regions can evolve independently through varying selection pressures. Greater attention needs to be paid to more species, for example, reptiles and amphibians, which are underrepresented and understudied within the brain evolution field, in order to build a better understanding of the evolutionary mechanisms influencing brain size.

6. ‘Why big bear brains?’ Literature review

Many mammalian species have developed large brains through divergent evolutionary pathways (Smaers et al., 2021). This is despite the fact that large brains have substantial developmental and energetic costs resulting in brains being expensive organs to grow and maintain (Aiello & Wheeler, 1995; Barton & Capellini, 2011; Isler & van Schaik, 2009; Niven & Laughlin, 2008; Weisbecker & Goswami, 2010). In fact, there are thought to be at least 30 significantly distinct allometric grade shifts between mammals (Smaers et al., 2021). Maintaining expensive neural tissue is believed to be worth the biological cost (Aiello, 1997; Kotrschal et al., 2013a; Laughlin et al., 1998), since an encephalised brain is thought to afford cognitive advantages (Boddy et al., 2012; Weisbecker et al., 2015), such as allowing behavioural flexibility (Sol, 2009a). However, the proposed relationship between brain size and cognitive ability remains controversial, with the advantages of increased brain size remaining ambiguous (Deaner et al., 2007; Deaner et al., 2000; Smaers et al., 2012; van Valen, 1974; Willerman et al., 1991). Work is still required in order to substantiate assumptions concerning the relationship between encephalisation and superior cognitive performance.

6.1. Superior abilities

As selection only favours changes that still reap benefits after costs, the mere presence of encephalisation raises many questions regarding what benefits are provided with increased brain size. One long-held assumption of the field is that the production of large brains promotes the production of superior cognitive abilities (Boddy et al., 2012;

Weisbecker et al., 2015). Thus, the presence of encephalisation or deviations from expected brain sizes, are thought to be determining factors in enhanced cognitive abilities (Boddy et al., 2012). Comparative studies lending credence to the assumption have started to arise, using indicators of superior abilities such as behavioural flexibility (Amici et al., 2018; Benson-Amram et al., 2016), invasion success (Amiel et al., 2011; Sol et al., 2005) and self-control (MacLean et al., 2014). These studies demonstrate how increased brain size can afford cognitive advantages through superior cognitive abilities. For example, MacLean et al. (2014) found increases in brain size provided the foundation for increases in self-control, whilst Amiel et al. (2011) found correlations between brain size and successful invasions, all of which points to the assertion that big brains provide a selective advantage across multiple domains. However, this theory is still controversial and much work is required in order to confirm that increased brain size equates to superior abilities.

6.2. Problem-solving abilities

One way to test for the presence of superior abilities is to study one's ability to innovate and solve unique socioecological problems, which has recently come to the fore in the field of animal cognition (Bandini & Harrison, 2020). Innovation is broadly defined as an animal's ability to utilise previous knowledge to solve a new problem or apply new techniques to solve an existing problem (Kummer et al., 1985; Reader & Laland, 2003). Innovative behaviours have become of specific interest to behavioural researchers (Arbilly & Laland, 2017), with innovation rate now commonly deployed as a tool to quantify differences in cognitive ability and thus test brain evolution hypotheses (Lefebvre et al., 2004). Whilst innovation is thought to be a direct product of cognition and directly selected for, innovativeness is best thought of as just one component of a larger array of traits, evolved to cope with the complexities of environmental variation (Griffin, 2016). Studies are now being developed to test problem-solving abilities and whether species can be innovative during socioecological challenges (Benson-Amram et al., 2016; Benson-Amram et al., 2013; Borrego & Gaines, 2016; Drea & Carter, 2009; von Bayern et al., 2009; Wat et al., 2020).

Problem-solving ability and innovativeness differ in that they do not focus on domain-*specific* abilities as seen with the SBH (see **2.1**). Instead, it relies on the presence of a domain-*general* capacity; therefore, using the innovation approach focuses on general cognitive abilities (Lefebvre et al., 2004). Ultimately, the existence of innovative abilities suggests species possess a general cognitive capacity, not as the result of a domain-*specific* challenge but selected to help cope with new, demanding or complex socioecological challenges. Thus, innovative behaviours are thought to be important indicators of high general intelligence (Ramsey et al., 2007; Reader et al., 2016), with such domain-general mechanisms considered powerful tools for attaining evolutionary goals (Chiappe & MacDonald, 2005). Thus, big brains are found to result in greater behavioural flexibility and higher innovation rates, which can be of use when facing complex challenges (Burkart et al., 2017). This in theory, is similar to the CBH (see **1.1**) and contrasts with the assertion of domain-specific skillsets targeted towards solving more specific problems.

One particular drawback to the use of innovation is the problem of defining precisely what innovative behaviours are, and thus, how to quantify such behaviour (Arbilly & Laland, 2017). Lefebvre et al. (1997) defined and measured innovation, using peer reviewed reports of ‘novel’ and ‘unusual’ behaviours, with their analyses revealing brain size to be positively correlated with innovation rates (Overington et al., 2009). However, terms such as ‘behavioural flexibility’ potentially confuse things further, leading to misconceptions about innovative and problem-solving behaviour (Audet & Lefebvre, 2017). Although, Griffin & Guez (2014) highlight how problem-solving ability can be a valid proxy for innovation as both appear to be determined by the same underpinning mechanisms. Despite this, the presence of inter-individual variation in cognitive ability is thought to further confound the situation, with greater appreciation and acknowledgement of the causes of such variation warranted, in order to better understand the evolution of cognition (Boogert et al., 2018). However, Johnson-Ulrich et al. (2020) did find innovative problem-solving ability to be a stable, reliable trait in wild spotted hyaenas, suggesting this proxy can be useful in predicting cognitive ability, despite between-individual variation. Furthermore, there is the perennial problem that differences in problem-solving abilities are often found to result from motivational differences rather than complex cognitive processes (van Horik & Madden, 2016). Selection for persistence can, therefore, be of greater benefit than selection for learning (Guez & Griffin, 2016). Careful consideration of the precise mechanisms behind cognitive abilities is essential to further the study of innovative behaviours and, in turn, better understand the potential benefits of increased brain size.

6.3. Order: Carnivora

Much of the cognitive literature has taxonomically-favoured primates, birds and domestic dogs (*Canis familiaris*) (Boesch, 2012; Emery & Clayton, 2004; Kubinyi et al., 2007; Miklósi et al., 2004; Seed et al., 2009; Seed & Tomasello, 2010). For example, rooks (*Corvus* *frugilegus*) were found to be capable of cooperative problem solving (Seed et al., 2008), and domestic dogs are able to use both human and conspecific social cues to locate hidden food items (Hare et al., 1998; Hare & Tomasello, 1999). However, one taxonomic group which is now starting to receive attention is carnivores (see e.g., Benson-Amram et al. (2016); Borrego and Gaines (2016); Daniels et al. (2019); Holekamp and Benson-Amram (2017)). This is perhaps because carnivores often engage in so-called intelligent behaviours, for example cooperative hunting, which is often cited as evidence for cognitive complexity (Borrego, 2017; Creel & Creel, 1995; Stander, 1992). Mammalian carnivores also show great variation in their brain and body size and have ranging social and physical environments, making them excellent models for testing for links between brain size and cognitive ability (also acknowledged by Benson-Amram et al. (2016) and Borrego (2017)).

Attention has primarily been focused on the social species of the order Carnivora, such as spotted hyaenas (see Benson-Amram and Holekamp (2012); Johnson-Ulrich et al. (2018)) and big cats (see Borrego (2017)) because their social groups often resemble that of primate societies (Gittleman, 1989; Holekamp et al., 2015; Smith et al., 2012; Stankowich et al., 2014), indicating they may possess similar levels of convergent cognitive capacity to those seen in primates (Holekamp et al., 2007), albeit limited to the social domain (Holekamp & Benson-Amram, 2017). For example, wild spotted hyaenas were proven to successfully innovate, with diversity of initial exploratory behaviours found to be determining problem-solving success (Benson-Amram & Holekamp, 2012). When compared, their captive counterparts were significantly more successful at problem-solving, pointing to decreased neophobia and increased explorative behaviours in captive individuals (Benson-Amram et al., 2013). Moreover, innovation has been suggested to have fitness consequences, with innovative female spotted hyaenas found to have higher annual cub production, but lower offspring survival, when compared to non-innovative females (Johnson-Ulrich, 2020; Johnson-Ulrich et al., 2019).

Albeit not as prevalent, studies are starting to surface investigating the capabilities of the asocial carnivore species, typically using a comparative approach to determine how non-social species compare in their ability to problem-solve. One example that compared lions, hyaenas, leopards and tigers, found the social species to be more successful innovators, suggesting a link between sociality, persistence and innovation (Borrego & Gaines, 2016). However, this association fails to remain present when using a larger sample size and including a greater variety of carnivore species. For example, Benson-Amram et al. (2016) fail to find support for the SBH, with social complexity failing to predict success in solving the problem. These contrasting results raise questions regarding how asocial species *truly* compare in their innovative abilities and the ‘true’ influence of sociality on cognitive performance; thus, it is clear that greater investigation into the order of Carnivora is warranted, especially focused on species that are solitary but who nonetheless have large relative brain sizes.

6.4. Family: Ursidae

One understudied family within the order is Ursids. Bears have unusually large relative brain sizes, showing similar encephalisation increases to Canidae (Finarelli & Flynn, 2009) despite living minimally social lives (Gittleman, 1999). This group has perhaps been overlooked as they fail to conform to the SBH by possessing relatively large brains but not being social-living (see **2.1**). Therefore, testing cognition in bears has been limited, meaning little is known about whether they too possess those cognitive abilities seen in large-brained social species. Moreover, it is not known why large brains have evolved in these species nor their function or specifically, what socioecological challenge has spurred increased brain size. For instance, American black (*Ursus americanus*) and brown bears (*Ursus arctos*) are classified as generalists, having high levels of foraging flexibility (Gittleman, 1986), with these flexible diets perhaps being important in driving increased brain size within this group, as found to be the case in primate species (Chambers et al., 2021; DeCasien et al., 2017; Powell et al., 2017).

Whilst relatively rare, studies examining the capabilities of bears can be found in the literature. Particular attention has been paid to their visual, spatial and numerical abilities (Bacon & Burghardt, 1976a, 1976b, 1983; Dungl et al., 2008; Kelling et al., 2006; Perdue et al., 2009; Perdue et al., 2011; Tarou, 2004; Vonk & Beran, 2012; Vonk et al., 2012; Vonk & Leete, 2017). Reports indicate that bears are capable of tool-use (Bentley-Condit & Smith, 2010; Deecke, 2012), a behaviour thought to be indicative of higher cognitive function (Emery & Clayton, 2009; Seed & Byrne, 2010). Indeed, six captive brown bears were found to be capable of tool-use, manipulating inanimate objects so as to obtain a food reward (Waroff et al., 2017). Sloth bears, however, failed in a similar scenario (Amici et al., 2019). Additionally, Benson-Amram et al. (2016) used puzzle boxes to test mammalian carnivores' ability to problem solve, finding species in the family Ursidae, including grizzly (*Ursus arctos horribilis*), polar (*Ursus maritimus*) and American black bears, to be most successful at solving the problem and accessing the puzzle box. The success of such research highlights the cognitive potential of bears; however, it is clear further research is needed to confirm their cognitive capabilities.

6.5. Species: Brown bears (*Ursus arctos*)

Generally, bear studies have tended to focus on American black bears (see e.g., Johnson-Ulrich et al. (2016); Myers and Young (2018); Vonk et al. (2012); Zamisch and Vonk (2012)), perhaps due to their prevalence and accessibility in the United States of America, meaning brown bears have seldom been evaluated. This is surprising from the standpoint that brown bears offer an excellent model system for testing the cognitive abilities of Ursids. They are the most widespread bears species, found across Europe, Asia and North America, occupying a diversity of habitats (Belant et al., 2010; Hilderbrand et al., 2018; Servheen et al., 1999). This is illustrated in Figure 4, taken from McLellan et al. (2017). Furthermore, they exhibit variable foraging strategies within populations, with diets ranging from highly mixed (i.e., meat and vegetation) to exceedingly specialised ones (Costello et al., 2016; Lafferty et al., 2015; Mangipane et al., 2018; Mangipane et al., 2020). Such factors are thought to demonstrate how brown bears come to display high levels of behavioural plasticity (Van Daele et al., 2012), especially in terms of foraging behaviour and that makes them excellent candidates for measuring cognitive ability.

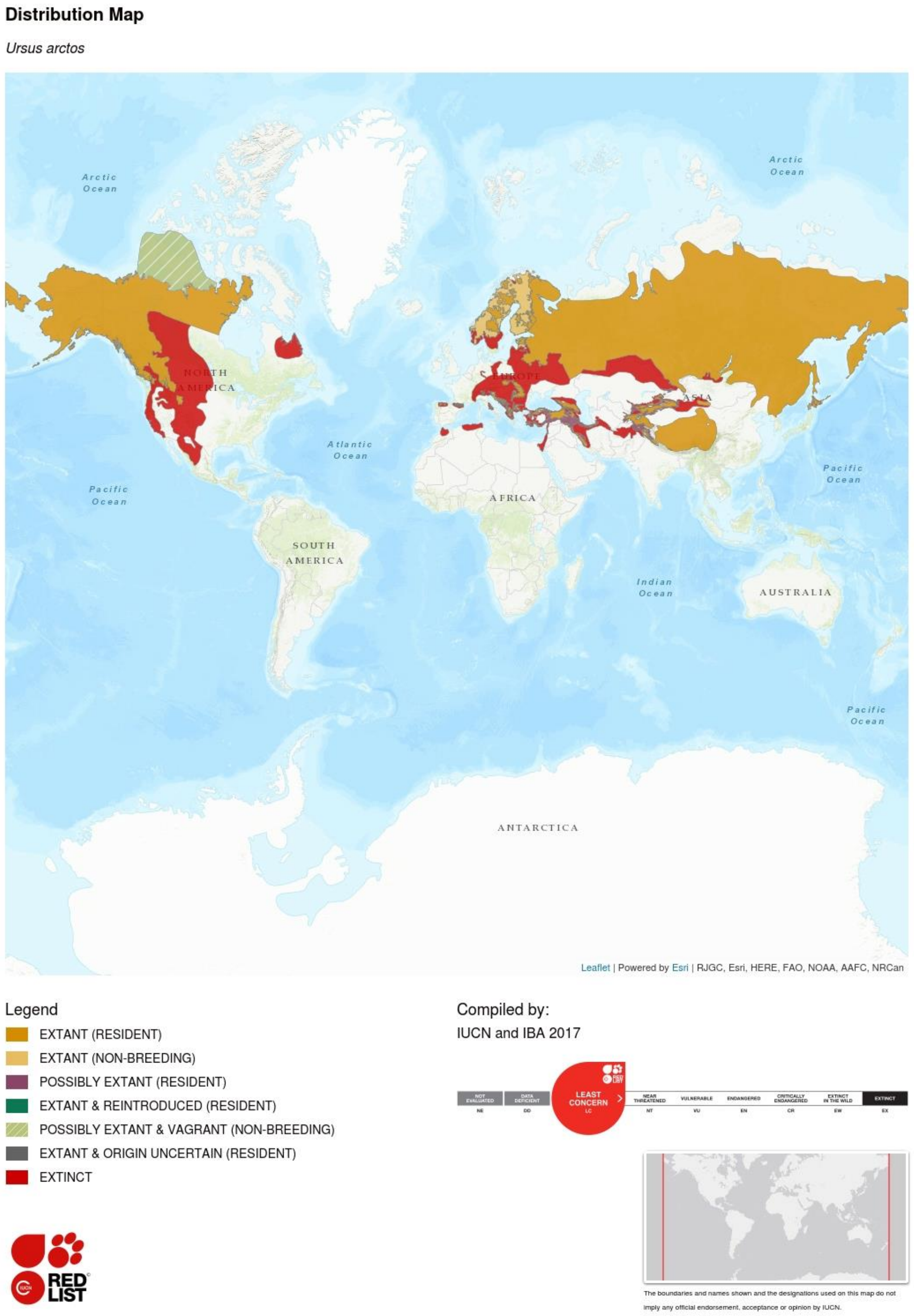

Figure 4. Geographic range of brown bears (*Ursus arctos*).

Credit. From Ursus arctos (amended version of 2017 assessment). By B. McLellan, M. F. Proctor, D. Huber & S. Michel. 2017. (https://dx.doi.org/10.2305/IUCN.UK.2017-3.RLTS.T41688A121229971.en). Copyright 2017 B. McLellan, M.F. Proctor, D. Huber & S. Michel.

7. ‘Why big bear brains?’ Methods

In efforts to further substantiate the assertion that large brains result in superior cognitive abilities and further elucidate whether studying one’s ability to innovate is a useful tool for testing such assumptions, here the cognitive abilities of captive European brown bears were tested. Bears have been relatively overlooked in the cognitive literature, brown bears even more so, which is surprising since they offer an excellent opportunity to investigate the presence of encephalisation and address theories of brain size evolution (see **6.4**, **6.5**). Albeit rarely tested, research is starting to surface suggesting bears exhibit enhanced cognitive abilities (see e.g., Benson-Amram et al. (2016)), and studying one’s ability to be innovative and solve unique socioecological problems has become prevalent in animal cognition studies (Bandini & Harrison, 2020). Therefore, here, two cognitive trials were implemented in order to test the cognitive abilities of bears. These trials have been previously implemented (see e.g., Benson-Amram et al. (2016); Waroff et al. (2017)) and proven useful in testing cognitive ability. Thus, the aim here was to determine whether bears possess problem-solving abilities, in terms of their ability to gain access to a puzzle box, whilst also testing their ability to manipulate an object in order to retrieve an out of reach food reward. Furthermore, using generalised linear mixed models (GLMM), analyses were conducted to determine which variables, if any, influenced cognitive performance. Particular attention was focused on the influence of age, sex, motivation levels, behavioural diversity and persistence on cognitive ability.

7.1. Ethics

This research received ethical approval from the University of Salford Research Ethics Committee (STR1819-64) and was granted a letter of support from the BIAZA Research

Committee (see Appendix 1). The research was conducted in accordance with the ASAB/ABS guidelines for the use of animals in research (Buchanan et al., 2012).

7.2. Pilot testing

From November 2019 to March 2020, preliminary trials of the previously *proposed* trials were conducted at Yorkshire Wildlife Park with four polar bears. This preliminary testing was conducted to ensure the viability, durability and suitability of the methods. Whilst it was intended to test both cognitive trials, the object-manipulation set-up (see **7.4**) proved challenging to implement, in terms of suspending an item at an acceptable height for polars and thus, only the puzzle box was implemented (Fig. 5). The results of this pilot testing allowed the reduction of the final puzzle box size and further refinement of the puzzle box *latch* to ensure the bears could manipulate it by either their mouth, nose or paws. Bear engagement in the trials was variable; however, this was most likely due to seasonality, as the trials were (unintentionally) implemented during the polar breeding season, and thus, the all-male group were often inattentive and distracted and failed to engage with the trials. Nevertheless, the pilot testing proved useful in terms of uncovering methodological challenges and refining intended techniques.

Figure 5. Polar bear interacting with the larger puzzle box.

Credit. By Helen Chambers, 2019.

7.3. Study sites and subjects

Experimental trials were implemented at seven zoological collections in the UK: Five Sisters Zoo, Wildwood Trust, Camperdown Wildlife Centre, Wildwood Escot, Welsh Mountain Zoo, Scottish Deer Centre and Port Lympne Reserve. Seventeen captive European brown bears (N = 17) were included in this study: eight adult females (Es, Ma, Br, At, Fi, Ne, En, Ne), one juvenile female (Lu), five adult males (Fl, Sc, Br, Lo, Ju), and three juvenile males (Mi, To, Ro). Ages ranged from twenty-three years to one year of age (mean = 10.35, ± 7.75). Weights ranged from 300 to 80 (kg). Fourteen of the bears were captive born and three were thought to be wild caught. None of the bears had previous experience with cognitive trials. However, all but two bears had previous experience with artificial enrichment, such as boomer balls (see Appendix 2 for bear information). Other physiological markers, such as individual bear health, stress levels, were not considered here, however they are important factors which could be influencing bear behaviour.

7.4. Experimental apparatus

Trials utilised: (i) a puzzle box and (ii) an object manipulation set-up. The puzzle box was a small (30cm x 30cm x 30cm) baited steel box (Fig. 6), which had a simple latch on the front that the bears needed to slide laterally for the door to open, allowing the bears to access the food reward inside. It was designed similarly to those used in previous studies which have proven useful in testing mammalian problem-solving ability (see Benson-Amram et al. (2016); Benson-Amram and Holekamp (2012); Benson-Amram et al. (2013); Borrego and Gaines (2016)). However, the latch was increased in size to accommodate the size and weight of the bears, which allowed the bears to move the latch using their mouth, nose or paws. The barred box design meant the bears could both see and smell the food reward inside. This task draws on the bear’s ability to manipulate small objects, similar to foraging challenges bears typically face, such as retrieving hard to reach berries or extracting honey from bee nests.

Figure 6. Brown bear interacting with the puzzle box.

Credit. By Kathryn Page, 2021.

The individual was considered “successful” in solving the problem if they gained access to the box using any technique; however, a further distinction was made if they used the latch to open the door. The box was chained during the trials, to reduce the likelihood of the box being pushed around and the latch “accidently” falling open. The ability to chain the box varied at the collections, which resulted in the trial data being split into two categories (i) box chained well with limited manoeuvrability, and (ii) box chained loosely with high manoeuvrability. The main distinction between the two categories was that the box could more easily be ‘tipped’ when loosely chained, sometimes resulting in the latch sliding open, which was not typically possible with the low manoeuvrability trials. This variability does limit the comparability of trials conducted across collections, but by defining how the box was chained, the two categories could be examined to better understand the presence of latch use (see Table 6).

The object-manipulation set-up involved suspending a food reward out of reach and providing tree stumps for the bears to manipulate so as to retrieve the reward. This typically involved securing a rope between two adjacent trees, with a food item hung in the middle and stumps provided underneath (Fig. 7). At certain collections, however, it was logistically easier to run trials in indoor enclosures with food suspended from roof meshing. Between one to three stumps were provided for the bears depending on age, weight and size. This task ultimately required the individual to work out that the food item could be accessed by repositioning the stump under the suspended item so as to reach it (Fig. 8) – a behaviour that could be considered tool-use (Waroff et al., 2017).

Figure 7. Object-manipulation set-up: a rope secured between two trees with a food item hung in the middle and stumps provided underneath.

Credit. By Helen Chambers, 2021.

Figure 8. Bear succeeding in acquiring the food reward using the stump in stage 1 of the object-manipulation task.

Credit. By Helen Chambers, 2021.

Variations of this set-up have been previously deployed in captivity (Amici et al., 2019; Waroff et al., 2017). Previous researchers have trained or provided cues for the bears; therefore, this task was divided into stages. Initially, the stump(s) provided were placed directly underneath the food reward, so the individual had only to approach and stand on the stump(s) to be successful. If successful, in the next trial, the stump(s) were placed on their side so that the individual would only need to push the stump(s) flat and stand on it/them to be successful. If successful, in the next trial, the stump(s) were positioned flat, however they were positioned away from the food reward, so the individual had to actively manipulate and manoeuvre the stump(s) in order to reach the food reward and be successful. Stages one and two are illustrated in Fig. 9, stage three was not reached. The full set-up is further illustrated in Fig. 10. The set-up presented only changed if stump use and manipulation was recorded. The individual was considered “successful” in solving the problem if they managed to retrieve the hung food reward using any technique; however, a further distinction was made if they used the stump(s) for elevation.

Figure 9. Object-manipulation stages one (left) and two (right).

Credit. By Helen Chambers, 2021.

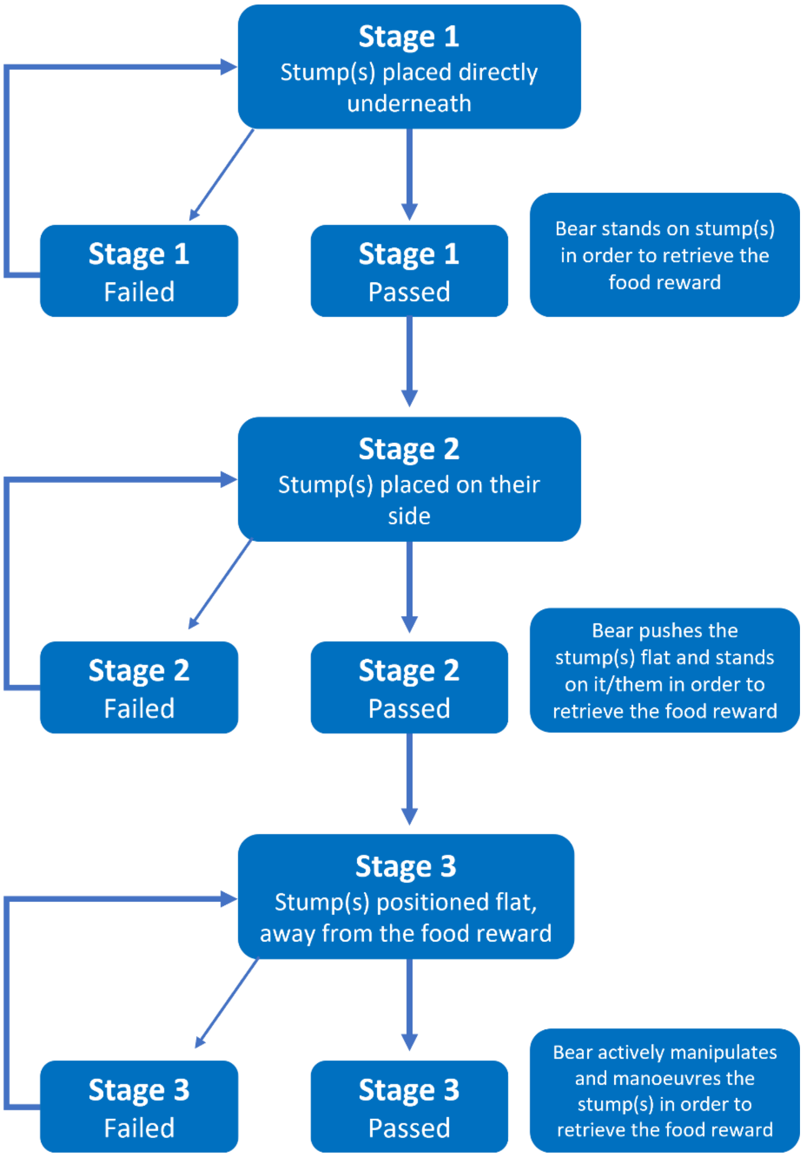

Figure 10. Object-manipulation stages and criterion.

Credit. By Helen Chambers, 2022.

7.5. Experimental procedure

Trials were implemented from June to October 2021. Separation of group-housed bears was rarely practical. This was of particular concern to many keepers who referenced that separation could possibly lead to anxiety or stereotypical behaviours in the bears. Therefore, trials were run with the bears collectively, meaning all bears had access to, and could interact with, the set-ups presented. Each bear was presented with at least three trials of each set-up; however, this was dependent on which bear engaged with the trials and whether one bear monopolised the trials. Thus, each set-up was repeated at least three times for each individual; however, as all bears had access at the same time, there was no way to guarantee which bear was going to interact with the trial. Whilst this ultimately resulted in not all bears having the same exposure time with the trials, this was unavoidable and highlighted how the social dynamics of group-housed bears may influence engagement with both cognitive trials and enrichment activities.

Running trials typically coincided with feeding times and thus, bears were usually fed at the same time as trials being run. Two to four trials were run per day, typically one in the morning and one in the afternoon. It is likely running trials in this way influenced bear motivation levels, as trials run in the morning were presented to bears who had not yet been fed, whereas bears had already been fed and had access to food prior to the afternoon trials. This is of interest as problem-solving abilities are often found to result from motivational differences rather than complex cognitive processes (van Horik & Madden, 2016). To ensure this was accounted for, it was noted how many bears had access to the set-up during each trial, whether they had already been fed and whether food was present at the same time (see **7.6**). The food chosen to use as bait was determined by keeper discussions, bear preferences and food availability. This usually was a ‘high value’ food item, such as monkey nuts, melon or quail; however, there were a few occasions where the food item used was not as high value, such as corn, which likely influenced engagement. Additionally, keepers acknowledged bear preferences change periodically (and seasonally) and thus, sometimes a high value item was not well received. However, such instances were few and most trials were baited with a high value item.

Trials commenced when the bear(s) had a direct line of sight to the set-up and ran for up to 30 minutes in duration, or until the food reward had been retrieved. However, trials run from September onwards were extended to last up to one hour in duration, to account for bears tested at this time of year having started to slow down for torpor and thus they were not as highly motivated to engage with the trials at first.

In total, trials involved 16 captive brown bears (nine females and seven males). One male bear did not engage with any of the trials. Similarly, one female only briefly engaged with one trial and motivation was very low. Another female failed to engage with the puzzle-box, but did engage with the object-manipulation trials. Only bears which engaged with one, or both, of the trials were considered for analyses.

7.6. Data extraction from videotaped trials

All trials were video recorded and behavioural data were extracted from the video recordings. For each individual, their best three trials were scored for each set-up. Video recordings were scored by one observer. However, to validate that the footage was scored accurately, 25% of trial recordings were reviewed by an independent observer, blind to the hypothesis. Interobserver reliability was very high across all measures (Latency R = 0.996; Time-to-solve R = 0.991; Behavioural diversity R = 0.9; Persistence R = 0.978; Latch use/Stump use R = 1, Successful R = 1; Spearman rank correlation).

In terms of measuring problem-solving ability for both set-ups, performance measures were used. Latency to approach (t^1) was recorded as the time taken (secs) to approach the set-up after first detecting it, as a measure of motivation to obtain the food reward. However, to also measure motivation, the following scoring system was additionally implemented: low (L), medium (M) and high (H). This was scored based on the time of day of the trial, whether the subject had already been fed, the number of bears with access, the availability of food alongside the trial and the overall activity levels of the bear prior to the trials. Time-to-solve (t^2) was recorded as the time taken (secs) to solve the test, after having had approached the set-up, during which the individual was oriented on the set-up and focused on solving the task, until successful. If unsuccessful, this was marked N/A. To score the range of behaviours seen during attempts (#), the same behavioural diversity score was used as Benson-Amram et al. (2016), including 12 different behaviours: *rub, foot on box, sniff, lick, dig, bite, pull box with mouth, push box with head, push box with paw, pull box with paw, stand on box,* and *tip box*. 'Flip box' was excluded as this was not possible and was instead replaced with '*claw*', used to represent the behaviour during which the bear used its front paw to 'claw' at the box, either in an attempt to open the box or to pull the food item through the bars. Thus, each individual received a score from 0 to 13. This score system was used only for the puzzle box trials. For both tests it was noted whether the individual was successful (Y/N); however, a further distinction was made in the puzzle box trials, in terms of the presence of latch use

(Y/N), and a further distinction was made in the object-manipulation trials, in terms of the presence of stump use (Y/N). Number of attempts (#), with an attempt being any behaviour used to try and retrieve the food reward, was used as a measure of persistence.

7.7. Statistical analyses

Interobserver reliability analyses were conducted in Minitab 21.1.0. (Minitab LLC, 2021). All further analyses were conducted in *R* 4.1.2 (R Core Team, 2021), using the packages 'lme4' (Bates et al., 2015), 'lmerTest' (Kuznetsova et al., 2017), 'car' (Fox & Weisberg, 2019), 'MuMIn' (Bartoń, 2010), 'r2glmm' (Byron, 2017) and several functions provided by Roger Mundry. Generalised linear mixed models (GLMM) were implemented to estimate effects of age, sex, behavioural diversity, persistence, number of successful trials, trial number, latency to approach, motivation score and the number of bears present on time-to-solve (Baayen, 2008). Five models in total were run, models one to three using the puzzle box data and models four and five using the object-manipulation data. In model one, behavioural diversity, persistence and their interaction were included as fixed effects. The interaction between behavioural diversity and persistence was included because it seemed likely there was to be a relationship between both the *number* and *types* of attempts. In model two, number of successful trials and trial number were included as fixed effects. The interaction between number of successful trials and trial number was included because it seemed possible for there to be a relationship between the number of *successful* trials and the trial *number*. In model three, latency to approach and motivation score were included as fixed effects. To avoid model convergence issues, the interaction between these two variables was not considered within this model. In model four, age, sex and their interaction were included as fixed effects. The interaction between age and sex was included because it seemed possible for them to interconnect. In model five, the number of bears present and the trial number were included as fixed effects. It did not seem likely that these two variables would be interconnected, and therefore the interaction between these two variables was not considered within this model. Time-to-solve was the response variable in the five models. In all models, subject was included as the as random effect, to control for the inclusion of multiple datapoints from one individual.

A series of preliminary models were implemented that included various combinations of the variables of interest to determine which variables best explained the data and to uncover any significant associations. These preliminary models included variables such as behavioural diversity, persistence, age, sex, trial number, number of successful trials, time of trial, latency to approach, number of bears present, month and motivation score. Thus, the five models (outlined above) were selected for use following this preliminary testing. Time of day and month were excluded from the final models as the inclusion of those variables did not improve the model fit or uncover any significant associations.

Prior to fitting the models, all predictors and responses were inspected for whether their distributions were symmetric. As a consequence, all continuous variables (time-to-solve, age, behavioural diversity, persistence, number of successful trials, trial number, latency to approach and number of bears present) were log transformed prior to analysis to satisfy the assumption of normality. In addition, continuous predictors (age, behavioural diversity, persistence, number of successful trials, trial number, latency to approach and number of bears present) were *z*-transformed to make model interpretation easier

(Schielzeth, 2010) and for easy model convergence. In order to handle the binary data, sex and motivation score were both dummy coded, with female and high (H) being the reference category, respectively. After fitting the models, it was checked that the assumptions of the residuals - to be normally distributed and homogeneous - were fulfilled. No deviations from these assumptions were indicated (see Appendix 4).

Full-null model comparisons were conducted in order to test the influence of the fixed effects and their interactions (Forstmeier & Schielzeth, 2011), whereby the null models lacked the interaction effects but were otherwise identical to the full model. The effect of individual fixed effects were tested by means of the Satterthwaite approximation (Luke, 2017). To test for the presence of multicollinearity, variance inflation factor (VIF) scores were checked. These were produced using models lacking the interactions between fixed effects, and collinearity appeared to be of no issue (maximum VIF = 3.53). Model stability was also assessed based on the levels of the estimated coefficients and standard deviations by excluding the levels of the random effects one at a time (Nieuwenhuis et al., 2012). All models appeared to be of acceptable stability, with the exception of the random effect (subject).

The sample for model one, two and three encompassed 32 trial values, from 14 individuals, with 10 observations per estimated term. The sample for model four encompassed 30 trial values, from 13 individuals, with 9.5 observations per estimated term. The sample for model five encompassed 30 trial values, from 13 individuals, with 12 observations per estimated term.

8. ‘Why big bear brains?’ Results

8.1. Puzzle box data

Out of 32 trials, latch use was present 17 times and alternative techniques were used in the other 15 trials (Table 6).

Table 6. Results of the puzzle box trials, including how the box was presented and presence/absence of latch use.

How puzzle box was chained	Total # of successful trials (1)	Trials with latch use (2)	Trials with no latch use
(i) Box chained well	23	17	6
(ii) Box chained loosely	9	0	9

Note. (1) When using up to three trials per bear, some individuals had more than three successful trials, (2) Whether accidental or intentional not distinguished.

8.1.1. Model one

Overall, the interaction between behavioural diversity and persistence failed to be significant (full-null model comparison: χ^2=1.353, *df*=1, *P*=0.245) and consequently, the model was re-run excluding the interaction terms. In this reduced model, behavioural diversity failed to be significant (*P*=0.054, R^2m = 0.722, R^2c = 0.852) (R^2m = marginal R^2 value including just fixed effects, R^2c = conditional R^2 value including fixed and random effects). However, persistence was positively correlated with time-to-solve and impacted success times (*P*=0.010, R^2m = 0.722, R^2c = 0.852). More specifically, as persistence (the number of attempts) increases, time-to-solve also increases (Table 7; Fig. 11).

Table 7. Results of generalised linear mixed model (GLMM), model one of behavioural diversity and persistence on log-time-to-solve (estimates and standard errors, together with confidence limits, results of tests, and the range of estimates obtained when dropping levels of random effects one at a time).

Term	**estimate**	**SE**	**lower CI**	**upper CI**	***t***	***df***	***P***	**min**	**max**
Intercept	1.47	0.066	1.355	1.597	22.415	12.809	0.000	1.405	1.507
Behavioural diversity **(1)**	0.199	0.099	-0.013	0.392	2.001	31.999	0.054	0.115	0.265
Persistence **(2)**	0.279	0.101	0.074	0.485	2.754	31.407	**0.010**	0.219	0.399

Note. (1)*z*-transformed to a mean of 0 and a standard deviation of 1; mean and SD of the original variable were 0.645 and 0.242, respectively,

(2)*z*-transformed to a mean of 0 and a standard deviation of 1; mean and SD of the original variable were 0.794 and 0.539, respectively.

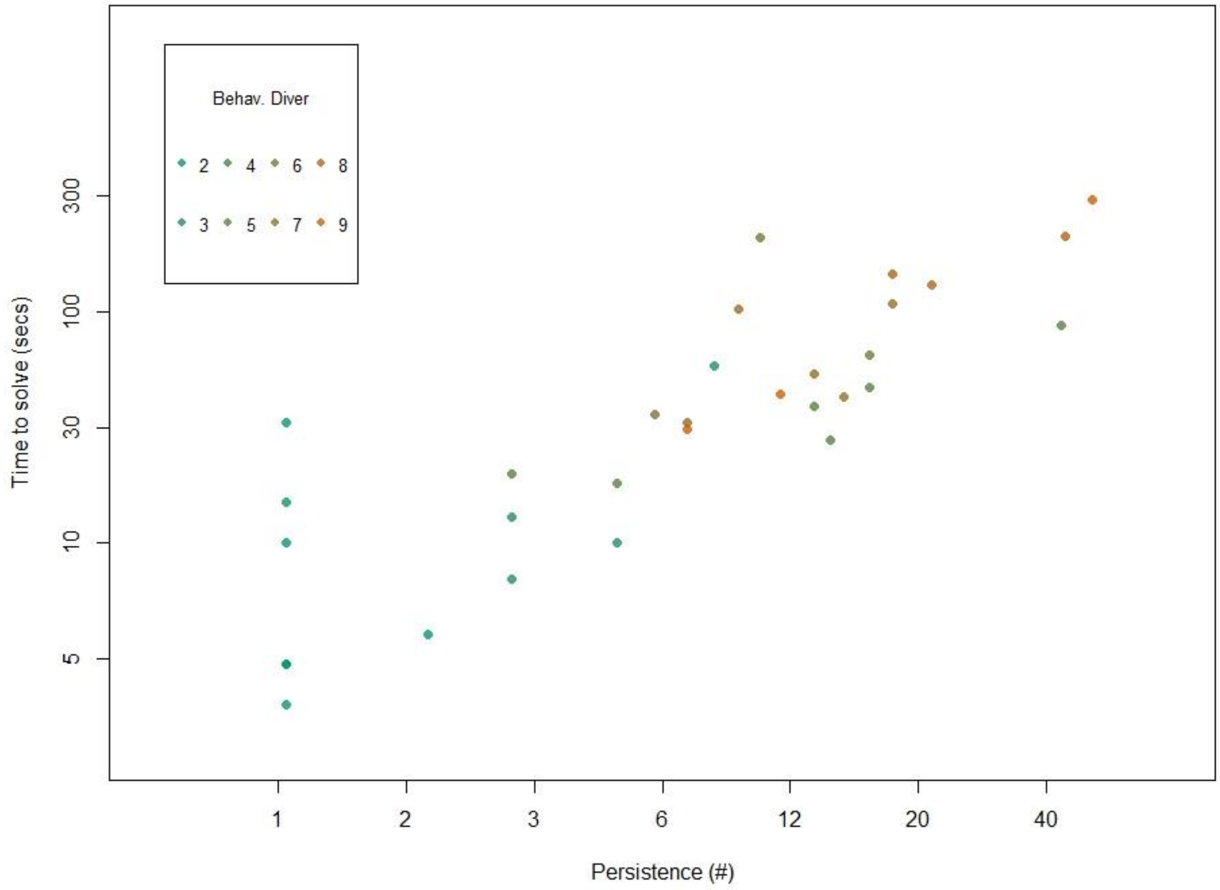

Figure 11. The influence of persistence and behavioural diversity on time to solve*. As time to solve increases both the number of attempts and the types of attempts increases (greater behavioural diversity displayed in orange dots). Data points represent all trial values (n = 32) from 14 individuals (mean number of trial values or data points per individual = 2.29, ± 0.91).

Note. *Axes are in $\log_{10}$ scale.

8.1.2. Model two

Overall, the interaction between the number of successful trials and trial number significantly improved the model and thus the full model was retained (full-null model comparison: χ^2= 6.233, *df*=1, *P*=0.013). In this model, the number of successful trials appeared to influence success times, as this was significantly negatively correlated with time-to-solve (*P*=0.020, R^2m = 0.563, R^2c = 0.653). However, trial number failed to be significant (*P*=0.336, R^2m = 0.563, R^2c = 0.653). In addition, there appears to be an interaction between number of successful trials and trial number, indicating that time-to-solve is dependent both on *exposure to success* and the exact trial *number* (*P*=0.009, R^2m = 0.563, R^2c = 0.653) (Table 8).

Table 8. Results of generalised linear mixed model (GLMM), model two of number of successful trials and trial number and their interaction on log-time-to-solve (estimates and standard errors, together with confidence limits, results of tests, and the range of estimates obtained when dropping levels of random effects one at a time).

Term	**estimate**	**SE**	**lower CI**	**upper CI**	***t***	***df***	***P***	**min**	**max**
Intercept	1.625	0.099	1.432	1.802	16.477	9.751	0.000	1.554	1.734
# Of successful trials (1)	-0.271	0.11	-0.460	-0.038	-2.470	28.733	**0.020**	-0.384	-0.212
Trial number (2)	-0.102	0.103	-0.313	0.083	-0.983	21.899	0.336	-0.165	-0.009
ST:TN	-0.234	0.08	-0.383	-0.078	-2.919	17.991	**0.009**	-0.317	-0.182

Note. (1)*z*-transformed to a mean of 0 and a standard deviation of 1; mean and SD of the original variable were 0.546 and 0.296, respectively,

(2)*z*-transformed to a mean of 0 and a standard deviation of 1; mean and SD of the original variable were 0.382 and 0.315, respectively.

8.1.3. Model three

In this model, latency to approach appeared to influence success times, as this was significantly positively associated with time-to-solve (*P*=0.028, $R^2m = 0.13$, $R^2c = 0.794$). Specifically, as latency to approach increases, time-to-solve also increases. However, this did fail to be significant when paired with a different variable (see Appendix 3). In addition, motivation score failed to be significant (*P*=0.166, *P*=0.259, $R^2m = 0.13$, $R^2c = 0.794$). This was the result produced when using high (H) as the reference category (Table 9).

Table 9. Results of generalised linear mixed model (GLMM), model three of latency to approach and motivation score on log-time-to-solve (estimates and standard errors, together with confidence limits, results of tests, and the range of estimates obtained when dropping levels of random effects one at a time).

Term	**estimate**	**SE**	**lower CI**	**upper CI**	***t***	***df***	***P***	**min**	**max**
Intercept	1.750	0.223	1.287	2.239	7.833	27.123	0.000	1.620	1.926
Latency $^{(1)}$	0.205	0.088	0.015	0.385	2.327	27.592	**0.028**	0.100	0.253
Motivation score L $^{(2)}$	-0.371	0.262	-0.919	0.132	-1.420	31.422	0.166	-0.587	-0.154
Motivation score M $^{(2)}$	-0.211	0.182	-0.555	0.151	-1.159	21.728	0.259	-0.426	-0.011

Note. $^{(1)}$*z*-transformed to a mean of 0 and a standard deviation of 1; mean and SD of the original variable were 1.284 and 0.436, respectively,

$^{(2)}$ coded as factor with high (H) being the reference category.

8.2. Object-manipulation data

Out of 30 trials, stump use was present 20 times and alternative techniques were used in the other ten trials (Table 10; Table 11).

Table 10. Results of the object-manipulation trials, including number of variations presented and presence/absence of stump use.

Object-manipulation stage	Total # of successful trials [(1)]	Trials with stump use	Trials with no stump use
1	26	20	6
2	4	0	4
3	0	0	0

Note. (1) When using up to three trials per bear, some individuals had more than three successful trials.

Table 11. The alternative techniques implemented by the bears when solving the object-manipulation set-up.

Techniques used (1)	Number of times witnessed	Object-manipulation stage
Climb tree and loosen rope leading to the food dropping down to a reachable height (2)	2	2
Climb apparatus and shake rope causing the food to drop to the floor	2	1
Climb apparatus and put pressure on the rope, causing the food to slide to the bear	3	1
Climb and hang from apparatus so the rope is in reach, then pull rope close and grab the food	1	1

Pull down on apparatus attached to chain (instead of rope) which brought the food down to a reachable height	2	2

Note. (1) Techniques are described how they happened, it was not obvious whether they were intentional or accidental,

(2) This individual even tried to suspend herself/hang from the rope, almost like she was going to pull herself along the rope to the food, but the rope did not hold (she tried this twice).

8.2.1. Model four

In terms of the interaction between age and sex, this significantly improved the model and thus the full model was retained (full-null model comparison: χ^2= 6.579, *df*=1, *P*=0.010). In this model, age appeared to influence success times, as age was significantly negatively correlated with time-to-solve (*P*=0.022, R^2m = 0.463, R^2c = 0.597) or simply, with increasing age comes increasing time to success. Similarly, sex seemed to have an impact on time-to-solve, with sex significantly negatively correlated with time-to-solve (*P*=0.004, R^2m = 0.463, R^2c = 0.597) (Fig. 12). This was the result produced when using female as the reference category, indicating that males typically have reduced time-to-solve in comparison to females. In addition, there appears to be an interaction between age and sex, indicating that time-to-solve is dependent on *both* age and sex (*P*=0.011, R^2m = 0.463, R^2c = 0.597) (Table 12).

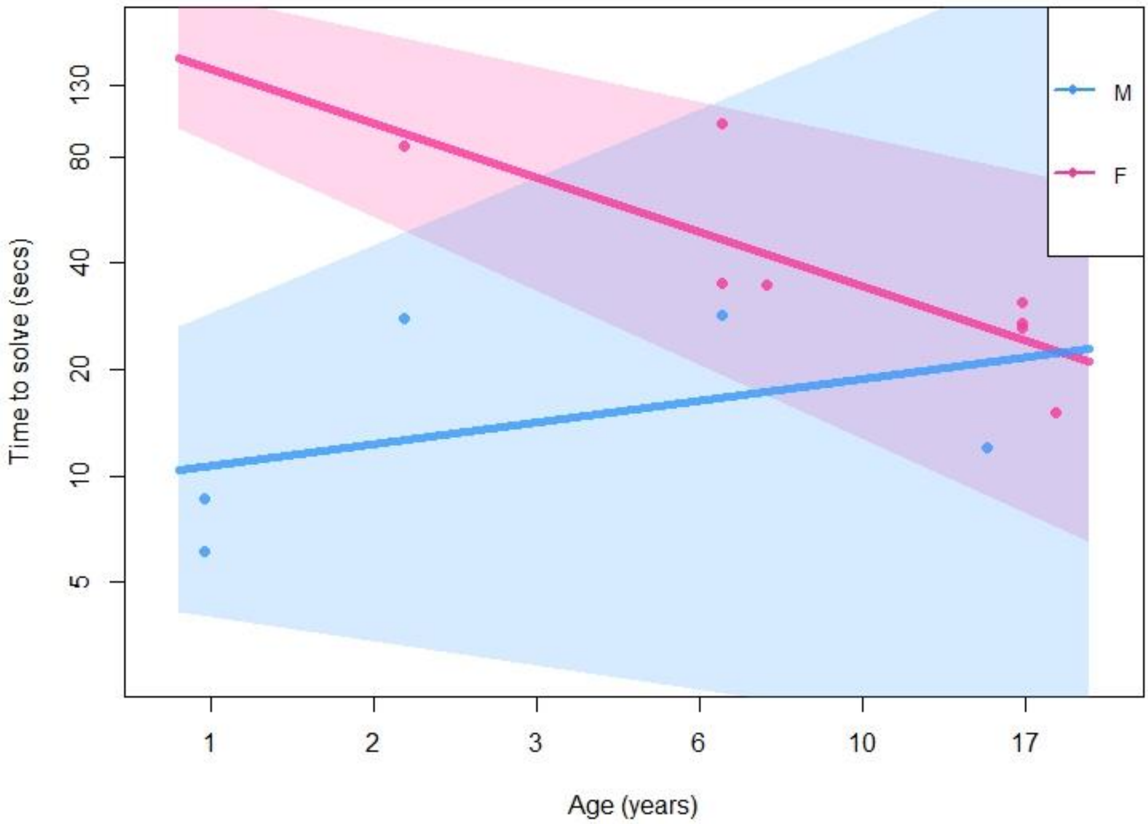

Figure 12. The influence of age and sex on time to solve*. Time to solve is dependent on both sex and age, with younger males typically showing improved scores. Coloured lines are the model predictions by sex (M – male; F – female), shaded areas are the 95% confidence intervals. Data points represent mean values of all trial values (n = 30) per individual (n = 13) (mean number of trial values per individual = 2.31, ± 0.85).

Note. *Axes are in $\log_{10}$ scale.

Table 12. Results of generalised linear mixed model (GLMM), model four of age, sex and their interaction on log-time-to-solve (estimates and standard errors, together with confidence limits, results of tests, and the range of estimates obtained when dropping levels of random effects one at a time).

Term	estimate	SE	lower CI	upper CI	*t*	*df*	*P*	min	max
Intercept	1.690	0.102	1.482	1.888	16.549	23.372	0.000	1.634	1.720
Age (1)	-0.306	0.124	-0.557	-0.058	-2.460	22.197	**0.022**	-0.337	-0.259
SexM (2)	-0.478	0.141	-0.740	-0.201	-3.398	16.420	**0.004**	-0.572	-0.153
A:S	0.428	0.151	0.131	0.729	2.825	17.700	**0.011**	0.343	0.684

Note. (1)*z*-transformed to a mean of 0 and a standard deviation of 1; mean and SD of the original variable were 0.744 and 0.489, respectively,

(2) dummy coded with female being the reference category.

8.2.2. Model five

In this model, the number of bears present appeared to influence success times, as this was significantly negatively associated with time-to-solve (*P*=0.004, R^2m = 0.442, R^2c = 0.537). Specifically, as the number of bears present during trials increases, time-to-solve decreases. However, trial number failed to be significant (*P*=0.11, R^2m = 0.442, R^2c = 0.537) (Table 13).

Table 13. Results of generalised linear mixed model (GLMM), model five of number of bears present and trial number on log-time-to-solve (estimates and standard errors, together with confidence limits, results of tests, and the range of estimates obtained when dropping levels of random effects one at a time).

Term	**estimate**	**SE**	**lower CI**	**upper CI**	***t***	***df***	***P***	**min**	**max**
Intercept	1.332	0.054	1.228	1.429	24.556	9.828	0.000	1.284	1.375
# Of bears present ⁽¹⁾	-0.224	0.056	-0.333	-0.117	-3.992	8.410	**0.004**	-0.297	-0.178
Trial number ⁽²⁾	-0.081	0.049	-0.177	0.020	-1.649	29.977	0.11	-0.126	-0.051

Note. ⁽¹⁾*z*-transformed to a mean of 0 and a standard deviation of 1; mean and SD of the original variable were 0.446 and 0.23, respectively,

⁽²⁾*z*-transformed to a mean of 0 and a standard deviation of 1; mean and SD of the original variable were 0.382 and 0.315, respectively.

9. ‘Why big bear brains?’ Discussion

The aim of the research presented here was to investigate problem-solving and object-manipulation abilities in European brown bears, whilst also determining which variables best explain success in cognitive trials. Using two experimental tests, a puzzle box testing problem-solving ability and an object-manipulation set-up measuring tool-use ability, the cognitive abilities of captive brown bears were examined. Puzzle box analyses revealed evidence of trial-and-error learning; however, two juveniles appeared to acquire an association between the latch and access to the box, suggesting some individuals have potential to draw perceptive associations. This was further reinforced by the presence of an interaction between number of successful trials and trial number, with the number of successful trials negatively associated with time-to-solve, indicating that the bears learnt to adopt successful strategies which improved their performance over time. Furthermore, latency to approach appeared to influence success times, suggesting individual variation in motivational levels is an important factor influencing cognitive performance. The bears failed to spontaneously use a tool, but still managed to retrieve the food reward, instead using alternative techniques to solve the problem. Object-manipulation analyses revealed an interaction between both age and sex, which were negatively associated with time-to-solve, indicating that younger male bears had improved time-to-solve. Nevertheless, the sample sizes were small and the confidence intervals for males were wide and funnel-shaped, indicating some caution is warranted. In addition, the number of bears present appeared to influence success times, suggesting that competition is a factor influencing cognitive engagement. These results are discussed further (see **9.2**), including the potential impacts of social dynamics on cognitive performance.

It is worth noting, however, due to certain limitations (such as the collective nature of testing or experimental limitations) which hinder data comparability, these results are likely the outcome of the techniques implemented and individuals tested, rather than being representative of, or generalisable to, brown bear populations. More work is necessary to further substantiate the results discussed here. In addition, other factors, such as bear personality and genetics, which have not been explored here, could also be influencing the results found. For example, the backgrounds of the bears were somewhat varied, including both wild caught and captive reared individuals. This background information was collected and considered prior to analyses; however, it was difficult to encapsulate these lived experiences into one quantifiable variable, and thus, whilst not considered during statistical analyses within the study, this may be having an impact on the behaviour of the bears and is a worthwhile avenue for future bear research. Similarly, the relatedness/genetics of the bears is another interesting variable which warrants further attention.

9.1. Puzzle box

All 14 bears that engaged with the puzzle box had at least one successful trial and were successful in solving the problem. This result concurs with Benson-Amram et al. (2016) who found that bear species were able to succeed at a similar task. Three bears did not engage with this scenario at all, likely due to the collective nature of testing, as those who did not engage with the box were identified by keepers as the more subordinate individuals in those groups. Thus, those individuals perhaps avoided interacting with the box for fear of agonistic repercussions from more dominate individuals. This result is of considerable interest in terms of bear personality and how this could be influencing the social interactions of group-living captive bears. Alternatively, a lack of motivation or fear of novel objects may have influenced their non-engagement behaviour. In future, greater attention should be paid to the food chosen as bait and ensuring this is consistent across trials, to reduce the risk of motivational levels influencing trial engagement and behaviour.

Data analysed from the puzzle box trials revealed persistence to be associated with time-to-solve. In addition, analyses revealed a potential association between behavioural diversity and time-to-solve, albeit this fell short of statistical significance, perhaps due to small sample sizes and/or individual variation. This suggests that with increasing time-to-solve, both the *number* and *types* of attempts to gain access to the box also increased. The first suggestion is typically expected during cognitive trials since as engagement time increases, the *number* of attempts also increases, as the individual increasingly tries to retrieve the food reward. The second suggestion is more interesting, as it hints toward the fact that the *types* of behaviours used also increases with time-to-solve. Thus, with increasing time, the individual broadens its approach, utilising different techniques (i.e., elaboration), until one is successful. This result is indicative of trial-and-error learning and suggests bears, alongside other species (Galef & Laland, 2005; Heyes, 1994), use this technique when facing novel challenges. Similar results were found by Waroff et al. (2017) who also suggest bears use trial and error techniques when approaching new tasks, usually invoking physical force.

On several occasions, the use of successful techniques was repeated during subsequence trials, suggesting the bears remembered previous exposures and adopted successful strategies. This was reinforced by the presence of an interaction between the number of successful trials and trial number, with the number of successful trials negatively associated with time-to-solve. This result indicates that as the number of successful exposures increases, the bears learn successful strategies, perhaps first uncovered by their use of trial-and-error learning, which ultimately improves their performance over time. Similarly, Borrego and Dowling (2016) found African lions (*Panthera leo*) to be capable of solving a novel problem, whilst also learning and remembering the task solution in subsequent trials. Benson-Amram et al. (2016) when presenting a similar task to a wide range of carnivoran species, likewise, found successful individuals improved their performance with experience. Thus, when compared to other carnivoran species, the bears were similarly capable of gaining an understanding of the puzzle and how to open it. However, it is important to note that it was observed that the bears frequently appeared to forget previous trials, once again adopting a trial-and-error technique. This apparent shortcoming could be down to the time between trials, low exposure and low motivation. It also points toward the investigation of discerning working and long-term memory in bears being a fruitful and beneficial aspect of future research.

Another variable which appeared important in terms of influencing success times was latency to approach. This was significantly positively associated with time-to-solve, indicating that as latency to approach increased, time-to-solve also increased. This suggests that individual variation in motivational levels is an important factor influencing cognitive engagement and performance. Similarly, Cooke et al. (2021) found variation in problem-solving performance to be best explained by motivational differences. This concurs with the idea that motivation is an important driver of innovative behaviour (Laland & Reader, 1999; Sol et al., 2012). Here, the result is most likely the consequence of motivational differences in terms of the food reward present, rather than the presence or influence of neophobia, as aside from a few individuals which showed signs of neophobia towards the puzzle box, most bears did not show signs of fear towards the novel object. Thus, the latency to approach result was most likely due to differing levels of interest to engage with the trials. This highlights how motivational differences are an important factor to consider when investigating the presence of superior cognitive abilities.

Frequent behaviours implemented in efforts to gain access to the box and food reward included tipping, shaking and pounding the box, as well as clawing at the food item through the bars. It worth noting, however, that this list is not exhaustive and the bears were frequently inventive with the techniques used. Despite this, whilst the bears often interacted with the door and latch, they frequently failed to draw associations between that and retrieving the food reward. From observations of trials, instead it appears the bears became hyper-focused on the food reward, failing to fully assess the situation. Amici et al. (2019) similarly note how the bears fail to "*cognitively represen*t" the situation. Two individuals, however, appeared to draw the association between latch-use and access to the box. The bears, both male and juvenile in age, by the end of their trials, were gaining access to the box in less than ten seconds, often with only one attempt and clear latch use (see Appendix 5). Whilst hesitant to make assumptions and broad generalisations of such behaviour, this hints at evidence that bears can make such associations, particularly through asocial learning. Waroff et al. (2017) likewise suggest that when physical force is not successful, bears often display '*insight-like*' behaviour, indicative of intelligent behaviour.

In evaluating why only two bears out of the 14 tested picked up the technique, there are a few potential explanations. Both bears had >5 trials with the puzzle box and this exposure time, paired with the curious nature of juvenile bears (see **9.2**), may explain why these individuals and not others, picked up the technique. Once they had picked up the technique, they tended to monopolise the trials, often returning to the box to check if it had been re-baited. In addition, the box was chained well at both collections, ergo less manoeuvrability, and thus, the bears were generally more likely to interact with the latch. If this were possible across all collections and if trials were run individually (thereby providing consistent exposure time between bears) it is plausible all of the bears involved could have followed suit, picking up the association.

9.2. Object-manipulation

Of 15 individuals who engaged with the object-manipulation set-up, 13 were successful in solving the problem. Of the two that were unsuccessful, one was likely due to low motivation levels, with only one short attempt at solving the problem. The second individual had several attempts and at first was highly motivated but for several reasons (perhaps lack of previous artificial enrichment experience, older in age so reduced mobility) failed to solve the problem. Of the two that were not tested, one did not engage with this scenario at all, likely due to collective testing (see **9.1**). The other bear did engage with the trials, but it was not possible to adequately suspend a food reward out of reach due to his large size and low hanging points. Therefore, this bear was excluded from further testing.

Data analysed from the object-manipulation set-up revealed that both age and sex were significantly influencing the time-to-solve measure, in particular, there was a significant interaction between age and sex. In this scenario, younger male bears had improved time-to-solve scores. Some caution is warranted, however, since the sample sizes for this task were small (males = 5, females = 8). The data show wide confidence intervals for males and is funnel-shaped, which is suggestive of the sample size not being adequate to provide an accurate representation of the population as a whole; instead, potentially being a product of the individuals examined and the sampling techniques implemented here. For example, there was some variation in the set-up presented, specifically in terms of the indoor versus outdoor variations of the scenario. Nevertheless, with due caution around this result acknowledged, this potentially intriguing finding is discussed below.

For age association, the direction of the relationship was negative, indicating that younger bears typically were quicker at solving the problem. This result contrasts with a long-held assumption that with increasing age comes increased knowledge in terms of certain environmental and social events, seen for example in elephants (McComb et al., 2001; McComb et al., 2011). Here, bears younger in age are found to be typically outperforming those older in age. This result is likely due to the fact that the younger bears were generally more excitable, receptive, and willing to engage with the trials. Benson-Amram et al. (2012) similarly found juvenile hyaenas to display greater exploratory behaviours, whilst also being more persistent and less neophobic than adults. In addition, with the juvenile subjects, they are at the age where the most social learning occurs and is transferred through the mother-offspring relationship (Breck et al., 2008), therefore cubs would typically be more curious in nature and receptive to the environment. For example, play behaviour in cubs has been found to influence survival (Fagen & Fagen, 2004, 2009). This highly receptive period, coupled with the investigatory nature of young bears (highlighted by (Bacon, 1980)), means they were more likely to engage with trials and greater predisposed to learning. This increased their exposure to the trials, allowing them to refine their skills or techniques in solving the problem, which over trials ultimately reduced their time-to-solve. Similarly, with the puzzle box trials, it was juvenile individuals which picked up the latch association; thus, this association appears to be consistent across both experimental tests.

Regarding the sex association, male bears typically had shorter time-to-solve scores and, as a result, were quicker at solving the problem. Generally, this would indicate that males have greater problem-solving abilities when compared to females and suggests there may be sex differences in the cognitive abilities of bears (see e.g., Carazo et al. (2014); Jonasson (2005); Jones et al. (2003)). However, this association is likely rather the result of collective testing and instead indicates that social dynamics are influencing cognitive performance. Specifically, because trials were run so that all bears had access to and could interact with the set-ups at the same time, this meant that those bears that were more dominant, i.e., males, would often monopolise the trials due to the food reward and competition present. Thus, as with the age result previously discussed, male bears typically had greater exposure to trials, which in turn allowed them to refine their technique and improve their time-to-solve. Therefore, whilst running trials individually is often preferred, it may perhaps be neglecting the influence of social dynamics on cognitive processes. For example, whilst individual testing is possible in some zoological collections, this does not represent the wild environment in which socioecological challenges are presented, where individuals may be influenced by those in their surrounding social environment (Hansen et al., 2021).

The suggestion that social dynamics are influencing cognitive engagement and performance, was further reinforced by the findings that the number of bears present during trials was significantly negatively associated with time-to-solve. This suggests that as the number of bears present increases, time-to-solve decreases. This result is likely the consequence of the collective nature of testing which caused increased competition between bears over the reward present. Although brown bears are considered obligatorily solitary (Gittleman, 1999), in captivity they are commonly kept in pairs or groups (mean group size here = 3), with this social environment likely influencing bear behaviour, especially in terms of engagement with enrichment devices or high-value food rewards. Thus, whilst collective testing can be advantageous in terms of evaluating cognition in a socially relevant context, there is also the risk of compromised performance due to competition over high-value and monopolisable resources (Jacobson et al., 2019). When considered with the previously discussed object-manipulation results, this suggests that the social dynamics of group-living captive bears may be influencing cognitive engagement and performance.

When specifically looking at the variations of the object-manipulation set-up, most trials were run with the stump already directly underneath the food reward. Bears often failed to identify the stump as an object to use to solve the problem and instead tried other techniques to solve the problem such as climbing the tree/apparatus involved and shaking the food reward free. Consequently, stump use was seldom seen. Whilst unexpected, the bears instead exhibited great resourcefulness in the techniques they used to solve the problem and almost all trials held were successful, even if stump use was not present. When stump use was present, and the set-up was subsequently altered in further trials, the bears often either failed to solve the problem or reverted to other techniques. Thus, here, the bears failed to manipulate an object in order to retrieve a food reward and these findings compliment those of Amici et al. (2019).

This result displays not a lack of ability, as bears have previously proven successful (Waroff et al., 2017), but rather that the scenario potentially fails to hold ecological relevance and neglects to draw on typical bear behaviours. For example, the most frequent reaction upon identifying the suspended food reward was to climb up high and retrieve it, which mirrors how bears would react to such a scenario in the wild. Therefore, without extensive training and obvious cues, bears fail to spontaneously use a tool. This suggests that a more ecologically-relevant scenario is required in order to test this cognitive ability i.e., tool-use which draws more readily on bear behaviours. However, it is also worth noting this outcome could instead be the result of certain experimental design limitations, such as the collective nature of testing or varying motivational levels, which possibly hindered bear engagement with the set-up.

9.3. Conclusion

Here, the problem-solving and object-manipulation abilities of captive European brown bears were examined. All 14 bears who engaged with the puzzle box were successful in solving the problem. Persistence was significantly associated with time-to-solve, and there appears to be potential for an association between behavioural diversity and time-to-solve, suggesting that as engagement time increases, both the *number* and *types* of attempts also increased, indicative of trial-and-error learning. However, two individuals did appear to acquire an association between the latch and access to the box. The number of successful trials was significantly negatively associated with time-to-solve, indicating that the bears learnt the task solution and remembered it in subsequent trials, which improved their performance over time. In addition, latency to approach appeared to influence success times, suggesting that varying motivational levels is an important factor to consider when investigating cognitive ability. Whilst the bears failed to spontaneously tool use, 13 out of 15 individuals were nonetheless successful in retrieving a food reward, instead using alternative techniques to solve the problem. Analyses revealed time-to-solve scores were dependent on *both* age and sex, indicating that younger male bears had significantly improved time-to-solve. This is likely due to the highly excitable, receptive nature of young bears, who refined their skills during increased exposure to trials. In addition, the collective nature of testing resulted in males dominating trials, and thus social dynamics appear to influence cognitive performance. This is further reinforced by the findings that the number of bears present was negatively associated with time-to-solve, suggesting that competition is a factor influencing cognitive engagement. Since this result may be 1) an artefact of the trial conditions and/or 2) a product of specific individuals sampled here, more work is needed to confirm these findings before extrapolation to the wider population. A more ecologically-relevant test seems necessary in order to test the tool using capabilities of bear species. In addition to future studies examining the cognitive abilities of bears, the underlying mechanisms influencing cognitive performance, in particular their social capabilities and potential for social learning, should be explored.

10. Overall conclusions

The research presented here investigated the selection pressures influencing brain size evolution in two well-studied orders: Primates and Carnivores, as well as the potential benefits afforded by encephalisation in a relatively understudied taxon: European brown bears. The results discussed are at the forefront of cognitive evolution research since much research effort is now focused on elucidating the selection pressures responsible for increased brain size, whilst also confirming how large brains benefit individuals through improved cognitive performance.

The first study presented herein, together with other recent re-examinations of brain size evolution (e.g., DeCasien et al. (2017); Powell et al. (2017)) are shifting long-standing viewpoints on the variables responsible for encephalisation, particularly challenging support for the social brain hypothesis. Thus, whilst support is found here for the SBH in primates, ecological variables appear to hold much greater prominence in both primate and carnivoran brain size evolution. These results reinstate the theories highlighted early on in the literature (e.g., Clutton-Brock and Harvey (1980); Parker and Gibson (1977)) which placed importance on the role of foraging ecology. Life-history associations corroborate with several hypotheses (such as the developmental cost (Barton & Capellini, 2011) and expensive brain (Isler & van Schaik, 2009) hypotheses), supporting the theory as to how the transition to slow life histories facilitates the production of big brains and bypasses the cost of expensive brain tissue. Future studies of brain size evolution should endeavour to integrate multiple variables, incorporating all the potential variables influencing brain size, whilst also investigating both whole brain and specific brain regions, as the inclusion of such may reveal further associations, highlighting how different brain regions can evolve independently through varying selection pressures.

The second study discussed, confirms the advanced cognitive abilities of European brown bears, in terms of their ability to be innovative and problem-solve. Little is known about cognition in bears, and thus, this study is one of the first to explore the cognitive abilities of captive European brown bears. Moreover, previous bears studies tended to focus on black bears (e.g., Vonk et al. (2012)) and are often limited by small sample sizes (e.g., (Johnson-Ulrich et al., 2016)), therefore, this study further improves on previously studies by using increased sample sizes and broadening the taxonomic approach. Results revealed bears use trial-and-error learning when interacting with novel challenges; however, evidence also suggests some individuals have potential to adopt successful strategies and draw perceptive associations. Individual variation in motivation levels appears to be an important factor influencing cognitive performance. The bears failed to spontaneously use tools (see also Amici et al. (2019)) but still managed to retrieve the food reward, instead using alternative techniques, further demonstrating their ability to innovate. Analyses revealed an interaction between age and sex, indicating that younger male bears had improved time-to-solve scores. This is explained by the highly excitable, receptive nature of young bears and the collective nature of testing which resulted in males dominating trials, raising questions regarding the influence of social dynamics of cognitive performance. This was further highlighted by an association between the number of bears present and time-to-solve scores, suggesting competition could be influencing success times. However, caution is warranted in terms of the generalisability of these results to the wider population. Future studies should aim to keep cognitive trials ecologically-relevant for bears, especially when testing their tool-use capabilities, thereby seeking to increase trial engagement and enrichment possibilities.

While not the reason for this study, the welfare of large-brained wide-roaming bears being held in captivity, is often a topic of public and professional concern. To be clear, the bears involved in this study were under both excellent care and conditions. However, cognitive stimulation, such as that provided in this study, can provide enriching and stimulating challenges for individuals living in zoological settings; and, ecologically-valid behaviour trials offer zoo-housed bears the opportunity to express wild bear behaviours, which are always going to be more limited in zoological settings than for bears in the wild. Moreover, even the best zoological facilities provide bears an environment that is different to the wild, leading to a different existence (though not necessarily a lesser existence) compared to their wild counterparts. Therefore, the results of this study highlight the use of zoo-housed cognition studies for what they can reveal about the lived-experiences of those individuals housed in zoological settings. Here, for example, the subjects were tested in groups as the idea of separation uncovered potential management concerns with the bears being group-housed. This study subsequently revealed the possible impact social behaviour has on zoo-housed group-living bears. In the United Kingdom there are currently housed: 32 brown bears, 12 polar bears, 12 American black bears, 3 Asiatic black bears (*Ursus thibetanus)*, 9 sun bears (*Helarctos malayanus)*, 16 Andean bears (*Tremarctos ornatus)*, 3 sloth bears (*Melursus ursinus)* and 2 giant pandas (*Ailuropoda melanoleuca)* (N=89). Such “ambassador” individuals warrant thorough attention to ensure they live the most fulfilled lives we can offer them.

In conclusion, brown bears show excellent promise as subjects for testing the cognitive abilities of Ursids and subsequently testing theories of cognitive evolution. The explanation for large brains in Ursids has been somewhat of an enigma since bears appear as an outliner in prominent explanations for the evolution of large brains (e.g., the social brain hypothesis) due to their relatively asocial nature. Selection for enhanced cognitive abilities, specifically in terms of their behavioural flexibility and ability to problem-solve and innovate, however, offers one explanation for their presence in these taxa.

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Appendix 1

BIAZA

BRITISH & IRISH ASSOCIATION
OF ZOOS & AQUARIUMS

BIAZA Research Committee

Letter of Support for Research Project

The BIAZA Research Committee promotes good quality basic and applied research by and within BIAZA's member collections.

Following critical consideration of the research proposal and subsequent satisfactory responses by the researcher, the committee has agreed to give a letter of support for this study by Helen Chambers of the University of Salford.

In the opinion of the BIAZA Research Committee the methodology proposed by this researcher will provide robust data that will answer their research question. In the interest of scientific training [and the furthering of science], the BIAZA Research Committee encourages BIAZA members to take part in this research project.

Please be advised that we would require an update or your completed project report within 1 year from today.

Yours faithfully,

Dr Kirsten Pullen
Chair, BIAZA Research Committee
28th October 2020

Figure 13. Letter of support from the BIAZA Research Committee.

Appendix 2

Table 14. Information on the bears involved in the research study.

Location	Name (ID)	Sex (m/f)	Age (years)	Weight (kg)	Prior experience of cognitive trials (y/n)	Prior experience of environmental enrichment (y/n)	Captive born or wild caught (C/W)	Time in captivity (years)	# of successful PB trials	# of successful OM trials
Five Sisters Zoo	Eso	F	7	200	N	Y	W	6.5	4	6
Wildwood Trust	Fluff	M	23	270	N	N	C	23	3	0
	Scruff	M	23	250	N	N	C	23	0	0
Camperdown	Brumm	M	6	220	N	Y	C	6	2	7
	Maja	F	6	180	N	Y	C	6	1	1
	Brumma	F	6	190	N	Y	C	6	6	1
Wildwood Escot	Mish	M	2	110	N	Y	W	1.5	9	8
	Lucy	F	2	90	N	Y	W	1.5	1	1
Welsh Mountain Zoo	Athena	F	17	180	N	Y	C	17	3	3
	Fivi	F	17	170	N	Y	C	17	0	2
Scottish Deer Centre	Loki	M	9	300	N	Y	C	9	1	0
	Nelly	F	17	200	N	Y	C	17	5	2
Port Lympne	Enciam	F	19	185	N	Y	C	19	2	2
	Julio	M	15	270	N	Y	C	15	1	4

	Neu	F	5	215	N	Y	C	5	0	0
	Rojo	M	1	80	N	Y	C	1	3	13
	Tornillo	M	1	80	N	Y	C	1	9	13

Appendix 3

Table 15. Results of generalised linear mixed model (GLMM), preliminary model of latency to approach and time of day on log-time-to-solve (estimates and standard errors, together with confidence limits, results of tests, and the range of estimates obtained when dropping levels of random effects one at a time).

Term	**estimate**	**SE**	**lower CI**	**upper CI**	***t***	***df***	***P***	**min**	**max**
Intercept	1.425	0.153	1.134	1.727	9.314	18.840	0.000	1.352	1.500
Latency (1)	0.156	0.093	-0.023	0.335	1.681	30.024	0.103	0.060	0.197
Time of day (2)	0.148	0.137	-0.120	0.393	1.083	24.703	0.289	0.057	0.281

Note. (1)*z*-transformed to a mean of 0 and a standard deviation of 1; mean and SD of the original variable were 1.284 and 0.436, respectively,

(2) dummy coded with PM being the reference category.

Appendix 4

Model 1:

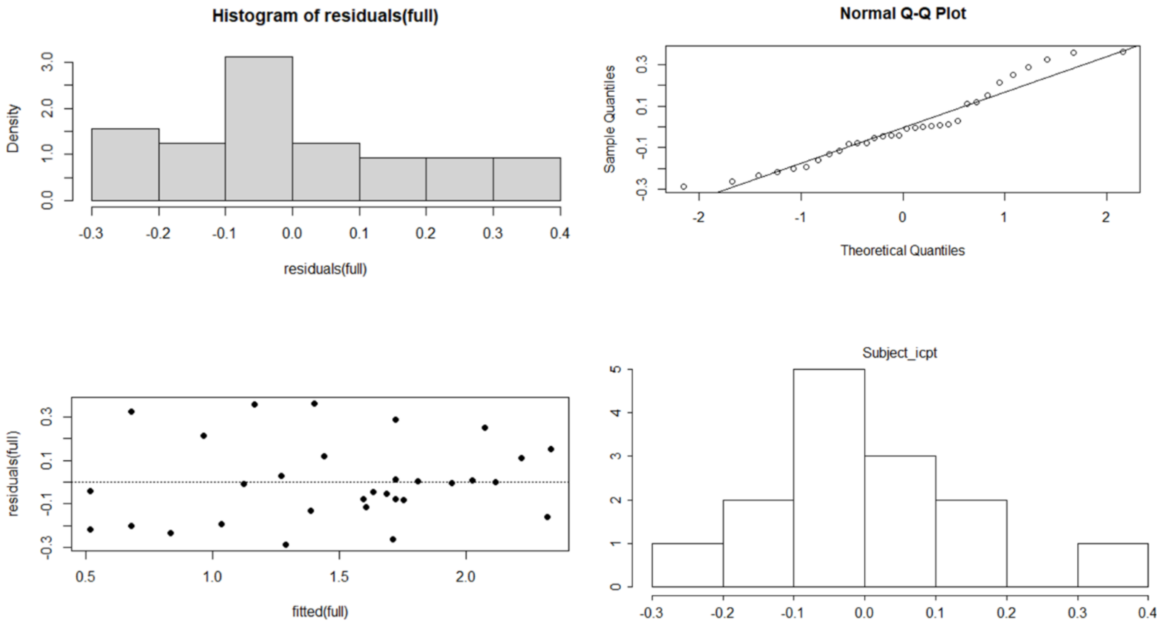

Figure 14. Normality of residuals for model one.

Model 2:

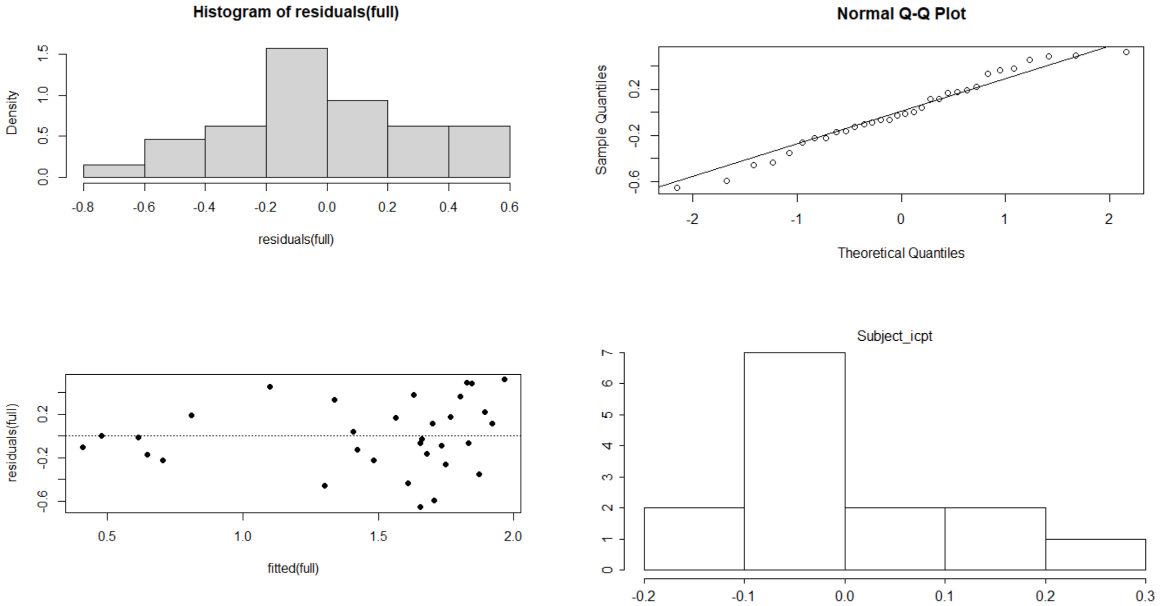

Figure 15. Normality of residuals for model two.

Model 3:

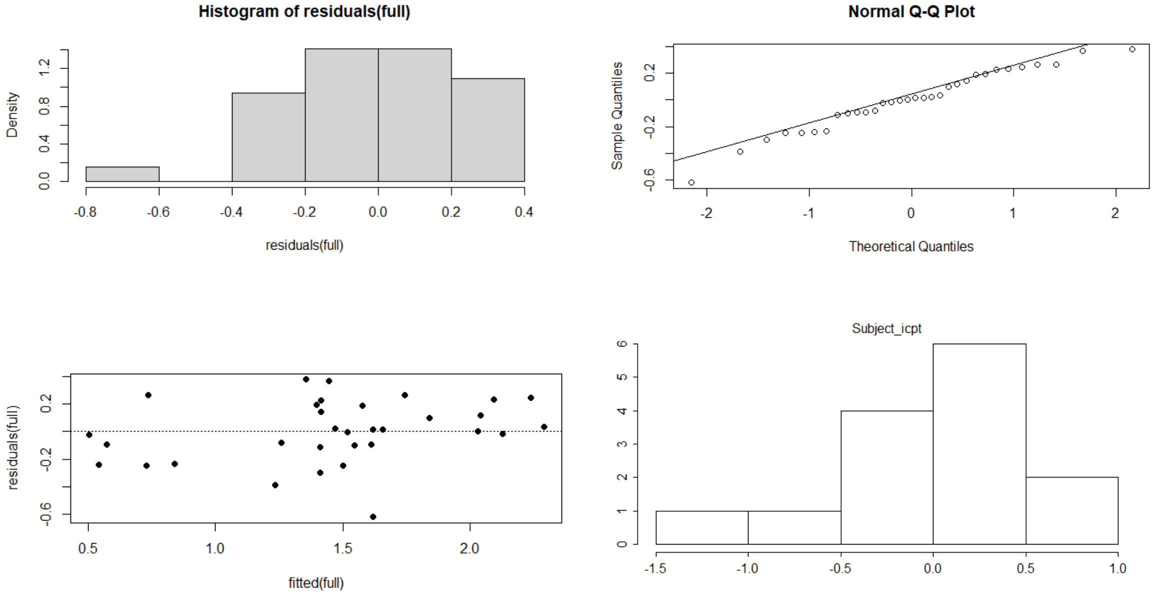

Figure 16. Normality of residuals for model three.

Model 4:

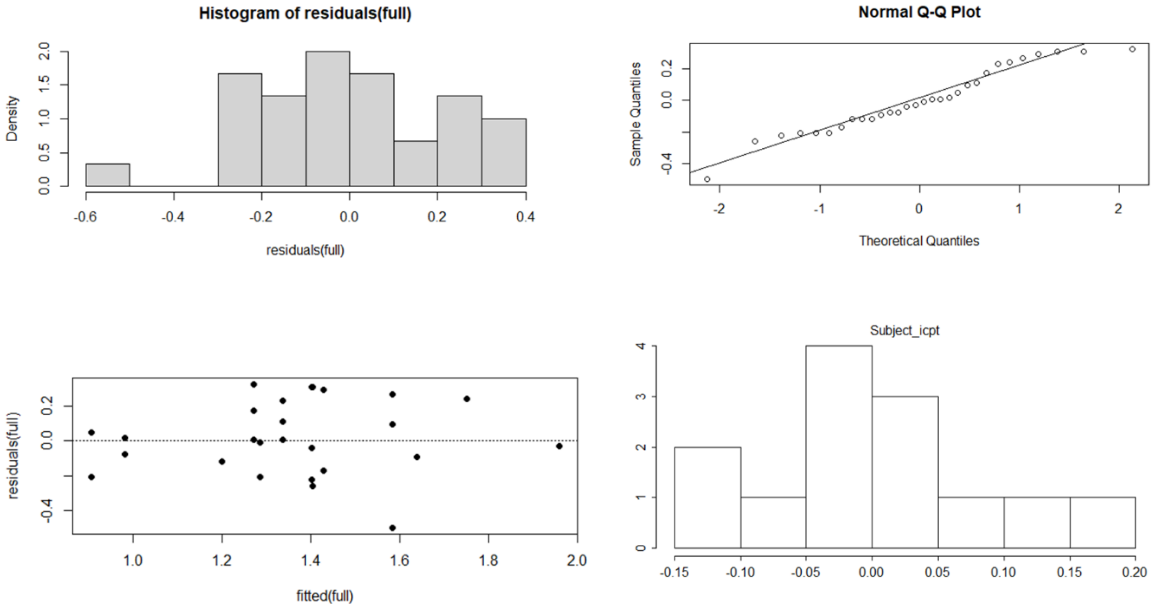

Figure 17. Normality of residuals for model four.

Model 5:

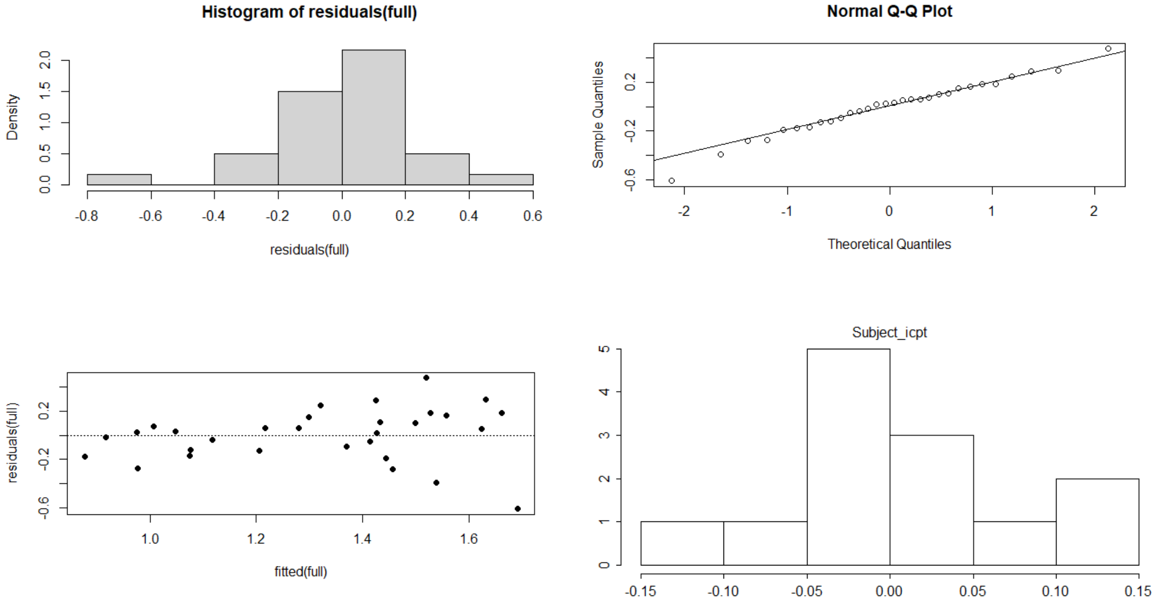

Figure 18. Normality of residuals for model five.

Appendix 5

Latch use footage.

https://1drv.ms/u/s!AjDJL8X7YalCg9V7L3qnZY3dYCfQnQ